ADVANCES IN UNGULATE ECOLOGY

EDITED BY: R. Terry Bowyer, Vernon Bleich, Paul Richard Krausman and
Jean-Michel Gaillard
PUBLISHED IN: Frontiers in Ecology and Evolution

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88966-910-3
DOI 10.3389/978-2-88966-910-3

About Frontiers

Frontiers is more than just an open-access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

Frontiers Journal Series

The Frontiers Journal Series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the Frontiers Journal Series operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

Dedication to Quality

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews.
Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view.
By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

What are Frontiers Research Topics?

Frontiers Research Topics are very popular trademarks of the Frontiers Journals Series: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area! Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers Editorial Office: frontiersin.org/about/contact

ADVANCES IN UNGULATE ECOLOGY

Topic Editors:
R. Terry Bowyer, University of Alaska Fairbanks, United States
Vernon Bleich, University of Nevada, Reno, United States
Paul Richard Krausman, University of Arizona, United States
Jean-Michel Gaillard, Université Claude Bernard Lyon 1, France

Citation: Bowyer, R. T., Bleich, V., Krausman, P. R., Gaillard, J.-M., eds. (2021). Advances in Ungulate Ecology. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88966-910-3

Table of Contents

frontiers
in Ecology and Evolution

EDITORIAL
published: 27 April 2021
doi: 10.3389/fevo.2021.675265

Editorial: Advances in Ungulate Ecology

R. Terry Bowyer[1]*, **Vernon C. Bleich**[2], **Paul R. Krausman**[3] **and Jean-Michel Gaillard**[4]

[1] Institue of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, United States, [2] Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV, United States, [3] School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, United States, [4] Laboratoire Biométrie & Biologie Évolutive, University Claude Bernard - Lyon I, Villeurbanne, France

Keywords: population ecology, behavioral ecology, nutritional ecology, conservation, life-histories

Editorial on the Research Topic

Advances in Ungulate Ecology

Edited and reviewed by:
Elise Huchard,
UMR5554 Institut des Sciences de l'Evolution de Montpellier (ISEM), France

****Correspondence:***
R. Terry Bowyer
bowyterr@isu.edu

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *02 March 2021*
Accepted: *30 March 2021*
Published: *27 April 2021*

Citation:
Bowyer RT, Bleich VC, Krausman PR and Gaillard J-M (2021) Editorial: Advances in Ungulate Ecology. Front. Ecol. Evol. 9:675265. doi: 10.3389/fevo.2021.675265

INTRODUCTION

Ungulates possess unique life-histories compared with other mammals, including long lives, large body size, delayed age at first reproduction, iteroparity, small litters with large progeny, high maternal allocation to offspring, and slow-paced life-histories with long generation times (Gaillard et al., 2016). Strong density-dependence, in body growth and recruitment, is typical (Eberhardt, 2002; Bonenfant et al., 2009). Those patterns, and the environments inhabited by ungulates, have been at the forefront of important discoveries in ecology (McCullough, 1979; Bleich et al., 1997), evolution (Boyce, 1988), and conservation (Cain et al., 2008; Krausman and Bleich, 2013). This Research Topic provides an overview and expansion of those advances, especially movement ecology (Mysterud et al., 2011), sociality and mating systems (Bowyer et al., 2020), the role of individual heterogeneity in population biology (Plard et al., 2012), responses to predation (Fortin et al., 2009), and evolutionary tradeoffs among biological functions (Gaillard et al., 2000).

Publications are organized into four broad sub-disciplines—**Population Ecology**, **Nutritional Ecology**, **Behavioral Ecology**, **and Conservation** that integrate them, with some venturing into a more general ecological context such as climate change. These publications offer expansive evolutionary underpinnings that will be of interest to biologists, and provide thought-provoking insights and directions for research.

POPULATION ECOLOGY

Many studies concentrate on the statistical evaluation of models, which has become a dominant Research Topic. Wisdom et al. provide practical guidelines for research on ungulates, especially those used in population ecology. They state that models should include seven key goals: cooperation between managers and scientists; explicit inference to space with supporting data; use of the appropriate scale for covariates; incorporation of ecologically plausible sets of competing models in development and selection; model evaluation; assessment of relationships with animals and population performance; and reliable interpretations for ecological understanding and use in management.

Many ungulates are partially migratory. Merrill et al. provide a detailed analysis of foraging behavior of migrant and resident North American elk during winter, an ecological context where foraging is constrained by vigilance of elk for gray wolves. They showed that this tradeoff alters foraging benefits between migratory tactics. If changes in winter density differentially influences forage-predation tradeoffs of migrant and resident elk, differences in winter foraging, along with grouping patterns, could shape the demographic advantage of a particular migratory tactic.

Gilbert et al. report that summer survival of young Sitka black-tailed deer is primarily determined by black bear predation and is positively influenced by mass at birth and sex. Winter fawn survival is affected by malnutrition in deep-snow winters and is influenced by an interaction between date of birth and snow depth. The prospective demographic analysis shows that adult female survival has the highest potential demographic effect on population growth. Conversely, the retrospective demographic analysis, which accounts for confounding effects of sampling variation, indicates that winter and summer fawn survival are most variable and most influential to variation in population growth.

Although effects of human disturbances on caribou survival are limited to specific regions and areas, Plante et al. detect a negative influence on survival, even at a low level of human development. This research highlights the importance of assessing effects of disturbances at various spatiotemporal scales, and of considering the relative influence of other non-anthropogenic factors to understand dynamics of ungulate populations subjected to a high human disturbance.

Parturition sites and nursery habitat for bighorn sheep constitute important components of habitat use and selection; strong selective pressures affect growth and survival of offspring. Robinson et al. document the birthing habitat for desert and Rocky Mountain bighorn sheep and determine that females raising lambs successfully prefer steep, north facing, rugged terrain in low elevations, and they avoid roads and trails. These results will aid in the management of bighorn sheep populations.

NUTRITIONAL ECOLOGY

Oates et al. report the importance of nutritional condition of female moose vs. remotely sensed data on vital rates in describing lambda (the finite growth rate). Nutritional condition has the stronger influence on pregnancy rates, parturition success, overwinter survival of adults, and influences survival more so than remotely sensed vital rates. Their work indicates that variation in vital rates and effects of resource limitation in a particular environment may be larger than previously thought.

Barboza et al. tracked body protein use in northern ungulates during late pregnancy when forage is limited and animals are beginning to move to spring and summer ranges to give birth. The capital breeding system of these ungulates relies on routing body proteins to simultaneously sustain maternal function and allocation to reproduction through common metabolic pathways that conserve body mass for survival.

At the population level, mule deer select high forage biomass at the landscape compared with the home-range scale, and during summer rather than spring (Merems et al.). Females that use vegetation with high biomass of preferred forage through spring and summer enter winter in the best condition. Patterns of forage use by ungulates may correlate more strongly with individual fitness than patterns of forage selection.

Pekins calculates the endogenous fat balance of pregnant moose by developing energy-balance equations that account for gestation, winter tick infestation, and lactation under two forage consumption levels. Those variables influence failed calving or calf mortality via a loss of endogenous protein in mid-sized and small cows, but not large ones. This population is confronted with a unique combination of environmental and parasitic conditions associated with a warming climate that affects its survival and reproduction.

Græsli et al. report seasonal differences in body temperature, heart rate, and activity of free-ranging female moose, with lower levels occurring during winter and higher values during summer. Metabolic rates decrease by 60% from the highest to the lowest point. Hypometabolism during winter is a tactic to reduce energy expenditure during periods with colder climate and limited availability of resources.

BEHAVIORAL ECOLOGY

Capital and income breeding relates energy used during reproduction to timing of its acquisition, typically focusing on females. Among male ungulates, Apollonio et al. report that capital breeders rely on previously accumulated resources for reproductive allocation. Income breeders use resources acquired primarily during reproductive activities, whereas capital breeders lose mass corresponding to body reserves acquired well before reproductive activities, and allocate a variable amount of energy to deal with different environmental or body conditions. A link exists between capital breeding and degree of polygyny.

Isvaran studies variable mating tactics of the blackbuck, which yielded a novel hypothesis explaining the small size of lek territories. Variation in the size of lek territories can be explained by competition arising from a female bias for mating on central territories. Reduced size of lek territories is likely a consequence of a central mating advantage in large aggregations, and consistent with a reduction in territory size and the evolution of male clustering, which can help explain other mating tactics.

Heffelfinger et al. use machine learning algorithms and resource selection functions to explore tradeoffs associated with reproductive stages in female mule deer. Pre-parturient females, mothers with young at heel, and females having lost their offspring all select areas with greater nutritional resources, that are closer to water, and that present lower predation risk than non-used areas. No tradeoff between safety of offspring and nutrient availability is detected, indicating predation risk and availability of nutritional resources are not mutually exclusive.

Young male white-tailed deer may be more successful when dominant males are absent, but it is uncertain if young males expend effort when those opportunities arise. Monteith et al. identify food intake, hormone levels, body mass, and somatic loss during rut as similar between yearling males that interact with adult males and those that do not. Male deer display risk-sensitive reproductive allocation. Reproductive allocation of resources garnered during the prior season are expended to avoid trading off survival for reproduction.

Weckerly reports that size of male-only groups of Roosevelt elk exhibit a positive relationship with male abundance and that the number of males in female groups exhibit an inverse relationship with female abundance. Social factors likely influence sizes of male-only groups and ecological factors probably influence male prevalence in female groups. These outcomes provide additional insights into the evolution of male gregariousness.

Cameron et al. report that calving sites of caribou are characterized by high-quality forage at the time of calving, and by a narrow range of distinct physiographic factors. During spring, pregnant females migrate to areas with high-quality forage, but upon arrival refine selection as a function of environmental stochasticity. Fidelity to calving grounds among caribou is supportive of spatial memory as a navigational mechanism to optimize foraging and energy acquisition.

CONSERVATION

Creech et al. explore influences of genetic structure, diversity, and isolation and then estimate relative vulnerability to climate change among populations of desert bighorn sheep. Genetic diversity decreases, and differentiation increases with isolation, and these patterns are stronger for native populations than for translocated populations. Native populations occupying intact landscapes are characterized by the lowest vulnerability. Results demonstrate the advantages of using multiple factors to maintain connectivity and potential for adaptation in areas experiencing rapid climate change.

Many ungulate populations exhibit a complex history of isolation and translocation. De Jong et al. report that spatial genetic structure and within-population genetic variation of red deer differ markedly from patterns assumed from present-day abundance and distribution. Those distortions on the genetic landscape can create management dilemmas that cannot be correctly anticipated without baseline genetic monitoring.

Queirós et al. report that non-native or hybrid red deer occur widely among Iberian populations. Mitochondrial introgression occurs across 15 populations, being more frequent in free-ranging individuals than in fenced populations but is absent from public-owned populations. Human-mediated translocations of non-native red deer into the Iberian Peninsula highlights the need to implement effective measures to avoid such practices to preserve the endogenous genetic patrimony of Iberian red deer populations.

Opportunities for creating new conservation areas in Africa are restricted by growing human populations and climate change. Whether the current protected-area network captures spatial priorities for conservation of 72 ungulate species is uncertain. Payne and Bro-Jørgensen illustrate how mapping of continent-wide conservation priorities for species can assist land-use planning and guide policies at national levels to enhance conservation.

Patterns of resilience become more difficult to observe as human domination of the Earth destabilizes systems beyond return points. Berger et al. focus on the modalities of ecological disruption that mitigate the changing role of ungulates in landscapes. Much of what was once generally predictable in terms of pattern and process no longer holds. Only messy projections of future community reorganization seem reasonable, whether related to food webs or assembly rules that once governed ungulate communities.

Contributors to this Research Topic provide the groundwork that will lead to important advances in subdivisions of ecology, and further enhance knowledge of these iconic mammals.

AUTHOR CONTRIBUTIONS

All authors have made substantial contributions to the Editorial and in organizing and editing the Research Topic.

ACKNOWLEDGMENTS

We thank authors who submitted manuscripts that made the Research Topic on ungulate ecology successful. We are grateful to the referees, acknowledged on the first page of each article, who provided timely and constructive comments on manuscripts. We thank Andrew J. MacIntosh for serving as Editor for a paper when one of the Editors was a co-author.

REFERENCES

Bleich, V. C., Bowyer, R. T., and Wehausen, J. D. (1997). Sexual segregation in mountain sheep: resources or predation? *Wildl. Monogr.* 134, 1–50.

Bonenfant, C., Gaillard, J.-M., Coulson, T., Festa-Bianchet, M., Loison, A., Leif, M. G., et al. (2009). Empirical evidence of density-dependence in populations of large herbivores. *Adv. Ecol. Res.* 41, 313–357. doi: 10.1016/S0065-2504(09)00405-X

Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., and Whiting, J. C. (2020). Evolution of ungulate mating systems: integrating social and environment factors. *Ecol. Evol.* 10, 5160–5178. doi: 10.1002/ece3.6246

Boyce, M. S. (1988). *Evolution of Life Histories: Theory and Patterns From Mammals, Evolution of Life Histories of Mammals: Theory and Pattern*, ed. M. S. Boyce, New Haven, CT: Yale University Press, 3–30.

Cain, J. W. I. I. I., Krausman, P. R., Morgart, J. R., Janse, B. D., and Pepper, M. P. (2008). Responses of desert bighorn sheep to removal of water sources. *Wildl. Monogr.* 171, 1–32. doi: 10.2193/2007-209

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* 83, 2841–2854. doi: 10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2

Fortin, D., Fortin, M. E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology* 90, 2480–2490. doi: 10.1890/08-0345.1

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Ann. Rev. Ecol. Syst.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., Lema?tre, J. F., Berger, V., Bonenfant, C., Devillard, S., Douhard, M., et al. (2016). In: Kliman, R. M. (ed.). *Encyclopedia of Evolutionary Biology*. Oxford: Academic Press, 2, 312–323. doi: 10.1016/B978-0-12-800049-6.00085-8

Krausman, P. R., and Bleich, V. C. (2013). Conservation and management of ungulates in North America. *Intern. J. Environ. Stud.* 70, 372–382. doi: 10.1080/00207233.2013.804748

McCullough, D. R. (1979). *The George Reserve Deer Herd: Population Ecology of a K-selected Species.* Ann Arbor, MI: Univ. Michigan Press.

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes —a role for density dependence? *Oikos* 120, 1817–1825. doi: 10.1111/j.1600-0706.2011.19439.x

Plard, F., Bonenfant, C., Delormeb, D., and Gaillard, J.-M. (2012). Modeling reproductive trajectories of roe deer females: fixed or dynamic heterogeneity? *Theor. Popul. Biol.* 82, 317–328. doi: 10.1016/j.tpb.2012.03.006

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 17 April 2020
doi: 10.3389/fevo.2020.00097

Determining Timing of Births and Habitat Selection to Identify Lambing Period Habitat for Bighorn Sheep

Rusty W. Robinson[1], Tom S. Smith[1], Jericho C. Whiting[2]*, Randy T. Larsen[1] and Justin M. Shannon[3]

[1] Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT, United States, [2] Department of Biology, Brigham Young University-Idaho, Rexburg, ID, United States, [3] Utah Division of Wildlife Resources, Salt Lake City, UT, United States

Edited by:
Paul Richard Krausman,
University of Arizona, United States

Reviewed by:
Clinton Wakefield Epps,
Oregon State University,
United States
Marco Festa-Bianchet,
Université de Sherbrooke, Canada

***Correspondence:**
Jericho Whiting
whitingj@byui.edu

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *18 December 2019*
Accepted: *26 March 2020*
Published: *17 April 2020*

Citation:
Robinson RW, Smith TS,
Whiting JC, Larsen RT and
Shannon JM (2020) Determining
Timing of Births and Habitat Selection
to Identify Lambing Period Habitat
for Bighorn Sheep.
Front. Ecol. Evol. 8:97.
doi: 10.3389/fevo.2020.00097

Timing of births in ungulates is influenced by ecological factors, and differences in seasonality of births have evolutionary implications for these mammals. Birthing habitat is one of the most important home-range attributes for ungulates, and disturbances during this time can decrease survival of young and population growth. We calculated timing of births and quantified habitat selected by nursery groups (i.e., females with young) of desert bighorn sheep (*Ovis canadensis nelsoni*) to produce and project a geographic information system (GIS) model of lambing period habitat (i.e., birthing locations and areas used up to 6 weeks post-parturition) in southeastern Utah, United States. We then applied that model to identify suitable lambing period habitat in an adjacent area for a population of Rocky Mountain bighorn sheep (*O. c. canadensis*). We monitored 19 global positioning system (GPS) collared females from 2012 to 2013 to delineate the birthing season. We used GPS locations during that time and logistic regression within a model-selection framework to differentiate between lambing period habitat and random locations based on habitat and anthropogenic covariates. We used model coefficients to produce and project a GIS model of lambing period habitat. Across both years, 89% of 45 births occurred in May (range = April 27–June 9). We quantified covariate values at 750 lambing period and 750 random locations during that time in the San Rafael study area. The top model included elevation, slope, terrain ruggedness, aspect, existing vegetation type, and distance to trails and roads. Those variables predicted lambing period habitat for desert bighorn sheep (*rho* = 0.99, *P* = 0.02). We then overlaid that model on 1,130 GPS locations from 17 female Rocky Mountain bighorns in the Green River study area. In both areas, a mean of 71% of locations were in the top two (of five) probability categories (San Rafael high = 37%, medium high = 31%; Green River high = 50%, medium high = 23%). Females in lambing period habitat preferred steep, north-facing slopes, rugged terrain, low elevation, and avoided roads. Our GIS model projected areas of lambing period habitat for adjacent desert and Rocky Mountain bighorns and provided land managers with a map of habitat in areas where resource extraction and recreation are increasing. Identifying timing of parturition, and high-probability lambing period habitat, will help managers mitigate temporal and spatial conflicts between bighorn sheep and anthropogenic activities. Similar data regarding timing of births and a GIS model can be applied to conserve habitat for other ungulates also.

Keywords: GIS model, *Ovis canadensis*, reintroductions, timing of births, translocations

INTRODUCTION

Timing of births in ungulates is influenced by many ecological factors (Sadleir, 1969; Bowyer, 1991; Loe et al., 2005), and differences in seasonality of births for these mammals can have evolutionary implications (Marshall and Cambridge, 1937; Rutberg, 1987; Ims, 1990), such as reduced survival of young and future reproductive potential (Clutton-Brock et al., 1987; Festa-Bianchet et al., 2000; Keech et al., 2000). For bighorn sheep (*Ovis canadensis*), latitude, elevation, growing season length, climate, nutrition, and photoperiod are factors influencing reproductive seasonality (Bunnell, 1982; Thompson and Turner, 1982; Whiting et al., 2012). Generally, bighorn sheep occupying northern latitudes and higher elevations give birth late in spring, because of a constricted birthing period and shortened growing season (Bunnell, 1982; Thompson and Turner, 1982). Conversely, bighorn sheep occupying southern latitudes can give birth during most months, likely because growing seasons are much less predictable (Lenarz, 1979; Thompson and Turner, 1982; Rubin et al., 2000). Understanding the timing of births for ungulates can guide conserving habitat by mitigating temporal conflicts between these mammals and anthropogenic activities (e.g., recreation and mining) during that time (Singh et al., 2010; Kaze et al., 2016).

Female ungulates select birth sites and habitat for nursery groups (i.e., females with young) based on a variety of trade-offs (Bowyer, 1991; Rachlow and Bowyer, 1991, 1994). These trade-offs include predation risk, exposure to extreme weather, and forage quality and availability for the mother to fulfill nutritional requirements during late gestation and lactation (Festa-Bianchet, 1988b; Berger, 1991; Severud et al., 2019). For example, female bighorn sheep often return to the same general area each year to give birth (Geist, 1971; Etchberger and Krausman, 1999; Whiting et al., 2012). Young are usually born in relatively flat areas of high elevation in rugged, steep terrain close to perennial water, on south and west facing slopes, and away from anthropogenic disturbance (Geist, 1971; Bangs et al., 2005; Smith et al., 2015). After giving birth, female bighorns generally form nursery groups with other females and young in rugged areas of high elevation and steep slopes (Geist, 1971; Bangs et al., 2005; Karsch et al., 2016). These groups then move cohesively among patches of nursery habitat for the subsequent months (Bangs et al., 2005; Whiting et al., 2012; Wiedmann and Bleich, 2014). In general, Rocky Mountain bighorn sheep (*O. c. canadensis*) give birth later in spring, and the birthing period is constricted allowing females to exploit the shortened growing season during summer (Bunnell, 1982; Thompson and Turner, 1982). Conversely, desert bighorn sheep (*O. c. nelsoni*) give birth in almost any month, ostensibly because of a less predictable growing season (Bunnell, 1982; Thompson and Turner, 1982; Rubin et al., 2000). Delineation of birthing habitat has important implications for the conservation, reproductive biology, and perpetuation of bighorn populations (Etchberger and Krausman, 1999; Wiedmann and Sargeant, 2014; Smith et al., 2015), and is a topic that is receiving increased attention for land-use planning (Severud et al., 2019).

Anthropogenic activities can influence habitat selection by female ungulates during birthing and when animals congregate in nursery groups (Stankowich, 2008; Dzialak et al., 2011; Kaze et al., 2016), which can reduce forage intake and suppress population growth (Ciuti et al., 2012b; Sproat et al., 2019). For example, Saiga antelope (*Saiga tatarica*) avoided areas of human use while selecting birthing sites (Singh et al., 2010). Parturient bison (*Bison bison*) selected birthing areas that were away from recreational trails, roads, and buildings (Kaze et al., 2016). In an area that was intentionally disturbed by humans during parturition, counts of young/female elk (*Cervus canadensis*) were 22.5% lower than in areas with undisturbed herds (Phillips and Alldredge, 2000). Populations of bighorn sheep can be negatively influenced by anthropogenic disturbances, especially during the birthing season (Papouchis et al., 2001; Wiedmann and Bleich, 2014; Smith et al., 2015). These disturbances can cause females to abandon previously used nursery habitat. Thereafter, females use less-suitable habitat (Longshore et al., 2013), which may increase predation risk for lambs (Papouchis et al., 2001), and lower recruitment of young, resulting in a declining population (Papouchis et al., 2001; Wiedmann and Bleich, 2014). Delineating birthing habitat and habitat for nursery groups of ungulates can reduce spatial conflict between these mammals and anthropogenic activities (Kaze et al., 2016; McLaren et al., 2017).

Conservation and land-use planning will increasingly rely on identifying preferred wildlife habitats in areas of varying levels of human use (Margules and Pressey, 2000; Dzialak et al., 2011; Harju et al., 2011). Biologists can reduce and mitigate disturbance from anthropogenic activities to female ungulates during birthing by identifying when and where animals give birth (Dzialak et al., 2011; Kaze et al., 2016; McLaren et al., 2017). Determining timing of parturition in ungulates to identify high probability nursery areas can help managers mitigate temporal and spatial conflicts (Kaze et al., 2016; McLaren et al., 2017), and guide habitat management (Severud et al., 2019). Global positioning system (GPS) data can effectively document such patterns at fine scales (Longshore et al., 2013), especially for parturient females (Smith et al., 2015; McLaren et al., 2017; Severud et al., 2019). We calculated timing of births to delineate habitat for nursery groups of GPS-collared desert bighorn sheep and Rocky Mountain bighorn sheep in two of the largest populations of those subspecies in Utah, United States. We used GPS locations during that time and logistic regression within a model-selection framework to differentiate between lambing period habitat (i.e., birthing locations and areas used up to 6 weeks post-parturition; Zeigenfuss et al., 2000) and random locations based on habitat and anthropogenic covariates. We then constructed a GIS model that projected lambing period habitat in both areas. That model provided biologists and managers with a map of high probability lambing period habitat. By identifying timing of parturition, and high-probability lambing period habitat, managers will be able to mitigate temporal and spatial conflicts between bighorn sheep and recreation, mining, and domestic livestock grazing. Data regarding timing of births and a similar GIS model can be applied to manage and conserve habitat for ungulate species in other areas as well.

MATERIALS AND METHODS

Study Areas

The population of desert bighorn sheep we studied occupied the North San Rafael Swell (hereafter, San Rafael). The San Rafael is located in Emery County, Utah (**Figure 1**; 38°58′N, 110°37′W). Bighorns were native and abundant in the San Rafael, but were likely extirpated from that area; the last confirmed sighting occurred in 1964 (Dalton and Spillett, 1971). That population was re-established in the 1970s and 1980s with five translocations of 57 bighorns from Canyonlands National Park and the San Juan Population, Utah (Utah Division of Wildlife Resources [UDWR], 2018). Those translocation efforts were successful, and in 2001 the UDWR estimated 543 animals in that population. However, bighorn sheep started to decline in the 2000s, and 1 month prior to our study, biologists estimated 143 individuals in that area.

The San Rafael is characterized by steep canyons in the Wingate Formation with broad mesa tops in Navajo and Entrada Sandstone formations (Rigby and Beus, 1987). Desert bighorn sheep habitat in that area ranged in elevation from 1,700 to 2,100 m. Vegetation consisted of species typical of salt desert shrub environments. Common shrubs included blackbrush (*Coleogyne ramosissima*) and fourwing saltbush (*Atriplex canescens*). Pinyon pine (*Pinus edulis*) and juniper (*Juniperus* spp.) were predominate on mesa tops and on north facing canyon slopes. The San Rafael is dry with annual precipitation averaging <20 cm per year. Daily high temperatures during summer (June–September) averaged 31°C and often exceeded 35°C. Winters (November–February) were typified with daily low temperatures averaging −12°C. Native populations of pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) inhabited the study area, although mule deer persisted at low densities. Wild burros (*Equus asinus*) and domestic cattle also occupied portions of the San Rafael. Mammalian predators included mountain lions (*Puma concolor*), bobcat (*Lynx rufus*), and coyotes (*Canis latrans*). The San Rafael study area was predominantly managed by the Bureau of Land Management (BLM). Recreation in the San Rafael included on and off-road travel, rock climbing, biking, hiking, camping, and hunting. Peak recreation occurred in spring during mild weather (Wade Paskett, pers. comm., UDWR).

We also studied a population of Rocky Mountain bighorn sheep in the Green River corridor (hereafter, Green River) located in Emery and Carbon counties, Utah (**Figure 1**). Bighorns were native to that area, but were extirpated by 1960 (Dalton and Spillett, 1971). Currently, bighorns in that area are a result of nine transplants beginning in 1970 with animals from Utah, Montana, Wyoming, and Colorado, United States and Alberta and British Columbia, Canada. Rocky Mountain bighorn in Green River form the largest metapopulation of this subspecies in Utah (**Figure 1**), and that area contains one of the largest contiguous sections of Rocky Mountain bighorn sheep habitat in Utah. An estimated 1,000 individuals occupied that area at the beginning of our study.

Elevation used by bighorn sheep in the Green River varied from 1,250 to 3,000 m. Riparian areas in that area were dominated by willow (*Salix* spp.), cottonwood (*Populus fremontii*), and box elder (*Acer negundo*) trees. General vegetation of the Green River was a desert environment dominated by salt shrubs, bunch grasses, pinyon, and juniper. Populations of pronghorn, mule deer, bison, elk, and domestic cattle occupied that area; and mammalian predators were the same as those that occurred in San Rafael, except the Green River has a large black bear *(Ursus americanus)* population. The Green River is of mixed land ownership, most of which is managed by the BLM. Recreation in the Green River included on and off-road travel, rock climbing, biking, hiking, camping, fishing, and hunting. The Green River corridor is also governed by the 1979 River Management Plan (Barry, 1979), which allows for private and commercial float permits and establishes a carrying capacity of 35,000 user days per year. The recreation season is divided into high and low use periods. High use occurred from May 15 through August 15. Total user days on the river have increased by 43% from 2003 to 2018 (Jaydon Mead, pers. comm., US BLM). Despite our two study populations being separated by <20 km, no genetic mixing has been documented between these populations.

Methods

In January 2012, 30 adult, female bighorn sheep were captured by aerial net gunning (Krausman et al., 1985) in the San Rafael, and 17 adult females were captured in the Green River. Efforts were made to sample a wide distribution of bighorns across the units by distributing collars proportionally to aerial count numbers and locations of bighorns established 2 months prior. Animals were equipped with Lotek 6000SD GPS/VHF collars (Lotek Wireless Inc., Ontario, Canada) with mortality transmitters and pre-programmable drop off mechanisms. Collars deployed in the San Rafael were programmed to acquire a GPS fix every 8 h, and collars deployed in the Green River were programmed to acquire a GPS fix on either a 2.5, 4, or 6 h schedule. In January 2013, eight additional females in the San Rafael and five in the Green River were captured and collared to replace mortalities, bringing the total number of collared females to 38 in the San Rafael and 22 in the Green River. Due to collar malfunctions and mortalities, we used data from 36 GPS collars (San Rafael = 19 and Green River = 17) for our GIS analyses; however, all females in the San Rafael with active collars at the time of lambing were observed for collection of data for parturition timing. We retrieved collars

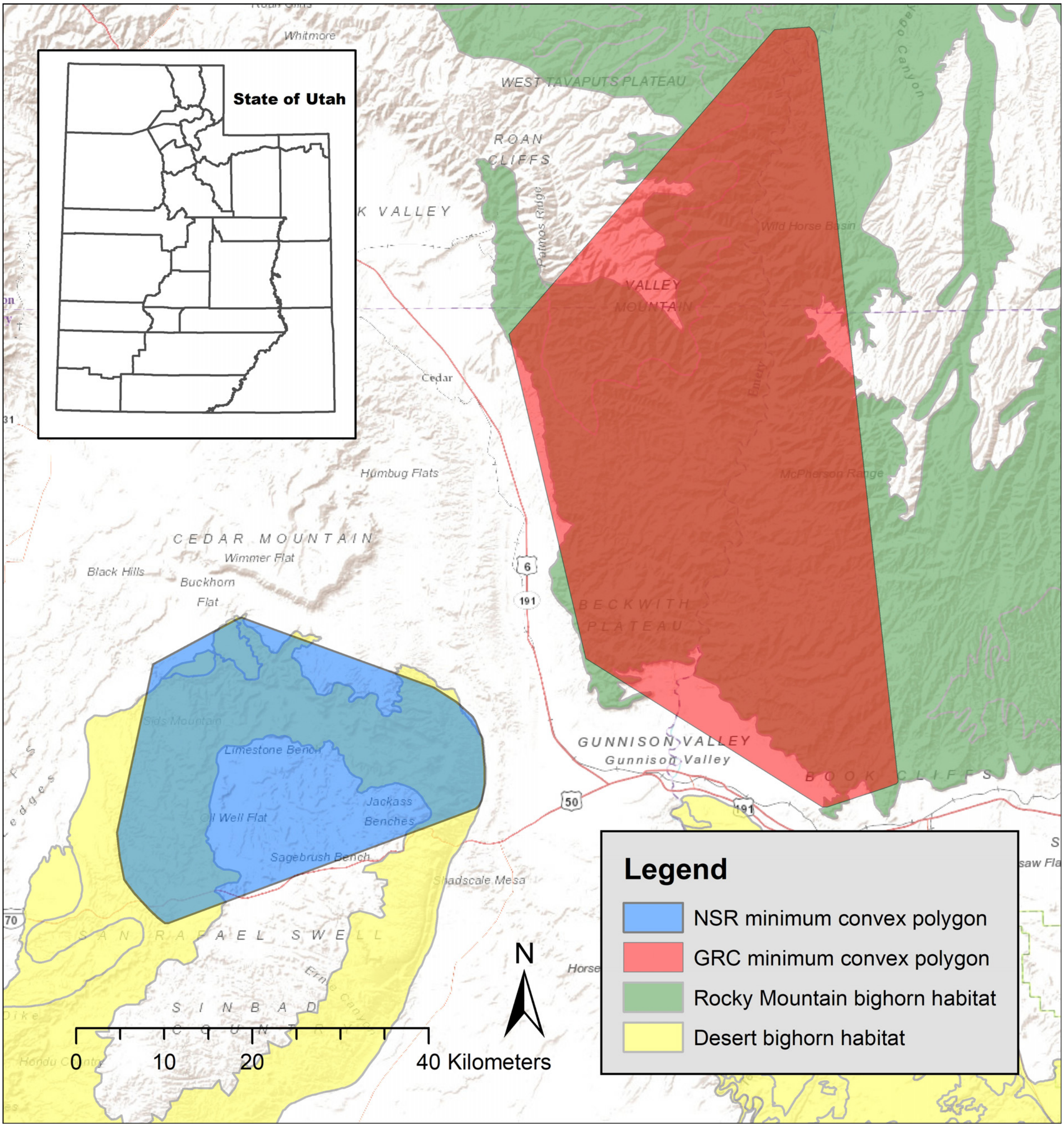

FIGURE 1 | Study areas where we documented lambing period habitat of 36 GPS collared bighorn sheep in eastern Utah, United States, 2012–2013. GRC, Green River Corridor; NSR, North San Rafael Swell.

after mortalities or at the end of the study in January 2014, and GPS locations were uploaded from the onboard data storage of the collars. Wildlife biologists from the UDWR used care in capturing, handling, and attaching GPS collars to bighorns (Sikes et al., 2016). Using GPS data is an extremely effective way to document parturition sites in bighorn sheep, and these data should be used over other sources (i.e., VHF collars) when delineating critical birthing habitat for this species (Smith et al., 2015), especially when considering anthropogenic influences on habitat use (Longshore et al., 2013).

To determine timing of births, we monitored collared bighorn sheep in the San Rafael weekly using radio telemetry for 2 years until January 2014. We relocated collared and uncollared females with binoculars and spotting scopes to record birthdates from

25 April to 25 June during 2012 and 2013. We searched the San Rafael a mean (±*SD*) of every 2 days ± 1.6 days in 2012, and a mean of every 2 days ± 1.7 days in 2013. To estimate parturition dates, we observed the behavior of marked females before, during, and after parturition; as well as first sighting, motor skills, size, and behavior of neonates (Festa-Bianchet, 1988a; Whiting et al., 2008, 2011). To determine birthdates for neonates of uncollared females, we compared their young with neonates of estimated ages of collared females when all females congregated in nursery groups after parturition (Côté and Festa-Bianchet, 2001; Whiting et al., 2008, 2012). When female and lamb pairings were questionable, we waited until the lamb nursed to identify its mother (Festa-Bianchet, 1988a). We exercised care not to disturb females with young (Sikes et al., 2016).

We estimated birthdates of young, pooled them into sampling intervals and calculated corrected means (timing of births) and *SD* values (synchrony of births) for the San Rafael population in each year (Johnson et al., 2004; Whiting et al., 2011). This technique allowed robust calculations of unequal sampling intervals (bin sizes) in determining timing and synchrony of births (Johnson et al., 2004). We then calculated a date range using ±2 *SD*s from the mean for lambing period habitat for our spatial analyses using data from GPS collars in the San Rafael population. A mean of 88 (±3.6) adult females occupied the San Rafael during our study.

We did not relocate collared and uncollared females with binoculars and spotting scopes in the Green River during our study. The general estimate of the peak birthing period, however, for that population was from 25 May to 5 June (Whiting et al., 2011). We therefore used the date range of May 1–June 10 for our analyses of lambing period habitat in that population. A mean (±*SD*) of 462 (±69.3) adult females occupied the Green River during our study.

Resource Selection Functions

Using the appropriate spatial scale when defining habitat availability to animals is critical when making inferences about habitat selection at the population level, making it important to define an area biologically relevant to the species of interest (Johnson, 1980; Boyce, 2006). We used the reproducible home range (rhr) package in Program R 3.1 to delineate a 95% minimum convex polygon for each study area (**Figure 1**). We created those polygons using bighorn birthing and lambing period locations during the date range calculated for both study populations.

We evaluated bighorn lambing period habitat selection in those 95% minimum convex polygons using a resource selection function within a use-availability study design (Manly et al., 2002) where the response variable was 1 for a use location or 0 for a random site. Random points were extracted with the random points tool in ArcMap 10.3 (Esri, Redlands, CA, United States) and R (R Core Team, 2015). We used a mixed-effects, logistic regression with a random intercept for individual bighorn (radio collar ID) and analyzed covariates at use versus random locations. We evaluated lambing period habitat using locations only from the San Rafael study area. We then produced a model from those variables and applied it to the Green River to verify if our GIS model captured lambing period habitat for that population.

We performed a database query in ArcGIS 10.3 (Redlands, CA, United States) to eliminate locations with <3D accuracy for both study areas. Because GPS collars across both study areas were programmed at different sampling intervals, we used only one randomly selected location per collar per day both for resource selection function analysis (San Rafael) and model testing (Green River). After removing <3D locations and locations that occurred outside the 95% minimum convex polygon, use locations totaled 750 for the San Rafael, and testing locations totaled 1,130 for the Green River. We generated 750 random locations within the San Rafael to be equal to the number of use locations and assigned them equal weight. Because random locations were cast within the boundary of the study area and not associated with individual home ranges, our modeling of resource selection generally corresponded to Johnson's second order of selection (Johnson, 1980). To ensure that 750 random locations adequately characterized our study area, we calculated the true mean values (i.e., mean of all pixels within the study area) for continuous variables and compared our sample means with 95% *CIs* to those values (Long et al., 2014). In every case, the confidence intervals of our samples overlapped the true mean values indicating that the 750 random locations were adequate to characterize our study area.

We selected the following landscape level features potentially influencing bighorn sheep habitat selection: slope, ruggedness, elevation, aspect, Landfire existing vegetation type (LANDFIRE[1]) (Smith et al., 1991; Bleich et al., 1997; Sappington et al., 2007; Rollins, 2009), and distance to trails and roads (Smith et al., 1991; Longshore et al., 2013; Wiedmann and Bleich, 2014). We extracted topographic features using a United States Geological Survey 30 m digital elevation model. We calculated slope using the slope tool in the Spatial Analyst Tools extension. We calculated ruggedness using the Vector Ruggedness Measure Tool in the Terrain Tools extension in ArcGIS (Sappington et al., 2007; Lowrey and Longshore, 2017). That tool measures terrain ruggedness as the variation in three-dimensional orientation of grid cells within a neighborhood. Vector Ruggedness Measure values can range from 0 (no terrain variation) to 1 (complete terrain variation). We calculated aspect using the aspect tool in the Spatial Analyst Tools extension and that variable was divided into the four cardinal directions (north, east, south, west). The LANDFIRE existing vegetation type layer consisted of five types (barren, sparse, herb, shrub, and tree). We calculated distance to roads and trails using the Generate Near Table Tool in the Analysis Tools extension. Distance to water sources was not included in our analysis. Because our study occurred in spring and due to the extensive nature of ephemeral water sources formed in holes in sandstone rock after rain or from seasonal seeps, it was not feasible to map water source locations accurately or comprehensively. Additionally, major rivers were in each study area. We evaluated explanatory variables for multicollinearity and did not include any variables with a correlation coefficient $|r| > 0.6$.

---

[1] http://www.landfire.gov

We developed models using an information theoretic approach (Burnham and Anderson, 2002) within a mixed-effects logistic regression (Hosmer et al., 2013) and used a random intercept to account for individual heterogeneity. We used R package lme4 for mixed-effect modeling analysis (Bates et al., 2013). We used combinations of covariates (all permutations) to build models. All continuous covariates (slope, ruggedness, elevation, distance to trails, and distance to roads) were standardized before model development ($x_i - \bar{X}/s$ (Baxter et al., 2017). We used AIC$_c$ values to identify the most supported models, and to identify which variables were informative (Burnham and Anderson, 2002; Arnold, 2010). We evaluated models based on AIC$_c$, ΔAIC$_c$ values, and AIC$_c$ model weight.

To assess predictive ability of our top model, we performed k-folds cross validation with $k = 5$ (Long et al., 2009; Villepique et al., 2015; Kaze et al., 2016) in the San Rafael. We randomly sorted observations into five partitions, with an equal number of locations in each partition. During each iteration of this procedure, we used four partitions (80% of the data) as the training set to estimate model coefficients and the remaining partition (20% of the data) to test model predictions. We repeated this procedure until all observations were used for the test set and part of the training set. We then applied the coefficients from the predictive model to calculate relative probability of use in the San Rafael and Green River study areas. We generated two predictive maps, one for the San Rafael and one for the Green River, by applying this procedure to each raster pixel in each study area. We then used five equal-area bins to categorize the relative probabilities of use for each pixel from low to high (Sawyer et al., 2007; Kaze et al., 2016).

RESULTS

In 2012, we estimated birthdates for 29 young. Mean (±2 *SDs*) birthdate for bighorn sheep in the San Rafael during that year was 21 May (±19 days). In 2013, we estimated birthdates for 16 young, and mean birthdate for bighorn sheep in that area during that year was 20 May (±21 days). In both years, 89% of 45 births occurred in May (range = April 27–June 9). The date range we used for our analyses of lambing period habitat from GPS collar data for 2012 was 2 May–9 June. Whereas, for 2013 that range of dates was 29 April–10 June.

Our habitat analyses resulted in two top models that accounted for 99% of the AIC*c* weight (**Table 1**). Because the top model accounted for 86% of AIC$_c$ weight and included all covariates from the second model, we did not need to model average and only report parameter estimates from the top model (**Table 2**). That model included measures of elevation, slope, ruggedness, aspect, existing vegetation type, distance to trails, and distance to roads. Estimates for variables with evidence of selection ($p < 0.05$) were positive for barren vegetation, slope, ruggedness, north facing slopes, and distance to roads (indicating a preference for areas farther from roads). Estimates for variables with significant negative correlation were elevation (indicating a preference for lower elevations), south facing slopes, herb, shrub, and tree vegetation types, and distance to trails (indicating a preference for areas closer to trails).

Five-fold cross validation (rho = 0.99, P = 0.02) indicated that these variables predicted lambing period habitat of bighorns in our study area. In the San Rafael, predicted high-probability habitat was clumped around canyon rims surrounding the mesa top. Large areas of low-use predicted habitat occurred in that area, and locations of females during birthing were concentrated in small canyons (**Figure 2**). Of our 750 GPS locations, 68% were in the top two probability categories (high = 37%, medium high = 31%), 17% were within the medium category, 11% in the medium-low category, and 4% were within the low category (**Figure 2**). In the Green River, predicted high-probability habitat occurred along the Green River; however, some locations of females during birthing were concentrated in small canyon draws near areas of low habitat suitability (**Figure 3**). In the Green River, of our 1,130 GPS locations, 73% were in the top two categories of probability (high = 50%, medium high = 23%), 14% fell into the medium category, 10% fell within the medium-low category, and 3% fell within the low category (**Figure 3**).

DISCUSSION

Management and conservation decisions for ungulates and their habitat are increasingly being made that emphasize birthing areas (Singh et al., 2010; Kaze et al., 2016; Severud et al., 2019). For bighorn sheep, additional research is needed to understand and predict habitat use during birthing and nursery periods (Bangs et al., 2005). Our description of timing of births and GIS model predicted lambing period habitat for adjacent populations of desert and Rocky Mountain bighorn sheep. In similar, adjacent habitat these methods could be applied to conserve and manage habitat for these ungulates and to identify lambing period habitat for reintroduction and translocation sites. Reintroduction and translocation continue to be useful management tools for bighorn conservation (Wiedmann and Sargeant, 2014; Boyce and Krausman, 2018; Robinson et al., 2019). In Utah >1,000 Rocky Mountain bighorn sheep and >850 desert bighorn sheep have been released in areas of historical habitat since 1966 (Olson et al., 2008; Shannon et al., 2008; Utah Division of Wildlife Resources [UDWR], 2018). Currently in Utah, 26 units/subunits are identified as potential sites for augmentation or reintroduction, and 27% of those units/subunits are in eastern Utah near our study area (Utah Division of Wildlife Resources [UDWR], 2018). Our results can provide a model that can identify potential lambing period habitat for both subspecies in these areas. Similar site-specific data could be used in other areas to identify birthing period habitat for other populations of adjacent ungulates.

Our GIS model showed where bighorn sheep gave birth and identified lambing period habitat; that model also indicated areas of low-probability lambing period habitat. These results can be important for land-use planning in our study areas. In these areas, outdoor recreation and energy development have increased in the last 40 years and are predicted to continually increase (Smith and Burr, 2011; Sproat et al., 2019). Several of the forms of recreation

TABLE 1 | Model results ($\geq$0.01 model weight) for habitat selection by 19 desert bighorn sheep females during lambing period in the North San Rafael Swell, Utah, United States, from 2012 to 2013.

Model	*K*	AIC*c*	ΔAIC*c*	ω*i*	LL
Elevation + slope + ruggedness + aspect + existing vegetation type + distance to trails + distance to roads	14	1585.60	0.00	0.86	−778.66
Elevation + slope + ruggedness + existing vegetation type + distance to trails + distance to roads	11	1589.45	3.85	0.13	−783.64

We report the number of parameters (K), Akaike's Information Criterion adjusted for small sample sizes (AICc), difference in AICc value from top model (ΔAICc), AICc model weight (ωi), and log likelihood (LL).

TABLE 2 | Scaled β coefficients (which can be used to compare relative strength and importance of each variable) for resource selection of lambing period habitat of 19 desert bighorn sheep females in the North San Rafael Swell, Utah, United States, from 2012 to 2013.

Parameter	β	SE	*Z*-value	*P*-value
(Intercept)	0.68	0.23	3.00	< 0.01
Elevation	−0.48	0.07	−6.57	**<0.001**
Slope	0.59	0.09	6.87	**<0.001**
Ruggedness	0.51	0.09	5.78	**<0.001**
Aspect (east)	0.02	0.18	0.09	0.93
Aspect (south)	−0.55	0.21	−2.61	**<0.01**
Aspect (west)	−0.20	0.18	−1.14	0.25
Existing vegetation type (herb)	−1.30	0.32	−4.11	**<0.001**
Existing vegetation type (shrub)	−1.09	0.20	−5.55	**<0.001**
Existing vegetation type (sparse)	−0.05	0.20	−0.23	0.82
Existing vegetation type (tree)	−1.11	0.34	−3.28	**<0.01**
Distance to trails	−0.25	0.08	−3.24	**<0.01**
Distance to roads	0.42	0.07	6.37	**<0.001**

Barren vegetation and north facing slopes are not included in this table because they were the intercept in the model for each variable category. Significant parameters are bolded.

that can potentially effect bighorn sheep are off-highway vehicles, mountain biking, hiking, rafting, rock climbing, canyoneering, and camping near rivers (Papouchis et al., 2001; Longshore et al., 2013; Sproat et al., 2019). Hiking can have a pronounced effect because of the unpredictable locations of that activity and people approaching bighorn sheep, especially in spring when females are giving birth (Macarthur et al., 1979; Papouchis et al., 2001; Wiedmann and Bleich, 2014). Researchers recommend that known habitat for nursery groups of bighorn sheep be closed to hiking to benefit females and lambs (Papouchis et al., 2001). Our results can be used by biologists and land managers in land-use planning to identify areas of low-probability lambing period habitat that can be designated for increased recreation and energy development. There is an increase in demand for special recreation or special-use permits granted by land management agencies for commercial, competitive, or organized purposes, often for large groups. Given the concentrated level of anthropogenic activity generally associated with these permits, they can be especially disruptive to bighorn sheep. Our results can be helpful for land managers when reviewing permit applications for uses that overlap timing of births and lambing period habitat.

Expectedly, slope and ruggedness were significant variables in our models. Many other researchers indicate that these habitat components are important to minimize risk of predation for bighorn sheep with young (Smith et al., 1991; Bleich et al., 1997; Zeigenfuss et al., 2000; Bangs et al., 2005). Smith et al. (2015) also documented these components selected for at parturition sites and south and west facing slopes. Our model indicated, however, a preference for north facing slopes and an avoidance of south facing slopes. That response was due to a difference in latitude and temperature relative to different study areas, because bighorns are ostensibly selecting north-facing slopes in our study area to avoid warm, south-facing slopes during lactation. Smith et al. (2015) were also modeling parturition sites specifically, while we analyzed lambing period habitat. Lactating females have high water demands (Geist, 1971; Robbins, 2001), and travel of young lambs is restricted, necessitating the use of areas near water (Zeigenfuss et al., 2000). This could explain the preference for north facing slopes and lower elevation where water collects and is retained in our study area.

While our GIS model indicated that bighorn sheep avoided roads, largely corroborating past work (Krausman et al., 1989; Smith et al., 1991; Papouchis et al., 2001), that model also indicated a preference for areas near trails. That result was unexpected and likely occurred because most trails in the San Rafael traverse up the bottoms and around the side rims of canyons. The locations of those trails allow recreationists easy access to unobstructed views of the scenery and landscape. Many of those areas were also used by nursery groups of bighorn sheep. Trail traffic, however, was relatively low in the San Rafael. For example, a motion-sensor camera placed on a canyon of rim trail within high-use lambing period habitat recorded 316 spring visitor days by hikers and bikers. Previous researchers have reported an avoidance of areas by bighorn sheep with more intensive human recreation ($\bar{X} = 15{,}925$ visitor days, $SD = 6{,}038$ visitor days) (Wiedmann and Bleich, 2014). Therefore, in the San Rafael the number of hikers might not be affecting bighorn sheep like other areas with high-use trails. We hypothesize that that effect will increase with increased recreation in these areas.

Our methods can be applied to other areas of desert and Rocky Mountain bighorn sheep habitat in Utah. For example, eastern Utah is the largest, contiguous area in the state consisting of important habitat for both subspecies of bighorn sheep (Utah Division of Wildlife Resources [UDWR], 2018). This area has been historically important bighorn sheep habitat (Flinders et al., 2002; Shannon et al., 2008), and some areas have experienced five times the growth in outdoor recreation since 1979 (Sproat et al., 2019), which often peaks in May (Papouchis et al., 2001). Oil and gas exploration and mining are also increasing industries in this area. Human disturbance has caused the abandonment of habitat by desert bighorn sheep (Etchberger et al., 1989; Lowrey and Longshore, 2017) and Rocky Mountain bighorn sheep (Wiedmann and Bleich, 2014), decreased population

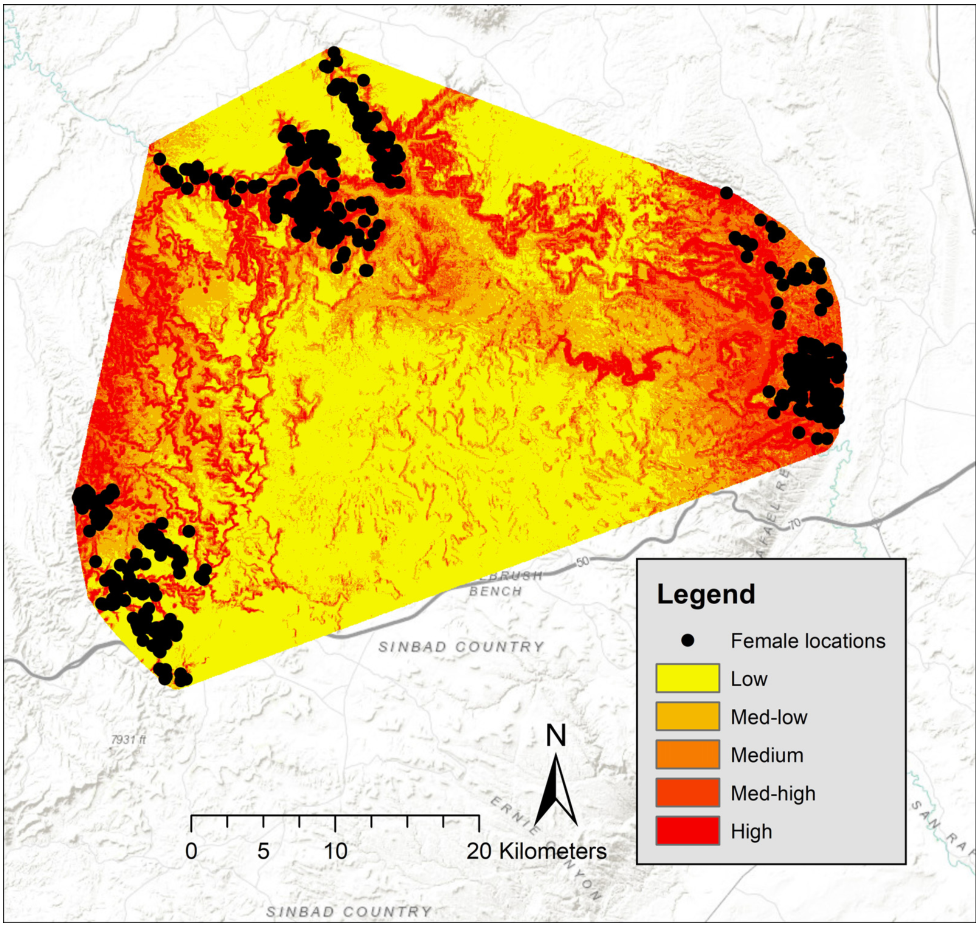

FIGURE 2 | Probabilities of desert bighorn sheep lambing period habitat in the North San Rafael Swell, spring 2012–2013, Utah, United States.

performance (Wiedmann and Bleich, 2014), and interrupted metapopulation dynamics for these animals (Epps et al., 2005; Bleich et al., 2016). The UDWR now has over 300 GPS collared bighorn sheep in 15 herds across the state. Our methods can be used in these areas to document lambing period habitat. Another important issue in southeastern Utah for which our GIS model can be used is in Grand Staircase-Escalante and Bears Ears national monuments. These areas are now being substantially reduced and opened for potential mining, livestock grazing, public access, and recreation (McBrayer and Roberts-Cady, 2018; Wilson et al., 2018; Reese, 2019). Timing of births data and a GIS model similar to ours could help inform natural resource managers about bighorn lambing period habitat in those areas facing immediate conservation and management changes.

Management of bighorn sheep habitat remains an important issue across much of western North America (Gutierrez-Espeleta et al., 2001; Lowrey and Longshore, 2017; Bleich, 2018; Boyce and Krausman, 2018). Proximity of bighorn sheep to domestic livestock allotments on public land (Cahn et al., 2011; Carpenter et al., 2014; O'Brien et al., 2014), and proximity of those wild ungulates to areas occupied by domestic sheep (*O. aries*) and goats (*Capra hircus*) on private land (Turner et al., 2004; Shannon et al., 2014), are controversial issues in the western United States. Domestic sheep and goats can transmit diseases to bighorn sheep (McClintock and White, 2007; Wehausen et al., 2011; Besser et al., 2012), and these issues are critical for the conservation and management of bighorn sheep populations (Cahn et al., 2011; Carpenter et al., 2014; O'Brien et al., 2014). Additionally, domestic cattle can affect habitat use by bighorns (Garrison et al., 2016). With female bighorn sheep showing general fidelity to birth sites and habitat for nursery groups (Etchberger and Krausman, 1999; Whiting et al., 2012), our data can be used to guide land-management decisions when assessing domestic livestock grazing allotments on public land, and when working with land owners on private land, which will help minimize conflict between these domestic and native ungulates.

Timing and synchrony of births in ungulates can have evolutionary implications (Marshall and Cambridge, 1937; Rutberg, 1987; Ims, 1990), such as reduced survival of young and reduced future reproductive potential (Clutton-Brock et al., 1987; Festa-Bianchet et al., 2000; Keech et al., 2000). Bighorn sheep from differing source populations that are released into adjacent areas can take up to 5 years to adapt timing of births

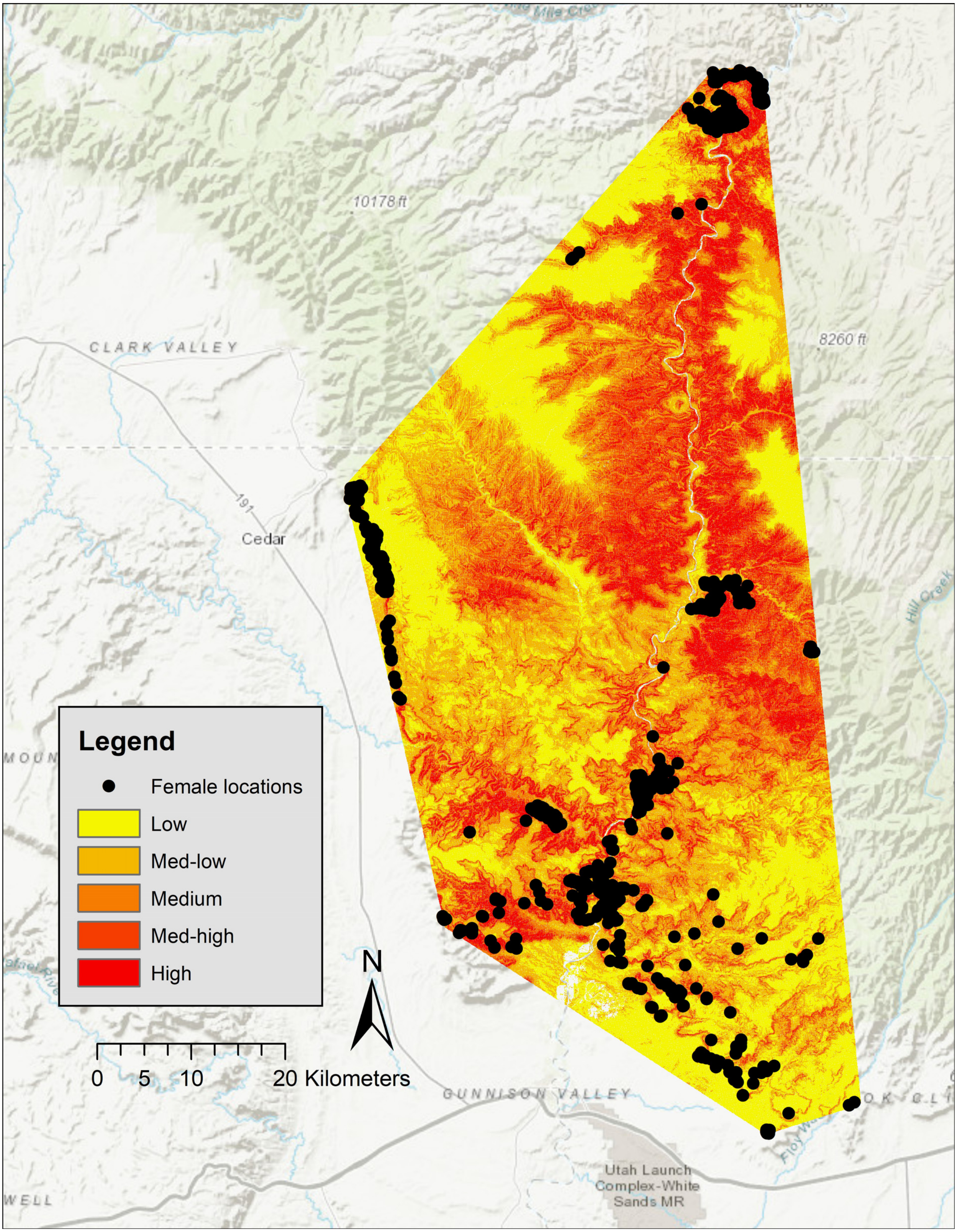

FIGURE 3 | Probabilities of Rocky Mountain bighorn sheep lambing period habitat in the Green River Corridor, spring 2012–2013, Utah, United States.

to local environments, which can hinder population growth (Whiting et al., 2011). Further, females in those populations do not compensate for late births by increasing maternal care, which possibly reduces survival of young (Whiting et al., 2010). After released bighorn sheep have adapted to local environments, differences of up to 29 days can still exist in timing of births across adjacent populations, because of discrepancies in peak green-up of vegetation (Whiting et al., 2012). All that information underscores the importance of collecting site-specific birthing data to produce GIS models of lambing period habitat for bighorn sheep.

Documenting the effects of human disturbance on ungulates is important for the ecology, evolution, and conservation of these animals, especially in an increasingly human-dominated world (Dzialak et al., 2011; Ciuti et al., 2012a,b). As anthropogenic activity increases in these areas, conservation planning and habitat management will increasingly rely on identifying habitats used by wildlife in areas of varying levels of human use (Goodson et al., 1999; Margules and Pressey, 2000; Harju et al., 2011). Biologists can substantially reduce effects from human activities to female ungulates by identifying where and when animals give birth and rear young (Singh et al., 2010; Kaze et al., 2016; McLaren et al., 2017), and this is a current, pressing conservation issue (Dzialak et al., 2011). Identification of lambing period habitat is becoming increasingly more important for bighorn conservation (Smith et al., 2015). Additionally, with GPS data being more readily accessible in wildlife studies, our methods can be used with site-specific timing of births and abiotic data and applied to other areas occupied by Rocky Mountain and desert bighorn sheep – and other ungulates – to identify important lambing period areas, which will aid in conservation and land-use planning.

DATA AVAILABILITY STATEMENT

The datasets analyzed for this study can be found by contacting the Utah Division of Wildlife Resources.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because all animal handling was done by the Utah Division of Wildlife Resources who held the pertinent permits to do such.

AUTHOR CONTRIBUTIONS

RR, JW, and JS designed the study. RR performed field work. JW, RR, and RL analyzed the data. RR, TS, and JW wrote an initial draft of the manuscript and all authors finalized it.

ACKNOWLEDGMENTS

We thank the UDWR, Utah Wild Sheep Foundation, and Brigham Young University for funding this project.

REFERENCES

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* 74, 1175–1178. doi: 10.1111/j.1937-2817.2010.tb01236.x

Bangs, P. D., Krausman, P. R., Kunkel, K. E., and Parsons, Z. D. (2005). Habitat use by desert bighorn sheep during lambing. *Eur. J. Wildl. Res.* 51, 178–184. doi: 10.1007/s10344-005-0098-8

Barry, R. (1979). *United States Bureau of Land Management Price River Resource Area*. Moab, UT: United States Bureau of Land Management.

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2013). *lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version 1.0–5*. Available online at: https://github.com/lme4/lme4/

Baxter, J. J., Baxter, R. J., Dahlgren, D. K., and Larsen, R. T. (2017). Resource selection by Greater Sage-Grouse reveals preference for mechanically-altered habitats. *Rangel. Ecol. Manage.* 70, 493–503. doi: 10.1016/j.rama.2017.01.007

Berger, J. (1991). Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim. Behav.* 41, 61–71.

Besser, T. E., Highland, M. A., Baker, K., Cassirer, E. F., Anderson, N. J., Ramsey, J. M., et al. (2012). Causes of pneumonia epizootics among bighorn sheep, western United States, 2008–2010. *Emerg. Infect. Dis.* 18, 406–414. doi: 10.3201/eid1803.111554

Bleich, V. C. (2018). Maintaining momentum for conservation: bighorn sheep as an example. *Wildl. Soc. Bull.* 42, 540–546. doi: 10.1002/wsb.914

Bleich, V. C., Bowyer, R. T., and Wehausen, J. D. (1997). Sexual segregation in mountain sheep: resources or predation? *Wildl. Monogr.* 134, 1–50.

Bleich, V. C., Whiting, J. C., Kie, J. G., and Bowyer, R. T. (2016). Roads, routes and rams: does sexual segregation contribute to anthropogenic risk in a desert-dwelling ungulate? *Wildl. Res.* 43, 380–388.

Bowyer, R. T. (1991). Timing of parturition and lactation in southern mule deer. *J. Mammal.* 72, 138–145. doi: 10.2307/1381988

Boyce, M. S. (2006). Scale for resource selection functions. *Divers. Distrib.* 12, 269–276. doi: 10.1111/j.1366-9516.2006.00243.x

Boyce, M. S., and Krausman, P. R. (2018). Controversies in mountain sheep management. *J. Wildl. Manage.* 82, 5–7. doi: 10.1002/jwmg.21400

Bunnell, F. L. (1982). The lambing period of mountain sheep: synthesis, hypotheses, and tests. *Can. J. Zool.* 60, 1–14. doi: 10.1139/z82-001

Burnham, K. P., and Anderson, D. A. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, NY: Springer-Verlag.

Cahn, M. L., Conner, M. M., Schmitz, O. J., Stephenson, T. R., Wehausen, J. D., and Johnson, H. E. (2011). Disease, population viability, and recovery of Endangered Sierra Nevada bighorn sheep. *J. Wildl. Manage.* 75, 1753–1766. doi: 10.1002/jwmg.232

Carpenter, T. E., Coggins, V. L., McCarthy, C., O'Brien, C. S., O'Brien, J. M., and Schommer, T. J. (2014). A spatial risk assessment of bighorn sheep extirpation by grazing domestic sheep on public lands. *Prev. Vet. Med.* 114, 3–10. doi: 10.1016/j.prevetmed.2014.01.008

Ciuti, S., Muhly, T. B., Paton, D. G., McDevitt, A. D., Musiani, M., and Boyce, M. S. (2012a). Human selection of elk behavioural traits in a landscape of fear. *Proc. R. Soc. B Biol. Sci.* 279, 4407–4416. doi: 10.1098/rspb.2012.1483

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., et al. (2012b). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS One* 7:e50611. doi: 10.1371/journal.pone.0050611

Clutton-Brock, T. H., Major, M., Albon, S. D., and Guinness, F. E. (1987). Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* 56, 53–67.

Côté, S. D., and Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* 127, 230–238. doi: 10.1007/s004420000584

Dalton, L. B., and Spillett, J. J. (1971). The bighorn sheep in Utah–past and present. *Trans. 1st North Am. Wild Sheep Conf.* 1, 32–53.

Dzialak, M. R., Harju, S. M., Osborn, R. G., Wondzell, J. J., Hayden-Wing, L. D., Winstead, J. B., et al. (2011). Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PLoS One* 6:e0014597. doi: 10.1371/journal.pone.0014597

Epps, C. W., Palsboll, P. J., Wehausen, J. D., Roderick, G. K., Ramey, R. R., and McCullough, D. R. (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecol. Lett.* 8, 1029–1038. doi: 10.1111/j.1461-0248.2005.00804.x

Etchberger, R. C., and Krausman, P. R. (1999). Frequency of birth and lambing sites of a small population of mountain sheep. *Southwest. Nat.* 44, 354–360.

Etchberger, R. C., Krausman, P. R., and Mazaika, R. (1989). Mountain sheep habitat characteristics in the Pusch Ridge Wilderness, Arizona. *J. Wildl. Manage.* 53, 902–907.

Festa-Bianchet, M. (1988a). Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J. Zool.* 214, 653–661. doi: 10.1007/s00442-008-1035-9

Festa-Bianchet, M. (1988b). Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75, 580–586. doi: 10.1007/BF00776423

Festa-Bianchet, M., Jorgenson, J. T., and Réale, D. (2000). Early development, adult mass, and reproductive success in bighorn sheep. *Behav. Ecol.* 11, 633–639. doi: 10.1093/beheco/11.6.633

Flinders, J. T., Rogers, D. S., Webber-Alston, J. L., and Barber, H. A. (2002). Mammals of the Grand Staircase-Escalante National Monument: a literature and museum survey. *Monogr. West. N. Am. Nat.* 1, 1–64. doi: 10.3398/1545-0228-1.1.1

Garrison, K. R., Cain, J. W., Rominger, E. M., and Goldstein, E. J. (2016). Sympatric cattle grazing and desert bighorn sheep foraging. *J. Wildl. Manage.* 80, 197–207. doi: 10.1002/jwmg.1014

Geist, V. (1971). *Mountain Sheep: A Study in Behavior and Evolution*. Chicago, IL: The University of Chicago Press.

Goodson, N. J., Stevens, D. R., McCoy, K., and Cole, J. (1999). "Effects of river-based recreation and livestock grazing on desert bighorn sheep on the Navajo Nation," in *Proceedings of the 2nd North American Wild Sheep Conference*, Reno, NV, 123–131.

Gutierrez-Espeleta, G. A., Hedrick, P. W., Kalinowski, S. T., Garrigan, D., and Boyce, W. M. (2001). Is the decline of desert bighorn sheep from infectious disease the result of low MHC variation? *Heredity* 86, 439–450. doi: 10.1046/j.1365-2540.2001.00853.x

Harju, S. M., Dzialak, M. R., Osborn, R. G., Hayden-Wing, L. D., and Winstead, J. B. (2011). Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. *Anim. Conserv.* 14, 502–511. doi: 10.1111/j.1469-1795.2011.00456.x

Hosmer, D. W. Jr., Lemeshow, S., and Sturdivant, R. X. (2013). *Applied Logistic Regression*. Hoboken, NJ: John Wiley & Sons.

Ims, R. A. (1990). The ecology and evolution of reproductive synchrony. *Trends Ecol. Evol.* 5, 135–140. doi: 10.1016/0169-5347(90)90218-3

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. doi: 10.2307/1937156

Johnson, D. S., Barry, R. P., and Bowyer, R. T. (2004). Estimating timing of life-history events with coarse data. *J. Mammal.* 85, 932–939. doi: 10.1644/bfw-009

Karsch, R. C., Cain, J. W., Rominger, E. M., and Goldstein, E. J. (2016). Desert bighorn sheep lambing habitat: parturition, nursery, and predation sites. *J. Wildl. Manage.* 80, 1069–1080. doi: 10.1002/jwmg.21092

Kaze, J., Whiting, J. C., Freeman, E. D., Bates, S. B., and Larsen, R. T. (2016). Birth-site selection and timing of births in American bison: effects of habitat and proximity to anthropogenic features. *Wildl. Res.* 43, 418–428.

Keech, M. A., Bowyer, R. T., Ver Hoef, J. M., Boertje, R. D., Dale, B. W., and Stephenson, T. R. (2000). Life-history consequences of maternal condition in Alaskan moose. *J. Wildl. Manage.* 64, 450–462.

Krausman, P. R., Hervert, J. J., and Ordway, L. L. (1985). Capturing deer and mountain sheep with a net-gun. *Wildl. Soc. Bull.* 13, 71–73.

Krausman, P. R., Leopold, B. D., Seegmiller, R. F., and Torres, S. G. (1989). Relationships between desert bighorn sheep and habitat in western Arizona. *Wildl. Monogr.* 53, 1–66.

Lenarz, M. S. (1979). Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). *J. Mammal.* 60, 671–678. doi: 10.2307/1380184

Loe, L. E., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Langvatn, R., Klein, F., et al. (2005). Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *J. Anim. Ecol.* 74, 579–588. doi: 10.1111/j.1365-2656.2005.00987.x

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., and Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol. Monogr.* 84, 513–532. doi: 10.1890/13-1273.1

Long, R. A., Muir, J. D., Rachlow, J. L., and Kie, J. G. (2009). A comparison of two modeling approaches for evaluating wildlife-habitat relationships. *J. Wildl. Manage.* 73, 294–302. doi: 10.1111/gcb.13900

Longshore, K., Lowrey, C., and Thompson, D. B. (2013). Detecting short-term responses to weekend recreation activity: desert bighorn sheep avoidance of hiking trails. *Wildl. Soc. Bull.* 37, 698–706. doi: 10.1002/wsb.349

Lowrey, C., and Longshore, K. M. (2017). Tolerance to disturbance regulated by attractiveness of resources: a case study of desert bighorn sheep within the river mountains, Nevada. *West. N. Am. Nat.* 77, 82–99.

Macarthur, R. A., Johnston, R. H., and Geist, V. (1979). Factors influencing heart-rate in free-ranging bighorn sheep-physiological approach to the study of wildlife harassment. *Can. J. Zool.* 57, 2010–2021. doi: 10.1139/z79-265

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., and Erickson, W. P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Boston, MA: Kluwer Academic.

Margules, C. R., and Pressey, R. L. (2000). Systematic conservation planning. *Nature* 405, 243–253. doi: 10.1038/35012251

Marshall, F. H. A., and Cambridge, F. R. S. (1937). On the change over in the oestrous cycle in animals after transference across the equator, with further observations on the incidence of the breeding seasons and the factors controlling sexual periodicity. *Proc. R. Soc. Lond. B* 122, 413–428. doi: 10.1098/rspb.1937.0034

McBrayer, J., and Roberts-Cady, S. (2018). The case for preserving Bears Ears. *Ethics Policy Environ.* 21, 48–51. doi: 10.1080/21550085.2018.1448035

McClintock, B. T., and White, G. C. (2007). Bighorn sheep abundance following a suspected pneumonia epidemic in Rocky Mountain National Park. *J. Wildl. Manage.* 71, 183–189. doi: 10.2193/2006-336

McLaren, A., Benson, J., and Patterson, B. (2017). Multiscale habitat selection by cow moose (*Alces alces*) at calving sites in central Ontario. *Can. J. Zool.* 95, 891–899. doi: 10.1139/cjz-2016-0290

O'Brien, J. M., O'Brien, C. S., McCarthy, C., and Carpenter, T. E. (2014). Incorporating foray behavior into models estimating contact risk between bighorn sheep and areas occupied by domestic sheep. *Wildl. Soc. Bull.* 38, 321–331. doi: 10.1002/wsb.387

Olson, D. D., Shannon, J. M., Whiting, J. C., and Flinders, J. T. (2008). History, status, and population structure of California bighorn sheep in Utah. *Proc. North. Wild Sheep Goat Counc.* 16, 161–177.

Papouchis, C. M., Singer, F. J., and Sloan, W. B. (2001). Responses of desert bighorn sheep to increased human recreation. *J. Wildl. Manage.* 65, 573–582.

Phillips, G. E., and Alldredge, A. W. (2000). Reproductive success of elk following disturbance by humans during calving season. *J. Wildl. Manage.* 64, 521–530. doi: 10.2307/3803250

R Core Team (2015). *A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rachlow, J. L., and Bowyer, R. T. (1991). Interannual variation in timing and synchrony of parturition in Dall's sheep. *J. Mammal.* 72, 487–492. doi: 10.2307/1382131

Rachlow, J. L., and Bowyer, R. T. (1994). Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy. *J. Mammal.* 75, 328–337. doi: 10.2307/1382551

Reese, A. (2019). The bones of Bears Ears. *Science* 363, 218–220. doi: 10.1126/science.363.6424.218

Rigby, J. K., and Beus, S. S. (1987). Stratigraphy and structure of the San Rafael Reef, Utah, a major Monocline of the Colorado Plateau. *Decade N. Am. Geol.* 2, 269–273. doi: 10.1130/0-8137-5402-x.269

Robbins, C. T. (2001). *Wildlife Feeding and Nutrition*. San Diego, CA: Academic Press.

Robinson, R. W., Whiting, J. C., Shannon, J. M., Olson, D. D., Flinders, J. T., Smith, T. S., et al. (2019). Habitat use and social mixing between groups of resident and augmented bighorn sheep. *Sci. Rep.* 9:14984. doi: 10.1038/s41598-019-51370-y

Rollins, M. G. (2009). LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *Int. J. Wildl. Fire* 18, 235–249. doi: 10.1071/wf08088

Rubin, E. S., Boyce, W. M., and Bleich, V. C. (2000). Reproductive strategies of desert bighorn sheep. *J. Mammal.* 81, 769–786. doi: 10.1644/1545-1542(2000)081<0769:rsodbs>2.3.co;2

Rutberg, A. T. (1987). Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *Am. Nat.* 130, 692–710. doi: 10.1086/284739

Sadleir, R. M. F. S. (1969). The role of nutrition in the reproduction of wild mammals. *J. Reprod. Fertil. Suppl.* 6, 39–48.

Sappington, J. M., Longshore, K. M., and Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* 71, 1419–1426. doi: 10.2193/2005-723

Sawyer, H., Nielson, R. M., Lindzey, F. G., Keith, L., Powell, J. H., and Abraham, A. A. (2007). Habitat selection of Rocky Mountain elk in a nonforested environment. *J. Wildl. Manage.* 71, 868–874. doi: 10.2193/2006-131

Severud, W. J., DelGiudice, G. D., and Obermoller, T. R. (2019). Association of moose parturition and post-parturition habitat with calf survival. *J. Wildl. Manage.* 83, 175–183. doi: 10.1002/jwmg.21570

Shannon, J. M., Olson, D. D., Whiting, J. C., Flinders, J. T., and Smith, T. S. (2008). "Status, distribution, and history of Rocky Mountain bighorn sheep in Utah," in *Proceedings of the Northern Wild Sheep and Goat Council*, (Heber, UT: Northern Wild Sheep and Goat Council), 178–195.

Shannon, J. M., Whiting, J. C., Larsen, R. T., Olson, D. D., Flinders, J. T., Smith, T. S., et al. (2014). Population response of reintroduced bighorn sheep after observed commingling with domestic sheep. *Eur. J. Wildl. Res.* 60, 737–748. doi: 10.1007/s10344-014-0843-y

Sikes, R. S., and Animal Care and Use Committee of the American Society of Mammalogists (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688. doi: 10.1093/jmammal/gyw078

Singh, N. J., Grachev, I. A., Bekenov, A. B., and Milner-Gulland, E. J. (2010). Saiga antelope calving site selection is increasingly driven by human disturbance. *Biol. Conserv.* 143, 1770–1779. doi: 10.1016/j.biocon.2010.04.026

Smith, J., and Burr, S. (2011). Environmental attitudes and desired social-psychological benefits of off-highway vehicle users. *Forests* 2, 875–893. doi: 10.3390/f2040875

Smith, J. B., Grovenburg, T. W., and Jenks, J. A. (2015). Parturition and bed site selection of bighorn sheep at local and landscape scales. *J. Wildl. Manage.* 79, 393–401. doi: 10.1002/jwmg.843

Smith, T. S., Flinders, J. T., and Winn, D. S. (1991). A habitat evaluation procedure for Rocky Mountain bighorn sheep in the Intermountain West. *Great Basin Nat.* 51, 205–225.

Sproat, K. K., Martinez, N. R., Smith, T. S., Sloan, W. B., Flinders, J. T., Bates, J. W., et al. (2019). Desert bighorn sheep responses to human activity in South-eastern Utah. *Wildl. Res.* 47, 16–24.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: a review and meta-analysis. *Biol. Conserv.* 141, 2159–2173. doi: 10.1016/j.biocon.2008.06.026

Thompson, R. W., and Turner, J. C. (1982). Temporal geographic variation in the lambing season of bighorn sheep. *Can. J. Zool.* 60, 1781–1793. doi: 10.1139/z82-231

Turner, J. C., Douglas, C. L., Hallam, C. R., Krausman, P. R., and Ramey, R. R. (2004). Determination of critical habitat for the endangered Nelson's bighorn sheep in southern California. *Wildl. Soc. Bull.* 32, 427–448. doi: 10.2193/0091-7648(2004)32[427:dochft]2.0.co;2

Utah Division of Wildlife Resources [UDWR] (2018). *Utah Bighorn Sheep Statewide Management Plan*. Salt Lake City, UT: Utah Division of Wildlife Resources.

Villepique, J. T., Pierce, B. M., Bleich, V. C., Andic, A., and Bowyer, R. T. (2015). Resource Selection by an endangered ungulate: a test of predator-induced range abandonment. *Adv. Ecol.* 2015:357080.

Wehausen, J. D., Kelley, S. T., and Ramey, R. R. (2011). Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. *Calif. Fish Game* 97, 7–24. doi: 10.1016/j.prevetmed.2012.11.018

Whiting, J. C., Bowyer, R. T., and Flinders, J. T. (2008). Young bighorn (*Ovis canadensis*) males: can they successfully woo females? *Ethology* 114, 32–41. doi: 10.1111/j.1439-0310.2007.01442.x

Whiting, J. C., Bowyer, R. T., Flinders, J. T., and Eggett, D. L. (2011). Reintroduced bighorn sheep: fitness consequences of adjusting parturition to local environments. *J. Mammal.* 92, 213–220. doi: 10.1644/10-mamm-a-145.1

Whiting, J. C., Olson, D. D., Shannon, J. M., Bowyer, R. T., Klaver, R. W., and Flinders, J. T. (2012). Timing and synchrony of births in bighorn sheep: implications for reintroduction and conservation. *Wildl. Res.* 39, 565–572.

Whiting, J. C., Stewart, K. M., Bowyer, R. T., and Flinders, J. T. (2010). Reintroduced bighorn sheep: do females adjust maternal care to compensate for late-born young? *Eur. J. Wildl. Res.* 56, 349–357. doi: 10.1007/s10344-009-0323-y

Wiedmann, B. P., and Bleich, V. C. (2014). Demographic responses of bighorn sheep to recreational activities: a trial of a trail. *Wildl. Soc. Bull.* 38, 773–782. doi: 10.1002/wsb.463

Wiedmann, B. P., and Sargeant, G. A. (2014). Ecotypic variation in recruitment of reintroduced bighorn sheep: implications for translocation. *J. Wildl. Manage.* 78, 394–401. doi: 10.1002/jwmg.669

Wilson, J. S., Kelly, M., and Carril, O. M. (2018). Reducing protected lands in a hotspot of bee biodiversity: bees of Grand Staircase-Escalante National Monument. *PeerJ* 6:e6057. doi: 10.7717/peerj.6057

Zeigenfuss, L. C., Singer, F. J., and Gudorf, M. A. (2000). Test of a modified habitat suitability model for bighorn sheep. *Restor. Ecol.* 8, 38–46. doi: 10.1046/j.1526-100x.2000.80064.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 21 April 2020
doi: 10.3389/fevo.2020.00098

Nutritional-Landscape Models Link Habitat Use to Condition of Mule Deer (*Odocoileus hemionus*)

Jennifer L. Merems[1], Lisa A. Shipley[2], Taal Levi[3], Joel Ruprecht[3], Darren A. Clark[4], Michael J. Wisdom[5], Nathan J. Jackson[6], Kelley M. Stewart[6] and Ryan A. Long[1]*

[1] Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, United States, [2] School of the Environment, Washington State University, Pullman, WA, United States, [3] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, United States, [4] Oregon Department of Fish and Wildlife, La Grande, OR, United States, [5] USDA Forest Service, Pacific Northwest Research Station, La Grande, OR, United States, [6] Department of Natural Resources and Environmental Science, University of Nevada, Reno, Reno, NV, United States

In heterogeneous landscapes, large herbivores employ plastic behavioral strategies to buffer themselves against negative effects of environmental variation on fitness. Yet, the mechanisms by which individual responses to such variation scale up to influence population performance remain uncertain. Analyses of space-use behaviors exemplify this knowledge gap, because such behaviors are often assumed, but rarely demonstrated, to have direct fitness consequences. We combined fine-scale data on forage biomass and quality with movement data and measures of somatic energy reserves to determine whether variation in use (the quantity of resource units, e.g., pixels on a landscape, that receive some level of investment by an animal during a specific sampling period) or selection (use of a resource unit relative to its availability to the animal during the same sampling period) of the nutritional landscape predicted early winter body condition of mule deer (*Odocoileus hemionus*). At the population level, mule deer exhibited stronger selection for high forage biomass at the landscape scale than at the home-range scale, and during summer than during spring. Use of the nutritional landscape varied among individual deer and had important consequences for early winter condition (an important determinant of survival and reproduction in capital-breeding ungulates). Females that consistently used vegetation communities that provided high biomass of preferred forage plants throughout spring and summer entered winter in better condition than females that used those vegetation communities less frequently. In contrast, selection (i.e., use relative to availability) of the nutritional landscape by individual deer was not significantly related to early winter condition at either the landscape or home-range scales. Our results highlight the value of using mechanistic, nutritional approaches to understand the potential fitness consequences of individual variation in behavior. In addition, our study suggests that patterns of forage use by ungulates may sometimes correlate more strongly with fitness than patterns of forage selection, which are scale-dependent and more vulnerable to biases stemming from the need to accurately quantify availability.

Keywords: crude protein, digestible energy, forage biomass, mule deer, nutritional condition, *Odocoileus hemionus*, Oregon, resource selection function

Edited by:
Paul Richard Krausman,
The University of Arizona,
United States

Reviewed by:
Mark Hebblewhite,
University of Montana, United States
Perry S. Barboza,
Texas A&M University, United States

***Correspondence:**
Ryan A. Long
ralong@uidaho.edu

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *02 December 2019*
Accepted: *26 March 2020*
Published: *21 April 2020*

Citation:
Merems JL, Shipley LA, Levi T, Ruprecht J, Clark DA, Wisdom MJ, Jackson NJ, Stewart KM and Long RA (2020) Nutritional-Landscape Models Link Habitat Use to Condition of Mule Deer (Odocoileus hemionus). Front. Ecol. Evol. 8:98. doi: 10.3389/fevo.2020.00098

INTRODUCTION

In heterogeneous landscapes, free-ranging animals often are forced to make complex tradeoffs among factors that influence fitness (e.g., forage versus predation risk; Berger, 1991; Barten et al., 2001). In the most fundamental life-history tradeoff experienced by animals in resource-limited environments, individuals must balance the costs of current reproduction against future reproduction and survival (Stearns, 1992; Monteith et al., 2013). Behavioral plasticity is one key mechanism by which animals cope with this tradeoff and buffer themselves against environmental variation (Huey et al., 2003). An increasing body of evidence suggests that behavioral strategies used by animals to overcome environmental constraints on fitness often vary with endogenous traits such as age (Montgomery et al., 2013), nutritional condition (Monteith et al., 2011, 2013; Long et al., 2014), immune function (Downs et al., 2015), or personality (Dall et al., 2004; Stamps and Groothuis, 2010). Yet, the mechanisms by which individual responses to variation in resource availability scale up to influence population performance remain unclear.

In temperate and polar environments, large terrestrial herbivores exhibit life-history strategies that revolve around seasonal changes in resource availability and the energetic demands imposed by key life-history events (Monteith et al., 2013). These long-lived mammals must accrue sufficient energy and protein reserves during summer to replenish reserves lost over winter, while also meeting the demands of lactation without endangering future survival and reproduction (Therrien et al., 2008; Bårdsen et al., 2010; Tollefson et al., 2010; Bårdsen and Tveraa, 2012). Large herbivores use a variety of physiological and behavioral strategies for coping with these tradeoffs (Monteith et al., 2013), and maximizing energy intake during summer is among the most critical (Cook et al., 2004; Monteith et al., 2013; Long et al., 2014, 2016). Small differences in the ratio of energy intake to expenditure during summer can have a disproportionate influence (i.e., a multiplier effect; White, 1983; Cook et al., 2004) on early winter body mass and condition that directly influences survival and reproductive success (Festa-Bianchet et al., 1997; Côté and Festa-Bianchet, 2001; Cook et al., 2004; Monteith et al., 2014). Nevertheless, a variety of factors (e.g., competition and risk of predation) may limit the ability of herbivores to optimize their use of the nutritional landscape (i.e., variation in the density of energy and protein across space and time; Pretorius et al., 2011). Under these conditions, differences in use of the nutritional landscape among individuals can have important fitness consequences (van Beest and Milner, 2013; Long et al., 2016).

Because nutrition integrates the responses of ungulates to their environment (Parker et al., 2009), research approaches that are grounded in the mechanistic principles of nutritional ecology are useful for predicting fitness consequences of behavior. In particular, patterns of movement and space use can be linked to fitness via their effects on energy balance, and thus nutritional condition, of individuals (e.g., Long et al., 2016). Measuring such behaviors is complicated, however, and there are multiple metrics designed to quantify the responses of ungulates to variation in the quality, abundance, or distribution of resources. Two such metrics commonly derived from telemetry data are resource use (i.e., the quantity of resource units (e.g., pixels on a landscape) that receive some level of investment (e.g., time spent in the unit) by an animal during a specific sampling period; Manly et al., 2002; Lele et al., 2013) and resource selection (i.e., use of a resource unit relative to its availability to the animal during the same sampling period; Manly et al., 2002). In contrast to resource use, resource availability is scale-dependent, and thus patterns of selection can change across spatial scales (e.g., geographic range, landscape, or home range scales) even as use remains constant (Johnson, 1980; Manly et al., 2002). Moreover, environmental covariates with the greatest potential to influence fitness often are selected most strongly at the largest scales. For example, if predation is the primary factor limiting an herbivore population, then individuals will often first locate their home range in a part of the landscape that reduces predation risk (2nd-order selection; Johnson, 1980), and then select the best forage available within that home range (3rd-order selection; Johnson, 1980; Bowyer and Kie, 2006). Both resource use and resource selection have value for understanding the causes and consequences of ungulate behavior (Millspaugh et al., 2006), but to our knowledge no previous study has compared the relative value of these metrics for linking patterns of movement or space use to fitness correlates such as nutritional condition.

Metrics of individual performance such as body mass and condition have been repeatedly demonstrated to influence survival and reproductive success of adult ungulates (Gaillard et al., 2000; Cook et al., 2004). Early winter condition in particular strongly affects overwinter survival of capital-breeding ungulates by determining the availability of fat stores that can be catabolized for energy when high-quality forage is unavailable in winter (Cook et al., 2004). Relationships between condition and individual fitness also scale up to influence population performance. For example, using a long-term dataset on mule deer in the Sierra Nevada, Monteith et al. (2014) demonstrated that population growth rate was dependent on condition, and that the rate of population change transitioned from positive ($\lambda > 1$) to negative ($\lambda < 1$) at a mean condition of approximately 12.4% ingesta-free body fat.

Our objective was to understand whether individual variation in use or selection (i.e., use relative to availability) of the nutritional landscape translated into variation in early-winter condition of female mule deer (*Odocoileus hemionus*). We hypothesized that:

1. H1: Mule deer will show stronger selection for the nutritional landscape at the landscape scale (i.e., 2nd-order selection) than at the home-range scale (i.e., 3rd-order selection.
2. H2: Mule deer will show stronger selection for the nutritional landscape during summer than spring because high-quality forage resources are more evenly dispersed, and therefore more easily accessible, during spring.
3. H3: Strength of selection (use relative to availability) for the nutritional landscape at the landscape scale will be

more strongly correlated with early-winter condition of individual deer than strength of selection at the home-range scale, because forage abundance and quality during summer are primary determinants of overwinter condition and survival of deer, and thus deer will select the nutritional landscape most strongly and consistently at the larger scale.

4. H4: Individual deer that use (i.e., spend more time in, independent of availability) vegetation communities with high biomass of preferred forages more consistently during spring and summer will enter winter in better condition than deer that spend less time in high-quality vegetation communities.
5. H5: Mean nutritional condition of mule deer in early winter will be above thresholds for maintaining positive population growth (∼12.4% ingesta-free body fat when $\lambda = 1$; Monteith et al., 2014) because mule deer are actively selecting areas where preferred forage plants are readily available (i.e., areas of high forage biomass).

MATERIALS AND METHODS

Study Area

We conducted our study at the Starkey Experimental Forest and Range, Blue Mountains, northeastern Oregon (45° 12′N, 118° 3′W), United States, during May–August of 2016 and 2017. Starkey is surrounded by a 2.4-m high fence that prevents movement of ungulates into or out of the study area (Rowland et al., 1997). Starkey encompasses 10,125 ha of the Wallowa-Whitman National Forest and supports a variety of large herbivores and predators [mule deer, elk (*Cervus canadensis*), cattle, mountain lions (*Puma concolor*), American black bears (*Ursus americanus*), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*)]. The estimated population size of female mule deer at Starkey was 51 deer (95% credible interval = 43 – 60), including yearlings, during the time of our study (T. D. Forrester, Oregon Department of Fish and Wildlife, unpublished data; 0.65 deer/km^2). Drainages and vegetation communities create a complex and varied foraging landscape at Starkey. Elevations range from 1,120 to 1,500 m, and annual precipitation is 510 mm, falling primarily during winter as snow. The study area supports a mosaic of grasslands, wet meadows, shrublands, and coniferous forests. A more detailed description of the study area is provided by Rowland et al. (1997).

Animal Capture and Handling

To quantify use of the nutritional landscape by mule deer, we collected data on space-use behavior of adult females (n = 32) during spring and summer, and on nutritional condition of a subset (n = 9 animal years) of those deer during early winter, using a combination of global positioning system (GPS)-collars, ultrasonography, and palpation scoring. Three deer were monitored during both years of the study, and we considered condition measurements from those deer to be independent based on longitudinal condition data obtained from mule deer in Wyoming (n = 72 pairs of early-winter body condition measurements from female mule deer sampled in ≥2 consecutive years, R^2 = 0.008 in a regression of condition in year t + 1 against condition in year t; K. L. Monteith, University of Wyoming, unpublished data). We baited adult female mule deer into wooden panel traps (Rowland et al., 1997) dispersed throughout the study area during mid-November to mid-December, or chemically immobilized them via darting (1–2 mL of the immobilization cocktail BAM: butorphanol, azaperone, and medetomidine; Miller et al., 2009). We hobbled (except during immobilizations, during which we placed deer in sternal recumbency) and blindfolded each deer to minimize stress. When all data were collected we were reversed immobilized deer with an intramuscular injection of 0.5 mL of naltrexone and 2–4 mL of atipamezole. During handling we removed GPS-collars from the previous year (if necessary), replaced them with new collars (model 4400S and 4500S, Lotek Wireless, Newmarket, ON, Canada or VERTEX Plus, Vectronic Aerospace GmbH, Berlin, Germany; Wisdom et al., 1993), measured body mass with an electronic scale (±1 kg), measured chest girth, and quantified nutritional condition using the methods of Cook et al. (2010). We programmed GPS-collars to record a location once every 90 min throughout most of the following year. We used ultrasonography (E.I. Medical Imaging, Ibex, with a 5-MHz linear transducer) to measure subcutaneous rump fat thickness (MAXFAT) and thickness of the bicep and loin muscles to the nearest 1 mm (Bishop et al., 2009; Monteith et al., 2011). In addition, we recorded a condition score via palpation of the sacrosciatic ligament (Cook et al., 2010). We combined condition data with data on body mass to estimate total percent ingesta-free body fat using the equations of Cook et al. (2010).

To quantify the effects of lactation status on nutritional condition of female mule deer in early winter, we monitored timing of parturition and subsequent survival of neonates born to a subset of GPS-collared females that represented ≥25% of the estimated adult female population at Starkey. We recaptured those deer (n = 9 animal years) in January–March, assessed them for pregnancy via ultrasonography, and fitted them with vaginal implant transmitters [VIT; M39/30L, Advanced Telemetry Solutions (ATS), Isanti, MN, United States] to monitor timing of parturition and aide in neonate capture (Bishop et al., 2007; Monteith et al., 2014). We captured neonates the following spring (typically within 48 h of parturition) and fitted them with an expandable very high frequency (VHF) radio-collar with a mortality sensor (M4210; Advanced Telemetry Solution, Isanti, MN, United States). We monitored neonates daily for survival during the first 2 months of life, and weekly thereafter. If mortality occurred, we located the carcass immediately and attempted to identify the cause of death (Walsh, 2016; Jackson, 2019).

Mapping the Nutritional Landscape

During spring (13 May–30 June) and summer (1 July–15 August) of 2016–2017, we conducted intensive vegetation sampling to map the nutritional landscape available to mule deer at Starkey. We used the Integrated Landscape Assessment Project (ILAP; Halofsky et al., 2014) potential vegetation layer to stratify Starkey into the following potential vegetation types

(PVTs): xeric grasslands dominated by a few grass and forb species (e.g., onespike oatgrass (*Danthonia unispicata*), ventenata (*Ventenata dubia*), and low gumweed (*Grindelia nana*); ~16% of the study area); xeric forests characterized by ponderosa pine (*Pinus ponderosa*; ~8% of the study area); and mesic forests dominated by grand fir (*Abies grandis*; ~31% of the study site), Douglas-fir (*Pseudotsuga menziesii*; ~32% of the study site), or grand/subalpine fir (*Abies spp.*; ~12% of the study site). We then selected transect locations for sampling mule deer forage using a stratified random design, wherein the number of transects within each PVT was proportional to the relative area of the PVT within Starkey. We also stratified our sampling by season (spring vs. summer) in each year, and transects did not overlap between seasons or years (i.e., sampling was without replacement). Transects were 100 m long and included five 4 × 10 m plots centered on the transect line and spaced at 10-m intervals. Each plot contained two 1-m^2 quadrats, located in opposite corners. We sampled quadrats to quantify forage biomass, and plots to quantify nutritional quality of key forage species for mule deer along each transect. We used published (Damiran, 2006; Stewart et al., 2011) and unpublished (R. C. Cook, National Council for Air and Stream Improvement; L.A. Shipley, Washington State University; unpublished data) data on mule deer diets in similar ecosystems to identify key forage species for mule deer at Starkey (i.e., forage plants that are commonly used proportionally greater than their availability (selected) or in proportion to their availability (neutral) by mule deer; **Supplementary Appendix A**).

We estimated green (i.e., uncured) biomass of forage species along each transect using the clip-and-weigh (CW) method (Butler and Wayne, 2007) and a double sampling scheme (Bonham, 1989). We started by visually estimating percent horizontal cover (Bonham, 1989) of each forage species within each 1-m^2 quadrat along a transect. We then selected the two most species-rich quadrats for biomass clipping. We clipped all forage species in those two quadrats at ground level, separated them by plant part (e.g., leaves and inflorescences for graminoids and forbs, and leaves and current annual growth for shrubs) and placed them into paper bags for drying. At the end of each day we placed biomass samples into a forced convection oven to dry at 100°C for 24 h. At the end of each drying period we removed and weighed samples using a Mettler platform scale (±0.1 g). We tallied biomass samples at the end of each season and conducted additional sampling at random locations within the associated PVT when necessary to ensure a minimum species-specific sample size of $n = 10$. When field sampling was completed, we estimated biomass of forage species in all unclipped quadrats by fitting simple linear regression models (Neter et al., 1996) to the biomass (response variable) and cover (predictor variable) data for each species (**Supplementary Appendix B**). We fit separate models for each season, and species with <10 paired biomass and cover measurements were grouped with similar species in either the same genus or family.

We quantified nutritional quality of forage along each transect by clipping additional samples within the 4 × 10 m plots. We used visual cover estimates (Bonham, 1989) from each transect to identify the 10 most abundant selected species and the 10 most abundant neutral species (separated by individual species). When necessary we also separated species by plant parts (e.g., stems and leaves of shrubs). We placed nutrition samples into paper bags and dried them at 40° C in a forced convection oven for 24 h; we dried all samples within 24 h of collection to minimize effects of respiration and fermentation. We aggregated nutrition samples at the PVT level within seasons by combining samples across transects for each species. We then ground composited samples in a Wiley Mill (1-mm screen) and analyzed them for crude protein (CP,%), neutral detergent fiber (NDF,%), and acid detergent lignin (ADL,%; Dairy One Forage Lab, Ithaca, NY, United States).

We obtained additional forage samples for analysis of protein-precipitating capacity of condensed tannins in the forage (mg Bovine Serum Albumin precipitate/mg forage) at the junction of the spring and summer seasons in 2017. We collected tannin samples opportunistically from each PVT and stored them in a freezer at −18° C. We subsequently freeze-dried those samples for 24 h, ground them in a Wiley Mill (1-mm screen), and analyzed them for tannin precipitation using the precipitation assay of Martin and Martin (1982) at the Wildlife Habitat Nutrition Laboratory at Washington State University. We were not able to obtain samples of all forage species for tannin analysis, and thus we used published values (Lopez-Perez, 2006; Wagoner, 2011; Ulappa, 2015) to estimate tannin precipitation for species not sampled in 2017. We were unable to obtain field estimates of ash (AIA, %) and gross energy (GE; kJ/g), so we obtained values from the same set of published data. We estimated the dry matter digestibility (DMD; %) using the summative equations of Robbins et al. (1987), which integrated our data on NDF, ADL, BSA precipitate, AIA, GE and tannins. We then calculated digestible energy (DE) content (kJ/g) of each composited forage sample from GE × DMD (Ulappa, 2015).

We used generalized additive models (GAMs; Zuur et al., 2009) to produce spatiotemporally dynamic maps of the nutritional landscape available to mule deer at Starkey during spring (15 May–30 June) and summer (1 July–15 August), 2016–2017 (**Supplementary Appendix C**). We used mean (averaged across quadrats) total biomass (kg/ha) of selected and neutral forage plants at each transect location as the response variable, and evaluated a suite of different spatial and temporal covariates as predictors of forage biomass. We constructed separate models for each year and season (four models total). We then applied each model to the Starkey landscape during the appropriate season and year to calculate spatiotemporally explicit estimates of predicted forage biomass (i.e., predicted biomass of selected and neutral forage plants) available to mule deer within each 30-m pixel in the study area (**Figure 1**).

Selection of the Nutritional Landscape by Mule Deer

We used resource selection functions (RSFs) to quantify strength of selection for the nutritional landscape by mule deer at the 2nd and 3rd orders of selection (Johnson, 1980). At the landscape scale (i.e., 2nd-order selection), we employed a use-availability design wherein GPS locations from individual mule

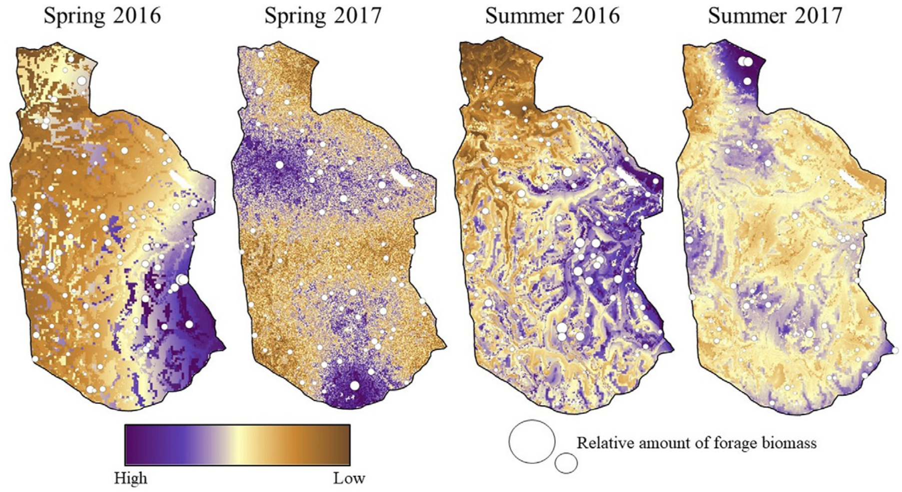

FIGURE 1 | Predicted spatiotemporal variation in the nutritional landscape (biomass of selected and neutral forage plants) available to mule deer during a representative week in mid-spring (29 May–5 June) and mid-summer (15–22 July), 2016 and 2017, at the Starkey Experimental Forest and Range, Oregon, United States.

deer (2016: $n = 18$; 2017: $n = 14$) represented used locations (coded 1 in our analyses), and randomly generated locations (coded 0 in our analyses; 750 total random locations/week, determined using the methods of Long et al., 2014) served as an index to availability of the nutritional landscape within the Starkey enclosure. To estimate RSFs we fit generalized linear mixed models with a logit link function and binomial error distribution to the used and random locations for mule deer (Gillies et al., 2006; Long et al., 2014). We extracted the model-predicted values of forage biomass on a week-by-week basis to the used and random locations, and we included a random intercept and an uncorrelated random slope (Zuur et al., 2009) for the nutritional landscape (the sole predictor variable), both of which were grouped by individual animal nested within week. This approach allowed us to account for autocorrelation among GPS locations within animals, and to ensure that use and availability of the nutritional landscape were compared at the appropriate time scale (exploratory analyses indicated that a weekly time step was sufficient for capturing changes in forage conditions through time; Long et al., 2014). The random slopes also facilitated subsequent analysis of selection at the individual level. We fit separate RSFs for each year and season (four models), and standardized the nutritional predictor variable prior to model fitting to facilitate direct comparison of coefficients across years and seasons. Statistical significance was inferred based on alpha $\leq$0.1.

At the home-range scale (i.e., 3rd-order selection) we used a 95% fixed-kernel home-range estimator (Horne et al., 2007) to delineate seasonal home-range boundaries for each individual mule deer within Starkey. We cast random locations within each home range based on its size, and in direct proportion to the point density used at the landscape scale. We then estimated 3rd-order RSFs using methods identical to those described for estimating 2nd-order RSFs. We evaluated the predictive strength of each model using k-fold cross-validation (Boyce et al., 2002). We conducted ten iterations for each model in which the model was fit to 80% of the data (i.e., 80% of the animals in the dataset) and the remaining 20% were held out as test data. In each iteration we grouped random locations from the test data into 10 equal bins based on their predicted probability of use (calculated from the model fit to the training data). We then compared the median predicted value of each bin to the number of actual used locations that fell into that bin using Spearman-rank correlation. We averaged Spearman-rank correlation coefficients (r_s) across all 10 iterations as a measure of the predictive strength of each model (Boyce et al., 2002).

As a measure of selection for the nutritional landscape at the individual level we extracted the random slopes for each individual deer and week from both the 2nd- and 3rd-order RSFs. Those conditional slopes represented, for each individual deer, strength of selection for the nutritional landscape relative to the population-level mean during each week of the study (Gillies et al., 2006; Long et al., 2014). We therefore used those conditional parameter estimates in subsequent analyses of the relationship between selection of the nutritional landscape and early-winter condition of individual deer.

Relating Use and Selection of the Nutritional Landscape to Early-Winter Condition of Deer

We used simple linear regression (Neter et al., 1996) to relate use and selection (both 2nd- and 3rd-order selection) of the nutritional landscape during spring and summer to early-winter condition of a subset of collared mule deer ($n = 9$ animal years). To quantify use of the nutritional landscape by deer we extracted the appropriate model-predicted values of the nutritional landscape (i.e., biomass of selected and neutral forage plants) to each deer's GPS locations. We chose to use all GPS locations from each deer (as opposed to, for example, nighttime locations only) because deer at Starkey do not exhibit strong diel variation in space-use behavior and may forage throughout the 24-h day (Ager et al., 2003). We then averaged those predicted use values across locations obtained during spring and summer to quantify the degree to which each deer consistently utilized high-quality foraging locations. We fit separate linear regression models for use, 2nd-order selection, and 3rd-order selection (we quantified selection using the conditional parameter estimates from the RSFs as described previously), and in each model early-winter condition (i.e., % ingesta-free body fat) of deer was the response variable. In addition, because of small sample size and the potential for outliers to influence regression results, we performed a jackknife analysis of each regression wherein we iteratively removed one point at a time from each dataset, refit the regression model, and recorded the resulting r^2 and *P*-values. For each jackknife analysis we report the mean r^2 and the percentage of regression iterations that produced a positive, statistically significant slope.

RESULTS

Forage Biomass

Mean estimates of forage biomass at sampled locations consistently were higher in spring than in summer across PVTs, but also were highly variable within PVTs (**Figure 2**). As a result, differences in biomass among PVTs rarely were significant within a season and year (based on overlap of 90% CIs; **Figure 2**). Models of the nutritional landscape performed considerably better during summer (adjusted R^2 = 0.39–0.66) than during spring (adjusted R^2 = 0.21–0.38; **Table 1**), because high-quality forage was more evenly dispersed across the landscape during spring. Top models for all year × season combinations included spatial and temporal smoothing terms, although the best-performing temporal smoother differed among models (**Table 1** and **Supplementary Appendix D**). The only spatial covariate that was retained in all four models was PVT (although at least one metric of topography also was included in all four models), suggesting that the different vegetation types at Starkey were not all equally valuable as foraging habitat for mule deer (**Table 1** and **Figure 2**). Model results also indicated that forage biomass varied among years, with available biomass peaking during spring in 2016 but during early summer in 2017, due to greater snowpack delaying phenology in 2017 (**Figure 1**).

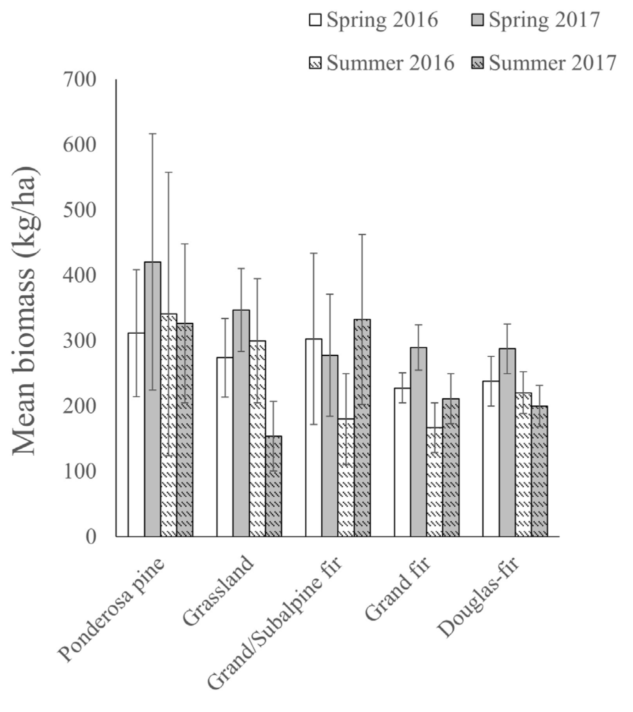

FIGURE 2 | Mean (±90% CI) biomass (kg/ha) of selected and neutral forage plants at transects sampled within each potential vegetation type during spring (13 May–30 June) and summer (1 July–11 August), 2016 and 2017, at the Starkey Experimental Forest and Range, Oregon, United States.

Nutritional Quality

Mean nutritional quality (i.e., $\bar{x}$ CP and DE of selected and neutral forage plants) of forage at sampled transect locations consistently was higher in spring than in summer across PVTs and years (**Figure 3**). Similar to forage biomass, however, forage quality also was highly variable within PVTs (**Figure 3**), and thus differences in CP and DE among PVTs generally were not significant (based on overlap of 90% CIs; **Figure 3**). When averaged across years, CP was higher in dry (i.e., xeric) PVTs than in wet (i.e., mesic) PVTs during spring, but this pattern was reversed during summer ($\bar{x} \pm SE$ spring: dry = 11.16 ± 0.50%, wet = 10.85 ± 0.42%; summer: dry = 9.87 ± 0.53%, wet = 9.93 ± 0.44%). In contrast, DE was highest in the dry PVTs during both seasons (spring: dry = 9.83 ± 0.29 kJ/g, wet = 9.64 ± 0.25 kJ/g; summer: dry = 9.11 ± 0.30 kJ/g, wet = 9.05 ± 0.26 kJ/g). Mean CP in forage during spring was higher in 2017 than in 2016 across all PVTs, whereas the opposite was true for mean DE in spring (CP: spring 2017 = 11.18 ± 0.41%, spring 2016 = 10.83 ± 0.51%; DE: spring 2017 = 9.51 ± 0.25 kJ/g, spring 2016 = 9.96 ± 0.27 kJ/g). During summer, however, both CP and DE were higher in 2016 than in 2017 (CP: summer 2017 = 9.81 ± 0.45%, summer 2016 = 9.98 ± 0.50%; DE: summer 2017 = 8.89 ± 0.27 kJ/g, summer 2016 = 9.27 ± 0.28 kJ/g).

Selection of the Nutritional Landscape by Mule Deer

At the landscape scale (i.e., 2nd-order selection), mule deer showed significant selection for the nutritional landscape in summer during both years (summer 2016 β = 1.29, $P < 0.001$; summer 2017 β = 0.98, $P < 0.001$; **Figure 4**). In contrast, mule deer were either indifferent to or avoided areas of high forage biomass during spring of both years (spring 2016 β = 0.08, $P = 0.25$; spring 2017 β = −0.16, $P = 0.02$; **Figure 4**). *K*-fold cross validation results also reflected this seasonal pattern; Spearman rank correlation coefficients averaged −0.01 and 0.47 across 10 iterations during spring of 2016 and 2017, respectively, whereas those coefficients averaged 0.73 and 0.63 during summers of those two years. These results suggest that deer selected for

TABLE 1 | Generalized additive models (GAMs) used to predict spatiotemporal variation in the nutritional landscape (i.e., biomass of selected and neutral forage plants) available to mule deer at the Starkey Experimental Forest and Range, Oregon, United States.

Year	Season	Best model[1]	Adjusted R^2	Deviance explained	GCV[2]
2016	Spring	Biomass ~ s(UTM_X, UTM_Y) + s(Total_Precipitation) + PVT + ln(Elevation)[3]	0.21	30.2%	12,595
2016	Summer	Biomass ~ s(UTM_X, UTM_Y) + s(Julian) + PVT + ln(Slope) + Elevation + SoilDepth^2	0.39	48.3%	19,911
2017	Spring	Biomass ~ s(UTM_X, UTM_Y) + s(Average_Temperature) + PVT + sin_Aspect	0.38	61.4%	17,821
2017	Summer	Biomass ~ s(UTM_X, UTM_Y) + s(Julian) + PVT + ln(Slope) + CanopyCover	0.66	77.5%	13,294

We fit separate models for spring (May 13–June 30) and summer (July 1–August 15) of 2016 and 2017. Spatial and temporal smoothing terms were fit using cubic regression splines, and cross-validation was used to determine the optimal amount of smoothing for each term. Model selection procedures are described in detail in the section "Materials and Methods." [1]*PVT, potential vegetation type.* [2]*Minimum generalized cross-validation score.* [3]*Weighted by the inverse of variance in each PVT; s, smoother.*

the nutritional landscape more strongly during summer, when availability of preferred forages declined.

Patterns of selection were less consistent at the home-range scale. During 2017 mule deer showed significant selection for the nutritional landscape within their home ranges during both spring and summer (spring 2017 $\beta = 0.34$, $P < 0.001$; summer 2017 $\beta = 0.40$, $P = 0.002$; **Figure 4**). In contrast, deer did not show selection for the nutritional landscape within their home ranges in either season during 2016 (spring 2016 $\beta = -0.43$, $P < 0.001$; summer 2016 $\beta = -1.28$, $P < 0.001$; **Figure 4**). Moreover, none of the 3rd-order models were highly predictive of patterns of space use by deer within their home ranges; Spearman rank correlation coefficients averaged 0.18 and 0.32 across 10 iterations during springs, and 0.29 and 0.27 during summers of 2016 and 2017, respectively. In addition, during the one season/year in which deer showed significant selection for the nutritional landscape at both scales (summer 2017), the standardized coefficient was more than twice as large in the 2nd-order model than in the 3rd-order model (**Figure 4**). Together, these results suggest that biomass of preferred forages had a greater influence on space-use decisions by mule deer at the landscape scale than at the home-range scale.

At the individual level, use of the nutritional landscape by deer during spring and summer was a significant predictor of early-winter condition ($P = 0.074$, $r^2 = 0.39$; **Figure 5**). Every 1-kg/ha increase in mean forage biomass at locations used by deer was predicted to produce a 2.84% increase in ingesta-free body fat in early winter (**Figure 5**). Mean r^2 from the jackknife analysis was 0.40, and 89% of regression iterations produced a positive, statistically significant relationship between use of the nutritional

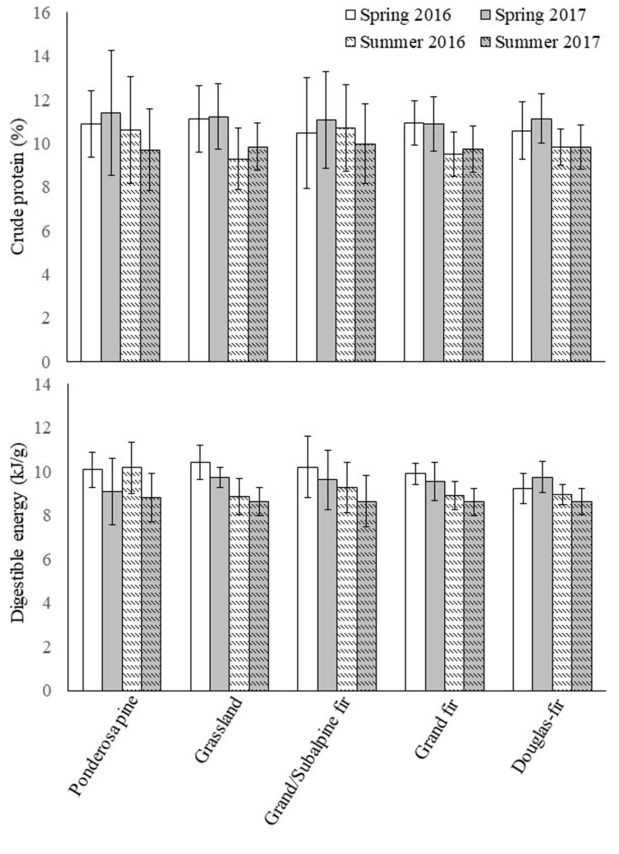

FIGURE 3 | Mean (±90% CI) values of crude protein (%) and digestible energy (kJ/g) in selected and neutral forage plants combined at transects sampled within each potential vegetation type during spring (13 May–30 June) and summer (1 July–11 August), 2016 and 2017, at the Starkey Experimental Forest and Range, Oregon, United States.

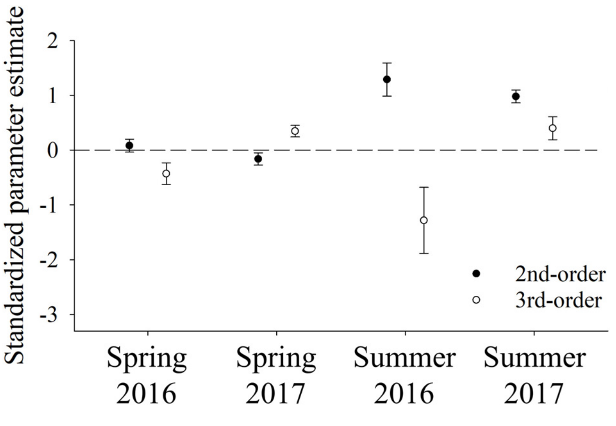

FIGURE 4 | Standardized parameter estimates (β) and associated 90% confidence intervals from 2nd- and 3rd-order resource selection functions that quantified the influence of forage biomass (i.e., biomass of selected and neutral forage plants) on space use by female mule deer during spring (13 May–30 June) and summer (1 July–11 August), 2016 ($n = 18$) and 2017 ($n = 13$), at the Starkey Experimental Forest and Range, Oregon, United States.

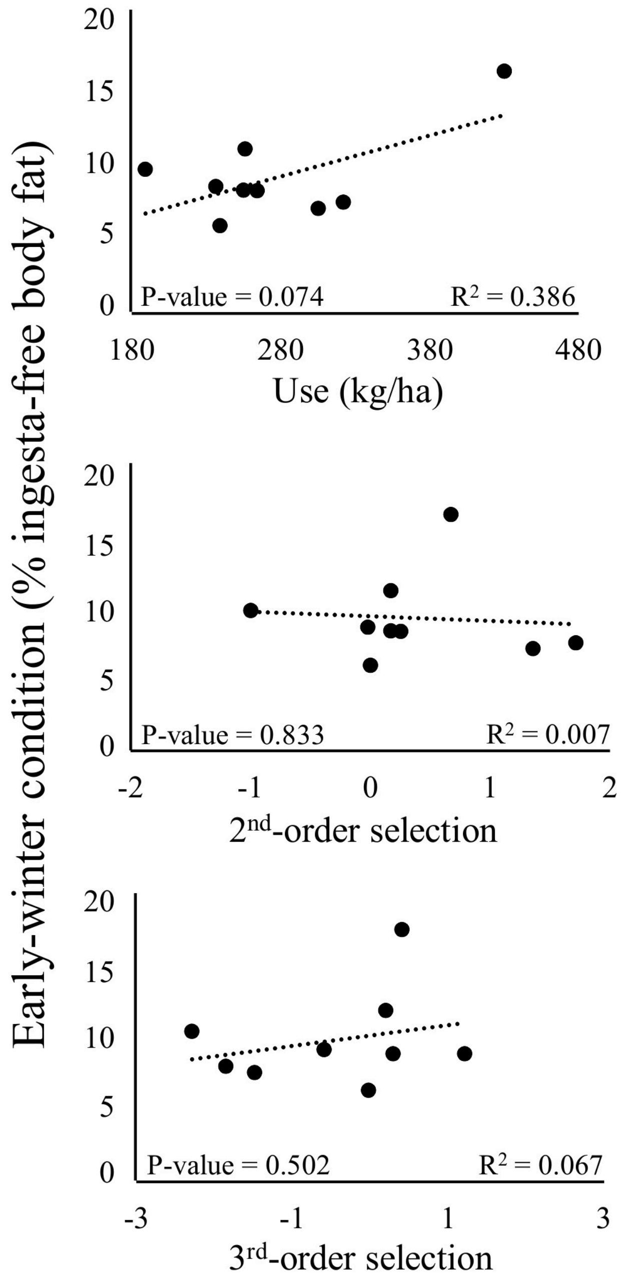

FIGURE 5 | Simple linear regression models of the effects of use (mean predicted biomass of selected and neutral forage plants at all locations used by each individual deer; **first panel**), 2nd-order selection (individual-level coefficients from landscape-scale mixed-effects RSFs; **second panel**), and 3rd-order selection (individual-level coefficients from home-range scale mixed-effects RSFs; **third panel**) of the nutritional landscape on early-winter nutritional condition (% ingesta-free body fat) of female mule deer ($n = 9$ animal years) at the Starkey Experimental Forest and Range, Oregon, United States.

landscape and early-winter condition of deer. In contrast to use, selection of the nutritional landscape by individual deer was not significantly related to early-winter condition at either spatial scale (**Figure 5**), and this result held across all iterations of the jackknife analyses for selection. Duration of lactation did not significantly affect early-winter condition of deer in multiple regression models that included either use or selection of the nutritional landscape, likely because all but three of the female deer in our early-winter sample lost their fawns within 4 weeks of parturition, and thus our data encompassed minimal variation in lactation costs.

Mean (± *SE*)% ingesta-free body fat of female mule deer in early winter was 8.48% ± 0.52 (**Table 2**). This estimate of condition is below the threshold for maintaining positive population growth (i.e., $\lambda > 1$) in mule deer reported by Monteith et al. (2014). Although our sample size for quantifying early-winter condition of deer was relatively small ($n = 9$ animal years), it likely represented ≥25% of the adult female population at Starkey), which has been declining for more than a decade.

DISCUSSION

Mule deer consistently showed stronger selection for high forage biomass at the landscape scale (2nd-order selection) than at the home-range scale (3rd-order selection), suggesting that deer chose to locate their home ranges in areas that provided ready access to high-quality forage, possibly limiting the need to strongly select those vegetation communities within their home ranges (Bowyer and Kie, 2006). This observation provides support for our first hypothesis (i.e., that selection for forage would be strongest at the largest scale) and highlights the importance of evaluating patterns of selection at multiple spatial scales (Long et al., 2008; Laforge et al., 2015; McGarigal et al., 2016). Because space-use decisions at smaller scales are constrained by choices made at larger scales (Bowyer and Kie, 2006; Mayor et al., 2009), and foraging decisions are scale-dependent (Senft et al., 1987), natural selection may favor behavioral strategies in which environmental covariates with the greatest effect on fitness (e.g., variables that influence energy acquisition or vulnerability to predation) are selected at the largest scales (Bowyer and Kie, 2006). In combination with our measurements of early-winter condition of deer, the scale-dependent pattern of selection for the nutritional landscape we documented at Starkey suggests the potential for nutritional limitation during summer.

Our second hypothesis, that mule deer would show stronger selection for the nutritional landscape during summer than spring, also was supported. Strength of selection for the nutritional landscape by mule deer (quantified by standardized parameter estimates from the resource selection models, and by results of *k*-fold cross validation) was considerably greater in summer than spring during both 2016 and 2017 (**Figure 4**). This seasonal change in behavior was due to the greater availability and more even dispersion of forage during spring. These conditions obviated the need for mule deer to select specific foraging areas during spring at the broad spatial scales we analyzed, because high-quality forage was readily available throughout the study area. Moreover, summer is a critical period for capital-breeding ungulates like mule deer because they must replenish energy and protein reserves lost over winter while meeting the demands of lactation (Therrien et al., 2008; Bårdsen et al.,

TABLE 2 | Body mass and condition metrics for female mule deer recaptured in early winter 2016 (November 22–December 18; $n = 5$) and 2017 (1–6 December; $n = 4$) at the Starkey Experimental Forest and Range, Oregon, United States.

Year	Animal ID	Mass (kg)	MAXFAT (cm)	rBCS[1]	IFBF[2] (%)	Number of fawns at parturition | capture	Duration of lactation (d)
2016	060104D01	71.89	0.4	3.50	7.71	2 | 0	53
2016	110104D01	68.49	0.8	3.50	10.03	1 | 1	120
2016	141125D01	59.42	0.0	3.00	8.83	1 | 0	17
2016	131218D01	66.18	0.1	2.25	6.10	1 | 0	10
2016	131216D02	64.18	0.3	2.50	7.29	1 | 0	25
2017	060104D01	73.66	1.1	2.00	11.44	2 | 0	3
2017	110104D01	67.85	2.0	4.00	16.85	1 | 0	23
2017	141125D01	60.96	0.5	3.00	8.56	1 | 0	4
2017	131216D03	61.69	0.5	1.60	8.53	1 | 0	8

Weight, MAXFAT, and rBCS measurements were obtained at the time of capture, and IFBF was calculated using the methods of Cook et al. (2010). The number of fawns was recorded at parturition (i.e., in the spring before body condition data were collected) and again at the time of winter capture (via radio collars affixed to fawns). Duration of lactation was estimated as the number of days between parturition and either the death of the fawn(s) or the estimated day of weaning (120 d; Sadleir, 1980).
[1] rBCS, body condition score. [2] IFBF, Ingesta-free body fat.

2010; Tollefson et al., 2010; Bårdsen and Tveraa, 2012), even as availability of high-quality forage declines (Cook et al., 2004; Monteith et al., 2013). This suggests the potential for strong evolutionary pressure to forage more selectively during summer to maximize energy intake in the face of a senescent forage base.

Our third hypothesis, that strength of selection (i.e., use relative to availability) for the nutritional landscape at the landscape scale would be more strongly correlated with early-winter condition of individual deer than strength of selection at the home-range scale, was not supported. Instead, strength of selection for the nutritional landscape by individual deer was unrelated to early-winter condition at both scales of analysis. This facet of our individual-level results highlights several important distinctions between analyses of resource use and resource selection. Analyses of resource selection have a long and diverse history of application in wildlife ecology (McLoughlin et al., 2010; McGarigal et al., 2016). Yet, one persistent criticism of studies that rely on RSFs is a failure to produce evidence in support of their most fundamental assumption; that patterns of resource selection have fitness consequences (Morrison, 2001; Manly et al., 2002). Although this failure commonly results from the many logistical challenges of directly relating complex behaviors to hard-to-measure components of fitness, our results suggest that even when it is possible to collect the necessary data, analyses of use may sometimes prove more useful than analyses of selection *per se* (Millspaugh et al., 2006). Even our relatively coarse measure of forage use by deer, which assumed that deer that used better foraging areas did, in fact, consume more high-quality forage, was sufficient to capture a significant relationship between behavior and condition at the individual level. When those measures of use were adjusted for availability in the context of a complex statistical model (RSF), however, we were no longer able to detect that relationship, despite the fact that strong selection for the nutritional landscape was evident at the population level, especially during summer and at the landscape scale. There are several potential explanations for this result. For example, available locations were randomly cast at both the landscape and home-range scales, which could have led to the inclusion of locations in the available sample that were not accessible to deer for either physical (e.g., topography) or behavioral (e.g., aversion behavior) reasons. Alternatively, despite increased availability of quality forage, individuals may switch their selection to other environmental features when necessary (i.e., select for vegetation communities that provide increased cover for thermoregulation or predator avoidance; Bjørneraas et al., 2012). Patterns of resource selection also may be density-dependent, although this seems unlikely at Starkey given the extremely low density of deer (0.65 female deer/km^2, including yearlings). Regardless, we suggest that future efforts to understand the fitness consequences of ungulate space-use behavior focus more strongly on quantifying what resources are actually used by animals in the context of testable, mechanistic hypotheses about how different patterns of use should influence nutrition and energy balance of individuals.

Our analysis of how individual-level responses to the nutritional landscape affected early-winter condition of mule deer was based on a relatively small sample size with correspondingly low statistical power. Nevertheless, the mule deer population at Starkey was similarly small, and our sample likely represented $\geq$25% of the adult female population. Moreover, despite our small sample size we detected a statistically significant relationship between use of the nutritional landscape and early-winter condition of female deer, suggesting that our test of this relationship was not underpowered (Rowland et al., 2018). Individuals that used, on average, areas that provided greater biomass of preferred forage plants during spring and summer entered winter in better condition. These results support our fourth hypothesis, and add to a small but growing body of literature linking space-use behaviors of ungulates to important correlates of fitness (Long et al., 2016). Similarly, our results highlight the value of nutritional approaches to understanding the fitness consequences of behavior, and in particular the measurement of nutritional condition, which integrates a suite of complex responses of ungulates to their environment (Parker et al., 2009; Cook et al., 2010; Monteith et al., 2013; Long et al., 2016).

Our study suggests that mule deer in northeastern Oregon may be nutritionally limited despite showing significant selection for the nutritional landscape at the population level; mean nutritional condition of mule deer in early winter was well below the estimated threshold for maintaining positive population growth (Monteith et al., 2014). These results refute our fifth hypothesis (i.e., that condition of deer would be high enough to promote population growth), and have important implications for mule deer in general, which have been declining throughout much of their range for several decades (Johnson et al., 2000; Manning, 2010; Bergman et al., 2015). One hypothesis for explaining poor condition of female mule deer in our study is that even the highest-quality forage available at Starkey is insufficient for supporting positive population growth. Critical thresholds of CP and DE for a female mule deer at peak lactation (with one fawn) are 12% CP and 11.5 kJ/g DE (Parker et al., 1999; Hanley et al., 2012). After peak lactation those thresholds drop to 8% CP and 9.5 kJ/g DE (Hanley et al., 1992, 2012; Parker et al., 1999). Maximum mean values of CP and DE available in PVTs at Starkey during spring were 10.97 and 9.73 kJ/g, respectively. During summer, maximum mean CP and DE were 9.90 and 8.94 kJ/g, respectively, suggesting that the ability of female mule deer to support lactation during summer could be limited by either CP or DE (although mule deer have considerable ability to locate the highest-quality forage available when mean quality is low; Ulappa, 2015; Hull, 2018). Nutritional limitation of this nature is one plausible explanation for our observation that few mule deer in our study successfully recruited a fawn, or even reared a fawn for more than 8 weeks. Total precipitation and spring snow-water-equivalent were both below long-term averages during 2016 and 2017. As a result, the limiting effects of low forage quality on mule deer reproduction may have been more pronounced during our study. In addition, the second winter of our study was characterized by later-than-normal snowfall, which delayed the onset of spring greenup. Variation in the timing, amount, and spatial distribution of precipitation can have marked effects on the distribution and quality of forage (**Figure 1**), and on ungulate vital rates and population dynamics (Hurley et al., 2014). This underscores the importance of mechanistic, nutritional approaches to explaining variation in performance of ungulate populations.

An alternative hypothesis for explaining nutritional limitation in our study area is that despite showing significant selection for the nutritional landscape at the population level, mule deer at Starkey faced tradeoffs between nutrition and other factors with potential to affect fitness. Previous researchers have hypothesized that inadequate nutrition may result indirectly from avoidance of competitors or predators (Cook et al., 2007). Interference competition with elk has been hypothesized to be a leading cause of mule deer population declines (Lindzey et al., 1997; Manning, 2010). Interference competition often produces strong patterns of avoidance or displacement that can dictate species' distributions, patterns of resource exploitation, and relative abundances (Johnson et al., 2000; Berger and Gese, 2007), and numerous studies have reported that mule deer avoid elk in space and time (Stewart et al., 2002; Ager et al., 2003; Manning, 2010). Direct and indirect effects of predators on mule deer behavior also may have contributed to the decline of this species (Salwasser, 1979; Lindzey et al., 1997). Mountain lions are a primary predator of mule deer across much of their range in North America (Ballard et al., 2001; Forrester and Wittmer, 2013) and rely on concealment to successfully kill prey (Laundré et al., 2014). This hunting mode limits the ability of mule deer to directly detect mountain lions, thus increasing their reliance on indirect cues of predation risk (Preisser et al., 2007; Schmitz et al., 2008). The result is a landscape of fear in which the perception of predation risk strongly influences patterns of space use (Brown et al., 1999; Kauffman et al., 2007; Laundré et al., 2014). During our study, Starkey supported the highest-density elk population in Oregon and abundant mountain lions, and thus strong potential existed for behaviorally mediated effects of competitors, predators, or both on nutritional condition of mule deer. Future research designed to shed light on the nutritional mechanisms by which predators and competitors indirectly influence fitness of mule deer would provide valuable insight into the complex causes of their range-wide decline.

Our results suggest that limited availability, whether absolute or functional (i.e., resulting from avoidance of predators or competitors), of high-quality forage during summer has resulted in poor early-winter condition of deer, which likely has contributed to the decline of mule deer at Starkey, despite those deer showing selection for the nutritional landscape during summer. More broadly, our work highlights the value of integrating the mechanistic principles of nutritional ecology with the theory and concepts that currently define our understanding of resource use and selection. We propose that an increased focus on understanding the nutritional consequences of individual resource-use behaviors could motivate new lines of inquiry and provide important and novel insights into the fitness consequences and evolutionary underpinnings of the diverse behavioral strategies exhibited by ungulates.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of Idaho Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

JM, DC, MW, and RL conceived and designed the study. JM, JR, NJ, and KS collected the field data. JM, LS, and RL conducted the nutritional analyses. JM, TL, and RL conducted analyses of space use. JM and RL wrote the manuscript with input from all authors.

FUNDING

This research was funded by Federal Aid in Wildlife Restoration Grants, the Oregon Department of Fish and Wildlife and the U.S. Forest Service, Pacific Northwest Research Station.

ACKNOWLEDGMENTS

This research would not have been possible without the support provided by the larger collaborative Starkey Project research group. We are indebted to B. L. Dick, R. Kennedy, D. Rea, P. K. Coe, J. M. Hafer, and B. J. Naylor for data structure and preparation from the United States Forest Service, Pacific Northwest Research Station, E. K. Strand from the University of Idaho, P. K. Coe from the Oregon Department of Fish and Wildlife, R. C. Cook from NCASI, and the many technicians and volunteers.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00098/full#supplementary-material

REFERENCES

Ager, A. A., Johnson, B. K., Kern, J. W., and Kie, J. G. (2003). Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *J. Mammal.* 84, 1076–1088. doi: 10.1644/bba-020

Ballard, W. B., Lutz, D., Keegan, T. W., Carpenter, L. H., and deVos, J. C. Jr. (2001). Deer-predator relationships: a review of recent Noth American studies with emphasis on mule deer and black-tailed deer. *Wildl. Soc. Bull.* 29, 99–115.

Bårdsen, B. J., and Tveraa, T. (2012). Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. *J. Anim. Ecol.* 81, 364–376. doi: 10.1111/j.1365-2656.2011.01913.x

Bårdsen, B. J., Tveraa, T., Fauchald, P., and Langeland, K. (2010). Observation evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia* 162, 627–639. doi: 10.1007/s00442-009-1537-0

Barten, N. L., Bowyer, R. T., and Jenkins, K. J. (2001). Habitat use by female caribou: tradeoffs associated with parturition. *J. Wildl. Manage.* 65, 77–92.

Berger, J. (1991). Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim. Behav.* 41, 61–77. doi: 10.1016/s0003-3472(05)80503-2

Berger, K. M., and Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* 76, 1075–1085. doi: 10.1111/j.1365-2656.2007.01287.x

Bergman, E. J., Doherty, P. F. Jr., White, G. C., and Freddy, D. J. (2015). Habitat and herbivore density: response of mule deer to habitat management. *J. Wildl. Manage.* 79, 60–68. doi: 10.1002/jwmg.801

Bishop, C. J., Freddy, D. J., White, G. C., Stepheson, T. R., Wolfe, L. L., and Watkins, B. E. (2007). Using vaginal implant transmitters to aid in capture of mule deer neonates. *J. Wildl. Manage.* 71, 945–954. doi: 10.2193/2006-123

Bishop, C. J., White, G. C., Freddy, D. J., Watkins, B. E., and Stepheson, T. R. (2009). Effect of enhanced nutrition on mule deer population rate of change. *Wildl. Monogr.* 172, 1–28. doi: 10.2193/2008-107

Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B. E., van Moorter, B., and Rolandsen, C. M. (2012). Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a larger herbivore. *Oecologia* 168, 231–243. doi: 10.1007/s00442-011-2072-3

Bonham, C. D. (1989). *Measurements for Terrestrial Vegetation*. New York, NY: John Wiley and Sons, 338.

Bowyer, R. T., and Kie, J. G. (2006). Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Divers. Distribut.* 12, 244–257. doi: 10.1111/j.1366-9516.2006.00247.x

Boyce, M. S., Vemier, P. R., Nielsen, S. E., and Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecol. Modell.* 157, 281–300. doi: 10.1016/s0304-3800(02)00200-4

Brown, J. S., Laundré, J. W., and Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399. doi: 10.2307/1383287

Butler, B. W., and Wayne, C. (2007). "The fire environment – innovations, management, and policy; conference proceedings," in *Proceedings of the RMRS-P-46CD, Destin, FL* (Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station), 662.

Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D., et al. (2004). Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildl. Monogr.* 155, 1–61.

Cook, R. C., Cook, J. G., Stephenson, T. R., Myers, W. L., Mccorquodale, S. M., Vales, D. J., et al. (2010). Revisions of rump fat and body scoring indices for deer, elk and moose. *J. Wildl. Manage.* 74, 880–896. doi: 10.2193/2009-031

Cook, R. C., Stephenson, T. R., Myers, W. L., Cook, J. G., and Shipley, L. (2007). Validating predictive models of nutritional condition for mule deer. *J. Wildl. Manage.* 71, 1934–1943. doi: 10.2193/2006-262

Côté, S. D., and Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* 127, 230–238. doi: 10.1007/s004420000584

Dall, S. R. X., Houston, A. I., and McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734–739. doi: 10.1111/j.1461-0248.2004.00618.x

Damiran, D. (2006). *Influence of Previous Cattle and Elk Grazing on the Subsequent Diet Quality and Nutrient Intake Rate of Cattle, Deer, and Elk Grazing Late-Summer Mixed-Conifer Rangelands.* Ph.D. Dissertation., Oregon State University, Corvallis.

Downs, C. J., Stewart, K. M., and Dick, B. L. (2015). Investment in constitutive immune function by North American elk experimentally maintained at two different population densities. *PLoS ONE* 10:e0125586. doi: 10.1371/journal.pone.0125586

Festa-Bianchet, M., Jorgenson, J. T., Bérubé, C. H., Portier, C., and Wishart, W. D. (1997). Body mass and survival of bighorn sheep. *Can. J. Zool.* 75, 1372–1379. doi: 10.1139/z97-763

Forrester, T. D., and Wittmer, H. U. (2013). A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. *Mamm. Rev.* 43, 292–308. doi: 10.1111/mam.12002

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Systemat.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gillies, C. S., Hebblewhite, M., Nielson, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898. doi: 10.1111/j.1365-2656.2006.01106.x

Halofsky, J. E., Creutzburg, M. K., and Hemstrom, M. A. (2014). *Integrating Social, Economic, and Ecological Values Across Large Landscapes. Gen.Tech. Rep. PNW-GTR*-896. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 206.

Hanley, T. A., Robbins, C. T., Hagerman, A. E., and MacArthur, C. (1992). Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. *Ecology* 73, 537–541. doi: 10.2307/1940759

Hanley, T. A., Spalinger, D. E., Mock, K. J., Weaver, O. L., and Harris, G. M. (2012). *Forage Resource Evaluation System for Habitat – Deer: an Interactive Deer-Habitat Model: General Technical Report PNW-GTR*-858. Portland, OR: USDA Forest Service, Pacific Northwest Research Station.

Horne, J. S., Garton, E. O., and Sager-Fradkin, K. A. (2007). Correcting home-range models for observation bias. *J. Wildl. Manage.* 71, 996–1001. doi: 10.2193/2005-678

Huey, R. B., Hertz, P. E., and Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161, 357–366. doi: 10.1086/346135

Hull, I. T. (2018). *Influences of Fuel Reduction Treatments on the Nutritional Ecology of Deer in Northeastern Washington.* Masters thesis., Washington State University, Pullman.

Hurley, M. A., Hebblewhite, M., Gaillard, J.-M., Dray, S., Taylor, K. A., Smith, W. K., et al. (2014). Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philos. Trans. R. Soc. B* 369:20130196. doi: 10.1098/rstb.2013.0196

Jackson, N. J. (2019). *Effects of Enhanced Winter Nutrition and Climatic Variation on Population Performance of A Large Herbivore.* Masters Thesis., University of Nevada-Reno, Reno.

Johnson, B. L., Kern, J. W., Wisdom, M. J., Findholt, S. L., and Kie, J. G. (2000). Resource selection and spatial separation of mule deer and elk during spring. *J. Wildl. Manage.* 64, 685–697.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. doi: 10.2307/1937156

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., and Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecol. Lett.* 10, 690–700. doi: 10.1111/j.1461-0248.2007.01059.x

Laforge, M. P., Vander Wall, E., Brook, R. K., Bayne, E. M., and McLoughlin, P. D. (2015). Process-focused, multi-grain resource selection functions. *Ecol. Modell.* 305, 10–21. doi: 10.1016/j.ecolmodel.2015.03.003

Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., et al. (2014). The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95, 1141–1152. doi: 10.1890/13-1083.1

Lele, S. R., Merrill, E. H., Keim, J., and Boyce, M. S. (2013). Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *J. Anim. Ecol.* 82, 1183–1191. doi: 10.1111/1365-2656.12141

Lindzey, F. G., Hepworth, W. G., Mattson, T. A., and Reeve, A. F. (1997). *Potential for Competitive Interactions Between Mule Deer and Elk in the Western United States and Canada*. Laramie, WY: Wyoming Cooperative Wildlife Research Unite.

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., Findholt, S. L., et al. (2016). Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. *Oecologia* 181, 709–720. doi: 10.1007/s00442-016-3604-7

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., and Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol. Monogr.* 84, 513–532. doi: 10.1890/13-1273.1

Long, R. A., Rachlow, J. T., and Kie, J. G. (2008). Effects of season and scale on response of elk and mule deer to habitat manipulation. *J. Wildl. Manage.* 72, 1133–1142. doi: 10.2193/2007-337

Lopez-Perez, E. (2006). *Natural Selenium and Planted Forages: Effects on Mule Deer and Elk in Washington.* Ph.D. Dissertation., Washington State University, Pullman.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., MacDonald, T. L., and Erickson, W. P. (2002). *Resource Selection by Animals. Statistical Design and Analysis for Field Studies*. London: Kluwer Academic Publisher.

Manning, J. A. (2010). *Population Dynamics of Rocky Mountain Elk and Mule Deer: Competition, Habitat Selection, Wolf Predation, and Predictions Under Climate Change.* Ph.D. Dissertation., University of Idaho, Moscow.

Martin, J. S., and Martin, M. M. (1982). Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. *Oecologia* 54, 205–211. doi: 10.1007/bf00378394

Mayor, S. J., Schneider, D. C., Schaefer, J. A., and Mahoney, S. P. (2009). Habitat selection at multiple scales. *Écoscience* 16, 238–247. doi: 10.2980/16-2-3238

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., and Cushman, S. A. (2016). Multi-scale habitat selection modelling: a review and outlook. *Landsc. Ecol.* 31, 1161–1175. doi: 10.1007/s10980-016-0374-x

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., and Contasti, A. L. (2010). Considering ecological dynamics in resources selection functions. *J. Anim. Ecol.* 79, 4–12. doi: 10.1111/j.1365-2656.2009.01613.x

Miller, B. F., Osborn, D. A., Lance, W. R., Howze, M. B., Warren, R. J., and Miller, K. V. (2009). Butorphanol-azaperone-medetomidine for immobilization of captive white-tailed deer. *J. Wildl. Dis.* 45, 457–467. doi: 10.7589/0090-3558-45.2.457

Millspaugh, J. J., Nielson, R. M., McDonald, L., Marzluff, J. M., Gitzen, R. A., Rittenhouse, C. D., et al. (2006). Analysis of resource selection using utilization distributions. *J. Wildl. Manage.* 70, 384–395. doi: 10.2193/0022-541x(2006)70%5B384:aorsuu%5D2.0.co;2

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2014). Life-History characteristics of mule deer: effects of nutrition in a variable environment. *Wildl. Monogr.* 186, 1–56.

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Klaver, R. W., et al. (2011). Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2:art47. doi: 10.1890/es10-00096.1

Monteith, K. L., Stephenson, T. R., Bleich, V. C., Conner, M. M., Pierce, B. M., and Bowyer, R. T. (2013). Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *J. Anim. Ecol.* 82, 377–388. doi: 10.1111/1365-2656.12016

Montgomery, R. A., Vucetich, J. A., Peterson, R. O., Roloff, G. J., and Millenbah, K. F. (2013). The influence of winter severity, predation and senescence on moose habitat use. *J. Anim. Ecol.* 82, 301–309. doi: 10.1111/1365-2656.12000

Morrison, M. L. (2001). A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *J. Wildl. Manage.* 65, 613–623.

Neter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. (1996). *Applied Linear Statistical Models*, 4th Edn. Boston: McGraw-Hill.

Parker, K. L., Barboza, P. S., and Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* 23, 57–69. doi: 10.1111/j.1365-2435.2009.01528.x

Parker, K. L., Gillingham, M. P., Hanley, T. A., and Robbins, C. T. (1999). Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildl. Monogr.* 143, 1–18.

Preisser, E. L., Orrock, J. L., and Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology* 88, 2744–2751. doi: 10.1890/07-0260.1

Pretorius, Y., de Boer, F. W., van der Waal, C., de Knegt, H. J., Grant, R. C., Knox, N. M., et al. (2011). Soil nutrient status determines how elephant utilize trees and shape environments. *J. Anim. Ecol.* 80, 875–883. doi: 10.1111/j.1365-2656.2011.01819.x

Robbins, C. T., Mole, S., Hagerman, A. E., and Hanley, T. A. (1987). Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology* 68, 1606–1615. doi: 10.2307/1939852

Rowland, M. M., Bryant, L. D., Johnson, B. K., Noyes, J. H., Wisdom, M. J., and Thomas, J. W. (1997). *The Starkey Project History, Facilities, and Data Collection Methods for Ungulate Research: Technical Report PNW-GTR-396*. Estacada, OR: United States Department of Agriculture Forest Service.

Rowland, M. M., Wisdom, M. J., Nielson, R. M., Cook, J. G., Cook, R. C., Johnson, B. K., et al. (2018). Modeling elk nutrition and habitat use in western Oregon and Washington. *Wildl. Monogr.* 199, 1–69. doi: 10.1002/wmon.1033

Sadleir, R. M. F. S. (1980). Milk-yield of black-tailed deer. *J. Wildl. Manage.* 44, 472–478.

Salwasser, H. (1979). *The Ecology and Management of the Devil's Garden Interstate Deer Herd and its Range.* Dissertation., Berkeley, CA: University of California, Berkeley.

Schmitz, O. J., Grabowski, J. H., Peckarsky, B. L., Preisser, E. L., Trussell, G. C., and Vonesh, J. R. (2008). From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology* 89, 2436–2445. doi: 10.1890/07-1030.1

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. *BioScience* 37, 789–795+798–799.

Stamps, J., and Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* 85, 301–325. doi: 10.1111/j.1469-185x.2009.00103.x

Stearns, S. R. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press, 264.

Stewart, K. M., Bowyer, R. T., Dick, B. L., and Kie, J. G. (2011). Effects of density dependence on diet composition of North America Elk *Cervus elaphus* and Mule Deer *Odocoileus hemionus*: an experimental manipulation. *Wildl. Biol.* 17, 417–430. doi: 10.2981/10-122

Stewart, K. M., Bowyer, T. R., Kie, J. G., Cimon, N. J., and Johnson, B. K. (2002). Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J. Mammal.* 83, 229–244. doi: 10.1093/jmammal/83.1.229

Therrien, J. F., Côté, S. D., Festa-Bianchet, M., and Ouellet, J. P. (2008). Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction. *Anim. Behav.* 75, 235–243. doi: 10.1016/j.anbehav.2007.04.030

Tollefson, T. N., Shipley, L. A., Myers, W. L., Keisler, D. H., and Dasgupta, N. (2010). Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *J. Wildl. Manage.* 74, 974–986. doi: 10.2193/2008-529

Ulappa, A. C. (2015). *Using Foraging Dynamics to Answer Landscape Management Questions: The Nutritional Ecology of Black-Tailed Deer.* Ph.D. Dissertation., Pullman: Washington State University.

van Beest, F. M., and Milner, J. M. (2013). Behavioural responses to the thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. *PLoS ONE* 8:e65972. doi: 10.1371/journal.pone.0065972

Wagoner, S. J. (2011). *The Effects of Spring Cattle Grazing on the Nutritional Ecology of Mule Deer (Odocoileus hemionus)* in *eastern Washington*. Ph.D. Dissertation., Pullman: Washington State University.

Walsh, D. R. (2016). *Birth Site Selection and Neonate Survival of Mule Deer in the Blue Mountains of Oregon.* Masters Thesis., University of Nevada-Reno, Reno.

White, R. G. (1983). Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40, 377–384.

Wisdom, M. G., Cook, J. G., Rowland, M. M., and Noyes, J. H. (1993). *Protocols for Care and Handling of Deer and Elk at the Starkey Experimental Forest and Range: General Technical Report PNW-GTR-311*. Portland, OR: U.S. Forest Service.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. H. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer-Verlag, New York.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 05 May 2020
doi: 10.3389/fevo.2020.00107

Seasonal Hypometabolism in Female Moose

Anne Randi Græsli[1]†, Alexandra Thiel[1]†, Boris Fuchs[1], Navinder J. Singh[2], Fredrik Stenbacka[2], Göran Ericsson[2], Wiebke Neumann[2], Jon M. Arnemo[1,2] and Alina L. Evans[1]*

[1] Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Inland Norway University of Applied Sciences, Koppang, Norway, [2] Department of Wildlife, Fish and Environmental Studies, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, Umeå, Sweden

How animals respond to a changing environment is a key question in ecological research. Animals living at higher latitudes are exposed to pronounced seasonal differences in both climate and in resource availability. Endotherms living in those environments have the ability to maintain a constant high body temperature (T_b), over a wide range of ambient temperatures (T_a). Nonetheless, many endotherms display seasonal shifts in metabolic rate (MR). Here, we studied the annual and circadian cycle of T_b and heart rate (HR) in female moose (*Alces alces*) in relation to activity and T_a. HR also can be used as a proxy of MR to calculate energy budgets. We deployed biologgers to 12 free-ranging female moose; a temperature sensor in the rumen, a HR logger subcutaneously, and a GPS collar equipped with acceleration and T_a sensors. We documented seasonal differences in T_b, HR and activity of moose, with lower levels during winter and higher values during summer. The highest daily mean T_b and HR were 38.64°C (10 July) and 71.9 beats per minute (bpm; 26 June), whereas the lowest daily mean T_b and HR were 38.03°C (17 March) and 40.5 bpm (6 March). High-resolution T_b and activity data allowed us to detect circadian and ultradian rhythmicity throughout the year. Based on previous calibration studies, MR decreased by 60% from the highest to the lowest point. Our results demonstrate hypometabolism including lower T_b and HR during winter as a strategy to reduce energy expenditure during periods with colder climate and limited availability of resources.

Keywords: activity, *Alces alces*, body temperature, global positioning system, heart rate, metabolic rate, moose, seasonal variation

OPEN ACCESS

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Ron Moen,
University of Minnesota Duluth,
United States
Rolf O. Peterson,
Michigan Technological University,
United States

***Correspondence:**
Anne Randi Græsli
anne.grasli@inn.no

†These authors have contributed equally to this work

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: 26 October 2019
Accepted: 01 April 2020
Published: 05 May 2020

Citation:
Græsli AR, Thiel A, Fuchs B, Singh NJ, Stenbacka F, Ericsson G, Neumann W, Arnemo JM and Evans AL (2020) Seasonal Hypometabolism in Female Moose. Front. Ecol. Evol. 8:107. doi: 10.3389/fevo.2020.00107

INTRODUCTION

Animals living in environments with ambient temperatures (T_a) below freezing are exposed to pronounced seasonal differences in both climate and resource availability. Nevertheless, endotherms living in these environments can maintain a constant high body temperature (T_b), over a wide range of T_a. Maintaining homeostasis in cold temperatures with limited food availability is energetically costly, and endotherms have adapted to seasonal differences through several strategies including increased insulation, hibernation, seasonal hypometabolism, and daily torpor (Geiser, 2004; Heldmaier et al., 2004; Lovegrove, 2005; Boyles et al., 2011). Hibernation in mammals usually lasts for months, during which animals rely on energy stores and reduce T_b and metabolic rate (MR). The basal MR for hibernating mammals is on average reduced by about 95% during hibernation (Geiser, 2004; Heldmaier et al., 2004; Ruf and Geiser, 2015).

A reduction in MR hypometabolism, is not limited to organisms entering hibernation or torpor, as other endotherms also can exhibit hypometabolism. The reason for entering this stage is not only to adapt to a colder climate, but also to cope with limited energy supplies as evidenced by endotherms in tropical climates (Heldmaier et al., 2004). Seasonal variations of MR, with hypometabolism during winter, occur in a variety of both captive and free-ranging ungulates living in temperate climates, including moose (*Alces alces*; Regelin et al., 1985; Kochan, 2007), red deer (*Cervus elaphus*; Arnold et al., 2004; Turbill et al., 2011), Przewalski horse (*Equus ferus przewalskii*; Arnold et al., 2006), Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Arnold et al., 2018), alpine ibex (*Capra ibex ibex*; Signer et al., 2011), and llama (*Lama glama*; Riek et al., 2019).

Circadian variations of MR also are reported in ungulates, e.g., as episodes of nocturnal hypometabolism independent of activity levels in alpine ibex and red deer (Arnold et al., 2004; Signer et al., 2011). A circadian rhythm is a biological process that displays an endogenous oscillation of about 24 h. Circadian organization in the activity pattern of different ungulate species have been reported previously (Arnold et al., 2004; Lowe et al., 2010; Signer et al., 2011; Pagon et al., 2013; Ensing et al., 2014). Studies of reindeer (*Rangifer tarandus tarandus*) living above the Arctic Circle, including animals on the Svalbard archipelago, reported only weak circadian organization of activity during constant darkness or light (Van Oort et al., 2005; van Oort et al., 2007). A more recent study of Svalbard reindeer, using biologgers, reported circadian rhythmicity in behavior, HR and T_b (Arnold et al., 2018). Circadian rhythmicity in moose could be caused by some combined adaptations to predator and/or human activity, T_a, light-dark cycles, food availability, feeding, and rumination (Van Ballenberghe and Miquelle, 1990; Gillingham and Klein, 1992; Scheibe et al., 1999; Klassen and Rea, 2008).

Several mammal species exhibit a significant correlation between heart rate (HR) and MR, which is attributed to the correlation between the rate of oxygen consumption (VO_2) and HR, when animals are in a metabolic steady state with aerobic metabolism (Green, 2011). Because of the correlation between HR and MR, HR measurements make it possible to calculate energy expenditures of animals under free-ranging circumstances (Renecker and Hudson, 1985). Calculations of energy expenditure are important when discussing potential stressful situations, especially in capital breeders (i.e., organisms relying on stored resources for reproduction) such as moose because increased MR could result in weight loss due to increased energy consumption and decreased time spent foraging. This relationship could further result in lower survival and reproduction rates.

Biologgers have made it possible to obtain data for characterization of the physiology of an animal in their environmental setting, and their reactions to humans over long periods of time (Rutz and Hays, 2009). In this study we used ruminal implants to obtain T_b. Ruminal and vaginal transmitters have previously been used in long-term (>1 year) studies of moose, and rumen temperature successfully predicts core T_b when censoring and filtering out drinking events (Herberg et al., 2018; Thompson et al., 2019). The few studies on moose using biologgers to monitor HR are short-term (weeks-months), usually with a limited number of animals in semi-captive conditions (Renecker and Hudson, 1985; Langvatn, 1992; Roshchevsky et al., 1999). In this study, we used the same type of HR loggers, as previously deployed in a variety of large mammals including domestic sheep (*Ovis aries*; Fuchs et al., 2019a), and Asiatic black bears (*Ursus thibetanus*) and Eurasian brown bears (*Ursus arctos*; Fuchs et al., 2019b).

There are relatively few long-term studies using biologgers that reports simultaneous measurements of T_b and HR in ungulates living in harsh climates (Arnold et al., 2006; Signer et al., 2011; Turbill et al., 2011; Arnold et al., 2018; Riek et al., 2019). Similar studies of moose are important, because similar to reindeer and caribou (*Rangifer tarandus* spp.), moose are a key herbivore in northern ecosystems that are ecologically, economically, and culturally important. Currently, we still lack knowledge on the physiological ability of moose to respond to ambient temperatures that are likely to come with changing climatic conditions. Previous studies have shown that moose are easily heat stressed with respiration rate, HR and energy expenditure rising with increasing T_a (Renecker and Hudson, 1986; Roshchevsky et al., 1999; McCann et al., 2013). In captive moose the respiration rate started to increase at 14°C and at 20°C they began open-mouthed panting (Renecker and Hudson, 1986). Thompson et al. (2019) suggested several other factors that also should be considered, including core T_b and daily variations of core T_b, in addition to the influence of body condition and season, when evaluating heat stress. Climatic changes resulting in increased T_a can be expected to result in habitat changes, decreased food availability and, therefore, poorer body condition (van Beest et al., 2012; van Beest and Milner, 2013).

In the present study, we used biologgers and global positioning system (GPS) collars to study the annual and circadian rhythms of HR and T_b, in relation to activity and T_a, in free-ranging female moose in Sweden. The obtained values and patterns are relevant background for evaluating the behavioral and physiological effects of potential stressors. Moreover, because HR can be a proxy for MR, values of HR also can be used to calculate energy budgets.

We hypothesized that moose would exhibit physiological and behavioral changes related to the dramatic seasonal differences present at northern latitudes. Firstly, we predicted lower T_b and HR in winter (Regelin et al., 1985; Langvatn, 1992; Kochan, 2007; Thompson et al., 2019). Secondly, we predicted a circadian rhythmicity in the HR, T_b, and activity of moose, as previously described in ungulates because of adaptations to feeding and rumination or environmental factors such as food availability, T_a and light-dark cycles, predation, and human activities (Scheibe et al., 1999; Arnold et al., 2004; Lowe et al., 2010; Signer et al., 2011; Pagon et al., 2013; Ensing et al., 2014). We also expected a change in these rhythms over the year (Klassen and Rea, 2008; Arnold et al., 2018). Thirdly, we predicted T_b to increase with increasing T_a because of the poor tolerance of moose to heat-stress (Renecker and Hudson, 1986; McCann et al., 2013; Thompson et al., 2019).

MATERIALS AND METHODS

Study Area and Animals

The study was conducted in the Nordmaling municipality (63°34′00′′ N, 19°30′00′′ E) in the county of Västerbotten in Sweden. The study area is characterized by boreal forests dominated by Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*) and birches (*Betula pendula* and *B. pubescens*). Yearly average T_a is 3°C and there are >150 days with snow cover from November to May. Mean and maximum daily snow depth from 1 November to 30 April was 0.15 and 0.5 m in 2016–2017 and 0.53 and 0.98 m in 2017–2018 (SMHI, 2019). The length of the growing season is between 150 and 160 days from late April to mid-October (SMHI, 2019).

We immobilized 12 female moose (>1.5 years old) in February 2017. The project was approved by the Animal Care Committee for Northern Sweden in Umeå (Dnr A3/2016 2016–02-26) and was conducted in accordance with Swedish laws concerning animal research ethics. Experienced veterinarians, pilots and field personnel were responsible for captures, monitoring, handling, collaring and surgeries. All personnel were trained and certified according to the standards of the Swedish Animal Welfare Agency and the Swedish Board of Agriculture.

Biologgers and Programming

We fitted moose with collars including a GPS receiver, a temperature recorder, an activity sensor, a mortality sensor, a very high frequency (VHF) transmitter, and a Global System for Mobile communication (GSM) modem (Vectronic-Aerospace, Berlin, Germany). Activity sensors measured acceleration in three orthogonal directions six to eight times per second. For each direction activity values were averaged for a recording interval of 5 min. To present overall activity, values of two of the three orthogonal directions (x and y) were summed, resulting in values ranging from 0–510, with 0 representing no activity and 510 highest activity (Gervasi et al., 2006). The GPS was scheduled to record positions from 1 min to 3 h depending on the ongoing studies, and together with the recorded T_a (every 5 min), those readings were sent using the GSM network to WRAM (Wireless Remote Animal Movement) database for storage (Dettki et al., 2014). Moose also were equipped with a mortality implant transmitter (MIT, Vectronic Aerospace GmbH, Berlin, Germany) in their rumen, which recorded T_b at 5-min intervals and then transmitted information to a collar unit, where it was archived. The MIT is a cylindrical device with a diameter of 21 mm, length 72 mm, and weight ca 100 *g* (VectronicAerospace, 2017). The most recently stored T_b was sent together with the GPS position message and the remaining data downloaded upon collar retrieval.

Additionally, we fitted moose with subcutaneous HR loggers (DST centi HRT; Star Oddi, Gardabaer, Iceland), which can simultaneously record long-term HR and subcutaneous T_b. The DST centi HRT is a cylindrical device with dimensions of 46 × 15 mm and weighs 19 grams. HR is automatically calculated from a 4 s electrocardiogram (ECG) strip with a 150 Hz measurement frequency and stored along with a quality index of signal clarity and the R-R interval regularity. The logger can store up to 699,051 HR and temperature measurements or 2,785 ECG buffer measurements and, according to the manufacturer, has a battery life of up to 19 month (StarOddi, 2017). We programmed the DST centi HRTs to record HR every second hour from the beginning of the study until 6 August; thereafter, they were programmed to record HR every second minute.

Immobilization Procedure

We immobilized moose from a helicopter using a CO_2 powered rifle (Dan-Inject, Børkop, Denmark) with the drug combination of 50 mg xylazine (Rompun Dry Substance, Bayer AG, Leverkusen, Germany) and 4.5 mg etorphine (Etorphine® HCl 9.8 mg/mL, Vericore Veterinary Products, Novartis Animal Health UK Ltd., Litlington, United Kingdom), according to previously described procedures (Evans et al., 2012; Lian et al., 2014). Pregnancy status was determined by rectal palpation (Solberg et al., 2003). Number of offspring (zero, single or twins) was verified the following spring by field observations. Biologgers were sterilized with ethylene oxide gas (Anprolene AN74i 60 L, Andersen Europe, Kortrijk, Belgium) before surgical implantation. Prior to surgery, moose were given analgesics, meloxicam (Metacam®, Boehringer Ingelheim Vetmedica GmBH, Ingelheim am Rhein, Germany) subcutaneously at a dose of 0.5 mg/kg. The DST centi HRT was implanted surgically at the right side of the most rostral part of the sternum, with the moose placed in lateral recumbency with the left side up. A cell phone device (KardiaMobile EKG Monitor, AliveCor Inc., Mountain View, CA, United States) and a corresponding application Kardia App (AliveCor Inc.; AliveCor, 2018), were used to find the best ECG signal, and the most appropriate site to implant the DST centi HRT. Surgery was performed according to best-practice guidelines (Fiorello et al., 2016) and a local anesthetic, bupivacaine (Marcain 5 mg/mL, AstraZeneca, Cambridge, United Kingdom), was administered at a total dose of 2.0–3.0 mg/moose. A 2-cm long skin incision was made and the DST centi HRT was placed between the subcutaneous fat and the muscle with the electrodes facing away from the muscle. The incision was closed with 2-0 monofilament absorbable suture PDS® II (polydioxanone) suture (Ethicon, Johnson & Johnson, New Brunswick, NJ, United States). After surgical implantation, we reversed the effects of xylazine with 5 mg atipamezole (Antisedan® 5 mg/mL, Orion Pharma Animal Health, Turku, Finland) injected intramuscularly or intravenously, to inhibit a swallowing reflex. We deployed MIT as previously described (Minicucci et al., 2018), before we reversed the immobilization with 50 mg naltrexone (Naltrexonhydroklorid vet. APL 50 mg/mL; Apotek Produktion och Laboratorier, Kungens Kurva, Sweden) intramuscularly or intravenously. There were no mortalities or known morbidities associated with the immobilization procedure. Two moose were shot during the study period, one during the annual moose hunt (September 2017) and one as a special action by the local government because of local damage to forests (February 2018).

In both instances, the loggers were collected and downloaded. We recaptured the remaining 10 moose 1 year after instrumentation (February 2018). The DST centi HRT was surgically removed, and data were downloaded, with the Mercury software program and a Communication Box (StarOddi, 2017). We downloaded all collar data and data from MITs stored in the collar unit in the field during recaptures.

Data Preparation

One of the instrumented moose was not pregnant the first season; the remainder gave birth in May–June 2017 (mean calving date 28 May, range 17 May to 10 June), as determined from GPS clustering and subsequent visual verification in the field. The following season two moose were not pregnant. We excluded the non-pregnant moose in the first season from the beginning of the study until 15 September 2017, and the non-pregnant moose in the second season from 15 September 2017 until the end of the study. We chose 15 September because of reports of mid-September as the beginning of oestrus in female moose in Sweden (Malmsten et al., 2014).

A strong positive correlation between temperature recorded by GPS collars on moose and T_a recorded by weather stations was previously reported, therefore collar temperatures are regarded as a reliable index for T_a (Ericsson et al., 2015). We used the offset for latitude 64°N and month reported by Ericsson et al. (2015) to correct the collar temperatures for each individual moose. Drinking and snow intake have been shown to influence ruminal temperature obtained by MITs (Herberg et al., 2018). We used the *R* package "anomalize" (Dancho and Vaughan, 2018) to detect outliers associated with water intake (low T_b values). To facilitate optimal outlier detection for T_b time series including visual inspection and filtering, we used the twitter method to detect outliers, set trend and frequency to 6 h and allowed for a total of 20% of outlier detection (Dancho and Vaughan, 2018).

We programmed the Star Oddi device to record raw ECG signals every second hour of which a subsample of 150 ECG strips were used to manually calculate HR. The manual ECG based HR was compared with the HR measurements automatically calculated by the algorithm of the Star Oddi device. Because of insufficient automatic R-R interval detection, the algorithm was adjusted by StarOddi and rerun on the entire raw ECG data set. Bjarnason et al. (2019) provides a more detailed description of the HR calculation. Ultimately only recalculated HR measurements with quality index 0 or 1 were included in the analysis. Limitations on data storage resulted in a decision to not record raw ECG data for the 2-min detailed HR data after 6 August. Because of the high noise level and insufficient automatic R-R interval detection, HR data were not reliable after that date.

One of the recaptured moose had lost the DST centi-HRT logger and was therefore excluded from the HR analysis. Data from two moose were excluded during the entire period because of high noise level in the ECG raw data and unsuccessful HR calculation. Days of capture and recapture were excluded from the analysis, because the capture event and the anesthetics were expected to affect HR, T_b, and activity (Kreeger and Arnemo, 2018).

Data Analysis

To investigate the seasonal patterns of T_b, HR, and activity, we fitted separate generalized additive mixed models (GAMM) with the function "bam" on daily mean T_b, HR activity and T_a as response variables (Wood, 2017). We added a fitted smooth term for day since capture, added a random intercept and slope for moose ID and an autoregressive model (AR1) structure to account for detected residual temporal autocorrelation (Pinheiro and Bates, 2000). We applied the "gam.check" function to choose adequate basis dimensions of the parameter k (Wood, 2017). We calculated the first derivatives of the smooth term for day since capture with the "fderiv" function, to determine periods of significant increase or decrease in daily mean T_b, HR and activity (Simpson, 2018).

We used Lomb-Scargle periodogram analysis to investigate circadian rhythms in T_b, HR, and activity (Ruf, 1999). We performed analyses on the raw data on a 15-day rolling window and tested for presence of circadian rhythms between 0.5 and 30 h. Significant periodicity was detected when peaks in the Lomb-Scargle periodogram exceeded the 95% confidence limit.

We visually investigated the intensity of T_b and activity variation over the year using the *R* package "ggplot2" to plot actograms of raw data of T_b and activity (Wickham, 2016). We calculated times for sunrise, sunset, dusk, and dawn at the following coordinates within the study area (Bivand and Lewin-Koh, 2017). We added the times to the actograms and defined sunrise and sunset as the time when the top edge of the sun reaches the horizon. Dusk and dawn were defined as the onset and end of civil twilight.

Daily energy expenditure was calculated on the days with the lowest and highest mean daily HR based on a pooled exponential equation:

$$y = 4.655e^{0.0071x},$$

where y is the MR and x is the HR normalised to $\text{BM}^{-0.25}$ (body mass). The equation was developed from a study of captive moose (Renecker and Hudson, 1985).

RESULTS

From February to September 2017, we obtained T_b data from eleven moose, and from September 2017 to February 2018, we obtained T_b data from nine moose. We had valid HR data from eight moose from February until the beginning of August 2017.

Female moose exhibited seasonal variation in T_b, HR and activity with higher levels in June-July and lower levels in January–March (**Table 1** and **Figure 1**). The seasonal trends followed the same patterns for all parameters throughout the year. Significantly increasing periods of activity, HR and T_b occurred between April and June and significantly decreasing periods occurred between July and November.

Estimated mean daily energy expenditure, for all individuals, for the days with the lowest and highest daily mean HR were 377 $\text{kJ/kg}^{0.75}$ and 935 $\text{kJ/kg}^{0.75}$, respectively, which represented

TABLE 1 | Overview of dates, daily mean values (Mean) and 95% CI of the daily mean (95% CI) for dates with lowest and highest values and start and stop for increasing and decreasing periods of body temperature (T_b), heart rate (HR), collar activity (activity), and ambient temperature (T_a) for female moose in Sweden.

	Date	Mean	95% CI	*n*
T_b				
Lowest	17 March	38.03°C	37.94–38.12	11
Increase start	27 March	38.50°C	37.96–38.14	11
Increase stop	30 June	38.62°C	38.52–38.73	11
Highest	10 July	38.64°C	38.53–38.75	11
Decrease start	17 July	38.63°C	38.52–38.74	11
Decrease stop	23 September	38.30°C	38.18–38.42	9
HR				
Lowest	6 March	40.5 bpm	37.7–43.2	8
Increase start	9 May	45.3 bpm	41.7–48.9	8
Break increasing period start	31 May	60.1 bpm	56.2–64.0	8
Break increasing period stop	3 June	61.2 bpm	57.2–65.2	8
Increase stop	20 June	71.2 bpm	66.9–75.5	8
Highest	26 June	71.9 bpm	67.6–76.3	8
Activity				
Lowest	14 February	13.7 AU	6.2–21.3	9
Increase start	21 April	19.6 AU	16.4–24.2	11
Increase stop	5 June	42.1 AU	38.1–46.1	11
Highest	17 June	44.0 AU	40.0–47.8	11
T_a				
Lowest	30 January	−2.1°C	−3.3 to −0.9	9
Increase start	21 April	7.6°C	6.5–8.8	11
Increase stop	17 June	20.3°C	19.2–21.5	11
Highest	16 July	22.4°C	21.2–23.5	11
Decrease start	13 September	16.3°C	15.0–17.3	11
Decrease stop	11 November	4.7°C	3.5–5.8	9

a 60% decrease in energy expenditure from summer to winter (calculations in **Supplementary Appendix A**).

Lomb-Scargle periodogram analyses detected circadian rhythmicity in T_b and activity, the schedule with HR measurements only every second hour was not adequate to detect circadian patterns in HR. Percentages of the displayed rhythms, based on the results of the periodograms for T_b and activity for one representative individual in January and September are presented in **Figure 2** (for the remainder of individuals, percentages of the displayed rhythms for each month are included in **Supplementary Appendix B**). A period length (τ) of 24 h of T_b was dominate during most of the year, whereas ultradian rhythms with τ of 3–8 h were more frequent in December and January, and to a small extent in June and July. Activity displayed ultradian rhythmicity with period length τ of 2–8 h throughout the year. Actograms of raw data of T_b and activity for the same individual in January and September are presented in **Figure 3** (for actograms for all individuals throughout the study period, see **Supplementary Appendix C**). A visual analysis of the actograms shows higher intensity of T_b and activity in September compared to January, as demonstrated in **Figure 1**.

DISCUSSION

Seasonal patterns displayed in the moose with low levels of T_b, HR and activity during winter compared with summer are similar to those reported in moose and other ungulates including alpine ibex, red deer, and Svalbard reindeer (Signer et al., 2011; Turbill et al., 2011; Arnold et al., 2018; Thompson et al., 2019). The interval from the lowest to the highest T_b recorded by vaginal implant transmitters in moose was 0.5°C (Thompson et al., 2019) compared with 0.61°C in our study using MITs, this is likely occurred because of the different types of biologgers used. The seasonal changes in T_b and HR are smaller than those reported for alpine ibex and Svalbard reindeer, which may be due to species differences, physiological state (i.e., pregnancy status, body-condition and mass, age, and sex), seasonal adaptations, the relatively mild coastal conditions and the unusually small amount of snow during the first winter of our study (mean and maximum daily snow depth was 0.15 and 0.5 m; Signer et al., 2011; Arnold et al., 2018). Maximum snow depths recorded from 2007/2008 to 2018/2019 ranged from 0.4 to 1.1 m (mean 0.66 m) and the mean snow depths from 0.13 to 0.53 m (mean of means 0.29 m; SMHI, 2019).

We calculated a 60% decrease in MR from summer to winter by decreasing HR. The calculation is based on an equation from Renecker and Hudson (1985). Mean daily MR was 377 kJ/kg$^{0.75}$ in winter and 935 kJ/kg$^{0.75}$ in summer. Calculated MR in this study is comparable to MRs obtained in earlier studies, and the decreased MR from summer to winter in these studies varies from 33–76% (Regelin et al., 1985; Renecker and Hudson, 1986, 1989). Differences between studies are likely related to dissimilarities in methods used to measure energy expenditure, study designs, and individual and environmental variation.

Voluntarily reduced food intake in winter, was demonstrated previously in moose receiving *ad libitum* high-quality food (Schwartz et al., 1984; Regelin et al., 1985). Differences in quality and intake of digestible nutrients could result in seasonal variations of HR and T_b, but do not result from food availability alone (Mesteig et al., 2000; Theil et al., 2004; Kochan, 2007; Signer et al., 2011). Decreased food intake could result in a decrease in both endogenous heat production from fermentation and metabolism in addition to reduced blood perfusion in abdominal organs, which results in lower HR and T_b (Mesteig et al., 2000; Signer et al., 2011). Seasonal variation in organ sizes corresponding to seasonal fluctuations in food and water intake occur in Sand gazelles (*Gazella subgutturosa*; Ostrowski et al., 2006), and it is assumed that this is a common feature in other ungulates as well (Arnold et al., 2006; Signer et al., 2011). A reduction in organ size could result from lower oxygen consumption with subsequent lower HR during winter.

The period with lowest levels of HR and T_b (March-April) coincides with the time of the year we would expect least natural food availability. Shortly after reaching the lowest values in mid-March, T_b started to rise, while HR was stable at its lowest level for a longer period. A similar relationship with T_b starting to rise prior to HR also was demonstrated in hibernating brown bears prior to den exit (Evans et al., 2016). Those authors suggested that the bears experienced passive

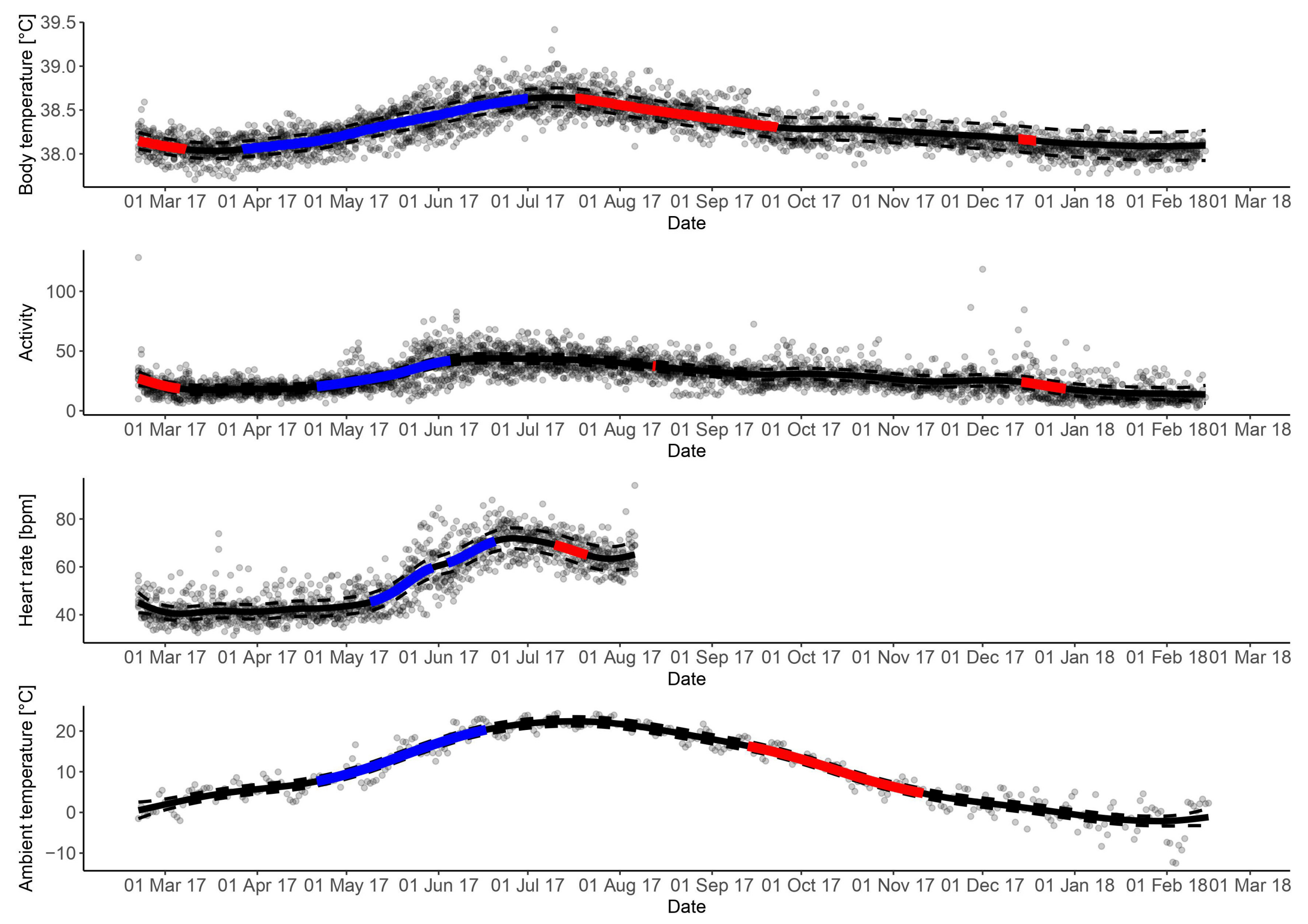

FIGURE 1 | Daily mean body temperature, collar activity, heart rate, and ambient temperature for 12 female moose in Sweden. Solid line represents daily mean body temperature, collar activity, heart rate, and ambient temperature, respectively, dashed lines represents 95% confidence interval of the daily mean. Significantly increasing and decreasing periods are presented as red and blue, respectively, of the solid line.

rewarming with increasing T_a, before they experienced increased activity of the sympathetic nervous system, decreased activity of the parasympathetic nervous system or a combination thereof, resulting in an increase in HR. Passive warming from basking in the sun, was also offered as a strategy in ungulates, by using exogenous heat, i.e., the sun, for thermoregulation and to reduce endogenous energy production (Signer et al., 2011). The earlier increase in T_b compared with HR and activity (and hence feeding behavior) after the lowest levels of those measurements during winter, in our study, might result from passive rewarming by the sun. Even if the T_a did not exhibit a significant increase during the period where T_b started to increase significantly, an increase in T_a was visible in the graph in March and April (**Figure 1**). Short days and cold nights might account for the lack of a significant increase in T_a.

Growing season, wind, light-dark cycle, snowfall, and snow cover are other external cues that influence HR and T_b in ungulates (Signer et al., 2011; Arnold et al., 2018). HR started to increase significantly at approximately the same time as the start of the growing season (mean daily $T_a > 5°C$; SMHI, 2019), likely because of increased nutrition content in the food (Brosh, 2007). The last month of pregnancy could also influence the increase in HR (Mauget et al., 1997).

Activity, measured in this study with motion sensitive collars, includes head movements in addition to locomotion; consequently, feeding behavior increases activity (Gervasi et al., 2006). A rise in activity before the start of the growing season, as demonstrated in this study, could reflect increased feeding behavior because of increased food availability when snow is melting. Another moose study in the same study area reported that about 80% of the animals were migratory and that the timing of the migration differed between years, and varied with food availability and calving time (Singh et al., 2012). We did not investigate the migratory patterns in this study, but migration likely affected the seasonal patterns we observed.

We demonstrated, based on our model, a break in the increasing period of HR from 31 May until 3 June, which coincides with the calving. Nonetheless, further investigation will be necessary to determine if this break in HR resulted from calving. Reproductive status influence T_b patterns in several wild

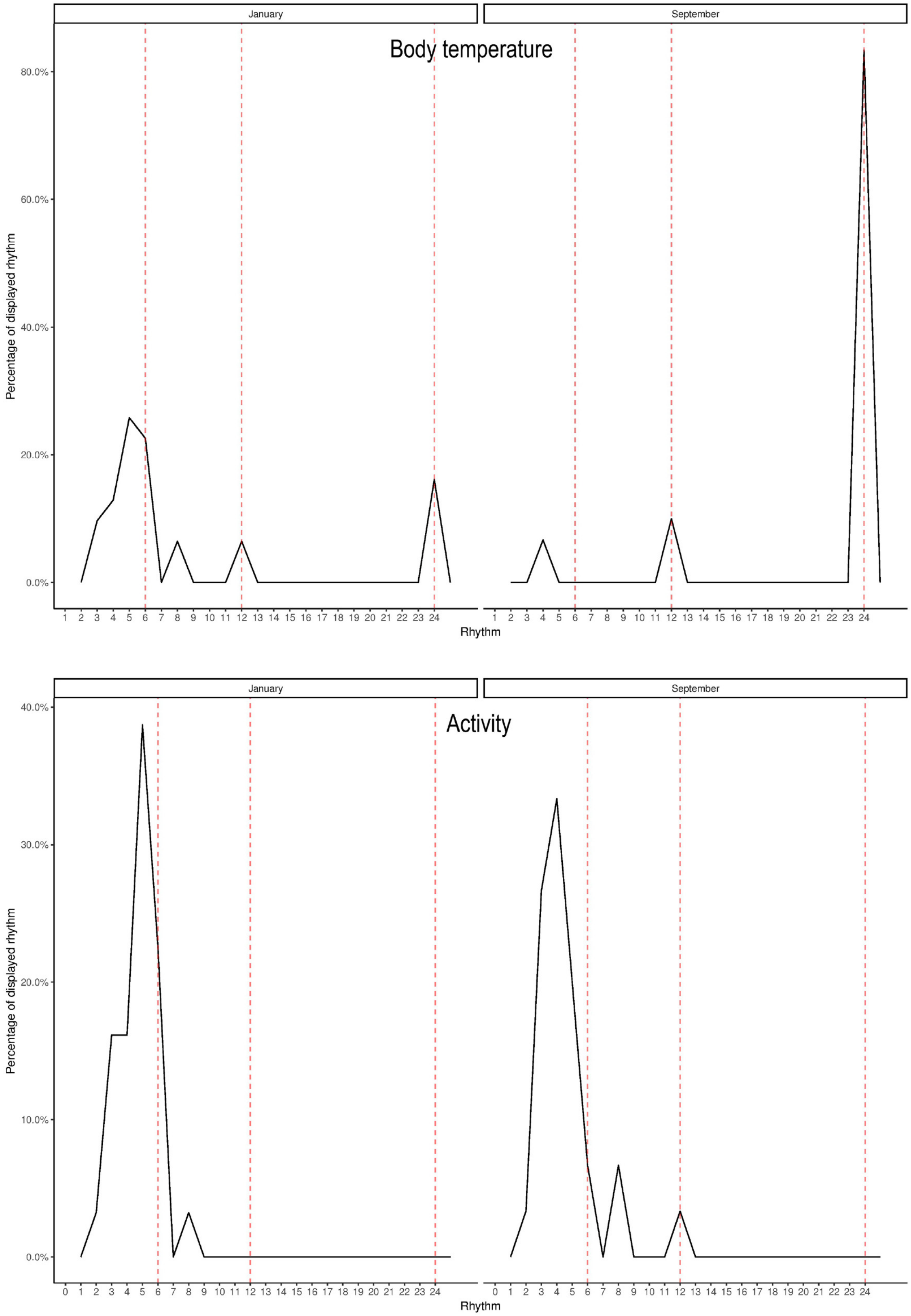

FIGURE 2 | Percentages of displayed rhythms based on Lomb-Scargle periodograms for body temperature (top) and activity (lower) for one representative moose in January and September. Vertical axis represents percentage of displayed rhythm and horizontal axis represents the rhythmicity in hours.

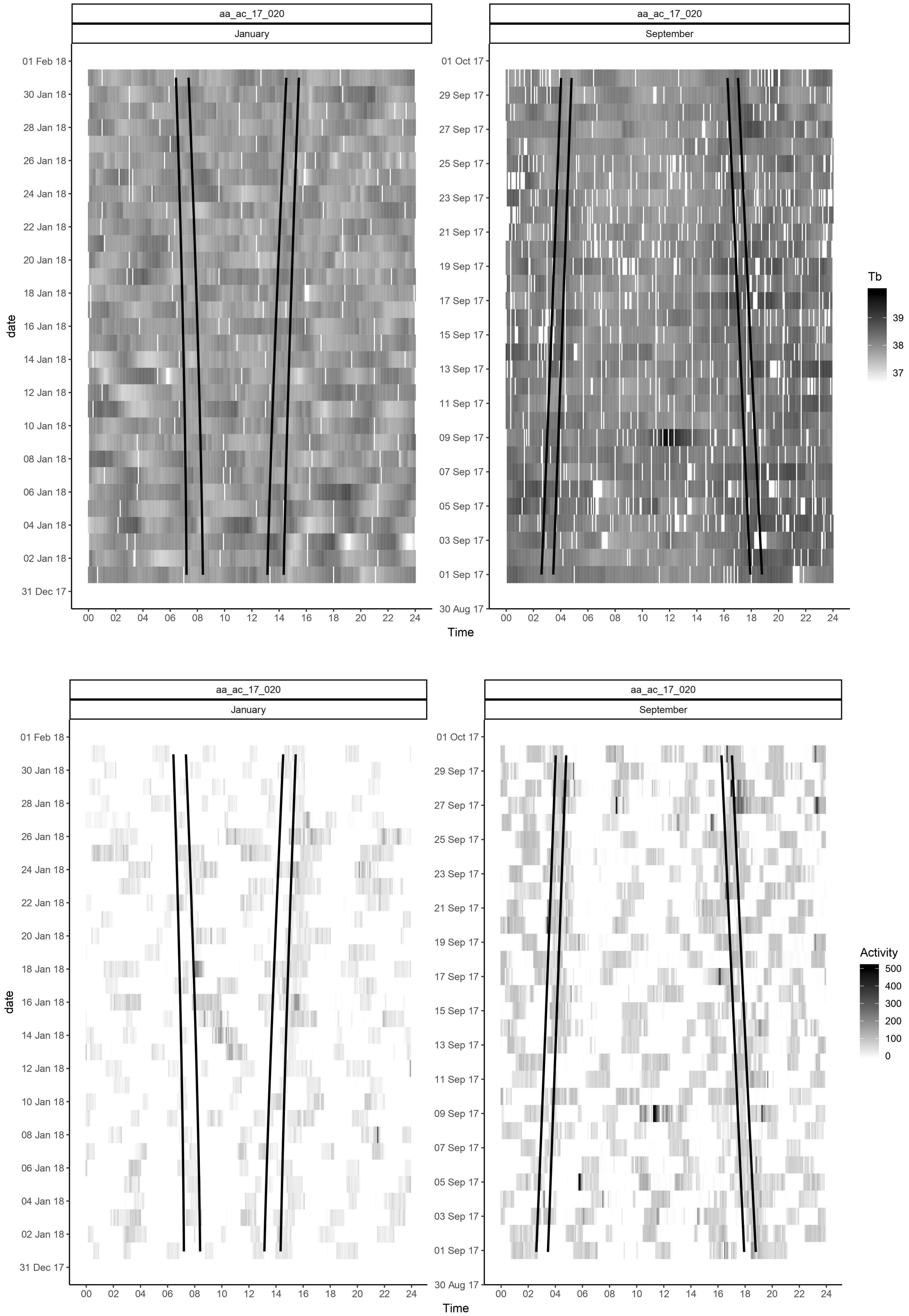

FIGURE 3 | Actograms for body temperature (T_b) and activity for one representative moose in January and September. Vertical axis represents the date and horizontal axis represents time of the day. The area between the black lines represents the twilight. Lightest color represents lowest T_b and activity, and darker color represents higher T_b and activity.

mammals. Reports exist of improved homeothermy in African lions (*Panthera leo*; Trethowan et al., 2016), wolverines (*Gulo gulo*; Thiel et al., 2019), muskox (*Ovibos moschatus*; Schmidt et al., 2020), and brown bears (Friebe et al., 2014) during gestation. Schmidt et al. (2020) also reported differences in seasonal T_b pattern between pregnant and non-pregnant muskoxen. The effect of reproductive status was not possible to detect in our study, because we only studied pregnant moose. MR in roe deer (*Capreolus capreolus*) increased during the last 2 months of gestation and during the first month of lactation, by 15 and 27%, respectively (Mauget et al., 1997). Regelin et al. (1985) documented no differences between sexes in MR in adult moose, when excluding last trimester of gestation and lactation. Thus, we would expect differences in T_b, HR and MR between pregnant and non-pregnant moose at the end of the gestation and the lactation. The skewed ratio of pregnant and non-pregnant females did not allow us to test for effects of pregnancy status on seasonal variation in HR and T_b.

Circadian rhythmicity in activity was demonstrated in this study, as previously reported in both moose (Van Ballenberghe and Miquelle, 1990; Gillingham and Klein, 1992) and other ungulates (Arnold et al., 2004; Lowe et al., 2010; Signer et al., 2011; Pagon et al., 2013; Ensing et al., 2014). In addition, we were able to demonstrate circadian organization of T_b, which has also been shown in Svalbard reindeer (Arnold et al., 2018). T_b displayed rhythms with τ of 24 h for most of the year, except December and January, where ultradian rhythms with τ 3–8 h were more dominate. In June and July, the months with the longest daylight periods, the 24 h rhythmicity was not as dominant as in the other months. This result is similar to the pattern reported in Svalbard reindeer by Arnold et al. (2018), who documented that during the periods with midnight sun and polar night the 24-h patterns were not as dominant as during the rest of the year. Even if there are no periods with constant daylight or darkness in our study area, the differences within the year could be affected by changes in the light-dark cycle. Other reasons for deviation from the 24-h cycle could be food availability, predation, and human disturbance (Ensing et al., 2014). We observed the same trend in the ultradian rhythms in activity as in moose in Alaska and Svalbard reindeer, with shorter periods in summer compared with winter (Van Ballenberghe and Miquelle, 1990; Arnold et al., 2018). Oscillation of rumination is demonstrated to be a regulatory function of activity, so the ultradian rhythmicity of activity is likely results from feeding behavior and ruminating (Scheibe et al., 1999). Diseases and stressful situations result in impairment of the ultradian rhythmicity of activity, and periodogram analysis could be used to detect irregular patterns (Scheibe et al., 1999; Berger, 2011).

Global climate change is an important concern regarding higher energetic cost with both fluctuating and increasing T_a (Boyles et al., 2011). The threshold for heat stress cannot only be explained by the T_a, but is also affected by factors such as wind speed, solar radiation, winter fur (i.e., in spring), physiological differences (e.g.,: age, sex, pregnancy status, body mass, and fitness), and immune status (Renecker and Hudson, 1986; McCann et al., 2013; Thompson et al., 2019). In this study, the highest mean daily T_a was 22.4°C, and >2 months had a mean daily $T_a > 14°C$, one reported threshold for heat stress (Renecker and Hudson, 1986); thus, the highest mean MR calculated in our study possibly represents a MR under heat stress and hypermetabolism. As a response to the increased MR, and to reduce heat generated from feeding, ruminants reduce dry matter intake under warm conditions (Beatty et al., 2008). Increasing T_a also could result in decreased availability of high-quality forage because of changes in vegetation phenology, habitat changes, and a shortened period with forage of high nutritional quality (Monteith et al., 2015). Cumulatively, loss of body mass and failure to accumulate fat will result in lower reproduction and survival, and increased infection risk (Lenarz et al., 2009; van Beest et al., 2012; McCann et al., 2013; van Beest and Milner, 2013).

In this study, T_b started to decline significantly 1 day after T_a peaked in July. Heat stress with voluntarily reduced food intake or habitat changes to habitats with forage of poorer quality could result in decreased endogenous heat production and thereby explain the decrease in T_b (Beatty et al., 2008; Monteith et al., 2015). The lack of HR data from the beginning of August, prevent us from commenting on the HR fluctuations from summer to winter. We strongly recommend performing pilot studies when using a HR detection algorithm on new species because validation is crucial to get reliable results.

CONCLUSION

Herein we documented the daily and annual pattern of T_b and HR of moose in northern Sweden. Annual variations of T_b and HR followed the same patterns with lowest levels in March and the highest levels from late June to early July. The decrease in HR from the highest to the lowest daily mean represents a 60% decrease in MR from summer to winter. The daily pattern of T_b varies throughout the year, with 24-h cycles as the predominant pattern in September, compared with ultradian cycles with τ 2–6 h as the predominant pattern in January. Our results indicate that hypometabolism is a vital strategy for energy saving with limited resources available in large are capital breeder in northern environment, with complexly regulated by both physiological and environmental factors. We hypothesize that hypermetabolism is also a strategy for gaining weight during summer.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by Animal Care Committee for Northern Sweden in Umeå (Dnr A3/2016 2016–02–26).

AUTHOR CONTRIBUTIONS

AE, JA, GE, WN, and NS designed and initiated the study. AG, AE, FS, JA, BF, and AT performed the data collection; data management was done by BF and AT. AG and AT drafted the manuscript. AT and AG performed the statistical analysis with advice from BF and NS. All authors participated in writing the manuscript and approved the submitted version.

FUNDING

The study was funded by the Norwegian Environmental Agency, the Inland Norway University of Applied Science, and the Swedish University of Agricultural Sciences (SLU) through the Beyond Moose program (financed by the Swedish EPA, the Kempe foundation, and the County Board of Västerbotten). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

ACKNOWLEDGMENTS

We acknowledge the collaboration with the research programs Beyond Moose and Governance in cooperation with local landowners and hunters, the county board of Västerbotten, and the Västerbotten chapter of the Swedish Association of Hunting and Wildlife Management. We will also thank Ada Viljanen and Helle Bernsdorf Hydeskov for excellent help during fieldwork, and Olivier Devineau for statistical advice.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00107/full#supplementary-material

APPENDIX A | Energy calculations for the day with the lowest and highest daily mean heart rate.

APPENDIX B | Percentages of displayed rhythms based on Lomb-Scargle periodograms for T_b and activity for all individuals in all months.

APPENDIX C | Actograms for T_b and activity for each individual during the study.

REFERENCES

AliveCor (2018). *KardiaMobile EKG Monitor [Online]*. Mountain View, CA: AliveCor.

Arnold, W., Ruf, T., and Kuntz, R. (2006). Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*) II. Energy expenditure. *J. Exp. Biol.* 209, 4566–4573. doi: 10.1242/jeb.02536

Arnold, W., Ruf, T., Loe, L. E., Irvine, R. J., Ropstad, E., Veiberg, V., et al. (2018). Circadian rhythmicity persists through the Polar night and midnight sun in Svalbard reindeer. *Sci. Rep.* 8:14466. doi: 10.1038/s41598-018-32778-4

Arnold, W., Ruf, T., Reimoser, S., Tataruch, F., Onderscheka, K., and Schober, F. (2004). Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *Am. J. Physiol. Regul. Integr. Compar. Physiol.* 286, R174–R181. doi: 10.1152/ajpregu.00593.2002

Beatty, D., Barnes, A., Taylor, E., and Maloney, S. (2008). Do changes in feed intake or ambient temperature cause changes in cattle rumen temperature relative to core temperature? *J. Ther. Biol.* 33, 12–19. doi: 10.1016/j.jtherbio.2007.09.002

Berger, A. (2011). Activity patterns, chronobiology and the assessment of stress and welfare in zoo and wild animals. *Int. Zoo Yearb.* 45, 80–90. doi: 10.1111/j.1748-1090.2010.00121.x

Bivand, R., and Lewin-Koh, N. (2017). *Maptools: Tools for Reading and Handling Spatial Objects. R package version 0.9–2.*

Bjarnason, A., Gunnarsson, A., Arnason, T., Oddgeirsson, M., Sigmarsson, A. B., and Gunnarsson, A. (2019). Validation of ECG-derived heart rate recordings in Atlantic cod (*Gadus morhua* L.) with an implantable data logging system. *Anim. Biotelemetr.* 7, 1–10. doi: 10.1186/s40317-019-0176-4

Boyles, J. G., Seebacher, F., Smit, B., and McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integr. Compar. Biol.* 51, 676–690. doi: 10.1093/icb/icr053

Brosh, A. (2007). Heart rate measurements as an index of energy expenditure and energy balance in ruminants: a review. *J. Anim. Sci.* 85, 1213–1227. doi: 10.2527/jas.2006-298

Dancho, M., and Vaughan, D. (2018). *Anomalize: Tidy Anomaly Detection. R package version 0.1.1.*

Dettki, H., Brode, M., Giles, T., and Hallgren, J. (2014). "Wireless remote animal monitoring (WRAM)–A new international database e-infrastructure for management and sharing of telemetry sensor data from fish and wildlife," in *Proceedings of the International Congress on Environmental Modelling and Software*, Colorado.

Ensing, E. P., Ciuti, S., de Wijs, F. A., Lentferink, D. H., ten Hoedt, A., Boyce, M. S., et al. (2014). GPS based daily activity patterns in European red deer and North American elk (*Cervus elaphus*): indication for a weak circadian clock in ungulates. *PLoS One* 9:e106997. doi: 10.1371/journal.pone.0106997

Ericsson, G., Dettki, H., Neumann, W., Arnemo, J. M., and Singh, N. J. (2015). Offset between GPS collar-recorded temperature in moose and ambient weather station data. *Eur. J. Wildl. Res.* 61, 919–922. doi: 10.1007/s10344-015-0968-7

Evans, A. L., Fahlman, A., Ericsson, G., Haga, H. A., and Arnemo, J. M. (2012). Physiological evaluation of free-ranging moose (*Alces alces*) immobilized with etorphine-xylazine-acepromazine in Northern Sweden. *Acta Vet. Scand.* 54:77. doi: 10.1186/1751-0147-54-77

Evans, A. L., Singh, N. J., Friebe, A., Arnemo, J. M., Laske, T. G., Fröbert, O., et al. (2016). Drivers of hibernation in the brown bear. *Front. Zool.* 13:7. doi: 10.1186/s12983-016-0140-6

Fiorello, C. V., Harms, C. A., Chinnadurai, S. K., and Strahl-Heldreth, D. (2016). Best-practice guidelines for field-based surgery and anesthesia on free-ranging wildlife. II. Surgery. *J. Wildl. Dis.* 52, S28–S39. doi: 10.7589/52.2S.S28

Friebe, A., Evans, A. L., Arnemo, J. M., Blanc, S., Brunberg, S., Fleissner, G., et al. (2014). Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears. *PLoS One* 9:e101410. doi: 10.1371/journal.pone.0101410

Fuchs, B., Sørheim, K. M., Chincarini, M., Brunberg, E., Stubsjøen, S. M., Bratbergsengen, K., et al. (2019a). Heart rate sensor validation and seasonal and diurnal variation of body temperature and heart rate in domestic sheep. *Vet. Anim. Sci.* 8:100075. doi: 10.1016/j.vas.2019.100075

Fuchs, B., Yamazaki, K., Evans, A. L., Tsubota, T., Koike, S., Naganuma, T., et al. (2019b). Heart rate during hyperphagia differs between two bear species. *Biol. Lett.* 15:20180681. doi: 10.1098/rsbl.2018.0681

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Ann. Rev. Physiol.* 66, 239–274. doi: 10.1146/annurev.physiol.66.032102.115105

Gervasi, V., Brunberg, S., and Swenson, J. E. (2006). An individual-based method to measure animal activity levels: a test on brown bears. *Wildl. Soc. Bull.* 34, 1314–1319. doi: 10.2193/0091-7648(2006)34[1314:aimtma]2.0.co;2

Gillingham, M. P., and Klein, D. R. (1992). Late-winter activity patterns of moose (*Alces alces* gigas) in western Alaska. *Can. J. Zool.* 70, 293–299. doi: 10.1139/z92-044

Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and recommendations. *Compar. Biochem. Physiol. Part A* 158, 287–304. doi: 10.1016/j.cbpa.2010.09.011

Heldmaier, G., Ortmann, S., and Elvert, R. (2004). Natural hypometabolism during hibernation and daily torpor in mammals. *Respir. Physiol. Neurobiol.* 141, 317–329. doi: 10.1016/j.resp.2004.03.014

Herberg, A. M., St-Louis, V., Carstensen, M., Fieberg, J., Thompson, D. P., Crouse, J. A., et al. (2018). Calibration of a rumen bolus to measure continuous internal body temperature in moose. *Wildl. Soc. Bull.* 42, 328–337. doi: 10.1002/wsb.894

Klassen, N. A., and Rea, R. V. (2008). What do we know about nocturnal activity of moose? *Alces* 44, 101–109.

Kochan, T. I. (2007). Seasonal adaptations of moose (*Alces alces*) metabolism. *Alces* 43, 123–128.

Kreeger, T. J., and Arnemo, J. M. (2018). *Handbook of Wildlife Chemical Immobilization*, 5th Edn. Published by authors.

Langvatn, R. (1992). Basissignal for hjerteaktivitet hos elg ved ulike typer fysisk aktivitet. *NINA Oppdragsmelding* 178, 1–15.

Lenarz, M. S., Nelson, M. E., Schrage, M. W., and Edwards, A. J. (2009). Temperature mediated moose survival in northeastern Minnesota. *J. Wildl. Manag.* 73, 503–510. doi: 10.2193/2008-265

Lian, M., Evans, A. L., Bertelsen, M. F., Fahlman, A., Haga, H. A., Ericsson, G., et al. (2014). Improvement of arterial oxygenation in free-ranging moose (*Alces alces*) immobilized with etorphine-acepromazine-xylazine. *Acta Vet. Scand.* 56:51. doi: 10.1186/s13028-014-0051-5

Lovegrove, B. G. (2005). Seasonal thermoregulatory responses in mammals. *J. Comp. Physiol. B* 175, 231–247. doi: 10.1007/s00360-005-0477-1

Lowe, S. J., Patterson, B. R., and Schaefer, J. A. (2010). Lack of behavioral responses of moose (*Alces alces*) to high ambient temperatures near the southern periphery of their range. *Can. J. Zool.* 88, 1032–1041. doi: 10.1139/Z10-071

Malmsten, J., Söderquist, L., Thulin, C.-G., Widén, D. G., Yon, L., Hutchings, M. R., et al. (2014). Reproductive characteristics in female Swedish moose (*Alces alces*), with emphasis on puberty, timing of oestrus, and mating. *Acta Vet. Scand.* 56:23. doi: 10.1186/1751-0147-56-23

Mauget, C., Mauget, R., and Sempéré, A. (1997). Metabolic rate in female European roe deer (*Capreolus capreolus*): incidence of reproduction. *Can. J. Zool.* 75, 731–739. doi: 10.1139/z97-094

McCann, N., Moen, R., and Harris, T. (2013). Warm-season heat stress in moose (*Alces alces*). *Can. J. Zool.* 91, 893–898. doi: 10.1139/cjz-2013-0175

Mesteig, K., Tyler, N., and Blix, A. (2000). Seasonal changes in heart rate and food intake in reindeer (*Rangifer tarandus* tarandus). *Acta Physiol.* 170, 145–151. doi: 10.1046/j.1365-201x.2000.00767.x

Minicucci, L., Carstensen, M., Crouse, J., Arnemo, J. M., and Evans, A. (2018). A technique for deployment of rumen bolus transmitters in free-ranging moose (*Alces alces*). *J. Zoo Wildl. Med.* 49, 227–230. doi: 10.1638/2017-0027R.1

Monteith, K. L., Klaver, R. W., Hersey, K. R., Holland, A. A., Thomas, T. P., and Kauffman, M. J. (2015). Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia* 178, 1137–1148. doi: 10.1007/s00442-015-3296-4

Ostrowski, S., Mésochina, P., and Williams, J. B. (2006). Physiological adjustments of sand gazelles (*Gazella subgutturosa*) to a boom-or-bust economy: standard fasting metabolic rate, total evaporative water loss, and changes in the sizes of organs during food and water restriction. *Physiol. Biochem. Zool.* 79, 810–819. doi: 10.1086/504614

Pagon, N., Grignolio, S., Pipia, A., Bongi, P., Bertolucci, C., and Apollonio, M. (2013). Seasonal variation of activity patterns in roe deer in a temperate forested area. *Chronobiol. Int.* 30, 772–785. doi: 10.3109/07420528.2013.765887

Pinheiro, J., and Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS*. Berlin: Springer Science & Business Media.

Regelin, W. L., Schwartz, C. C., and Franzmann, A. W. (1985). Seasonal energy metabolism of adult moose. *J. Wildl. Manag.* 42, 388–393. doi: 10.2307/3801539

Renecker, L. A., and Hudson, R. J. (1985). Telemetered heart rate as an index of energy expenditure in moose (*Alces alces*). *Compar. Biochem. Physiol. Part A* 82, 161–165. doi: 10.1016/0300-9629(85)90721-2

Renecker, L. A., and Hudson, R. J. (1986). Seasonal energy expenditures and thermoregulatory responses of moose. *Can. J. Zool.* 64, 322–327. doi: 10.1139/z86-052

Renecker, L. A., and Hudson, R. J. (1989). Ecological metabolism of moose in aspen-dominated boreal forests, central Alberta. *Can. J. Zool.* 67, 1923–1928. doi: 10.1139/z89-275

Riek, A., Stölzl, A., Bernedo, R. M., Ruf, T., Arnold, W., Hambly, C., et al. (2019). Energy expenditure and body temperature variations in llamas living in the High Andes of Peru. *Sci. Rep.* 9:4037. doi: 10.1038/s41598-019-40576-9

Roshchevsky, M., Chermnykh, N., and Azarov, J. (1999). Cardiac reactions in the behaviour of young moose. *Alces* 35, 143–151.

Ruf, T. (1999). The Lomb-Scargle periodogram in biological rhythm research: analysis of incomplete and unequally spaced time-series. *Biol. Rhythm Res.* 30, 178–201. doi: 10.1076/brhm.30.2.178.1422

Ruf, T., and Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biol. Rev.* 90, 891–926. doi: 10.1111/brv.12137

Rutz, C., and Hays, G. C. (2009). New frontiers in biologging science. *Biol. Lett.* 5, 289–292. doi: 10.1098/rsbl.2009.0089

Scheibe, K., Berger, A., Langbein, J., Streich, W., and Eichhorn, K. (1999). Comparative analysis of ultradian and circadian behavioural rhythms for diagnosis of biorhythmic state of animals. *Biol. Rhythm Res.* 30, 216–233. doi: 10.1076/brhm.30.2.216.1420

Schmidt, N. M., Grøndahl, C., Evans, A. L., Desforges, J.-P., Blake, J., Hansen, L. H., et al. (2020). On the interplay between hypothermia and reproduction in a high arctic ungulate. *Sci. Rep.* 10, 1–7. doi: 10.1038/s41598-020-58298-8

Schwartz, C. C., Regelin, W. L., and Franzmann, A. (1984). Seasonal dynamics of food intake in moose. *Alces* 20, 223–244.

Signer, C., Ruf, T., and Arnold, W. (2011). Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. *Funct. Ecol.* 25, 537–547. doi: 10.1111/j.1365-2435.2010.01806.x

Simpson, G. L. (2018). *gratia: ggplot-based Graphics and Other Useful Functions for GAMs Fitted Using mgcv. R package version 0.1–4.*

Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., and Ericsson, G. (2012). From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecol. Appl.* 22, 2007–2020. doi: 10.1890/12-0245.1

SMHI (2019). *Swedish Weather Data [Online]*. Norrköping: SMHI.

Solberg, E. J., Heim, M., Arnemo, J. M., Sæther, B.-E., and Os, Ø (2003). Does rectal palpation of pregnant moose cows affect pre-and neo-natal mortality of their calves? *Alces* 39, 65–77.

StarOddi (2017). *DST centi-HRT Heart Rate and Temperature Logger [Online]*. Reykjavík: StarOddi.

Theil, P. K., Coutant, A. E., and Olesen, C. R. (2004). Seasonal changes and activity-dependent variation in heart rate of roe deer. *J. Mammal.* 85, 245–253. doi: 10.1644/1545-1542(2004)085<0245:SCAAVI<2.0.CO;2

Thiel, A., Evans, A. L., Fuchs, B., Arnemo, J. M., Aronsson, M., and Persson, J. (2019). Effects of reproduction and environmental factors on body temperature and activity patterns of wolverines. *Front. Zool.* 16:21. doi: 10.1186/s12983-019-0319-8

Thompson, D. P., Barboza, P. S., Crouse, J. A., Mcdonough, T. J., Badajos, O. H., and Herberg, A. M. (2019). Body temperature patterns vary with day, season, and body condition of moose (*Alces alces*). *J. Mammal.* 100, 1466–1478. doi: 10.1093/jmammal/gyz119

Trethowan, P. D., Hart, T., Loveridge, A. J., Haw, A., Fuller, A., and Macdonald, D. W. (2016). Improved homeothermy and hypothermia in African lions during gestation. *Biol. Lett.* 12:20160645. doi: 10.1098/rsbl.2016.0645

Turbill, C., Ruf, T., Mang, T., and Arnold, W. (2011). Regulation of heart rate and rumen temperature in red deer: effects of season and food intake. *J. Exp. Biol.* 214, 963–970. doi: 10.1242/jeb.052282

Van Ballenberghe, V., and Miquelle, D. G. (1990). Activity of Moose during Spring and Summer in Interior Alaska. *J. Wildl. Manag.* 54, 391–396. doi: 10.2307/3809645

van Beest, F. M., and Milner, J. M. (2013). Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. *PLoS One* 8:e65972. doi: 10.1371/journal.pone.0065972

van Beest, F. M., Van Moorter, B., and Milner, J. M. (2012). Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim. Behav.* 84, 723–735. doi: 10.1016/j.anbehav.2012.06.032

Van Oort, B. E., Tyler, N. J., Gerkema, M. P., Folkow, L., Blix, A. S., and Stokkan, K.-A. (2005). Circadian organization in reindeer. *Nature* 438, 1095–1096. doi: 10.1038/4381095a

van Oort, B. E., Tyler, N. J., Gerkema, M. P., Folkow, L., and Stokkan, K.-A. (2007). Where clocks are redundant: weak circadian mechanisms in reindeer living under polar photic conditions. *Naturwissenschaften* 94, 183–194. doi: 10.1007/s00114-006-0174-2

VectronicAerospace (2017). *Mortality Implant (MIT) [Online]*. Berlin: VectronicAerospace.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Berlin: Springer.

Wood, S. (2017). *Mixed GAM computation vehicle with automatic smoothness estimation. R package versions 1.8–22.*

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 27 May 2020
doi: 10.3389/fevo.2020.00147

Deciphering Anthropogenic Effects on the Genetic Background of the Red Deer in the Iberian Peninsula

João Queirós[1]*, *Christian Gortázar*[2] *and Paulo Célio Alves*[3,4]

[1] Centro de Investigacão em Biodiversidade e Recursos Genéticos (CIBIO)/InBio Laboratório Associado, Universidade do Porto, Campus de Vairão, Porto, Portugal, [2] SaBio Research Group, Instituto de Investigación en Recursos Cinegéticos (CSIC-UCLM-JCCM), Ciudad Real, Spain, [3] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, Porto, Portugal, [4] Wildlife Biology Program, University of Montana, Missoula, MT, United States

Edited by:
Jean-Michel Gaillard,
Université Claude Bernard Lyon 1,
France

Reviewed by:
Sébastien Devillard,
Université Claude Bernard Lyon 1,
France
Fabio Pinheiro,
University of Campinas, Brazil

***Correspondence:**
João Queirós
joao.queiros@cibio.up.pt

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 05 December 2019
Accepted: 29 April 2020
Published: 27 May 2020

Citation:
Queirós J, Gortázar C and Alves PC (2020) Deciphering Anthropogenic Effects on the Genetic Background of the Red Deer in the Iberian Peninsula. Front. Ecol. Evol. 8:147. doi: 10.3389/fevo.2020.00147

Anthropogenic hybridization is one of the greatest threats to global biodiversity. It incites human-mediated gene flow between non-native/exotic and native taxa, which can have irreversible effects on native species or locally adapted populations, eventually leading to extinction. The red deer, *Cervus elaphus*, is a game species that, due to its extraordinary economic value, has been introduced in several regions throughout Europe. However, the consequences of those introductions on native populations, namely on their genetic background, have been poorly addressed. This study is focused on the Iberian Peninsula and aims to: (i) assess the extent of anthropogenic hybridization/introgression of introduced red deer into the native Iberian populations; (ii) evaluate the impact of red deer management regimes on the observed hybridization/introgression patterns; and (iii) assess how hybridization/introgression influence the current genetic diversity of native Iberian populations. A set of 11 microsatellites and a 329 bases pair fragment of the mitochondrial D-loop gene were used to estimate nuclear admixture and mitochondrial introgression in 1,132 individuals sampled across 46 red deer populations throughout Iberia. A Bayesian approach implemented in the STRUCTURE program was employed to investigate the proportion of admixture between native populations and non-native red deer. Results showed that 17% of individuals presented signs of non-native recent ancestors and 10.1% had non-native mitochondrial haplotypes, reaching an overall hybridization/introgression rate of 23%. Non-native or hybrid individuals were found throughout 40 Iberian red deer populations, and the percentages per population varied between 3.3 and 75.0%, independently of the management regime. Mitochondrial introgression was observed across 15 Iberian red deer populations, being more frequent in free-ranging individuals (16.2%) than in fenced populations (9.2%) but was completely absent from public-owned populations. Nuclear genetic diversity correlated positively with the proportion of hybrid individuals in public-owned populations. The genetic footprint of historical and current human-mediated translocations of non-native red deer into the Iberian Peninsula is evidenced in this study, highlighting the need to implement effective measures to avoid such practices both in Portugal and Spain, in order to preserve the endogenous genetic patrimony of the Iberian red deer populations.

Keywords: hybridization, introgression, human-mediated gene flow, *Cervus elaphus*, hunting management regimes, conservation genetics

INTRODUCTION

Anthropogenic factors are important drivers of the evolutionary history of species and populations (Miraldo et al., 2016; Hendry et al., 2017). Humans have been influencing the natural distribution and population dynamics of organisms (i.e., by hunting) for a long time. Nevertheless, the current rate and pace that such human-mediated actions have on the genetic background of many species is huge, threatening wildlife populations worldwide (Macdougall et al., 2013; Mimura et al., 2017). Global changes in land use, commercial trade and climate warming, promoted mainly by the rising trend of the size of the human population, are posing new challenges to the conservation of natural resources, especially concerning preserving the intraspecific genetic diversity of species and populations that have evolved and adapted to local ecosystems over millennia (Taylor-Brown et al., 2019). The widespread and traditional practice (intentional or accidental) of translocating foreign (non-native/exotic) organisms and introducing them to areas where they have never naturally occurred, is amongst the human-mediated factors that directly contribute to increasing the crossbreeding of genetically differentiated taxa (i.e., distinct species, subspecies, or evolutionary units), fostering the disruption of local gene-adapted complexes and increasing the risk of extinction (Muhlfeld et al., 2009; Senn et al., 2010; Huisman et al., 2016). Although a wide range of organisms is facing anthropogenic hybridization (human-mediated gene flow), animals and plants with high economic or cultural values are more vulnerable to this phenomenon (Allendorf et al., 2001).

The red deer, *Cervus elaphus*, is one of the most widespread wild ungulates across Europe and a species with a great economic, social, and ecosystem value (Milner et al., 2006; Apollonio et al., 2010). Several subspecies have been recognized using phenotypic or biogeographical traits, though there is still an ongoing debate about this subspecific taxonomy since it is not congruent with the evolutionary units that have been described by genetic studies (Zachos and Hartl, 2011; Meiri et al., 2018). Due to its importance and wide distribution, red deer have been largely studied over their geographical range, with numerous studies focused on understanding their evolutionary history (Ludt et al., 2004; Skog et al., 2009; Meiri et al., 2013; Stanton et al., 2016; Queirós et al., 2019). Despite being intensively exploited as a natural resource since the Pleistocene (Sommer et al., 2008), studies based on mitochondrial DNA have shown a natural wide-scale phylogeographic pattern of red deer across Europe (Niedziałkowska et al., 2011; Zachos and Hartl, 2011; Meiri et al., 2013; Queirós et al., 2019). Three main mitochondrial D-loop lineages have been described, with a clear spatial pattern: A Western European lineage distributed in Western Europe; an Eastern European lineage distributed in the Balkans (Eastern Europe); and a Mediterranean lineage distributed in Africa and the islands of Sardinia and Corsica. Furthermore, in the particular case of the Western European linage, distinct evolutionary sub-linages from the rest of Western Europe have been described for the Iberian peninsula, highlighting the singularity of Iberian red deer populations (Carranza et al., 2016; Queirós et al., 2019). Besides mitochondrial differentiation, studies have shown a clear nuclear differentiation between the Iberian and the remaining European populations (Carranza et al., 2016; Frantz et al., 2017; Queirós et al., 2019), with divergent evolution (followed by geographic isolation) estimated around the Last Glacial Maximum, 19,000 to 27,000 years before present (Queirós et al., 2019). Since the last century, however, human-mediated actions, namely habitat destruction, change in land use, intensive management and translocations have favored the genetic diversity loss and promote the hybridization of red deer with other non-native species, subspecies or evolutionary units all over its distribution range, putting the preservation of the natural endogenous genetic resources of each region at risk (Hartl et al., 2003; Nussey et al., 2006).

Anthropogenic hybridization, defined here as human-mediated gene flow between individuals from different species, subspecies or evolutionary units, in red deer has proved to be relatively frequent throughout Europe (review in Iacolina et al., 2019). However, there is still a knowledge gap concerning its extent in many European countries, including the Iberian Peninsula (Portugal and Spain), where introductions of red deer from Central, Northern and Eastern Europe have been reported since, at least, the middle of the twentieth century (Carranza, 2003; Vingada et al., 2010). Anthropogenic hybridization in Iberia is mainly focused on improving the trophy, through crossbreeding with higher performance individuals from Central, Northern, and Eastern Europe, traditionally classified as different subspecies (*C. e. elaphus*). Commercial trophy hunting increased during the 1970–80s and relied mostly on the intensive management of red deer in high-fenced enclosures, where individuals are food-supplemented seasonally or even all the year round (Azorit et al., 2002; Queiros et al., 2014). The majority of these fenced populations are located in central-southern Iberia, while free-ranging populations are more common in the north. In addition, there are fenced and unfenced public-owned red deer populations, managed from a conservation-oriented perspective.

In this study we aim to unveil the impact of human-mediated actions on the genetic pattern of red deer in the Iberian Peninsula, namely by: (i) quantifying the extent of nuclear admixture and mitochondrial introgression of non-native red deer in the native Iberian populations; (ii) evaluating the impact of management regimes on the anthropogenic hybridization/introgression patterns; and (iii) understanding how anthropogenic hybridization/introgression influence the genetic diversity of the Iberian populations.

MATERIALS AND METHODS

Study Populations and Sampling

Forty-six sites were sampled throughout the Iberian Peninsula, which comprised red deer populations subjected to distinct management regimes: 23 fenced populations; 17 free-ranging populations; and 6 public-owned populations (**Figure 1**). In addition, nine free-ranging red deer populations from the Center

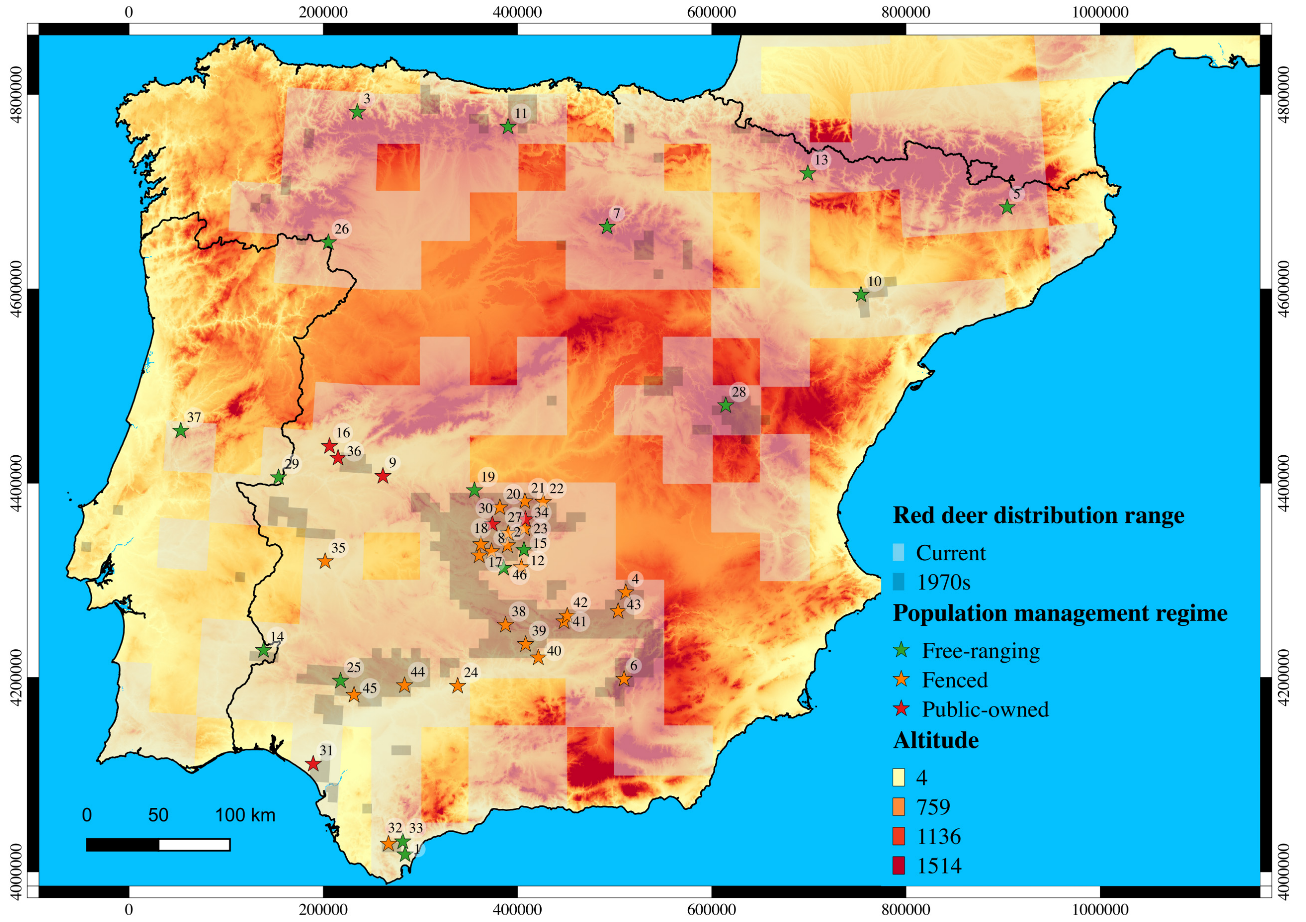

FIGURE 1 | Red deer populations sampled throughout the Iberian Peninsula under the hunting management regime. Current and past (1970s) distribution range of species is depicted in light and dark gray, respectively (Ministerio de Agricultura, 1968; Mitchell-Jones et al., 1999; Salazar, 2009). Population codes are represented within circles.

(France, *n* = 27; Switzerland, *n* = 31; and Italy, *n* = 10), the West (England, *n* = 17), the North (Norway, *n* = 5 and Sweden, *n* = 6), and the East (Czech Republic, *n* = 9; Hungary, *n* = 7; and Romania, *n* = 35) of Europe were sampled to investigate the proportion of admixture between native Iberian populations and non-native Central, Northern and Eastern European populations. The samples consisted of a portion of the spleen taken from each individual. In total, 1,281 samples were collected, 1,132 in the Iberian Peninsula and 149 across Europe (see details in **Supplementary Table S1**).

DNA Extraction, Microsatellite Amplification and Analysis

Genomic DNA was extracted using the EasySpin Genomic DNA Tissue Minipreps Kit according to the manufacturer's instructions. Individual multilocus genotypes were determined using a set of 11 microsatellite markers (Ceh31, Ceh34, Ceh38, Ceh43, Ceh44, Ceh45, Ceh49, Ceh53, Ceh73, Ceh77, and Ceh79) selected from the 35 microsatellites specifically developed for red deer (Queirós et al., 2015). These markers have shown a high polymorphism content and genotype accuracy (i.e., absence of null alleles and scoring errors and reduced allelic dropout) in previous studies (Queirós et al., 2015, 2019). They were amplified in a single multiplex reaction following the conditions described by Queirós et al. (2015). Multiplex PCR products were run on an ABI3100xl genetic analyzer together with the 400 LIS^{TM} size standard. Fragment analysis was conducted using the software GENEMAPPER 4.0 (Applied Biosystems) and checked manually by two researchers independently. The genotype dataset can be consulted on **Supplementary Material (Raw Datasets)**. Deviations from the Hardy–Weinberg equilibrium and linkage equilibrium were tested for each red deer population using heterozygote excess/deficit tests and considering the log likelihood ratio statistic implemented in GENEPOP 4.0.10 (Raymond and Rousset, 1995). Significance levels estimated by Markov Chain Analysis (10^4 dememorization steps, 10^3 batches, and 10^4 iterations per batch) were adjusted using Bonferroni's sequential method for multiple comparisons (Rice, 1989). Moreover, in the case of the Iberian populations, these tests were also conducted including only the native individuals (*n* = 872, see section "Results"). Hardy–Weinberg equilibrium within each population was observed for the majority of loci analyzed, with some exceptions (**Supplementary Table S2**). However, none of these exceptions shown a deviation pattern across loci and populations. Furthermore, some pairwise combinations of markers showed to be in linkage disequilibrium in eight Iberian populations when all the individuals were considered. However, all markers were in linkage equilibrium in the Iberian populations when the non-native/hybrid individuals were removed from the analyses.

Mitochondrial D-Loop Amplification

A fragment of mitochondrial D-loop comprised of 329 base pair was amplified using the primer pair LD5 and HD6, and following the PCR conditions reported by Nagata et al. (1998). Successful amplifications were purified using the enzymes exonuclease I and shrimp alkaline phosphatase, and then sequenced with BigDye chemistry (Applied Biosystems), using the HD6 primer and following the BigDye Terminator v3.1 cycle sequencing protocol (Applied Biosystems). Electropherograms were checked and aligned using SEQSCAPE 2.5 (Applied Biosystems).

Admixture of Native Iberian Populations With Non-native Red Deer

A Bayesian clustering analysis implemented in the STRUCTURE 2.3.3 program (Pritchard et al., 2000; Falush et al., 2003) was used to assign individuals to Iberian (native) and European (non-native) populations ($K = 2$) and to identify hybrids between native and non-native red deer. The analyses were conducted using the admixture model with correlated allele frequencies and no prior information for individual identification. STRUCTURE was run with five repetitions of 50^6 MCMC iterations following a burn-in period of 50^5 steps. The average proportion of membership of native and non-native red deer populations was inferred for each cluster, and the individual membership proportion (qi-values) of each sample to those two clusters.

Simulations were performed with both parental and hybrid genotypes in HYBRIDLAB 1.0 (Nielsen et al., 2006) to evaluate the performance of the markers and models used in the admixture analyses to distinguish among parental (native and non-native red deer) and hybrid classes (F1, F2, backcrosses with native red deer), and establish the range of qi-values expected for all possible admixed generations. Based on a previous study (Queirós et al., 2019) in which 35 microsatellite markers were used to characterize the genetic profile of individuals, we selected 100 parental native red deer and the 100 parental non-native red deer, individuals that showed qi-values above 99% on STRUCTRUE analysis, to generate 50 genotypes of each parental and hybrid class: native red deer, non-native red deer, F1, F2 and respective first and second generation backcross with native red deer (for both F1 and F2). Ten independent replicates were simulated for each hybrid class. The simulated genotypes can be consulted on **Supplementary Material (Simulated Datasets)**. Simulated genotypes were then used in STRUCTURE in order to assess the efficiency of the admixture analyses in estimating the membership proportion of each class in the simulated data set and to establish the cut-off threshold between Iberian and non-native/hybrid individuals. Non-parametric Mann–Whitney tests were employed to compare the qi-values obtained for each parental/hybrid class using SPSS (IBM Corp, New York). In addition, NEWHYBRIDS 1.1 (Anderson and Thompson, 2002) was used to achieve a more detailed analysis of admixture proportions and hybrids ancestry, by inferring the posterior probability assignment of each individual identified as hybrid in STRUCTURE (see section "Results") to eight genotype frequency classes: native, non-native, F1, F2, first and second backcross with native. Individuals sampled outside the Iberian Peninsula (non-native) were used as priors in the program.

The fragment of mitochondrial D-loop comprised of 329 bases pairs was used to infer the past maternal introgresion of non-native red deer into the Iberian populations. Native and non-native mitochondrial haplotypes were defined based on natural phylogeographic patterns previously established for red deer in Europe, and particularly in the Iberian Peninsula (Carranza et al., 2016; Queirós et al., 2019). GenBank accession numbers KT202236–KT202280 for Carranza et al. (2016) and MK092836–MK092885 for Queirós et al. (2019). Details about the haplotype classification can be consulted in **Supplementary Table S1** in Queirós et al. (2019). Native, non-native/hybrids and introgressed individuals were classified according to the membership proportion estimated from admixture analysis and mitochondrial haplotypes. The proportion of nuclear hybrids, mitochondrial introgressed individuals and both (non-native/hybrid/introgressed individuals) were quantified by sampling points and compared among management regimes using non-parametric Kruskal–Wallis and Mann–Whitney tests in SPSS (IBM Corp, New York). Furthermore, Spearman correlation tests were also used to address the impacts of anthropogenic hybridization/introgression on the current patterns of population's genetic diversity, which was evaluated through nuclear allelic richness and observed heterozygosity. These parameters were calculated for each population using FSTAT 2.9.3.2 (Goudet, 2001) and GENEALEX 6.5 (Peakall and Smouse, 2012), respectively. Only populations with more than ten sampled individuals were considered for this analysis.

RESULTS

HYBRIDLAB Simulations

Parental and hybrid genotypes simulated in the HYBRIDLAB program showed significantly different values of membership proportion (qi-values) between native and non-native red deer ($Z = -27.37$, $p < 0.001$) and between native and hybrid classes (F1: $Z = -27.26$, $p < 0.001$; F2: $Z = -27.07$, $p < 0.001$; BC1-F1: $Z = -22.98$, $p < 0.001$; BC1-F2: $Z = -23.66$, $p < 0.001$; BC2-F1: $Z = -15.32$, $p < 0.001$; BC2-F2: $Z = -15.10$, $p < 0.001$). Significant differences on qi-values were also observed between F1/F2 and BC1/BC2 classes, but not between F1 and F2 within each hybrid class (**Figure 2**). The genotypes simulated for parental native red deer showed an average qi-value of 92.14% (95% confidence interval ranged between 91.7 and 92.5%) for the Iberian cluster, while parental non-native red deer ranged between 5.98 and 6.72%, with an average value of 6,33%. Thus,

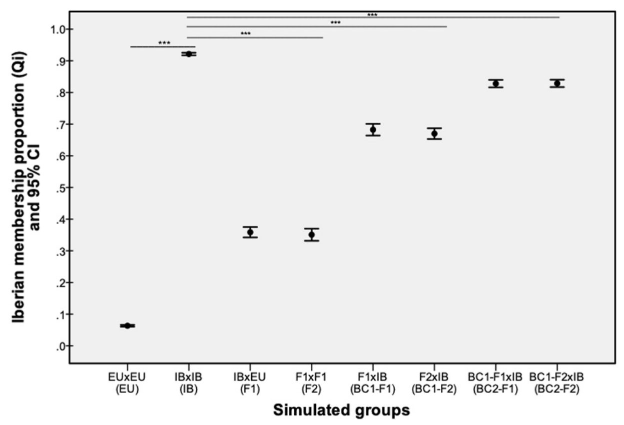

FIGURE 2 | The proportion of Iberian membership (qi) values estimated using the STRUCTURE program for the admixed generations of parental (native – IB; non-native – EU) and hybrid (F1, F2, BC1, and BC2) genotypes simulated by the HYBRIDLAB program. Bars with asterisks represent the statistically significance differences observed between simulated native red deer and non-native/hybrid classes (p-value < 0.001).

individuals with qi-values from the Iberian cluster above 91,7% were classified as native red deer, below 6.72% as non-native deer, and between 91.7 and 6.72% as hybrids.

Native or Non-native Red Deer

Bayesian admixture analyses performed with STRUCTURE, and allowing two clusters, suggested the presence of two differentiated groups that splits the Iberian from the other European red deer populations (**Figure 3**). Given the threshold value of 91.7, previously established from the simulated nuclear DNA data, 940 individuals were identified as native Iberian red deer, representing 83% of all the samples analyzed. A total of 21 individuals were considered as non-native (1.9%) and 171 as hybrids (15.1%). No hybrids were detected in the populations from Central, Northern and Eastern Europe (average qi-values of 1.7 and 95% confidence interval between 1.6 and 1.8%). From the 192 individuals identified as non-native or hybrid (17%), 79 were sampled from free-ranging populations (19.8%, $n = 399$), 94 from fenced populations (16.6%, $n = 567$) and 19 from public-owned populations (11.4%, $n = 166$) (**Figure 4**). The non-native or hybrid individuals were found in 40 out of the 46 Iberian populations studied, with percentages varying between 3.3 and 75% per population (**Supplementary Figure S1**). Pure non-native individuals were observed in six free-ranging/fenced populations, representing between 4.2 and 39.1% of all the individuals sampled in each population. The admixture proportions and hybrids ancestry estimated by NEWHYBRIDS indicate that the great majority of the 171 hybrids belong to second-generation backcross of F2 with native individuals (BC2-F2), although the posterior probability assignment for each individual was either for non-native or BC2-F2 classes (**Figure 5**).

Mitochondrial introgression with non-native haplotypes was found in 114 (10.1%) out of the 1,107 Iberian red deer individuals for which successful amplifications were obtained (no data for 25 individuals). Most of these non-native haplotypes (110 individuals) belong to the Western European lineage (Hap011, Hap043, Hap048, Hap050, Hap070, Hap073, and Hap078 as in Queirós et al. (2019), haplotypes described in the British Isles, France and Norway. In addition, two haplotypes from Eastern (Hap031 and Hap038) and one from Mediterranean (Hap028 in two individuals) European lineages were also detected in four individuals sampled in the Iberian Peninsula. Individuals harboring non-native haplotypes were found in 15 populations, with percentages per population varying between 4.0% and 85.2% (**Supplementary Figure S2**). Considering both mitochondrial and nuclear DNA information, 260 (23.0%) individuals were identified as non-native Iberian red deer, with percentages per population varying between 3.3 and 85.2%. These non-native Iberian red deer individuals were located in 42 populations that are widespread throughout the Iberian Peninsula (**Figure 6**).

When assessing the levels of anthropogenic hybridization/introgression under the management regime, significant differences between free-ranging, fenced and protected populations were observed in the proportions of introgressed ($\text{Chi}^2 = 34.17$, df = 2, $p < 0.05$) and non-native/hybrid/introgressed individuals ($\text{Chi}^2 = 17.74$, df = 2, $p < 0.05$). The highest proportion of introgressed individuals was observed for free-ranging populations (16.2%), followed by fenced populations (9.2%). Non-native mitochondrial haplotypes were not observed in public-owned populations (0.0%). Two-pairwise comparisons between management regimes showed statistically significant differences between free-ranging and fenced populations ($Z = -3.29$, $p < 0.05$), free-ranging and public-owned populations ($Z = -5.45$, $p < 0.05$),

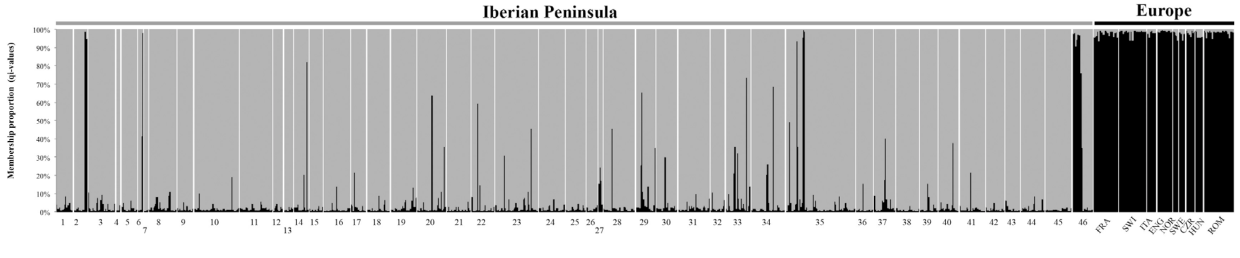

FIGURE 3 | Bayesian clustering analyses conducted in STRUCTURE for $K = 2$. Individual membership proportion to each cluster is indicated in gray for the Iberian populations (codes as in **Figure 1**) and black for the European populations (FRA, France; SWI, Switzerland; ITA, Italy; ENG, England; NOR, Norway; SWE, Sweden; CZR, Czech Republic; HUN, Hungary; ROM, Romania).

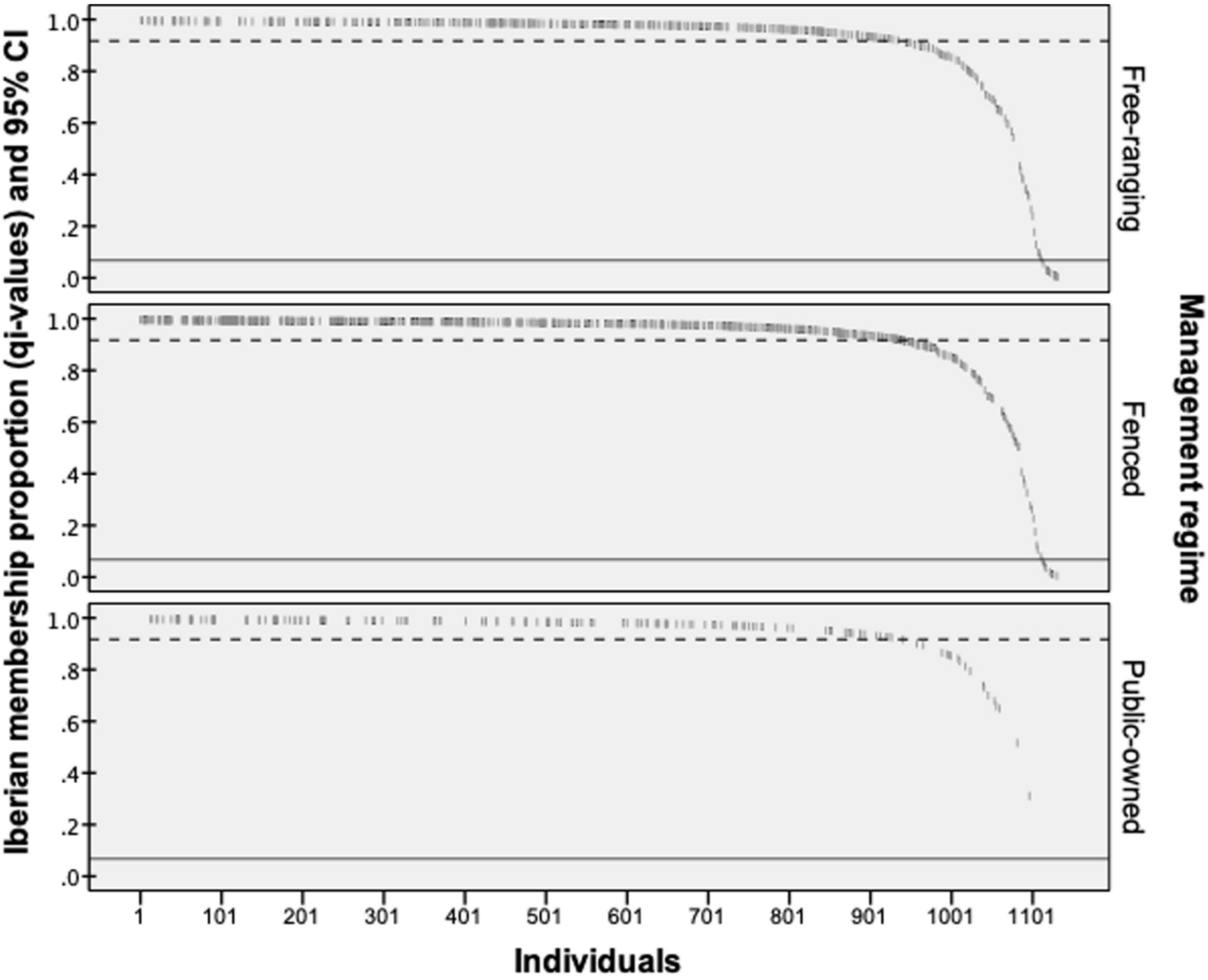

FIGURE 4 | The proportion of Iberian membership (qi-values) estimated in the STRUCTURE program for the 1,132 red deer sampled in the Iberian Peninsula. Dashed line indicates the threshold value (qi = 91,7%) used to consider native individuals (above line), while continuous line establishes the limit (6.72%) between non-native (below) and hybrid (above) classes.

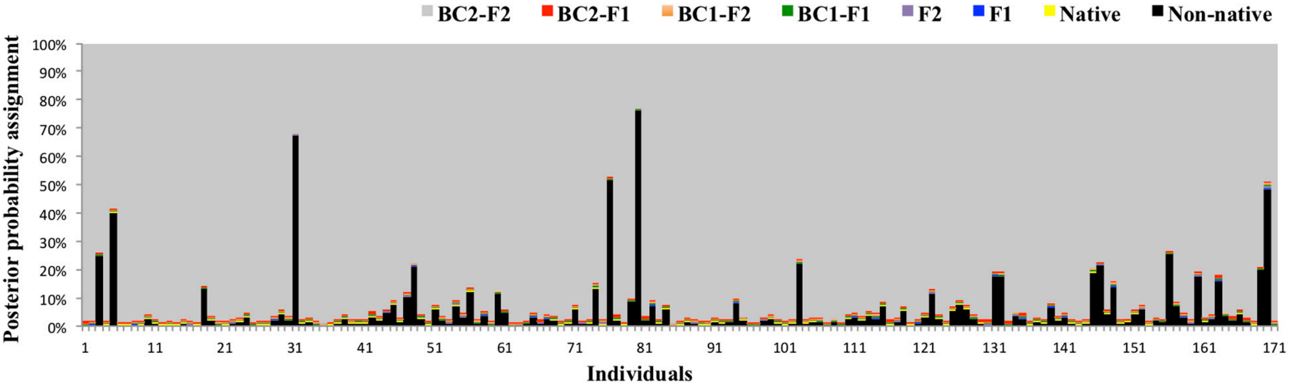

FIGURE 5 | Posterior probability assignment values obtained in NEWHYBRIDS for the 171 individuals identified as hybrids in STRUCTURE. Genotype classes are represented by different colors: native (yellow), non-native (black), F1 (blue), F2 (purple), F1 backcross with native (BC1-F1, green), F2 backcross with native (BC1-F2, orange), BC1-F1 backcross with native (BC2-F1, red) and BC1-F2 backcross with native (BC2-F2, gray).

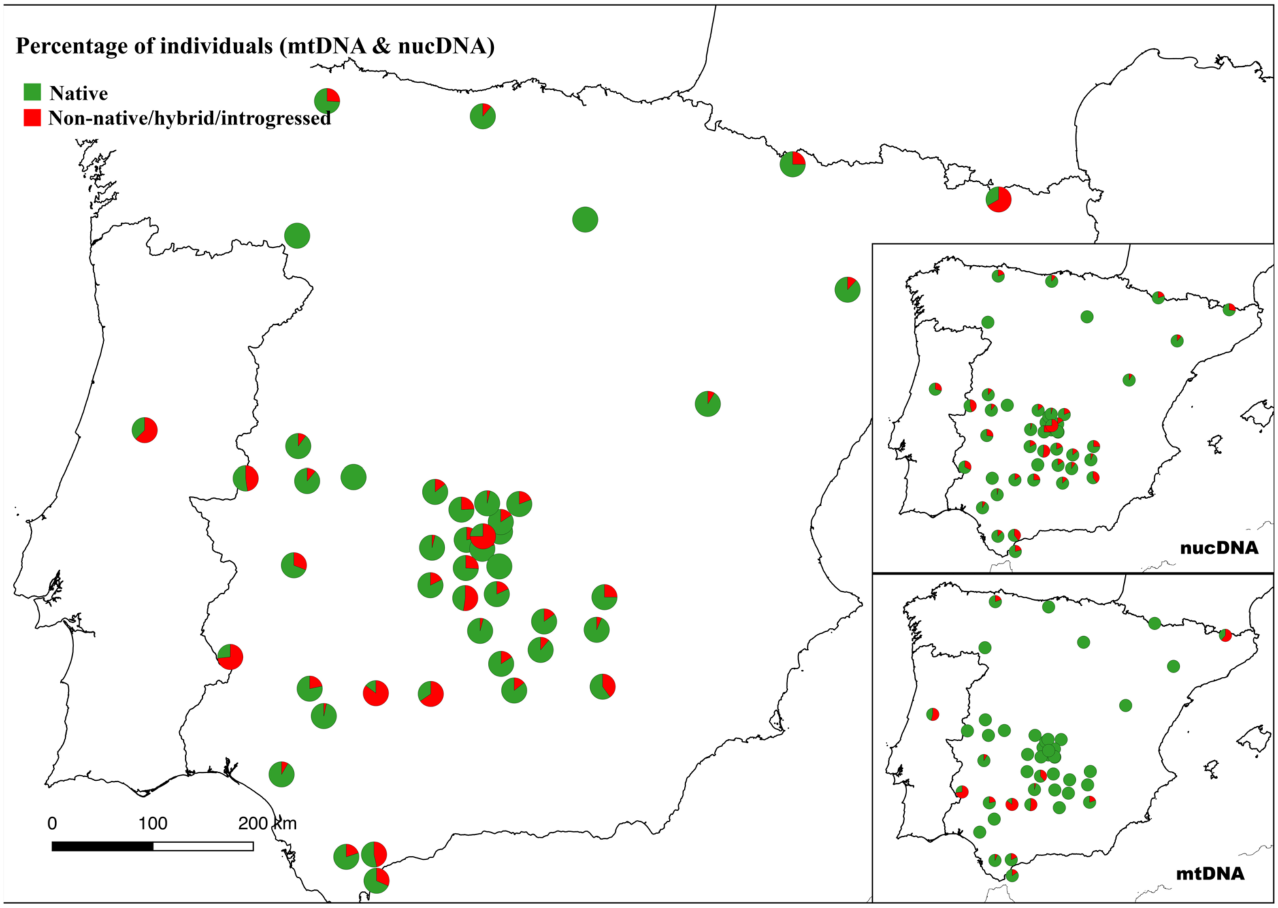

FIGURE 6 | Proportion of native and non-native red deer by population in the Iberian Peninsula. Individuals were classified according to both nuclear (nucDNA) and mitochondrial (mtDNA) DNA content (see section "Materials and Methods").

and fenced and public-owned populations ($Z = -3.99$, $p < 0.05$; **Figure 7a**). In the case of non-native/hybrid/introgressed individuals, significant differences on two-pairwise comparisons were only observed between free-ranging and public-owned populations ($Z = -4.20$, $p < 0.05$), and between fenced and public-owned populations ($Z = -3.19$, $p < 0.05$). No significant differences were observed between free-ranging and fenced populations ($Z = -1.79$, $p > 0.05$) (**Figure 7c**). Regarding nuclear DNA information alone (non-native/hybrid individuals), no significant differences between populations were observed ($Chi^2 = 5.92$, df = 2, $p > 0.05$), although a similar trend in the proportion of non-native/hybrid individuals was recorded (free-ranging 19.8%; fenced 16.6%; protected 11.4%; **Figure 7b**).

The genetic diversity of populations was evaluated through nuclear allelic richness and observed heterozygosity. The values of allelic richness ranged between 2.64 and 4.08 (**Supplementary Figure S4**), while the values of observed heterozygosity ranged between 0.487 and 0.753 (**Supplementary Figure S5**). These population parameters were then correlated, separately for each management regime, with the levels of anthropogenic hybridization/introgression observed in each population. No significant correlations were found between population's allelic richness and the proportion of non-native/hybrid individuals (free-ranging populations: Spearman's correlation = −0.07, $p = 0.778$; fenced populations: Spearman's correlation = 0.432, $p = 0.057$; public-owned populations: Spearman's correlation = 0.638, $p = 0.173$), between population's allelic richness and the proportion of introgressed individuals (free-ranging populations: Spearman's correlation = 0.19, $p = 0.473$; fenced populations: Spearman's correlation = 0.26, $p = 0.264$), and between population's allelic richness and the proportion of non-native/hybrid/introgressed individuals (free-ranging populations: Spearman's correlation = −0.09, $p = 0.745$; fenced populations: Spearman's correlation = 0.27, $p = 0.251$; **Supplementary Figure S4**). Regarding population heterozygosity, similar results were found, with the exception of a positive significant correlation observed for the proportion of non-native/hybrid individuals in public-owned populations (Spearman's correlation = 0.89, $p < 0.05$; **Supplementary Figure S5**). Thus, overall, no significant associations were found between population heterozygosity and the proportion of non-native/hybrid individuals in free-ranging (Spearman's correlation = −0.25, $p = 0.349$) and fenced populations (Spearman's correlation = 0.32, $p = 0.163$). In addition, no

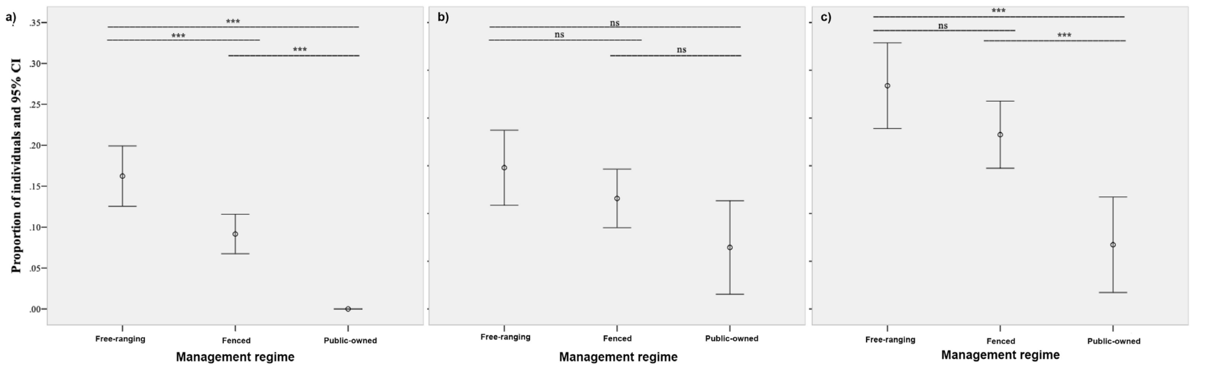

FIGURE 7 | Proportions of individuals with signs of mitochondrial introgression **(a)**, nuclear DNA admixture and non-native individuals **(b)**, and both introgressed and non-native/hybrid individuals **(c)**. The significance of two-pairwise comparisons between hunting management regimes is also shown (***significant at p-value < 0.05; ns, non-significant).

significant correlations were observed between population heterozygosity and the proportion of introgressed individuals (free-ranging populations: Spearman's correlation = 0.32, $p = 0.217$; fenced populations: Spearman's correlation = −0.11, $p = 0.660$), and between population heterozygosity and the proportion of non-native/hybrid/introgressed individuals (free-ranging populations: Spearman's correlation = −0.08, $p = 0.770$; fenced populations: Spearman's correlation = 0.08, $p = 0.748$).

DISCUSSION

We disclosed the extent of nuclear admixture and mitochondrial introgression of non-native red deer into native Iberian populations for the first time in the Iberian Peninsula. The results show the widespread presence of non-native nuclear genetic background across autochthonous Iberian red deer populations, with free-ranging populations showing the highest proportion of non-native/hybrid individuals, followed by fenced and public-owned populations, respectively. Non-native mitochondrial haplotypes are less frequent throughout Iberia, and are even absent in public-owned populations. Under the latter management regime, nuclear genetic diversity correlated positively with the proportion of hybrid individuals in the population.

Nuclear Admixture and Mitochondrial Introgression

Anthropogenic hybridization in the red deer between autochthonous European populations and introduced sika deer (*Cervus nippon*) or wapiti deer (*Cervus canadensis*) has been often documented (McDevitt et al., 2009; Senn and Pemberton, 2009; Biedrzycka et al., 2012; Smith et al., 2014, 2018). However, anthropogenic admixture between red deer is more challenging to address because of the inconsistent support between subspecies defined using morphological characteristics or biogeography and the genetic evolutionary units (Zachos and Hartl, 2011; Meiri et al., 2018). In addition, such analysis requires large genetic databases to accurately infer non-native or hybrid individuals across Europe. Recently, an attempt to detect non-native red deer was conducted in Belgium, using a large European microsatellite database, and the authors estimated 3.7% of individuals as being non-native, with the majority of the non-native individuals introduced by humans from the British Isles and Germany/Poland (Frantz et al., 2017). Here, 17% of the individuals sampled in the Iberian Peninsula showed signs of non-native recent ancestors and 10.1% had non-native mitochondrial haplotypes, reaching an overall hybridization/introgression rate of 23%. It is noted, however, that the methodology used in this study to assess nuclear admixture only distinguishes native from non-native individuals until the second-generation backcross (**Figure 2**), which in fact may be an underestimation of the real status of hybridization levels (McFarlane and Pemberton, 2019). Indeed, this overall result (nuclear and mitochondrial DNA information) was expectable given the previous reports and *in situ* observations showing that translocations of non-native red deer to the Iberian Peninsula have occurred since, at least, the middle of the twentieth century (Carranza, 2003; Vingada et al., 2010). Thus, the introgression of non-native mitochondrial DNA haplotypes together with the degree of admixture suggested by NEWHYBRIDS (**Figure 5**) is consistent with past introductions of non-native red deer followed by frequent crossbreeding with native individuals. Actually, it was during the second half of the last century that Iberian populations experienced a rapid population expansion, after a strong decline in distribution and abundance as a consequence of overexploitation during and after the Spanish Civil War. This expansion was promoted through the establishment of public game reserves and restocking operations for hunting (Gortázar et al., 2000; Acevedo and Cassinello, 2009). The British Isles and Eastern Europe have been described as the main source of these translocated individuals, which is consistent with mitochondrial data that point to haplotypes previously described in the British Isles (Western lineage) and Hungary (Eastern lineage). Detailed inferences on the origin of non-native individuals was not conducted for nuclear data due to the limited sample size of the Central, North and Eastern European populations included in this study. Despite historical introductions of non-native red deer, it is remarkable that over 75% of the individuals analyzed are not non-native neither hybrids, demonstrating quite a strong resilience of the native genetic characteristics throughout Iberia, and eventually an inappropriate adaption of non-native individuals. The preservation of the native genetic characteristics of the Iberian red deer has deserved special attention from researchers and society in general over the last two decades, owing to increasing conservation concerns and the need to protect endogenous resources. Thus, genetic assessments of translocated animals have become frequent, which together with trophy certification assessments have limited this practice over the last years (Carranza, 2003; Vingada et al., 2010). However, pure non-native individuals are still detected in Iberian populations (21 individuals, 1.9%). It should be emphasized, that besides the genetic deterioration that occurs when exotic species or non-native populations are introduced, it also represents a high risk of the introduction of pathogens into natural populations (Fèvre et al., 2006), with farm-reared ungulates being particularly prone to carry infectious diseases such as tuberculosis (Mackintosh et al., 2004). Sanitary risks together with the loss of native genetic diversity may have a great impact on the health and fitness of natural populations, and therefore, both represent major threats to the conservation of natural populations (Queirós et al., 2016; Queirós and Vicente, 2018).

Hunting Management Regimes and Hybridization/Introgression Patterns

Hunting is one of the most ancestral humans practices, and therefore, has contributed to the evolutionary process of their prey over millennia (Hendry et al., 2017; Mimura et al., 2017). However, in the case of the Iberian red deer, hunting practices have changed tremendously since the last century, from a supply of meat and commodities to a hunting-sport focused on trophies (Azorit et al., 2002). Selective hunting for bigger trophies has been accompanied by the emergence of a trophy hunting industry. This industry has promoted the intensive management of animals in high-fenced enclosures and translocations of foreign and farm-reared individuals mostly in the center and south of Iberia. Therefore, it would be expectable to find a higher proportion of non-native, hybrid and/or introgressed individuals in populations under this management regime, when compared with free-ranging or public-owned populations, which, however, was not the case. When looking for nuclear DNA content alone, there were no statistical differences among management regimes, which is consistent with the historical translocations of non-native red deer (mostly males, but also females) followed by a certain dissemination/homogenization of non-native genes throughout Iberia, owing to past re-introductions and restocking events that took place during the middle of the last century (Acevedo and Cassinello, 2009). Movements between close populations are also possible, principally during hunting events, despite artificial barriers (high fences). In contrast to nuclear data and our expectations, higher levels of mitochondrial introgression were observed in the free-ranging populations when compared with the fenced and public-owned populations. This result could be explained by past translocations of non-native red deer to these regions followed by the maintenance of certain mitochondrial haplotypes, possibly due to some adaptive advantage to environmental conditions, and/or the lower turnover of females (which maintain the matrilineal age of the mtDNA) in these populations when compared with fenced populations (Torres-Porras et al., 2014). Moreover, removal of translocated individuals is more difficult to occur under this free-ranging regime, favoring the maintenance of non-native mitochondrial haplotypes over time.

Public-owned populations under the conservation-oriented perspective showed the lowest levels of nuclear admixture and mitochondrial introgression (absence of non-native haplotypes). This result is consistent with our understanding that national parks and natural reserves promote and preserve the genetic resources of autochthonous populations or species. Most of these reserves were established during the middle of the last century (1960–1970) and have not been directly influenced by human-mediated factors related to intensive hunting. Indeed, some of these populations were used as source populations during the restocking events that took place over the middle of the last century (Acevedo and Cassinello, 2009).

Anthropogenic Hybridization Impact on Population Genetic Diversity

The impact of anthropogenic hybridization on the evolution of organisms is difficult to evaluate in natural populations because it entails a long term monitoring of several fitness-related traits (Allendorf et al., 2001). Nevertheless, it is well known that hybridization may reduce fitness, disrupt gene-adapted complexes and alter the genetic structure of populations (Muhlfeld et al., 2009; Haanes et al., 2010; Senn et al., 2010; Huisman et al., 2016). However, what are the hybridization effects on the genetic diversity of populations? In this study we have shown that only red deer populations under the public-owned regime (conservation-oriented perspective) seem to be influenced by the levels of hybrid individuals. The positive correlation observed between population heterozygosity and nuclear admixture is consistent with the absence of recent introductions to these populations, no non-native individuals were detected, indicating only backcrossing (**Figure 5**). Furthermore, during the beginning of the last century, like in other Iberian populations, public-owned populations underwent several fluctuations in distribution and abundance, namely strong population reductions, which may have had a great impact on their natural genetic background, principally in those populations that remained isolated for a long time (Queirós et al., 2019). Thus, the influence of non-native genes, possibly coming from neighboring populations, or past introductions, seems to be more marked in these theoretically unmanaged populations. Although hybridization enhances a population's genetic diversity, which is usually positive regarding a population's viability and fitness (Allendorf and Luikart, 2007; Queirós et al., 2016), it represents a serious risk to the conservation of natural endogenous resources (Rhymer and Simberloff, 1996). Furthermore, hybridization may have negative impacts on the fitness of native populations over the long term due to outbreeding depression (Asher et al., 2005; Muhlfeld et al., 2009). Therefore, the impact of non-native (or exotic in case of other deer species) genes on natural populations and the individual fitness of the Iberian red deer should be further addressed in the future, namely by the implementation of a transnational genetic monitoring program.

CONCLUSION

Most of the Iberian red deer individuals analyzed (77%) did not show signs of nuclear admixture with non-native genes nor past mitochondrial introgression. However, these phenomena are widespread across the native Iberian red deer populations sampled, with 42 out of 46 populations showing signs of non-native ancestors. Current patterns of nuclear anthropogenic admixture are not influenced by a population's management regime, while mitochondrial introgression is more frequent in free-ranging populations than in fenced populations. Non-native mitochondrial haplotypes are absent from public-owned populations, which curiously, is the only system for which populations showed a positive correlation between nuclear admixture and genetic diversity. Past and recent human-mediated translocations of non-native red deer are evidenced in this study, highlighting the need to implement transnational genetic monitoring programs to avoid new introductions of non-native red deer or exotic deer species and to deal with the historical admixture/introgression already present in the Iberian populations.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in the article/**Supplementary Material**.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because all animal sampling took place post-mortem. Samples were obtained from individuals harvested during hunting events (fenced and free-ranging populations) or control programmes (national and natural parks) between the 2005/2006 and 2015/2016 hunting seasons, independent of our research. According to EU and National legislation (the 2010/63/UE Directive and Spanish Royal Decree (53/2013) and to the University of Castilla – La Mancha guidelines, no permission or consent is required to conduct the research reported herein.

AUTHOR CONTRIBUTIONS

JQ conceived the study, performed the genetic and statistical analysis and wrote the manuscript with support of PA and CG.

FUNDING

This work was supported by AGRIGEN – NORTE-01-0145-FEDER-000007, supported by Norte Portugal Regional Operational Programme (NORTE2020), under the PORTUGAL 2020 Partnership Agreement, through the European Regional Development Fund (ERDF). The authors wish to thank all the gamekeepers and many colleagues at IREC and CIBIO/InBIO for their kind support and contribution during the sampling and laboratory procedures.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00147/full#supplementary-material

REFERENCES

Acevedo, P., and Cassinello, J. (2009). Human-induced range expansion of wild ungulates causes niche overlap between previously allopatric species: red deer and Iberian ibex in mountainous regions of southern Spain. *Ann. Zool. Fenn.* 46, 39–50.

Allendorf, F., and Luikart, G. (2007). *Conservation and the Genetics of Populations*. Oxford: Blackwell.

Allendorf, F. W., Leary, R. F., Spruell, P., and Wenburg, J. K. (2001). The problems with hybrids: setting conservation guidelines. *J. Archaeol. Sci.* 16, 613–622.

Anderson, E. C., and Thompson, E. A. (2002). A model-based method for identifying species hybrids using multilocus genetic data. *Genetics* 160, 1217–1229.

Apollonio, M., Andersen, R., and Putman, R. J. (2010). *European Ungulates and their Management in the 21st Century*. Cambridge: Cambridge University Press.

Asher, G. W., Archer, J. A., Scott, I. C., O'Neill, K. T., Ward, J., and Littlejohn, R. P. (2005). Reproductive performance of pubertal red deer (*Cervus elaphus*) hinds: effects of genetic introgression of wapiti subspecies on pregnancy rates at 18 months of age. *Anim. Reprod. Sci.* 90, 287–306. doi: 10.1016/j.anireprosci.2005.01.020

Azorit, C., Analla, M., Carrasco, R., and Muñoz-Cobo, J. (2002). Influence of age and environment on antler traits in Spanish red deer (*Cervus elaphus hispanicus*). *Z. Jagdwiss.* 48, 137–144.

Biedrzycka, A., Solarz, W., and Okarma, H. (2012). Hybridization between native and introduced species of deer in Eastern Europe. *J. Mammal.* 93, 1331–1341.

Carranza, J. (2003). Game species: extinction hidden by census numbers. *Anim. Biodivers. Conserv.* 26, 81–84.

Carranza, J., Salinas, M., de Andrés, D., and Pérez-González, J. (2016). Iberian red deer: paraphyletic nature at mtDNA but nuclear markers support its genetic identity. *Ecol. Evol.* 6, 905–922. doi: 10.1002/ece3.1836

Falush, D., Stephens, M., and Pritchard, J. K. (2003). Inference of population Structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* 164, 1567–1587.

Fèvre, E. M., Bronsvoort, B. M. D. C., Hamilton, K. A., and Cleaveland, S. (2006). Animal movements and the spread of infectious diseases. *Trends Microbiol.* 14, 125–131. doi: 10.1016/j.prevetmed.2013.01.008

Frantz, A. C., Zachos, F. E., Bertouille, S., Eloy, M. C., Colyn, M., and Flamand, M. C. (2017). Using genetic tools to estimate the prevalence of non-native red deer (*Cervus elaphus*) in a Western European population. *Ecol. Evol.* 7, 7650–7660. doi: 10.1002/ece3.3282

Gortázar, C., Herrero, J., Villafuerte, R., and Marco, J. (2000). Historical examination of the status of large mammals in Aragon, Spain. *Mammalia* 64, 411–422.

Goudet, J. (2001). *FSTAT, a Program to Estimate and Test Gene Diversities and Fixation Indices*. Available online at: http://www2.unil.ch/popgen/softwares/fstat.htm (accessed June 7, 2018).

Haanes, H., Røed, K. H., Mysterud, A., Langvatn, R., and Rosef, O. (2010). Consequences for genetic diversity and population performance of introducing continental red deer into the northern distribution range. *Conserv. Genet.* 11, 1653–1665.

Hartl, G. B., Zachos, F., and Nadlinger, K. (2003). Genetic diversity in European red deer (*Cervus elaphus* L.): anthropogenic influences on natural populations. *C. R. Biol.* 326, 37–42. doi: 10.1016/s1631-0691(03)00025-8

Hendry, A. P., Gotanda, K. M., and Svensson, E. I. (2017). Human influences on evolution, and the ecological and societal consequences. *Philos. Trans. R. Soc. B Biol. Sci.* 372:20160028. doi: 10.1098/rstb.2016.0028

Huisman, J., Kruuk, L. E. B., Ellis, P. A., Clutton-Brock, T., and Pemberton, J. M. (2016). Inbreeding depression across the lifespan in a wild mammal population. *Proc. Natl. Acad. Sci. U.S.A.* 113, 3585–3590. doi: 10.1073/pnas.1518046113

Iacolina, L., Corlatti, L., Buzan, E., Safner, T., and Šprem, N. (2019). Hybridisation in European ungulates: an overview of the current status, causes, and consequences. *Mamm. Rev.* 49, 45–59.

Ludt, C. J., Schroeder, W., Rottmann, O., and Kuehn, R. (2004). Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Mol. Phylogenet. Evol.* 31, 1064–1083.

Macdougall, A. S., McCann, K. S., Gellner, G., and Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494, 86–89. doi: 10.1038/nature11869

Mackintosh, C. G., de Lisle, G. W., Collins, D. M., and Griffin, J. F. T. (2004). Mycobacterial diseases of deer. *N. Z. Vet. J.* 52, 163–174.

McDevitt, A. D., Edwards, C. J., O'Toole, P., O'Sullivan, P., O'Reilly, C., and Carden, R. F. (2009). Genetic structure of, and hybridisation between, red (*Cervus elaphus*) and sika (*Cervus nippon*) deer in Ireland. *Mamm. Biol.* 74, 263–273.

McFarlane, S. E., and Pemberton, J. M. (2019). Detecting the true extent of introgression during anthropogenic hybridization. *Trends Ecol. Evol.* 34, 315–326. doi: 10.1016/j.tree.2018.12.013

Meiri, M., Kosintsev, P., Conroy, K., Meiri, S., Barnes, I., and Lister, A. (2018). Subspecies dynamics in space and time: a study of the red deer complex using ancient and modern DNA and morphology. *J. Biogeogr.* 45, 367–380.

Meiri, M., Lister, A. M., Higham, T. F. G., Stewart, J. R., Straus, L. G., Obermaier, H., et al. (2013). Late-glacial recolonization and phylogeography of European red deer (*Cervus elaphus* L.). *Mol. Ecol.* 22, 4711–4722. doi: 10.1111/mec.12420

Milner, J. M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S., and Stenseth, N. C. (2006). Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol.* 43, 721–734.

Mimura, M., Yahara, T., Faith, D. P., Vázquez-Domínguez, E., Colautti, R. I., Araki, H., et al. (2017). Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evol. Appl.* 10, 121–139. doi: 10.1111/eva.12436

Ministerio de Agricultura (1968). *Mapa Cinegético Nacional*. Madrid: Ministerio de Agricultura.

Miraldo, A., Li, S., Borregaard, M. K., Flórez-rodríguez, A., Gopalakrishnan, S., Rizvanovic, M., et al. (2016). An Anthropocene map of genetic diversity. *Science* 353, 24–27. doi: 10.1126/science.aaf4381

Mitchell-Jones, A. J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P. J. H., Spitzenberger, F., et al. (1999). *The Atlas of European Mammals*. London: T & AD Poyser Ltd.

Muhlfeld, C. C., Kalinowski, S. T., McMahon, T. E., Taper, M. L., Painter, S., Leary, R. F., et al. (2009). Hybridization rapidly reduces fitness of a native trout in the wild. *Biol. Lett.* 5, 328–331. doi: 10.1098/rsbl.2009.0033

Nagata, J., Masuda, R., Kaji, K., Kaneko, M., and Yoshida, M. C. (1998). Genetic variation and population structure of the Japanese sika deer (*Cervus nippon*) in Hokkaido Island, based on mitochondrial D-loop sequences. *Mol. Ecol.* 7, 871–877. doi: 10.1046/j.1365-294x.1998.00404.x

Niedziałkowska, M., Jêdrzejewska, B., Honnen, A.-C., Otto, T., Sidorovich, V., Perzanowski, K., et al. (2011). Molecular biogeography of red deer *Cervus elaphus* from eastern Europe: insights from mitochondrial DNA sequences. *Acta Theriol.* 56, 1–12. doi: 10.1007/s13364-010-0002-0

Nielsen, E. E., Bach, A. L., and Kotlicki, P. (2006). Hybridlab (version 1.0): a program for generating simulated hybrids from population samples. *Mol. Ecol. Notes* 6, 971–973.

Nussey, D. H., Pemberton, J., Donald, A., and Kruuk, L. E. B. (2006). Genetic consequences of human management in an introduced island population of red deer (*Cervus elaphus*). *Heredity* 97, 56–65. doi: 10.1038/sj.hdy.6800838

Peakall, R., and Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics* 28, 2537–2539. doi: 10.1093/bioinformatics/bts460

Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155, 945–959. doi: 10.1111/j.1471-8286.2007.01758.x

Queirós, J., Acevedo, P., Santos, J. P. V., Barasona, J., Beltran-Beck, B., González-Barrio, D., et al. (2019). Red deer in Iberia: molecular ecological studies in a southern refugium and inferences on European postglacial colonization history. *PLoS One* 14:e0210282. doi: 10.1371/journal.pone.0210282

Queirós, J., Godinho, R., Lopes, S., Gortazar, C., de la Fuente, J., and Alves, P. C. (2015). Effect of microsatellite selection on individual and population genetic inferences: an empirical study using cross-specific and species-specific amplifications. *Mol. Ecol. Resour.* 15, 747–760. doi: 10.1111/1755-0998.12349

Queirós, J., and Vicente, J. (2018). Inbreeding shapes tuberculosis progression in female adult badgers (*Meles meles*). *J. Anim. Ecol.* 87, 1497–1499. doi: 10.1111/1365-2656.12901

Queirós, J., Vicente, J., Alves, P. C., de la Fuente, J., and Gortazar, C. (2016). Tuberculosis, genetic diversity and fitness in the red deer, *Cervus elaphus*. *Infect. Genet. Evol.* 43, 203–212. doi: 10.1016/j.meegid.2016.05.031

Queiros, J., Vicente, J., Boadella, M., Gortázar, C., and Alves, P. C. (2014). The impact of management practices and past demographic history on the genetic diversity of red deer (*Cervus elaphus*): an assessment of population and individual fitness. *Biol. J. Linn. Soc.* 111, 209–223.

Raymond, M., and Rousset, F. (1995). GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *J. Hered.* 86, 248–249.

Rhymer, J. M. and Simberloff, D. (1996). Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27, 83–109. doi: 10.1146/annurev.ecolsys.27.1.83

Rice, W. (1989). Analyzing tables of statistical tests. *Evolution* 43, 223–225.

Salazar, D. C. (2009). *Distribuição e Estatuto do Veado e Corço em Portugal*. Master's thesis, Universidade de Aveiro, Aveiro.

Senn, H. V., and Pemberton, J. M. (2009). Variable extent of hybridization between invasive sika (*Cervus nippon*) and native red deer (*C. elaphus*) in a small geographical area. *Mol. Ecol.* 18, 862–876. doi: 10.1111/j.1365-294X.2008.04051.x

Senn, H. V., Swanson, G. M., Goodman, S. J., Barton, N. H., and Pemberton, J. M. (2010). Phenotypic correlates of hybridisation between red and sika deer (genus *Cervus*). *J. Anim. Ecol.* 79, 414–425. doi: 10.1111/j.1365-2656.2009.01633.x

Skog, A., Zachos, F. E., Rueness, E. K., Feulner, P. G. D., Mysterud, A., Langvatn, R., et al. (2009). Phylogeography of red deer (*Cervus elaphus*) in Europe. *J. Biogeogr.* 36, 66–77.

Smith, S. L., Carden, R. F., Coad, B., Birkitt, T., and Pemberton, J. M. (2014). A survey of the hybridisation status of Cervus deer species on the island of Ireland. *Conserv. Genet.* 15, 823–835.

Smith, S. L., Senn, H. V., Pérez-Espona, S., Wyman, M. T., Heap, E., and Pemberton, J. M. (2018). Introgression of exotic *Cervus* (*nippon* and *canadensis*) into red deer (*Cervus elaphus*) populations in Scotland and the English Lake District. *Ecol. Evol.* 8, 2122–2134. doi: 10.1002/ece3.3767

Sommer, R. S., Zachos, F. E., Street, M., Jöris, O., Skog, A., and Benecke, N. (2008). Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe. *Quat. Sci. Rev.* 27, 714–733.

Stanton, D. W. G., Mulville, J. A., and Bruford, M. W. (2016). Colonization of the Scottish islands via long-distance Neolithic transport of red deer (*Cervus elaphus*). *Proc. R. Soc. B Biol. Sci.* 283:20160095. doi: 10.1098/rspb.2016.0095

Taylor-Brown, A., Booth, R., Gillett, A., Mealy, E., Ogbourne, S. M., Polkinghorne, A., et al. (2019). The impact of human activities on Australian wildlife. *PLoS One* 14:e0206958. doi: 10.1371/journal.pone.0206958

Torres-Porras, J., Carranza, J., and Pérez-gonzález, J. (2014). The tragedy of the commons: unsustainable population structure of Iberian red deer in hunting estates. *Eur. J. Wildl. Res.* 60, 351–357.

Vingada, J., Fonseca, C., Cancela, J., Ferreira, J., and Eira, C. (2010). "'Ungulates and their management in Portugal,'" in *European Ungulates and their Management in the 21st Century*, eds M. Apollonio, R. Andersen, and R. J. Putman (Cambridge: Cambridge University Press).

Zachos, F. E., and Hartl, G. B. (2011). Phylogeography, population genetics and conservation of the European red deer *Cervus elaphus*. *Mamm. Rev.* 41, 138–150.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 28 May 2020
doi: 10.3389/fevo.2020.00150

Winter Is Coming: Conserving Body Protein in Female Reindeer, Caribou, and Muskoxen

Perry S. Barboza[1,2,3]*, *Rachel D. Shively*[1,2], *Dave D. Gustine*[1,4] *and J. A. Addison*[1]

[1] *Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, United States,* [2] *Department of Rangelands, Wildlife and Fisheries, Texas A&M University, College Station, TX, United States,* [3] *Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, United States,* [4] *Grand Teton National Park, National Park Service, Moose, WY, United States*

Northern ungulates undergo pregnancy in winter when food supplies are low. Consequently, females employ a capital breeding strategy that relies upon maternal body stores of energy and protein for fetal growth. We studied captive female reindeer (*Rangifer tarandus tarandus*; $n = 6$; 118 kg), caribou (*Rangifer tarandus granti*; $n = 6$; 97 kg), and muskoxen (*Ovibos moschatus*; $n = 8$; 205 kg) in late winter (February to April) to track body protein use in late pregnancy when feeding is often interrupted by snow storms and when wild animals begin movements to spring and summer ranges where they give birth. We used high and low protein rations (14–16 and 8% protein) as complete diets for *Rangifer* and high protein ration as a supplement (500 g/day) to hay (7.3% protein; $\delta^{15}N = 1.1‰$) for *Ovibos*. Animals were fasted for 2 days to evaluate isotopic responses to an acute deficit of energy and protein on each diet in a sequence from $\delta^{15}N$ 1.6‰, to 6.9‰ to 3.2‰ over 58 days. Dietary shifts in $\delta^{15}N$ were reflected in plant fibers in the feces (fecal fiber) but not in blood cells (*Rangifer* 6.5 ± 0.3‰; *Ovibos* 5.2 ± 0.1‰). Serum proteins were higher in $\delta^{15}N$ than blood cells whereas serum amino acids were lower in $\delta^{15}N$ than blood cells and more responsive to changes in dietary $\delta^{15}N$ indicated by fecal fiber. Fasting did not affect $\delta^{15}N$ of serum proteins or serum amino acids. Values for $\delta^{15}N$ in urea were strongly affected by both shifts in diet and by fasting, which indicated that excretory urea N was derived from cellular proteins and isotopically heavy proteins released from organs into the serum. Inter-organ exchanges of transport proteins may minimize oxidation of stored amino acids and conserve body protein stores for fetal growth and milk production in *Rangifer* and *Ovibos*. A capital breeding strategy in these long-lived, iteroparous herbivores relies upon routing of body proteins to simultaneously sustain maternal function and maternal investment through common metabolic pathways that conserve lean body mass for survival.

Keywords: arctic, herbivore, protein, stable isotopes, ungulate

OPEN ACCESS

Edited by:
Paul Richard Krausman,
The University of Arizona,
United States

Reviewed by:
Niels Martin Schmidt,
Aarhus University, Denmark
Mark S. Boyce,
University of Alberta, Canada

****Correspondence:***
Perry S. Barboza
psbarboza@tamu.edu

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *15 February 2020*
Accepted: *04 May 2020*
Published: *28 May 2020*

Citation:
Barboza PS, Shively RD,
Gustine DD and Addison JA (2020)
Winter Is Coming: Conserving Body
Protein in Female Reindeer, Caribou,
and Muskoxen.
Front. Ecol. Evol. 8:150.
doi: 10.3389/fevo.2020.00150

INTRODUCTION

The phrase "winter is coming" always applies to northern ungulates because summers are shorter than winters for populations of reindeer (*Rangifer tarandus tarandus*), caribou (*Rangifer tarandus granti*), and muskoxen (*Ovibos moschatus*; Blix, 2005; Parker et al., 2009). Muskoxen forage on a fibrous diet of graminoids throughout the year [e.g., sedges (*Carex* spp.)] with browse [e.g., willow (*Salix* spp.)] in summer whereas reindeer use a less fibrous diet of forbs [e.g., wooly lousewort

(*Pedicularis* spp.)], browse and emerging sedges in summer with lichens in winter (Kristensen et al., 2011; Thompson et al., 2015; Mosbacher et al., 2016; Denryter et al., 2017). Forages are highest in quality and abundance during spring and mid-summer but low in quality and abundance through winter when plants are dormant and covered by snow (Kazmin et al., 2011; Barboza et al., 2018). In summer, digestible content of nutrients such as protein and minerals decline more quickly than that of digestible energy, which results in a short window for nutrient gain in all herbivores (Barboza et al., 2018; Oster et al., 2018). Dramatic seasonal changes in plant growth and temperature at high latitudes select for behavioral and physiological mechanisms that allow herbivores to switch from growing and storing energy and nutrients in body tissues through summer, to conserving those stores to sustain body function through winter. In females, body stores may also support reproduction through the growth of a fetus and uterine tissue through late winter and the production of milk for their offspring through early summer. Consequently, body mass affects the survival of the mother and also the viability of her calves through maternal stores of body energy and nutrients (Taillon et al., 2012; Berger et al., 2018; Desforges et al., 2019; Paoli et al., 2019).

Lipids in fat depots are the principal store of energy for physical (e.g., movements) and metabolic activities, which includes maintenance functions (e.g., thermoregulation and cellular turnover) and the synthesis of new tissues. In northern ungulates, the subcutaneous depot of fat on the rump is an easily measurable index of body energy, especially among the more sedentary reindeer and muskoxen (Rombach et al., 2002a; Milner et al., 2003; Gustine et al., 2007). Body nutrients are more difficult to assess because the amino acids and minerals in proteins are part of the structure of the body in muscles, organs, and bone (Barboza et al., 2009). Some muscles can provide an index of body protein but these are more difficult to measure than body fat (Taillon et al., 2011). The rate of change in body protein may be more important than the absolute size of the store because nutrients mobilized to maintain body functions and synthesize fetal tissues in winter are part of a dynamic process of turnover and exchange among tissues (Barboza et al., 2009).

All proteins contain nitrogen (N), which can be tracked by using the isotopic ratios of ^{15}N:^{14}N (δN^{15}) in diet, tissues, isolated proteins, amino acids and metabolites (Barboza and Parker, 2006). Metabolic processes of digestion, absorption, transport and turnover discriminate between light and heavy isotopes of N to raise isotopic ratios from diet to muscle. Conversely, the breakdown of proteins and their constituent amino acids to urea discriminates between isotopes of N to lower isotopic ratios between body protein and the N excreted in urine. Isotopic ratios can be used to distinguish the source of N in a product; high ratios of isotopic N in urea indicates the oxidation of body protein whereas low ratios in urea indicate that body protein is being conserved and that sufficient dietary N is available for body function (Gustine et al., 2011a,b). Similarly, allocation of maternal body N and dietary N to the fetus during pregnancy can be measured by ratios of isotopic N in neonates that are typically greater than those of the mother in reindeer and caribou because maternal body protein is the principal source of fetal protein (Barboza and Parker, 2008; Taillon et al., 2013). Maternal protein stores are closely guarded in winter; pregnant reindeer, caribou and muskoxen lose <10% of their body protein over the course of pregnancy and that loss matches the investment of protein in their offspring (Barboza and Parker, 2006, 2008; Gustine et al., 2010).

Isotopic ratios of N have been used to monitor body protein status of wild caribou and muskoxen by sampling urinary N from snow and the muscle and blood of captured animals (Gustine et al., 2011a,b, 2012, 2014a; Taillon et al., 2013). Isotopic assessments of body protein status have been used to assess constraints of habitat quality such as snow depth and diet that ultimately affect the supply of N for individuals and thus the productivity of the population. However, those assessments have been limited by our understanding of isotopic responses to changes in N supply. In this study, we examine the conservation of N in captive female reindeer, caribou, and muskoxen. We examine the effect of changing N supply on isotopic ratios of N in metabolic pools of free amino acids, circulating protein and urinary urea by changing dietary N content, dietary isotopic ratios of N and by withholding food. We use the isotopic responses to develop a model of N dynamics for predicting the depletion of body protein stores used for reproduction in wintering ungulates.

MATERIALS AND METHODS

Animals and Treatment

All procedures for animal care, handling, and experimentation were approved by the Animal Care and Use Committee, University of Alaska Fairbanks under protocol 06-049, which conforms to the American Society of Mammalogists guidelines for the use of mammals in research (Sikes, 2016).

We studied female reindeer (n = 6), caribou (n = 6), and muskoxen (n = 8) from a captive population maintained by the Institute of Arctic Biology in Fairbanks, Alaska (64.8795, −147.8640). Air temperature (°C) and solar radiation were measured on site (HOBO, Onset Computer, Bourne, MA, United States). All animals were bred in captivity and maintained on formulated rations with access to natural vegetation and grass hay in outdoor pens of one to two hectares. Water was available *ad libitum* as snow or from heated water troughs. This study was conducted during late winter (ordinal days 41–99; 11 February to 10 April 2009; **Figure 1**) when snow depths minimized foraging on natural vegetation. All females were held in harem with males during the breeding season in the autumn before the study and monitored for production of calves in the spring after the study.

We used three formulated rations that were provided as pellets: a high N "Control," a high N "Spike" with high δN^{15}, and low N ration with intermediate δN^{15} (**Table 1**; Alaska Pet and Garden, Anchorage, AK, United States). High N rations were similar to growing forbs that are available to wild reindeer, caribou and muskoxen in spring whereas the low N ration is similar to the low-quality forages available in winter (Parker et al., 2005; Barboza et al., 2018). The high N rations therefore foster maintenance or gain of body protein whereas the low

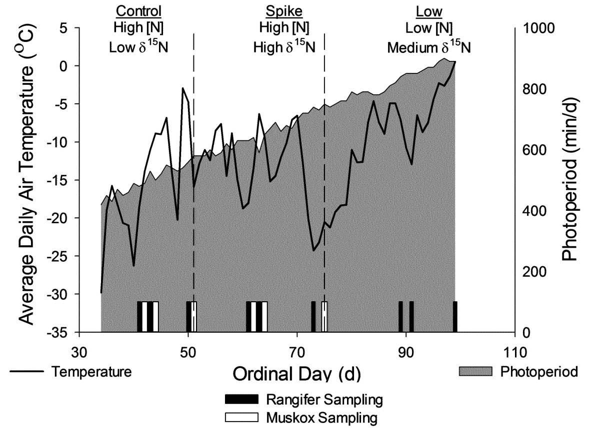

FIGURE 1 | Environmental conditions for experiments on female reindeer, caribou (*Rangifer*) and muskoxen (*Ovibos*) during late winter from February to April of 2009 in Fairbanks, AK, United States. Reindeer and caribou were fed all three rations as complete diets whereas muskoxen were fed hay *ad libitum*, which was supplemented with the control or the spike rations. Sampling days for collection of blood and excreta and for measures of body condition are indicated as vertical bars on the *X*-axis.

TABLE 1 | Composition of foods provided to reindeer, caribou, and muskoxen from February to April 2009 in Fairbanks, AK, United States.

Dry matter composition	Hay	High N control	High N ^{15}N spike	Low N
δ^{15}N (‰)	1.10	1.57	6.88	3.19
Ash (%)	4.4	6.7	7.2	4.4
Neutral detergent fiber (NDF; %)	68.9	35.4	36.3	28.3
Acid detergent fiber (%)	39.6	18.0	17.2	12.7
Lignin (%)	8.51	8.40	9.57	6.45
Nitrogen (%)	1.2	2.2	2.5	1.3
Nitrogen in NDF (%)	0.7	0.6	0.9	0.3

N ration simulated conditions that are likely to limit protein gain and foster conservation of body N. The acute shift in isotopic value from the control to the spike ration was used to simulate an acute change in range from an area without marine derived N to an area with N subsidies from anadromous fish such as Pacific salmon (*Oncorhynchus tshawytscha*). Reindeer and caribou were provided with *ad libitum* ration in a shared feeding trough whereas muskoxen were provided each ration as an individual supplement each day (500 $g \cdot d^{-1}$) with *ad libitum* grass hay (*Bromus* spp.). Muskoxen did not readily accept the Low N ration, which was as low in N content as the grass hay (**Table 1**). Consequently, muskoxen were only studied on the High N rations through ordinal day 75 (17 March).

We fed all animals each diet in three sequential periods. The control ration was used to maintain caribou and reindeer throughout the year whereas muskoxen were maintained on a mineral supplement (M ration Alaska Pet and Garden, Anchorage, AK, United States) with the same ingredients as the control ration but with a different mineral vitamin premix (Gustine et al., 2010). Animals were transitioned to each new ration for 3 days before feeding that ration for 7 days prior to sampling. We fasted animals for 2 days by removing rations from the reindeer and caribou pens and by removing hay and withholding supplemental ration from the muskoxen. Animals were allowed to feed again for 7 days before sampling in the "refed" state (**Figure 1**). Sampling days occurred before fasting, at the end of fasting, and 7 days after fasting ended for each period (**Figure 1**).

Sample Collection

Individual animals were observed to collect fresh feces and urine on sampling days (**Figure 1**). We moved caribou and muskoxen into small handling pens (<0.4 ha) for up to 4 h to observe and collect excreta from snow as soon as it was voided by each individual in the pen. Reindeer were haltered and accustomed to standing while tethered in stalls, which allowed us to collect voided excreta directly into a cup without snow. All excreta samples were collected into 60 ml plastic bottles and frozen.

Animals were weighed on electronic load scales (± 0.1 kg; Tru-Test Model 703, San Antonio, TX, United States) after collection of excreta. Animals were manually restrained in handling chutes or stalls to collect blood samples from the jugular vein. Blood was collected into glass tubes (Vacutainer, Becton Dickinson, Franklin Lakes, NJ, United States) without additives and allowed to coagulate. Clear sera were decanted from blood after centrifugation at 3,000 $\times$ g for 10 min and frozen for analysis. The clot of blood cells and clotting proteins was retained and frozen after draining residual sera.

We measured subcutaneous rump fat via ultrasound on reindeer and muskoxen standing in the handling chute without chemical immobilization (Rombach et al., 2002a; Barboza and Parker, 2006). Rump fat was not measured in caribou to minimize the stress of repeated handling.

Lab Analysis

Urine samples were freeze dried and rehydrated with 25 mL deionized water for analysis. We used steam distillation to collect urinary urea N from urine samples (Nolan and Leng, 1972; Barboza et al., 1997). Fecal samples were dried to constant mass at 50°C in a forced-air oven then ground in a Wiley mill (Arthur Thompson, Philadelphia, PA, United States) through a 1 mm screen. We isolated fibrous residues from feces by using polyester filter bags to individually boil ground fecal samples in separate beakers of deionized water (F57 filter bags, Ankom Technology, Macedon, NY, United States) for 20 min followed by 3 rinses with hot water (Gustine et al., 2011b, 2014b).

Clotted blood was freeze dried for analysis. Proteins were precipitated from blood sera with Na_2WO_4 (Barboza et al., 1997) and freeze-dried. We measured urea concentrations of deproteinized serum by reaction with diacetyl monoxime (Barboza et al., 2004). Serum amino acids were collected from deproteinized serum by ion-exchange chromatography (Gustine et al., 2010).

We assayed ^{15}N by continuous flow isotope ratio mass spectrometry by using a Finnigan Delta V plus mass spectrometer (Thermo Scientific, Waltham, MA, United States) combined with a Costech Elemental Analyzer (Costech Analytical Technologies

Inc., Valencia, CA, United States) at the Alaska Stable Isotope Facility at University of Alaska Fairbanks. Isotopic values for nitrogen were reported in delta notation and expressed in parts per thousand, relative to air {δ = [(isotope ratio sample/isotope ratio standard)−1] × 1000} (Gustine et al., 2011a). Peptone was used as a reference standard with an expected δ^{15}N value of 7.00‰, which was assayed with an accuracy of ±0.28‰ (Vansomeren et al., 2017).

The distribution of N in blood was measured in triplicate samples of blood from four female reindeer and two female caribou during winter. We collected blood samples without additive for serum and with sodium heparin for plasma. Heparinized blood was used to measure the relative proportions of packed red cells and plasma as hematocrit. Whole blood, packed cells, serum, and plasma were subsampled and dried to constant mass in a freeze drier to measure dry matter content. We used plasma to measure total soluble protein (i.e., including clotting proteins) by reaction with Bradford reagent (Coomassie Blue dye at 595 nm; Sigma Chemicals, St. Louis, MO, United States). Urea and amino acid contents of deproteinized serum were measured as above. Total N of freeze-dried blood fractions were measured by elemental analyzer (LECO, St. Joseph, MO, United States). We allocated total N to red cells, plasma protein, free amino acids, and urea. Creatinine and other metabolites were estimated as the residual N from blood plasma.

Statistical Analysis

We used two sets of mixed effects regression models with individual animal (constant) and time (ordinal days; covariate) as random effects to account for repeated measures. The first set of models examined body condition by using the following five dependent variables (Y_C): body mass, rump fat, serum urea concentration, δ^{15}N of fecal fiber, and δ^{15}N of blood clot. Each model included the fixed effect of taxon (TAXON; reindeer, caribou, or muskox). The first set of models on body condition included the fixed effects of reproductive status (REPRO; pregnant or not pregnant), diet treatment (DIET; Control, Spike, Low), and phase (PHASE; fed, fasted, refed) with interactions between taxon and reproductive status, taxon and diet treatment, and taxon and phase.

The full model for condition variables was:

$$\begin{aligned} Y_C = {} & \text{TAXON} + \text{REPRO} + \text{DIET} + \text{PHASE} + \text{TAXON} \\ & \times \text{REPRO} + \text{TAXON} \times \text{DIET} + \text{TAXON} \times \text{PHASE}. \end{aligned}$$

The second set of models examined isotopic changes in three pools of body N as dependent variables (Y_N): δ^{15}N value of serum amino acids, δ^{15}N value of serum protein, and δ^{15}N value of urinary urea. The second set of models included the fixed effects of taxon, phase, and their interaction. Reproduction was initially included but that fixed effect was not significant and thus removed from this second set of models. We also used δ^{15}N of fecal fiber (FIBER15N) and δ^{15}N of blood clot (CLOT15N) as covariates to represent isotopic endpoints of diet and body N, respectively, in the second set of models (Taillon et al., 2013; Gustine et al., 2014b).

The full model for variables of isotopic N was:

$$\begin{aligned} Y_N = {} & \text{TAXON} + \text{PHASE} + \text{TAXON} \times \text{PHASE} \\ & + \text{FIBER15N} + \text{CLOT15N}. \end{aligned}$$

In each set of models, we used backward elimination of fixed effects by starting with the full model and progressively excluding interactions and independent variables with beta coefficients that were not significantly different from zero ($P > 0.05$). Margins ($\bar{X}$ ± standard error) were calculated for the observed range of each fixed effect in the final model. We used Bonferroni's adjustment for pairwise comparisons and contrasts of margins between diets and between phases (e.g., fasted vs. fed) within each taxon (STATA 16, StataCorp, College Station, TX, United States).

Finally, we derived simple linear relationships using a single fixed effect in the mixed model for two comparisons among taxa with individual animal (constant) and time (ordinal days; covariate) as random effects to account for repeated measures. Firstly, the relationship between the isotopic endpoint of the body (CLOT15N) and the isotopic endpoint of the diet (FIBER15N) on the High N control treatment (**Figure 1**). Secondly, relationships between body N pools (Y_N) and clotted blood cells among taxa.

RESULTS

Body Condition

Daily average air temperature ranged from −30°C to + 0°C as daily photoperiod increased from 420 to 900 min·day^{-1} over the course of the study (**Figure 1**). All females were exposed to intact males before the study but one of six reindeer, two of six caribou, and five of eight muskoxen did not produce calves because they did not enter estrus or because they resorbed the fetus *in utero*. Births occurred on ordinal days 99–104 for reindeer, 128–136 for caribou, and 113–119 for muskoxen. Body mass was not significantly affected by reproductive state (**Table 2**) but did decline over the course of the study by −10.8 ± 2.8 kg in reindeer, −2.1 ± 1.0 kg in caribou, and −2.6 ± 0.8 kg in muskoxen (**Table 2** and **Supplementary Table S1**). Reindeer lost 15.9 ± 1.9 mm of subcutaneous fat at the rump as body mass declined by 9.1% whereas muskoxen maintained rump fat depth over the course of the study even though body mass declined by 1.3%. Fasting did not significantly affect rump fat depth in reindeer or muskoxen (**Table 2**). However, body mass was lost in each 2-day fast by 2.3 ± 0.6 kg in reindeer, 2.1 ± 0.2 kg in caribou, and 5.8 ± 0.4 kg in muskoxen. Fasting increased serum urea concentrations by +5.1 ± 2.0 mg·dl^{-1} in reindeer, +6.0 ± 1.9 mg·dl^{-1} in caribou, and +16.2 ± 1.6 mg·dl^{-1} in muskoxen. Serum urea was not significantly affected by the change from High N ration to High N Spike ration but the subsequent change to the Low N ration decreased serum urea by −5.7 ± 1.6 mg·dl^{-1} in reindeer and by −11.8 ± 2.2 mg·dl^{-1} in caribou.

Values for δ^{15}N in fecal fiber were significantly affected by diet. An increase in δ^{15}N value of the ration from High N Control to High N Spike (**Table 1**) significantly increased fecal fiber δ^{15}N values by 2.2 ± 0.1‰ in reindeer, 1.7 ± 0.1‰ in caribou, and 0.8 ± 0.2‰ in muskoxen (**Table 2** and **Supplementary Table S1**).

TABLE 2 | Results of mixed model regression for evaluation of body condition variables (Y_C) in female reindeer, caribou, and muskoxen from February to April 2009 in Fairbanks, AK, United States.

Parameters	**Level**	**Dependent variable (Y_C)**				
		Body mass (kg)	**Rump fat (mm)**	**Serum urea (mg·dL^{-1})**	**Fecal fiber δN^{15} (‰)**	**Blood clot δN^{15} (‰)**
Observations		156	102	153	153	154
χ^2		12261	111	405	8810	857
[df]		[15]	[8]	[15]	[15]	[13]
P		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Fixed effects						
Intercept	Reindeer (base)	119*	39.5*	12.7*	5.32*	6.37*
Taxon	Caribou	−21*	–	10.5*	0.55*	−0.32
	Muskox	+86*	−18.9*	−4.3*	−1.90*	−1.02*
Phase	Fasted	−2.28*	0.6	5.1*	0.54*	0.21*
	Refed	−2.30*	−2.3*	2.7	−0.24*	0.35*
Taxon*phase	Caribou-fasted	0.23	–	0.9	−0.25	−0.19*
	Caribou-refed	0.62	–	−3.6	−0.10	−0.28
	Muskox-fasted	−3.56*	−1.1	11.1*	−0.43*	−0.23*
	Muskox-refed	−1.08*	−1.7	−3.8	0.95*	−0.45*
Diet	Spike	−1.62*	−5.2*	−1.2	2.21*	0.08
	Low	−10.8*	−15.9*	−7.0*	−0.19	0.29
Taxon*diet	Caribou-spike	2.24*	–	3.4	−0.54*	0.17
	Caribou-low	8.70*	–	−2.7	0.40	0.17
	Muskox-spike	−0.99	5.2*	−0.1	−1.43*	−0.24
Reproductive	Pregnant	–	–	9.4*	0.68*	–
Reproductive*taxon	Caribou-pregnant	–	–	−9.6*	−0.63*	–
	Muskox-pregnant	–	–	−7.2*	−0.83*	–
Random effects						
Variance	Individual	396.4	167.1	2.2725	0.0038	0.4165
	Time	0.0090	0.0054	0.0017	< 0.0001	< 0.0001
	Individual × Time	−0.2824	−0.8417	−0.0548	−0.0041	−0.0041
	Residual	2.6151	8.9300	29.7732	0.1898	0.0575

Asterisks denote significant beta coefficients for fixed effects ($P < 0.05$), dashes (–) represent fixed effects that were not significant and subsequently removed from the model ($P > 0.05$). Fed non-pregnant reindeer on the control diet were the basis for comparison in each model.

The subsequent change to the Low N ration with a lower δ^{15}N value (**Table 1**) significantly reduced fecal fiber δ^{15}N values by 2.4 ± 0.2‰ in reindeer and by 1.5 ± 0.1‰ in caribou (**Table 2** and **Supplementary Table S1**). Values for δ^{15}N in fecal fiber were also significantly affected by fasting. Fasting increased fecal fiber δ^{15}N values by 0.5 ± 0.1‰ in reindeer and by 0.3 ± 0.1‰ in caribou, which was reversed when the ration was fed *ad libitum*. In muskoxen, the 2-day fast did not significantly change values for δ^{15}N in fecal fiber but resumption of *ad libitum* feeding decreased those values by −0.7 ± 0.1‰.

The random effects of individual and ordinal day accounted for less than 0.1% of the variance in the model for δ^{15}N values in fecal fiber but more than 98% of the variance in δ^{15}N values of the blood clots (**Table 2**). Most of the variance in δ^{15}N values of the blood clots during the study was associated with changes over time within animals: values rose by +0.8 ± 0.3 and +0.5 ± 0.1‰ in reindeer and caribou, respectively, whereas values for muskoxen fell by −0.3 ± 0.1‰ over the course of the study (**Supplementary Table S1**). Fasting significantly affected blood clot δ^{15}N values (**Table 2**) but pairwise differences between phases were only significant for reindeer, which increased by +0.2 ± 0.1‰ between the fed and fasted state. In reindeer and caribou, δ^{15}N values of the blood clots increased by +0.2 ± 0.1‰ with each change in diet even though the δ^{15}N values of those rations increased and then decreased (**Table 1** and **Supplementary Table S1**). Conversely, δ^{15}N values of the blood clots decreased by −0.2 ± 0.1‰ in muskoxen as the δ^{15}N value of the ration increased (**Table 1** and **Supplementary Table S1**).

Body N Pools

The initial isotopic endpoints for the body were positively related to the long-term diet at the start of the study. Values for δ^{15}N in blood clots increased by +0.21 ± 0.07‰ for each unit increase in δ^{15}N values of fecal fiber during the first period of the study when animals were provided with the Control High N diet, which was similar to the diet provided through the previous year (**Figure 2**).

Values for δ^{15}N in serum amino acids, serum protein, and urinary urea were not significantly affected by variation in the isotopic endpoint for the body indicated by blood clot δ^{15}N values within taxon (**Table 3**). However, simple linear relationships across taxa indicated that each unit increase in δ^{15}N value of the body endpoint was associated with an increase in

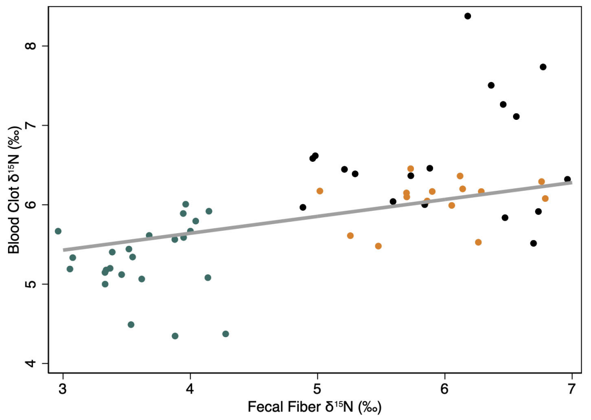

FIGURE 2 | Linear relationship between the isotopic endpoints [δ^{15}N (‰)] of the body (i.e., clotted blood cells) and the diet (i.e., fecal fiber) when animals were fed the control High N diet to which they were accustomed for the previous year. The thick gray line indicates the predicted linear relationship from a mixed model regression with fecal fiber as the only fixed effect, and individual animal (constant) and time (ordinal days; covariate) as random effects to account for repeated measures. Symbols indicate observations for female reindeer (black), caribou (orange), and muskoxen (green) in late winter. All measures were conducted during late winter from February to April of 2009 in Fairbanks, AK, United States.

+0.50 ± 0.20‰ of serum amino, and +1.61 ± 0.28‰ in urinary urea values (**Figure 3**).

Values for δ^{15}N in serum amino acids, serum protein, and urinary urea were significantly affected by the dietary isotopic endpoint indicated by fecal fiber δ^{15}N values (**Table 3**). Each unit increase in δ^{15}N value of the dietary endpoint increased serum amino acid and protein values by only +0.28 ± 0.07 and +0.14 ± 0.04‰, respectively, whereas urinary urea values increased by +0.88 ± 0.1‰ (**Figure 3**). Fasting for 2 days did not affect δ^{15}N values for either serum amino acids or protein (**Table 3**). However, δ^{15}N values for urinary urea increased during fasting by +2.11 ± 0.40‰ in reindeer, +2.41 ± 0.30‰ in caribou, and +1.05 ± 0.34‰ in muskoxen. Values for δ^{15}N of urinary urea declined again after *ad libitum* feeding resumed in each taxon.

Distribution of N in Blood

Blood cells accounted for 48 ± 3% of the volume of heparinized whole blood. Cells accounted for more dry matter than plasma (15.67 ± 0.29 vs. 4.38 ± 1.28 g dry mass·dL^{-1} in whole blood) but those dry components were similar in N concentration (15.93 ± 0.50 vs. 14.53 ± 2.09% N). Consequently, whole blood contained 20.05 ± 1.07 g dry mass·dL^{-1}, which was 15.78 ± 2.28% N. Plasma accounted for 21.6 ± 4.9% of dry mass and 19.8 ± 2.7% of total N in whole blood whereas blood cells were 78.4 ± 4.9% of dry mass and 80.2 ± 2.7% of N in whole blood (**Figure 4**). Serum contained 77.3 ± 5.9 mg of protein·mL^{-1} that accounted for 12.82 ± 0.96 mgN·mL^{-1}, which was 19.2 ± 0.3% of total N in whole blood. Serum contained only 387 ± 201 µgN·mL^{-1} as urea and only 12 ± 4 µgN·mL^{-1} as amino acids, which was only 0.36 and 0.02% of the total N in whole blood, respectively. Residual N that was associated with creatinine and other metabolites was only 0.22% of N in whole blood (**Figure 4**).

DISCUSSION

Body mass loss of reindeer, caribou, and muskoxen during this study were consistent with our previous studies at this location when animals were fed *ad libitum* through winter (Barboza and Parker, 2008; Gustine et al., 2010). Winter mass loss is associated with net loss of body fat and body protein that reflect low voluntary food intakes (Parker et al., 2005; Thompson and Barboza, 2017) and increased costs of thermoregulation during periods of cold weather when temperatures dropped below −20°C (Munn et al., 2009; Schmidt et al., 2020). In late winter when temperatures were mild, fat loss was associated with increasing energy demands in the third trimester of pregnancy especially in reindeer that gave birth within 5 days of the end of this study (Barboza and Parker, 2006, 2008).

Changes in winter diet were reflected in oxidation of proteins from the diet. Serum urea declined with dietary N content in reindeer and caribou. In muskoxen, serum urea concentrations were consistently low on the two high N supplements because >70% of the N intake is derived from hay, which was low in N content (**Table 1**) (Peltier and Barboza, 2003; Peltier et al., 2003). However, δ^{15}N values for urinary urea closely followed those of dietary N in all three taxa (**Figure 3**), which indicates that dietary N was the principal source of urea N when animals were fed *ad libitum*. This suggestion is consistent with previous estimates of more than 60% of urinary urea from dietary N in muskoxen and reindeer fed High N rations through winter (Barboza and Parker, 2006; Gustine et al., 2010). Conversely, fasting increased serum urea concentrations on each diet treatment in all taxa. The increase in serum urea concentration during fasting reflects oxidation of body protein and recycling of urea-N to minimize the loss of both N and water from the body. In reindeer, the pool of urea N turns over every 12 h with 70% of the N that enters the urea pool being degraded and returned to amino acids (Barboza and Parker, 2006). Moreover, δ^{15}N values for urinary urea increased dramatically, which indicates that body proteins were oxidized during the fast. The subsequent decline in urea δ^{15}N values is consistent with a rapid return to oxidation of dietary N when feeding is resumed (**Supplementary Table S1** and **Figure 3**). Body protein is therefore conserved by an oxidative system that responds rapidly to changes in dietary N supply, limits oxidation of body N and extensively recycles oxidized N when N intakes are low (Parker et al., 2005; Barboza and Parker, 2006). Increases in serum urea concentration of pregnant females were most evident for reindeer especially at the end of the experiment when N intakes may have been further depressed by low intakes of the low N diet in the last few weeks before parturition (**Table 2**) (Barboza and Parker, 2008).

Isotopic changes in diet were reflected in fecal residues of fiber but the discrimination between diet and fecal fiber varied from 3.3 to 5.3‰ in reindeer and caribou and from 1.4 to 2.7‰ in muskoxen on the control diet (**Supplementary Table S1**). Isotopic variation in fecal residues is probably due to variation

TABLE 3 | Results of mixed model regression for evaluation of body N pools (Y_N) in female reindeer, caribou, and muskoxen from February to April 2009 in Fairbanks, AK, United States.

Parameters	Level	Dependent variable (Y_N)		
		Serum amino acids δN^{15} (‰)	**Serum protein δN^{15} (‰)**	**Urinary urea δN^{15} (‰)**
Observations		149	151	146
χ^2		354	466	567
[df]		[10]	[10]	[10]
P		$P < 0.001$	$P < 0.001$	$P < 0.001$
Fixed effects				
Intercept	Reindeer (base)	1.25	6.19*	1.79
Taxon	Caribou	0.24	0.00	−0.90*
	Muskox	−1.21*	−1.43*	−2.11*
Phase	Fasted	−0.12	0.08	2.17*
	Refed	−0.62*	−0.13	−0.65*
Taxon*phase	Caribou-fasted	−0.35	0.01	0.25
	Caribou-refed	0.94*	0.23*	0.34
	Muskox-fasted	0.76*	0.01	−1.12*
	Muskox-refed	0.66*	0.17*	0.36
Fecal fiber δN^{15} (‰; diet endpoint)		0.28*	0.13*	0.87*
Blood clot δN^{15} (‰; body endpoint)		0.15	0.10	−0.34
Random effects				
Variance	Individual	1.8321	1.2643	7.2093
	Time	0.0006	0.0006	0.0019
	Individual × Time	−0.0327	−0.0261	−0.1143
	Residual	0.3543	0.0739	1.5036

Asterisks denote beta coefficients for fixed effects that were significantly different from zero (P < 0.05). Fed reindeer on the control diet were the basis for comparison in each model.

in the contribution of endogenous N from digestive secretions and microbial colonization of the fiber matrix (Gustine et al., 2014b; Ungerfeld et al., 2018). Variation in the flow of particles through the digestive tract may further affect isotopic variation in fiber residues because mean retention of particles in the digestive tract ranges from 60–100 h in reindeer and muskoxen (Lechner et al., 2010). However, dietary transitions were accomplished over 10 days and continued for a total of 20 days, which is equivalent to 8–20 times the mean retention of particles. Periods of 7–10 days are usually sufficient for equilibration of digestive and metabolic functions in these animals (Barboza et al., 2009). Fecal fiber residues track isotopic changes in dietary endpoints for northern ungulates within 10 days but fractionation may vary with the digestion and flow of dietary components (Gustine et al., 2014b; Vansomeren et al., 2017). Small increases in δ^{15}N values of fecal fiber in pregnant females may reflect small differences in the contribution of endogenous N to feces when compared with those females that did no calve (**Table 2**).

The effect of dietary isotopes of N on the body endpoint probably occurs on a seasonal scale of time in northern ungulates. Values for δ^{15}N in blood cells were related to long term diet indicated by fecal fiber residues on the control diet – reindeer and caribou were fed the control diet through the previous summer whereas muskoxen were fed a supplement of the same formulation as the control diet with a different mineral mix (**Figure 2**). During winter, low N intakes are accompanied by conservation of N and preferential oxidation of dietary N that tends to preclude the incorporation of that dietary N in body protein. Consequently, δ^{15}N values of blood cells decline slowly in reindeer and caribou fed the same diet at both high and low concentrations of N through winter (Barboza and Parker, 2006, 2008). The slow changes in δ^{15}N values of blood clots is consistent with slow turnover of a large metabolic pool of N that accounts for the majority of circulating N in blood (**Figure 4**). The slow changes in blood cells during winter are probably representative of the protein in muscle, which is isotopically similar to blood clots in caribou (Taillon et al., 2013). In pregnant females, the tissues that are synthesized in winter appear to be allocated from body protein to produce fetal protein with δ^{15}N values that exceed those of maternal muscle, blood cells and diet (Barboza and Parker, 2006, 2008; Taillon et al., 2013).

Circulating pools of amino acids can arise from digestion of dietary protein and turnover of tissue protein but δ^{15}N values of serum amino acids are consistently lower than those of the blood clot and closer to the dietary endpoint (**Supplementary Table S1**). In these ungulates, dietary plant proteins are mixed with microbial proteins from ruminal fermentation to produce the full complement of essential and non-essential amino acids (Lapierre et al., 2008). Circulating amino acids are therefore an admixture of 20 pools connected by interorgan exchanges and pathways of intermediary metabolism that probably buffer the relatively small isotopic pool (**Figure 4**). Consequently, changes in dietary δ^{15}N values were reflected in δ^{15}N values of the serum amino acid pool but interruption of dietary N supply by fasting did not affect δ^{15}N values of the serum amino acid pool (**Figure 3**). Dietary amino acids appear to be routed

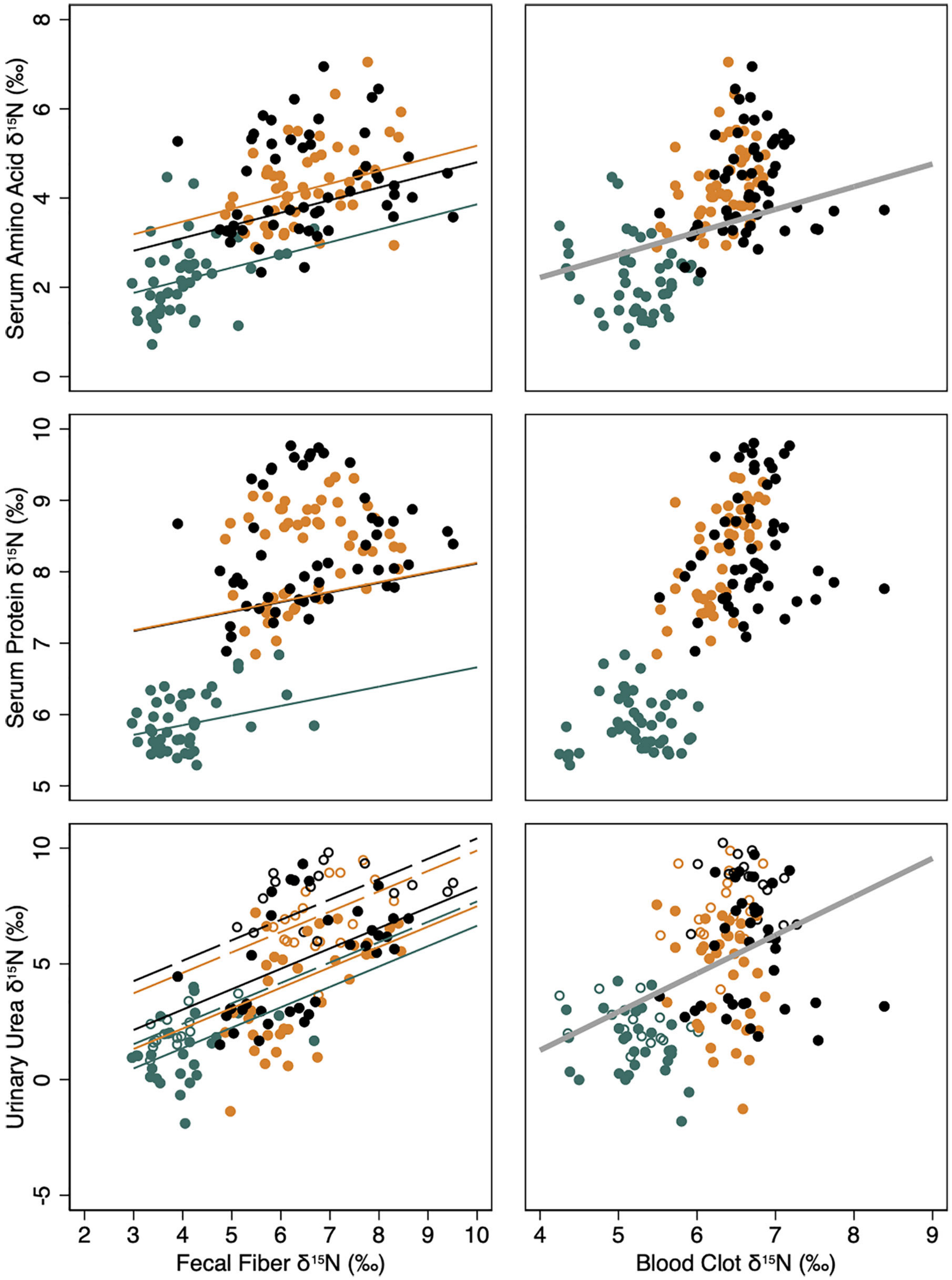

FIGURE 3 | Isotopic pools of body N [δ^{15}N (‰); Y_N] in serum amino acids, serum protein and urinary urea and their relationship to the respective isotopic value of the diet, indicated by fecal fiber (left column) or the body protein, indicated by clotted blood cells (right column). Lines indicate predicted linear relationships from mixed model regressions for female reindeer (black), caribou (orange), and muskoxen (green) in late winter from February to April of 2009 in Fairbanks, AK, United States. Solid lines and solid symbols indicate relationships and observations when food was provided *ad libitum* whereas dashed lines and open symbols indicate relationships and observations when food was restricted. Thick gray lines indicate linear relationships between body N pools and clotted blood cells as a single fixed effect among taxa. All regression models included individual animal (constant) and time (ordinal days; covariate) as random effects to account for repeated measures.

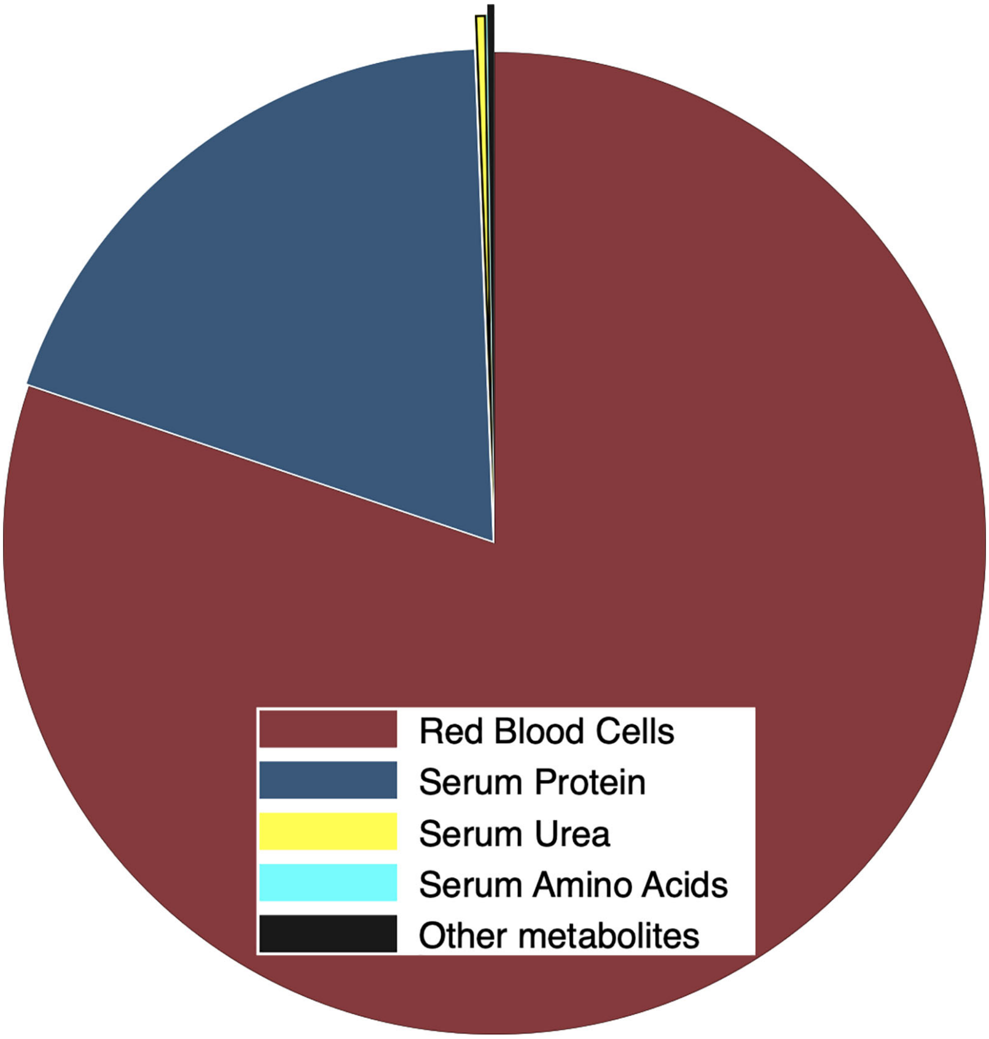

FIGURE 4 | Proportional distribution of total N ($g \cdot g^{-1}$) in whole blood from female reindeer during March 2009 in Fairbanks, AK, United States. Nitrogen was allocated to red cells (maroon), plasma protein (navy), free amino acids (cyan), and urea (yellow). Creatinine and other metabolites (black) were estimated as the residual N in blood plasma.

differently than tissue amino acids for urea formation. The isotopic correspondence between urea and diet was greater than that between amino acids and diet (+0.88 vs. +0.28‰ per unit change in fecal $\delta^{15}N$ value), which suggests that dietary amino acids are preferentially oxidized to urea in the liver. Amino acids flow to the liver through two major blood vessels – absorbed dietary amino acids are received at the liver via the portal vein whereas recirculating amino acids enter the liver via the hepatic artery (Barboza et al., 2009). Metabolic routing of amino acids can therefore spare body protein during winter. Furthermore, routing reduces energy costs by avoiding futile cycles of degradation and synthesis of non-essential amino acids.

Values for $\delta^{15}N$ of serum protein were affected by the dietary endpoint but much more slowly than the circulating amino acid pool that is the precursor for protein synthesis (+0.14 vs. +0.28‰ per unit change in fecal $\delta^{15}N$ value). Serum protein is a mix of molecules responsible for interorgan exchanges of amino acids and nutrients that collectively maintain the osmotic potential of blood (Madden and Whipple, 1940; Lobley et al., 2000). Consequently, serum proteins maintain fluid distributions between extracellular spaces of blood, lymph and tissue. Fasting did not affect $\delta^{15}N$ values of serum protein, which is consistent with the relatively large size of this metabolic pool (**Figure 4**). Serum protein values for $\delta^{15}N$ were greater than those of the blood clot in all three taxa in this study, which suggests that the N in this diverse pool of protein was derived from recirculating body proteins (Anderson, 2002; Schaller et al., 2008). However, variation in $\delta^{15}N$ of serum protein was not related to that of the body endpoint indicated by red blood cells. Similarly, serum protein values for $\delta^{15}N$ were not correlated with those of muscle in wild caribou, which suggests that serum protein operates as a separate pool of N that could be a labile store of amino acids for synthesis of fetal tissue in pregnancy (Taillon et al., 2013).

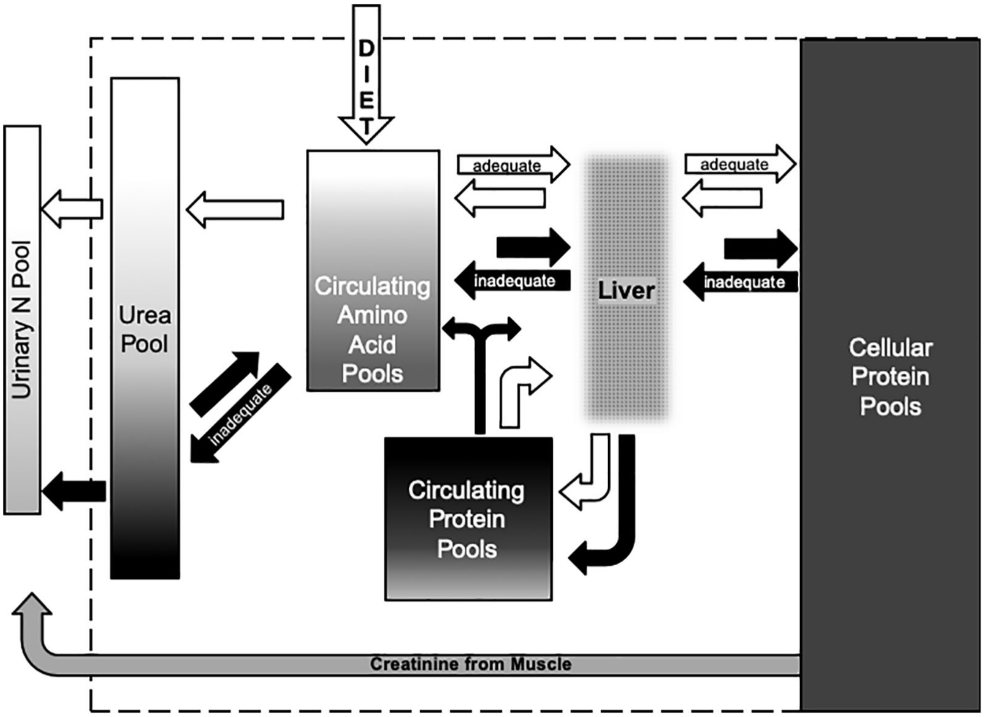

FIGURE 5 | Conceptual model of the flows of N among metabolic pools in the body and the excretion of N in urine from female ungulates during winter. White arrows indicate flows at adequate N balance when dietary N intake is at or above the requirements for maintaining the body and investing in reproductive tissues during winter. Black arrows indicate inadequate N balance when body N is mobilized to sustain body function and limit reproductive investment. Dietary N is absorbed as amino acids that enter the portal vein to the liver where the flow of essential and non-essential amino acids that are released into the hepatic vein are integrated with flows recirculated from the body to the liver via the hepatic artery. The liver also synthesizes serum proteins such as albumens from dietary and recirculating amino acids. Turnover of cellular proteins in other organs and muscles add and remove protein and amino acids from the circulation. Breakdown of circulating and cellular proteins to amino acids for energy substrates such as glucose results in oxidation of N to form urea that is excreted from the body when dietary N supplies are high (positive N balance) but conserved by recycling when supplies of N are low (negative N balance). Shading within the boxes that represent each pool indicates the range of δ^{15}N values. The large pool of N in cellular proteins of muscles and blood cells has δ^{15}N values that are higher than those of the diet. Values for δ^{15}N in amino acids are intermediate to the diet and cellular proteins whereas values for serum proteins often exceed those of blood cells. Values for δ^{15}N in urea vary with the source of N – values are lowest when amino acids from the diet are oxidized and highest when those amino acids are released from catabolism of proteins in cells or sera. Nitrogen excreted in urine includes urea and other metabolites such as creatinine – an energy substrate from muscle with δ^{15}N values that reflect the values of proteins in those cells.

Model of N Dynamics

The conceptual relationships between the metabolic pools of N and diet (**Figure 5**) characterize flows when body N is maintained or gained at positive N balance (i.e., when diet is sufficient to sustain the body store of protein for reproductive investments in the fetus during winter and in milk during spring). More importantly, the model characterizes flows of N when reproductive investments would be compromised by depletion of body N in a negative N balance. Values of δ^{15}N in urinary urea can indicate short term (∼1 day) declines from adequate to negative N balance when diet is stable (Gustine et al., 2012). Amino acids may reflect medium term (∼7 days) switches in diet at positive balance but it may not indicate negative balance very quickly because it is buffered by intermediary metabolism. Similarly, clots can indicate changes in dietary values of δ^{15}N over the long term (∼30–90 days) but isotopic changes in this large metabolic pool of N may be quite subtle. The projected effect of changing N balance on the average δ^{15}N value of female reindeer was less than 1‰ when animals were held at positive or negative N balance observed on a high N diet during winter (Barboza and Parker, 2006).

Serum protein may provide the best indication of a declining body protein store in northern ungulates. Gustine et al. (2014a) hypothesized that serum protein could be compared with red blood cells to indicate relative increases in δ^{15}N value of the circulating protein. However, the experimental data we present in this study indicates that the δ^{15}N value of serum protein would probably decline not increase when N balance was negative. Removal of serum proteins from circulation by deposition in tissue or by oxidation to urea would remove N with δ^{15}N values that exceed the values of dietary and circulating amino acids and muscle. Consequently, serum protein concentrations would be maintained by replacement from diet or tissue proteins with lower δ^{15}N values that would likewise decrease the average value of the serum protein pool. Gustine et al. (2014a) reported values of δ^{15}N in serum protein that were negatively related to those of red blood cells in female caribou during severe winters that resulted in low body mass of mothers and birth mass of their calves. Conditions that would predispose animals to depletion of body protein were associated with serum protein values that declined as isotopic values for red blood cells rose.

The investment of body stores in reproduction entails more than one currency because those investments are not just the loss of maternal body mass but a controlled mobilization of energy, protein, and minerals (Barboza and Parker, 2006). Body capital is used sparingly in relation to the supplies from diet and the costs of activity and weather. Female reindeer, caribou, and muskoxen are able to mobilize energy from body fat while conserving and reallocating protein and minerals to their offspring during pregnancy and lactation when food supplies are low in abundance and quality. Body protein is not an inert depot but a dynamic pool of nitrogen in cellular and circulating proteins and metabolites. Conservation of protein is therefore a process of controlling N flows rather than simply managing the loss from a static reserve (Barboza et al., 2009). Conservation of protein is achieved in two ways through the liver: control of flows to oxidation and routing protein in circulation. Firstly, dietary amino acids are burned before stored amino acids, that is stored amino acids are spared from oxidation to urea and that oxidized urea N is recycled. Secondly, the distribution of N from tissues such as muscle to the fetus is apparently managed with circulating proteins (Sand et al., 2015).

Capital breeding allows animals to uncouple primary production of food supplies from their reproductive investments to allow longer times for development and to facilitate flexibility in timing of births (Gustine et al., 2017). Capital breeding is most evident in northern ungulates, phocid seals, whales, and bears that schedule pregnancy or lactation when food intakes are low. However, most animals use some body stores to offset dietary supplies of lipid, protein, minerals, and vitamins when food supplies are low (McCue, 2010). Some degree of capital investment is involved in energy or nutrients for most animals. In muskoxen, copper is transferred from maternal stores in the liver to establish large hepatic stores of copper that the neonate uses until weaning (Rombach et al., 2002b; Swor, 2002). Calcium from bone is routed to developing offspring and milk in most mammals – the delay of restoring bone calcium from diet may be a few days in small animals but a season in large ungulates (Baksi and Newbrey, 1989; Schmidt and Hood, 2014). Behavioral and metabolic adaptations for intermittent feeding allow animals to reduce exposure to weather extremes or predation over diurnal to seasonal scales of time (Barboza and Hume, 2006). Capital breeding extends the duration and intensity of those metabolic adaptations to accomplish both survival and reproduction. In northern ungulates, the strategy is constrained by environmental variance in the quality and duration of forage available in summer and the capacity to store enough nutrients and energy for the variable demands of winter in both migratory and sedentary populations. Species that are widely distributed from north to south such as white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) alter seasonal movements in relation to forage availability and body stores to balance maternal survival and maternal investments in offspring (van Beest et al., 2013; Monteith et al., 2014; Henderson et al., 2017). Summer foraging conditions and winter severity affect reproductive rates in northern populations of white-tailed deer (Simard et al., 2014; Ayotte et al., 2019), which is consistent with a capital breeding strategy that begins in a narrow seasonal window of mating before winter. Southern populations of white-tailed deer mate and birth over wider seasonal windows than their northern conspecifics (Bronson, 1985). Southern deer may be able to use the dietary income of energy and nutrients from forage available in winter and spring for pregnancy and lactation whereas growth and maturation may be constrained by summer forage production especially in stochastic environments with high temperatures and low precipitation (Ginnett and Young, 2000; Cain et al., 2006; DeYoung et al., 2019). Survival in these drought prone environments is favored by conservation of body water and body protein through the same metabolic routes that limit oxidation and facilitate recycling of body N in northern ungulates during winter (Barboza et al., 2009).

DATA AVAILABILITY STATEMENT

The data are summarized in the **Supplementary Table S1** of the **Supplementary Material** and are available at https://doi.org/10.18738/T8/MCNOWH.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care and Use Committee, University of Alaska Fairbanks (Protocol: 06-049).

AUTHOR CONTRIBUTIONS

PB and DG designed the study. PB, RS, DG, and JA were responsible for animal handling and sample collection. JA and RS were responsible for laboratory analysis. PB analyzed the data and prepared the manuscript with RS. The manuscript was reviewed by all authors and revised by the corresponding author to address all comments.

FUNDING

This research was supported by the Institute of Arctic Biology, University of Alaska Fairbanks. This publication was prepared with support from Boone & Crockett Club Dr. James H. "Red" Duke Endowment for Wildlife Conservation and Policy at Texas A&M University.

ACKNOWLEDGMENTS

T. Howe and L. Oliver assisted with laboratory analysis. J. Jack assisted with animal handling.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00150/full#supplementary-material

REFERENCES

Anderson, N. L. (2002). The human plasma proteome: history, character, and diagnostic prospects. *Mol. Cel. Proteomics* 1, 845–867. doi: 10.1074/mcp.R200007-MCP200

Ayotte, P., Simard, M. A., and Cote, S. D. (2019). Reproductive plasticity of female white-tailed deer at high density and under harsh climatic conditions. *Oecologia* 189, 661–673. doi: 10.1007/s00442-019-04337-4339

Baksi, S. N., and Newbrey, J. W. (1989). Bone metabolism during antler growth in female reindeer. *Calcified Tissue Int.* 45, 314–317. doi: 10.1007/BF02556025

Barboza, P. S., Farley, S. D., and Robbins, C. T. (1997). Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus* and *U.arctos*). *Can. J. Zool.* 75, 2129–2136.

Barboza, P. S., Hartbauer, D. W., Hauer, W. E., and Blake, J. E. (2004). Polygynous mating impairs body condition and homeostasis in male reindeer (*Rangifer tarandus* tarandus). *J. Comp. Physiol. B* 174, 309–317. doi: 10.1007/s00360-004-0416-6

Barboza, P. S., and Hume, I. D. (2006). Physiology of intermittent feeding: integrating responses of vertebrates to nutritional deficit and excess. *Physiol. Biochem. Zool.* 79, 250–264. doi: 10.1086/499984

Barboza, P. S., and Parker, K. L. (2006). Body protein stores and isotopic indicators of N balance in female reindeer (*Rangifer tarandus*) during winter. *Physiol. Biochem. Zool.* 79, 628–644. doi: 10.1086/502811

Barboza, P. S., and Parker, K. L. (2008). Allocating protein to reproduction in arctic reindeer and caribou. *Physiol. Biochem. Zool.* 81, 835–855. doi: 10.1086/590414

Barboza, P. S., Parker, K. L., and Hume, I. D. (2009). *Integrative Wildlife Nutrition*. Heidelberg: Springer - Verlag.

Barboza, P. S., VanSomeren, L. L., Gustine, D. D., and Bret-Harte, M. S. (2018). The nitrogen window for arctic herbivores: plant phenology and protein gain of migratory caribou (*Rangifer tarandus*). *Ecosphere* 9:e02073.

Berger, J., Hartway, C., Gruzdev, A., and Johnson, M. (2018). Climate degradation and extreme icing events constrain life in cold-adapted mammals. *Sci. Rep.* 8:1156. doi: 10.1038/s41598-018-19416-19419

Blix, A. S. (2005). *Arctic Animals and their Adaptations to Life on the Edge*. Trondheim: Tapir Academic Press.

Bronson, F. H. (1985). Mammalian reproduction: an ecological perspective. *Biol. Reprod.* 32, 1–26. doi: 10.1095/biolreprod32.1.1

Cain, J. W. III, Krausman, P. R., Rosenstock, S. S., and Turner, J. C. (2006). Mechanisms of thermoregulation and water balance in desert ungulates. *Wildlife Soc. Bull.* 34, 570–581.

Denryter, K. A., Cook, R. C., Cook, J. G., and Parker, K. L. (2017). Straight from the caribou's (*Rangifer tarandus*) mouth: detailed observations of tame caribou reveal new insights into summer–autumn diets. *Can. J. Zool.* 95, 81–94. doi: 10.1139/cjz-2016-2114

Desforges, J.-P., Marques, G. M., Beumer, L. T., Chimienti, M., Blake, J., Rowell, J. E., et al. (2019). Quantification of the full lifecycle bioenergetics of a large mammal in the high arctic. *Ecol. Model.* 401, 27–39. doi: 10.1016/j.ecolmodel.2019.03.013

DeYoung, C. A., Fulbright, T. E., Hewitt, D. G., Wester, D. B., Draeger, D. A., DeYoung, C. A., et al. (2019). Linking white-tailed deer density, nutrition, and vegetation in a stochastic environment. *Wildlife Monogr.* 202, 1–63. doi: 10.1002/wmon.1040

Ginnett, T. F., and Young, E. L. B. (2000). Stochastic recruitment in white-tailed deer along an environmental gradient. *J. Wildlife Manag.* 64, 713–720. doi: 10.2307/3802741

Gustine, D. D., Barboza, P. S., Adams, L. G., Farnell, R. G., and Parker, K. L. (2011a). An isotopic approach to measuring nitrogen balance in caribou. *J. Wildlife Manag.* 75, 178–188. doi: 10.1002/jwmg.11

Gustine, D. D., Barboza, P. S., Lawler, J. P., Arthur, S. M., Shults, B. S., Persons, K., et al. (2011b). Characteristics of foraging sites and protein status in wintering muskoxen: insights from isotopes of nitrogen. *Oikos* 120, 1546–1556. doi: 10.1111/j.1600-0706.2011.19215.x

Gustine, D. D., Barboza, P. S., Adams, L. G., Griffith, D. B., Cameron, R. D., and Whitten, K. R. (2017). Advancing the match-mismatch framework for large herbivores in the arctic: evaluating the evidence for a trophic mismatch in caribou. *PLoS One* 12:e0171807. doi: 10.1371/journal.pone.0171807

Gustine, D. D., Barboza, P. S., Adams, L. G., and Wolf, N. B. (2014a). Environmental and physiological influences to isotopic ratios of N and protein status in a montane ungulate in winter. *PLoS One* 9:e103471. doi: 10.1371/journal.pone.0103471

Gustine, D. D., Barboza, P. S., Addison, J., Shively, R., and Oliver, L. (2014b). Isotopic nitrogen in fecal fiber as an indicator of winter diet in caribou and muskoxen. *Rapid Commun. Mass Spectrom.* 28, 625–634. doi: 10.1002/rcm.6825

Gustine, D. D., Barboza, P. S., and Lawler, J. P. (2010). Dynamics of body protein and the implications for reproduction in captive muskoxen (*Ovibos moschatus*) during winter. *Physiol. Biochem. Zool.* 83, 687–697. doi: 10.1086/652729

Gustine, D. D., Barboza, P. S., Lawler, J. P., Adams, L. G., Parker, K. L., Arthur, S. M., et al. (2012). Diversity of nitrogen isotopes and protein status in caribou: implications for monitoring northern ungulates. *J. Mammal.* 93, 778–790. doi: 10.1644/11-mamm-a-164.1

Gustine, D. D., Parker, K. L., and Heard, D. C. (2007). Using ultrasound measurements of rump fat to assess nutritional condition of woodland caribou in Northern British Columbia. Canada. *Rangifer* 17, 249–256.

Henderson, C. R., Mitchell, M. S., Myers, W. L., Lukacs, P. M., and Nelson, G. P. (2017). Attributes of seasonal home range influence choice of migratory strategy in white-tailed deer. *J. Mammal.* 99, 89–96. doi: 10.1093/jmammal/gyx148/4645407

Kazmin, V. D., Kholod, S. S., Rozenfeld, S. B., and Abaturov, B. D. (2011). Current state of forage resources and feeding of reindeer (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) in the arctic tundras of Wrangel Island. *Biol. Bull.* 38, 747–753. doi: 10.1134/s106235901107003x

Kristensen, D. K., Kristensen, E., Forchhammer, M. C., Michelsen, A., and Schmidt, N. M. (2011). Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C3 plants, faeces, and wool. *Can. J. Zool.* 89, 892–899. doi: 10.1139/z11-073

Lapierre, H., Ouellet, D. R., Berthiaume, R., Martineau, R., Holtrop, G., and Lobley, G. E. (2008). Distribution of 15N in amino acids during 15N-leucine infusion: impact on the estimation of endogenous flows in dairy cows. *J. Dairy Sci.* 91, 2702–2714. doi: 10.3168/jds.2007-2871

Lechner, I., Barboza, P. S., Collins, W., Fritz, J., Gunther, D., Hattendorf, B., et al. (2010). Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. taurus), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents stratification. *Comp. Biochem. Physiol. A* 155, 211–222. doi: 10.1016/j.cbpa.2009.10.040

Lobley, G. E., Milano, G. D., and van der Walt, J. G. (2000). "The liver: integrator of nitrogen metabolism," in *Ruminant Physiology: Digestion, Metabolism, Growth and Reproduction*, ed. P. B. Cronjé (Wallingford: CAB International), 149–167.

Madden, S. C., and Whipple, G. H. (1940). Plasma protreins: their source, production and utilization. *Physiol. Rev.* 20, 194–217.

McCue, M. D. (2010). Starvation physiology: reviewing the different strategies animals use to survive a common challenge. *Comp. Biochem. Physiol. Part A Mol. Integrat. Physiol.* 156, 1–18. doi: 10.1016/j.cbpa.2010.01.002

Milner, J. M., Stien, A., Irvine, R. J., Albon, S. D., Langvatn, R., and Ropstad, E. (2003). Body condition in Svalbard reindeer and the use of blood parameters as indicators of condition and fitness. *Can. J. Zool.* 81, 1566–1578.

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monogr.* 186, 1–56.

Mosbacher, J. B., Michelsen, A., Stelvig, M., Hendrichsen, D. K., and Schmidt, N. M. (2016). Show me your rump hair and i will tell you what you ate - the dietary history of muskoxen (*Ovibos moschatus*) revealed by sequential stable isotope analysis of guard hairs. *PLoS One* 11:e0152874. doi: 10.1371/journal.pone.0152874

Munn, A. J., Barboza, P. S., and Dehn, J. (2009). Sensible heat loss from muskoxen (*Ovibos moschatus*) feeding in winter: small calves are not at a thermal disadvantage compared with adult cows. *Physiol. Biochem. Zool.* 82, 455–467. doi: 10.1086/605400

Nolan, J. V., and Leng, R. A. (1972). Dynamic aspects of ammonia and urea metabolism in sheep. *Br. J. Nutr.* 27, 177–193. doi: 10.1079/bjn19720081

Oster, K. W., Barboza, P. S., Gustine, D. D., Joly, K., and Shively, R. D. (2018). Mineral constraints on arctic caribou (*Rangifer tarandus*): a spatial and phenological perspective. *Ecosphere* 9:e02160. doi: 10.1002/ecs2.2160

Paoli, A., Weladji, R. B., Holand, Ø, Kumpula, J., and Jia, Z.-Y. (2019). The onset in spring and the end in autumn of the thermal and vegetative growing season affect calving time and reproductive success in reindeer. *Curr. Zool.* 66, 123–134. doi: 10.1093/cz/zoz032

Parker, K. L., Barboza, P. S., and Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* 23, 57–69.

Parker, K. L., Barboza, P. S., and Stephenson, T. R. (2005). Protein conservation of female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. *J. Mammal.* 86, 610–622.

Peltier, T. C., and Barboza, P. S. (2003). Growth in an arctic grazer: effects of sex and dietary protein on yearling muskoxen. *J. Mammal.* 84, 915–925.

Peltier, T. C., Barboza, P. S., and Blake, J. E. (2003). Seasonal hyperphagia does not reduce digestive efficiency in an arctic grazer. *Physiol Biochem. Zool.* 76, 471–483. doi: 10.1086/377744

Rombach, E. P., Barboza, P. S., and Blake, J. E. (2002a). Costs of gestation in an Arctic ruminant: copper reserves in muskoxen. *Comp. Biochem. Physiol.* 134C, 157–168. doi: 10.1016/s1532-0456(02)00222-3

Rombach, E. P., Barboza, P. S., and Blake, J. E. (2002b). Utilization of copper during lactation and neonatal development in muskoxen. *Can. J. Zool.* 80, 1460–1469.

Sand, K. M. K., Bern, M., Nilsen, J., Noordzij, H. T., Sandlie, I., and Andersen, J. T. (2015). Unraveling the interaction between FcRn and albumin: opportunities for design of albumin-based therapeutics. *Front. Immunol.* 5:682. doi: 10.3389/fimmu.2014.00682

Schaller, J., Gerber, S., Kampfer, U., Lejon, S., and Trachsel, C. (2008). *Human Blood Plasma Proteins Structure and Function*. Chichester: John Wiley and Sons.

Schmidt, C. M., and Hood, W. R. (2014). Bone loss is a physiological cost of reproduction in white-footed mice (*Peromyscus leucopus*). *Mamm. Biol. Z. Säugetie.* 79, 96–100. doi: 10.1016/j.mambio.2013.09.003

Schmidt, N. M., Grøndahl, C., Evans, A. L., Desforges, J.-P., Blake, J., Hansen, L. H., et al. (2020). On the interplay between hypothermia and reproduction in a high arctic ungulate. *Sci. Rep.* 10:1514. doi: 10.1038/s41598-020-58298-58298

Sikes, R. S. (2016). 2016 guidelines of the American society of mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688. doi: 10.1093/jmammal/gyw078

Simard, M. A., Huot, J., de Bellefeuille, S., and Côté, S. D. (2014). Linking conception and weaning success with environmental variation and female body condition in a northern ungulate. *J. Mammal.* 95, 311–327. doi: 10.1644/13-mamm-a-036

Swor, R. M. (2002). *The Effect of Marginal Copper Diet on Muskox Calf Growth and Immune Function*. Fairbanks, AK: University of Alaska.

Taillon, J., Barboza, P. S., and Cote, S. D. (2013). Nitrogen allocation to offspring and milk production in a capital breeder. *Ecology* 94, 1815–1827. doi: 10.1890/12-1424.1

Taillon, J., Brodeur, V., Festa-Bianchet, M., and Côté, S. D. (2011). Variation in body condition of migratory caribou at calving and weaning: which measures should we use? *Ecoscience* 18, 295–303. doi: 10.2980/18-3-3447

Taillon, J., Brodeur, V., Festa-Bianchet, M., and Côté, S. D. (2012). Is mother condition related to offspring condition in migratory caribou (*Rangifer tarandus*) at calving and weaning? *Can. J. Zool.* 90, 393–402. doi: 10.1139/z2012-001

Thompson, D. P., and Barboza, P. S. (2017). Seasonal energy and protein requirements for siberian reindeer (*Rangifer tarandus*). *J. Mammal.* 98, 1558–1567. doi: 10.1093/jmammal/gyx132

Thompson, I. D., Wiebe, P. A., Mallon, E., Rodgers, A. R., Fryxell, J. M., Baker, J. A., et al. (2015). Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus* tarandus) in boreal forests in Ontario. *Can. J. Zool.* 93, 87–98. doi: 10.1139/cjz-2014-2140

Ungerfeld, E. M., Leigh, M. B., Forster, R. J., and Barboza, P. S. (2018). Influence of season and diet on fiber digestion and bacterial community structure in the rumen of muskoxen (*Ovibos moschatus*). *Microorganisms* 6:89. doi: 10.3390/microorganisms6030089

van Beest, F. M., Vander Wal, E., Stronen, A. V., and Brook, R. K. (2013). Factors driving variation in movement rate and seasonality of sympatric ungulates. *J. Mammal.* 94, 691–701. doi: 10.1644/12-mamm-a-080.1

Vansomeren, L. L., Barboza, P. S., Gustine, D. D., and Bret-Harte, M. S. (2017). Variation in del15N and del13C values of forages for arctic caribou: effects of location, phenology and simulated digesti. *Rapid. Commun. Mass Spectrom.* 31, 813–820. doi: 10.1002/rcm.7849

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 10 June 2020
doi: 10.3389/fevo.2020.00128

Disassembled Food Webs and Messy Projections: Modern Ungulate Communities in the Face of Unabating Human Population Growth

Joel Berger[1,2]*, *Tshewang Wangchuk*[3,4], *Cristobal Briceño*[5], *Alejandro Vila*[6]* and *Joanna E. Lambert*[7]

[1] Department FWC-Biology, Colorado State University, Fort Collins, CO, United States, [2] Wildlife Conservation Society–Global Program, The Bronx, NY, United States, [3] Bhutan Foundation, Washington, DC, United States, [4] Bhutan Foundation, Thimphu, Bhutan, [5] ConserLab, Departamento de Medicina Preventiva Animal, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile, [6] Wildlife Conservation Society, Chile Program, Punta Arenas, Chile, [7] Program in Environmental Sciences, Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, United States

OPEN ACCESS

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Stan Boutin,
University of Alberta, Canada
Matt W. Hayward,
University of Newcastle, Australia
Evelyn Hunter Merrill,
University of Alberta, Canada

***Correspondence:**
Joel Berger
jberger@wcs.org
Alejandro Vila
avila@wcs.org

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 28 January 2020
Accepted: 20 April 2020
Published: 10 June 2020

Citation:
Berger J, Wangchuk T, Briceño C,
Vila A and Lambert JE (2020)
Disassembled Food Webs and Messy
Projections: Modern Ungulate
Communities in the Face
of Unabating Human Population
Growth. Front. Ecol. Evol. 8:128.
doi: 10.3389/fevo.2020.00128

The human population grows inexorably. When Charles Darwin explored the southern cone of South America in 1830, fewer than 1.2 billion people inhabited Earth. When Ehrlich's *Population Bomb* appeared in 1968, there were ∼3.5 billion people. We approach eight billion today, and biospheric impacts do not abate. We have affected most life forms through climate modification, harvest, erasure and fragmentation of habitat, disease, and the casting of alien species. Given the lack of abatement in human population growth, herein we focus on the modalities of ecological disruption–direct and indirect–that mitigate the changing role of ungulates in landscapes. Much of what was once generally predictable in terms of pattern and process is no longer. Offshore climatic events have strong onshore consequences, as exemplified by toxic algal blooms in the Patagonian Pacific. These have diminished the harvest of fish and likely resulted in fishermen using dogs to hunt huemul (*Hippocamelus bisulcus*), the most endangered large terrestrial mammal of the Western Hemisphere. Similarly, human economies foment change in the Himalayan realm and Gobi Desert by increasing the number of cashmere-producing goats, and where dogs that once followed tourists or guarded livestock now hunt a half-dozen threatened, endangered, and rare ungulates, including kiang (*Equus kiang*), chiru (*Pantholops hodgsonii*), saiga (*Saiga tatarica*), and takin (*Budorcas taxicolor*), spread disease, and displace snow leopards (*Panthera uncia*). In North America's Great Basin Desert, 100 years of intense livestock grazing created a phase shift by which changed plant communities enabled mule deer (*Odocoileus hemionus*) colonization. An altered predator–prey system ensued with the arrival of pumas (*Puma concolor*). Patterns of resilience postulated by Holling (1973) become more difficult to witness in the absence of humans as our domination of

Earth destabilizes systems beyond return points. These include ungulates both in and out of protected areas. Consequently, only messy projections of future community reorganization seem reasonable, whether related to *food webs* or *assembly rules* that once governed ungulate communities of the very recent past.

Keywords: human disturbance, trophic relationships, apex carnivores, mammals, endangered species, predator prey, climate change

INTRODUCTION

The human population is increasing inexorably. When Charles Darwin explored South America in 1830, fewer than 1.2 billion people inhabited Earth (Goldewijk, 2005). One hundred forty years later, when *The Population Bomb* (Ehrlich, 1968) appeared, the population was ∼3.5 billion. Now, only 50 years since, we approach eight billion; 30 years hence we will near 10 billion (United Nations Department of Economic and Social Affairs Population Division, 2019), and the biospheric impacts do not abate. Globally, livestock and people constitute 97% of the world's mammal biomass (Thomas, 2017). We have affected most life forms, restructuring ecological dynamics on six continents not only by climate modification but also by erasing species and fragmenting their habitats and by casting of alien species and disease. So great are the similarities between marine and terrestrial systems that a heuristic contrast using hoofed mammals would reveal that green turtles and whales were the equivalent of bison (*Bison bison*) or wildebeest (*Connochaetes taurinus*), yet all suffered reductions in excess of 99% (Springer et al., 2003; Jackson, 2008; Sanderson et al., 2008).

Ungulates, many of which have regularly played trophic roles through top-down and bottom-up effects, are clearly among those assemblages that have been impacted by anthropogenic pressures (Ripple et al., 2015; Bowyer et al., 2019). Although systems involving these large and small hoofed mammals have operated unhinged from humans, or have only been slightly affected by them/us for millennia, they no longer operate evolutionarily or ecologically as they did across deep time (Vrba and Schaller, 2000). Even ecological baselines that once framed our knowledge of the recent past are often of little modern relevance (Lovejoy and Hannah, 2019). The huemul (*Hippocamelus bisulcus*), for instance, a cervid that Darwin observed on Patagonia's eastern Atlantic shore and which extended across the Andes to the Pacific, no longer exists across 99% of their range (Eisenberg and Redford, 1989; Diaz, 1993; Vila et al., 2006). Six of the seven species of wild equids are on the IUCN Red List as endangered.

While the best-studied large protected areas–Yellowstone, Serengeti, and Kruger–offer essential baselines for understanding the recent past in which species had persisted with only slight human impact (Arcese and Sinclair, 1997; Smith et al., 2003), these sites today are but mere postage stamps for the once universal conditions with intact prey and predator assemblages. Although these places no longer have human harvest, the concept of ecological 'stability' was never meant to be a strong hallmark of these protected areas (Sinclair et al., 2010). Today, by definition, we co-exist with rapid biological change. Its pace now and into the future (will) only escalate(s).

Given the lack of abatement in human population growth and the immeasurable impacts, we focus herein on the modalities of disruption–direct and indirect–that mitigate the changing role of ungulates in global ecosystems (**Figure 1**). We evaluate what is known about various disruptors and how these altered community dynamics and structure the nature of ecological interactions now and likely will in coming decades. Much of what was once generally predictable in terms of pattern and process is no longer, and ecological surprises are regular occurrences (Doak et al., 2008). Consequently, only messy projections of future community reassembly are reasonable. Below, we first illustrate the limitations of our predictive power in interpreting assembly rules in deep time. We then move to extant systems, using the interrelated themes of *food webs* and *assembly*, and describe the human-induced extrinsic and intrinsic variables that shape modern ungulate communities and attendant challenges (**Figure 1**). We close by pointing to lessons of the past and reluctantly suggest that, unless human behavior changes in unprecedented ways, future communities of ungulates will not look much like those of the recent past or even today.

ASSEMBLY AND DISASSEMBLY RULES IN DEEP TIME

That geological and climatic perturbations create evolutionary opportunity for plants and animals has been well appreciated across parts of three centuries (Darwin, 1859; Wallace, 1876; Simpson, 1944; Webb and Barnosky, 1989). A scrambling of species with vastly different origins not only alters community composition but also leads to extinction and speciation, innovation, and altered niches. Prominent cases involving ungulates include climate-induced "turnover pulses" (*sensu* Vrba, 1993) of East African antelopes (2.8–2.5 mya) and the ecological reassembly of camelids, suids, cervids, and tapirids that resulted once the Panamanian land bridge re-connected the Americas (∼3 mya) (Webb, 2006). More ephemeral connections farther north involved Beringia, which ultimately enabled the entry of human colonists of Asian descent into the Americas (Webb, 2006). The patterns by which communities assemble or fall apart are often context specific and governed by both type of ecological disruptor and species composition with time as a mitigating factor (Strong et al., 1984; Croll et al., 2005; Woodroffe and Ginsberg, 2005). Yet beyond some generalities of species–area relationships and competition theory, the fuzziness of past rules may be ineffective

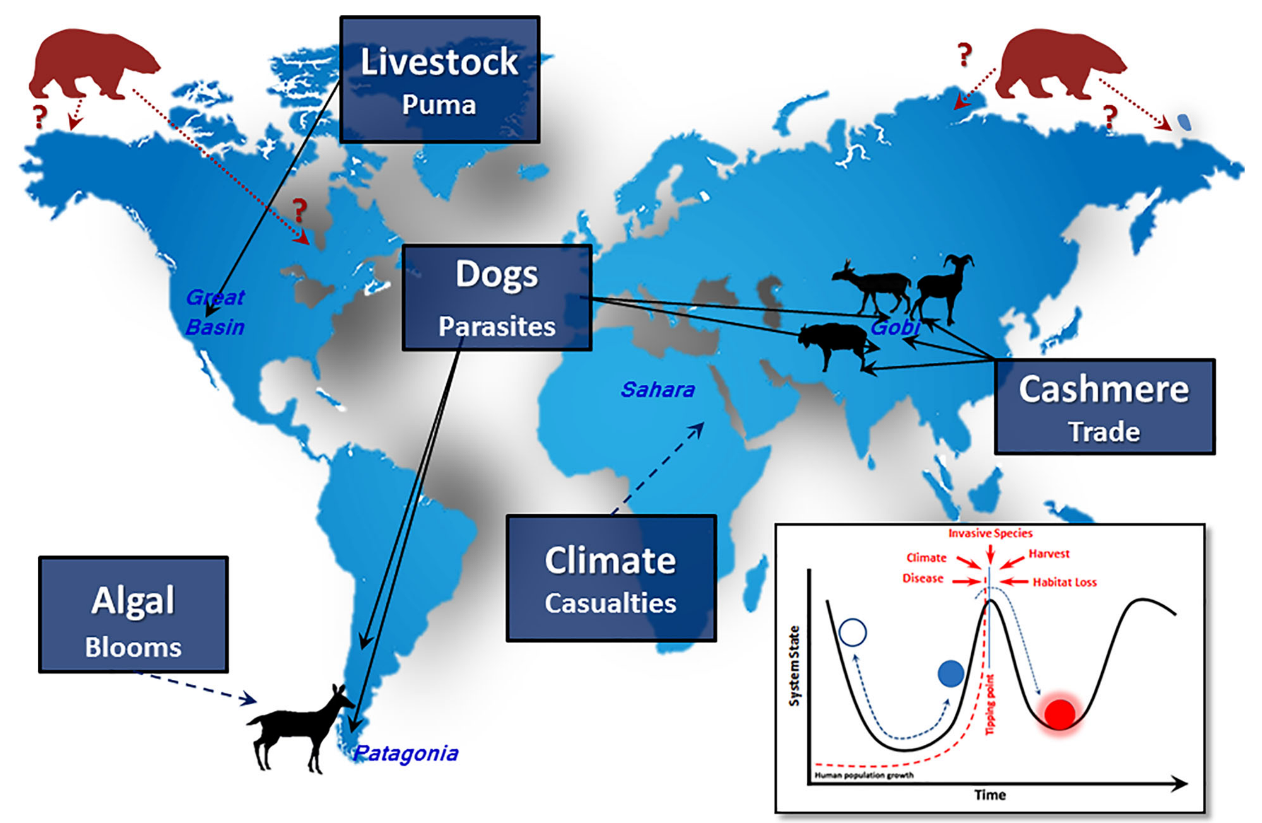

FIGURE 1 | Overview of locations, ungulates, and ecological disruptors. Species silhouettes are pointed out in the text. Inset–modification of Holling's (1986) resiliency model with biotic and climate disruptors coupled with exponential human growth.

predictors of future ungulate communities. The few rules available today for predicting winners and losers in our briskly changing landscapes may not be much other than the admitted oversimplification that generalists tend to out-prosper specialists in human-dominated landscapes (Roemer et al., 2009).

Deeper in time and prior to any human impacts, it is still unclear whether geological events coupled with the loss of species predictably yield to patterned replacement. With 50 million years of mammalian evolution, some ecosystems shared similarities where globally proboscidean-sized species occurred on every continent (Smith and Lyons, 2013; Smith et al., 2015). In other cases, replacement of lost species or colonization of new lands follows varied pathways with uncertain and stochastic representation (Graham and Lundelius, 1984; Strong et al., 1984). Even where the loss or expansion of a species opened or reduced habitat for others, it has not been especially clear which scenario would lead to more species packing or the numerical proliferation of a single dominate one. The African buffalo (*Syncerus caffer*), for example, collapsed across parts of Africa due to anthrax early in the 20th century while zebra and gazelles flourished (Sinclair et al., 2010), but in North America, why bison became so abundant and whether this occurred at the expense of other species, humans included (Noss, 2012), or may have been predisposed by others is subject to diverse interpretations (MacPhee, 2019). In South America, perhaps it was its long-isolated history with a concomitant reduction in browsing competitors and the loss of equids and proboscideans that enabled the radiation of cervids into some 15 species and into unusual previously unoccupied niches, including huemul (Wemmer, 1987; Geist, 1998; Weber and Gonzalez, 2003; Vila et al., 2006, 2010). The tempo and the mode of past change have guided our understanding of ecosystem structure.

Whatever ecological stability may have once occurred in deeper time is widely challenged today by disturbance dynamics and runaway human population growth (**Figure 1**). Holling (1973, 1986) refocused attention on resiliency and argued it was the magnitude and the variance incumbent within a system that, coupled with disturbance, could shift it to a different state. It is the shape and the scale of modern disruptors and subsequent altered states that complicate projections about stasis and reorganization in future ecosystems that involve not only ungulates but also life support processes.

EXTANT UNGULATES WITH AND WITHOUT PREDATORS

Despite diversity, visibility, and global geography, much remains unknown about how the world's ~250 ungulates interact with their environments. Among the array of hoofed mammals are specialists and generalists, for which lifestyles and life histories vary based on size, digestive strategies, and vulnerability to predators (Jarman, 1974; Eisenberg, 1981; Barboza and Bowyer, 2000). Variation in body size can be extreme, from the 1- to 2-kg Javan mouse deer (*Tragulus javanicus*) to African elephants (*Loxodonta africana*) at nearly 7 tons. Regardless of size, ungulates carry the stamp of 'prey' which, by definition, connotes predation. Even adults of species like elephants and rhinos, once considered immune due to their extraordinary size, can become prey (Brain et al., 1999; Loveridge et al., 2006; Power and Compion, 2009), and they certainly defend their young from predators (Cunningham and Berger, 1997). Knowledge of such prey–predator interactions stems from large protected areas where these sorts of dynamics can unfold and be recorded.

The situation differs in most tropical, temperate, and sub-Arctic zones (Geldmann et al., 2014) as the world accentuates its transformation (Redford, 1992; Lovejoy and Hannah, 2019). Nearly 80% of the world's carnivores 15 kg or larger are in decline (Ripple et al., 2014; Bauer et al., 2015), and predation on larger ungulates has been relaxed or lost as a selective force. The world's largest felids, tigers and lions, are absent from ∼95% of their modern historic ranges (Walston et al., 2010), and wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) are gone from 85 to 100% of their respective North American desert and shrub biomes (Laliberte and Ripple, 2004). Although some carnivores may regulate ungulate populations under specific conditions (Sinclair et al., 2003; Bowyer et al., 2005), a complex interplay among many competing factors also operate (Sinclair et al., 2010; Pierce et al., 2012; Smith and Ferguson, 2012; Bowyer et al., 2014). Nevertheless, the history of large herbivore overabundance as a consequence of predator removal is a rich one (Leopold, 1949; Serrouya et al., 2011; Krausman and Bleich, 2013), with frequent suggestions that replacement by human hunting is functionally redundant–but this is not the case due to both direct and indirect effects (Berger, 2005). The notion that prey–predator dynamics have been strongly altered is not contestable nor is that change has consequence for understanding current and future trophic dynamics (Terborgh and Estes, 2010; Estes et al., 2012; Bonacic et al., 2019).

Super Abundant Herbivores

In the recent past, mostly within the last century or so, saiga (*Saiga tatarica*), white-tailed gazelles (*Gazella subgutturosa*), and perhaps guanacos (*Lama guanicoe*) exceeded one million individuals in Kazakhstan, Mongolia, and Patagonia (Milner-Gulland et al., 2001; Novaro et al., 2004; Novaro and Walker, 2005; Olson et al., 2005). The East and Southern African grasslands shared in uncountable numbers of wildebeest and springbok (*Antidorcas marsupialis*), and as recently as the 1980s, African elephants exceeded one million (Wittemyer et al., 2014). Such population numbers may arise due to migratory behavior where predation is avoided (Fryxell et al., 1988).

Among other super abundant large mammals were the North American bison, variously estimated at 10–30 million (Berger and Cunningham, 1994); their large populations may be associated with the colonization of a relatively young grassland system in the early Holocene (Geist, 1978; Stebbins, 1981; Sanderson et al., 2008). Whatever the multiple routes to numerical domination, it is unlikely that predation controlled their numbers or that of caribou, although some 80% plus of Arctic caribou (*Rangifer tarandus*) populations are in decline (Vors and Boyce, 2009). A few optimistic spots have emerged with saiga and guanacos rebounding (see below). While super abundant populations of some species occur today, these tend to be beneficiaries of habitat change like white-deer (*Odocoileus virginianus*) and feral species such as pigs (*Sus scrofa*) and horses (*Equus caballus*). The conditions of the past will not be those of the future.

Altered and Unaltered States of Ungulates

The default condition for most of earth's living history has been one of predator and/or parasite and prey accompanied by periods of slow and rapid change (Vermeij, 1993). Variations occur and lead to evolutionary innovation. Prior to massive human-induced habitat alterations, Wallace (1876) wondered about causes of differences among Malayan archipelago faunas and why different arrays of carnivores and ungulates assembled. Indeed some northern islands like Svalbard, those close to the Norwegian and Alaskan coastlines, and even those in Lake Superior have had moose (*Alces alces*) or caribou in the absence of large carnivores (Peterson, 2007; White et al., 2014). The native wild reindeer of Svalbard, for instance–following a pattern of dwarfism on islands–are small, about the size of pronghorn (*Antilocapra americana*), and fat and have only polar bears (*Ursus maritimus)* to flee (Tyler et al., 2008). While polar bear numbers increase on land due to reductions of sea ice, the overarching effects at the terrestrial food level (Rode et al., 2015a,b), especially as predators of ungulates, are not clear (**Figure 1**), although instances of predation on Arctic ungulates exist (Derocher et al., 2000; Berger, 2018).

With the advent of human weaponry and poisons, however, much of these past putatively non-human-influenced distributions of ungulates and carnivores are now intensely modified. All large carnivores suffer range reductions (Ripple et al., 2014; Wolf and Ripple, 2017), some so massively that these ungulates no longer face predators (Caro, 2005), a deviation from the default state of functional relationships (Soulé et al., 2003) which is achieved only by maintaining carnivores or restoring them (Pyare and Berger, 2003; Berger, 2007b). Wolves, for instance, were reintroduced back into Yellowstone after nearly 60 years of absence (Smith and Ferguson, 2012) and currently number ∼1,500 in the western United States; wolves are also now recovering in Scandinavia, France, Italy, Germany, and Eastern Europe (Boitani and Linnell, 2015). Also rebounding are cougars (*Puma concolor*) in the United States, expanding into Canada's Yukon and, at the hemisphere's other extreme, recolonizing parts of Patagonia where they had been previously extirpated (Walker and Novaro, 2010). Both wolves and pumas excise strong impacts on prey populations, sometimes because individuals learn to specialize and this behavior can reduce a population's growth rate for more than a generation (Festa-Bianchet et al., 2006), so can weather including North Pacific Oscillations, El Niño, and other off-shore currents (Hebblewhite, 2005; Post et al., 2009, 2013; Loe et al., 2016).

Ungulates and Recognition of Native Carnivores

Beyond climate, short-term weather events, and large carnivores, prey must have regularly dealt with altered predation regimes and (re-)colonizing native predators (as opposed to alien ones) (Blumstein and Daniel, 2005), but predation regimes change, and common examples involve coyotes (*Canis latrans*), which colonized the east coast of the United States, and golden jackals (*Canis aureus*), now moving into southern Europe (Ćirović et al., 2015; Trouwborst et al., 2015). Similarly, the colonization of the Great Basin a century ago brought cougars into a system where they had not occurred (see below), yet little was known about the potential sensitivity of prey to a novel carnivore as the dynamics of ecological systems shift.

A relaxation or cessation in predation due to human-caused extirpation of effective carnivores has consequences including diminished recognition of predation risk to putatively 'novel' carnivores (Berger et al., 2001b; Carthey and Blumstein, 2018). Field experiments and observations, however, reveal both curiosity and trepidation when exposed to carnivores (**Figure 2**), and those sensory modalities of predator recognition return once re-exposure happens (Berger, 2007a, 2008a). Conversely, demographic effects will proliferate as habitat is altered, carnivore ranges shift, and when prey lack appropriate or effective defense responses.

Meso-Predators and Ungulates

The persistence, loss, or return of large native carnivores has notable direct and indirect effects on ungulates *via* meso-predators. The interactions and the outcomes between different-sized carnivores and potential prey species in the Greater Yellowstone region of Wyoming are illustrative (**Figure 3**). During periods that persisted until the early and mid-19th century, including the present-day Yellowstone National Park (YNP; formally created in 1872), there were seven native ungulates including bison, pronghorn, and elk; four carnivores at 40 kg or more also existed–grizzly bears, black bears (*Ursus americanus*), cougars, and wolves. Elk, bison, and mule deer (*O. hemionus*) currently comprise important components of wolf diet, and both species of bears prey on neonate elk (Metz et al., 2012; Middleton et al., 2013). Wolves were extirpated in YNP and in adjacent Grand Teton National Park to the south; they were re-introduced into YNP in 1995 and re-colonized Grand Teton late in 1997. The 21st century fauna of YNP and adjacent Grand Teton now is probably much like what it was prior to modern weapons (**Figure 3**), although species abundances have certainly changed as hunting and other forces outside and within parks excise prominent effects (Smith et al., 2003, 2004). Fencing and habitat conversions, for instance, have blocked migration routes beyond parks (Berger et al., 2006), whereas the establishment of food stations to subsidize elk at 23 winter feed grounds through the Greater Yellowstone Ecosystem inflates their population sizes (Smith et al., 2004). That elk are key components of wolf diet (**Figure 3**) or that their high densities coupled with protection facilitate local coyote population sizes within the parks is not a leap of faith.

The inverse relationship between coyote and wolf density (Berger and Gese, 2007) suggests that coyote predation on pronghorn fawns is highest when protected and wolf densities are low–which is the case in protected areas like Grand Teton (**Figure 3**) where annual juvenile mortality approaches 90%; beyond park boundaries, it is less intense than in wolf-occupied areas (Berger et al., 2008). Similar patterns of fawn mortality occur in YNP (Barnowe-Meyer et al., 2009), where migration beyond the park no longer occurs (Berger et al., 2006). A complicating factor in understanding meso-predator release (Prugh et al., 2009) is that bottom-up forces also mediate prey availability, especially rodents and hares, the availability of which should affect predation rates in generalist carnivores like coyotes (Cypher and Spencer, 1998; Garrott et al., 2007).

In both Grand Teton and Yellowstone national parks, white-tailed jack rabbits (*Lepus townsendii*) are gone from the former and much reduced in the latter, a situation that has changed from when the parks were established (Berger, 2008b). Elsewhere hares are key dietary elements of coyotes, as once they were in the Teton region; when hares are of low density, predation on domestic animals may increase (Stoddart et al., 2001). Consequently, in both parks, it is uncertain whether high predation rates on pronghorn fawns are a consequence of the loss of alternative prey (hares) or if these arise because high ungulate densities reduce fawn hiding cover and therefore increase their vulnerability (Berger, 2008b). Regardless of the process–prey switching, apparent competition (see below), or something else, ecological dynamics within even protected areas have changed as a consequence of human management beyond boundaries.

As a global phenomenon, meso-predator release can impact ungulates (Brashares et al., 2010). Where grizzly bears have been lost or reduced, black bears subdue growth in moose populations through reduced recruitment of young (Schwartz and Franzmann, 1991); for elk, calf mortality can approach 50% (Zager and Beecham, 2006). In western Africa, where lions (*Panthera leo*) and leopards (*Panthera pardus*) have been extirpated, baboons (*Papio cynocephalus*) assume a meso-predator role and kill the young of different ungulates (Brashares et al., 2010). Elsewhere leopards apparently adopt a similar niche as their feasting on ungulates changes in the presence of tigers (*Panthera tigris*) (Harihar et al., 2011; Athreya et al., 2013). More broadly, only recently has data been accumulating on how meso-predator release alters predation on ungulate neonates or adults (Roemer et al., 2009; Grovenburg et al., 2011; Benson and Patterson, 2013; Quintana et al., 2016). Information also accumulates on how the loss or the retention of carnivores affects prey spacing, distribution, and movement (Ripple et al., 2014).

Buffer Zones and Unintended Vulnerability

In 1910, the Scottish-born naturalist John Muir traveled to Africa and suggested that human entry into the system mediated a complex three-way interaction among prey, predator, and people:

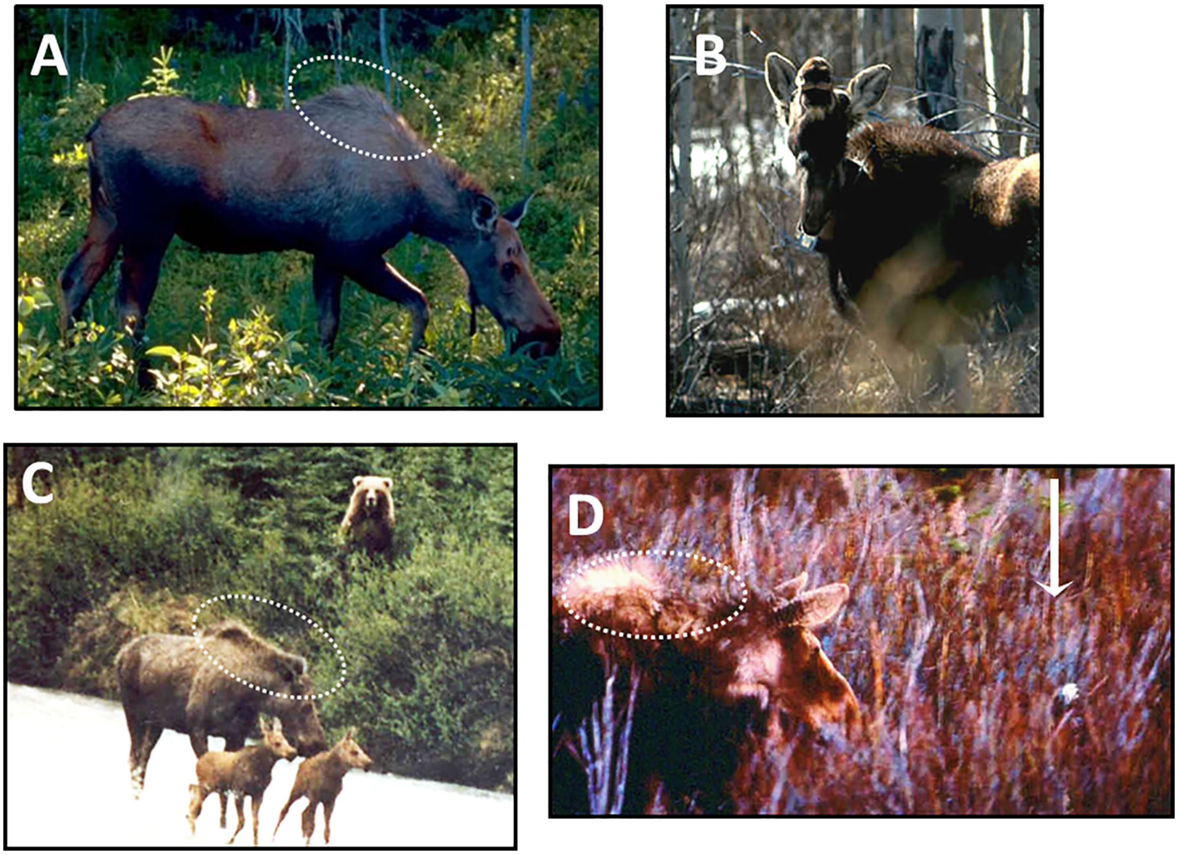

FIGURE 2 | Typical response of moose when exposed to a familiar predator and its cues. **(A)** Moose with little obvious concerns of eternal threat. **(B)** Olfactory response to exposure of wolf urine delivered by a projectile. **(C)** Pilo-erection and retraction of ears during interaction with a grizzly bear. **(D)** Pilo-erection but no ear retraction in a naïve moose with no prior exposure to grizzly bear feces (wrapped in porous tissue).

'Most of the animals seen today were on the Athi Plains (Kenya) and have learned that the nearer the railroad the safer they are from the attack of either men or lions.' He watched zebras and giraffe (Berger, 2007b). In the intervening 110 years, we have created deliberate and inadvertent refuges to favor and diminish bio-complexity to the point where even large protected areas may not do justice to represent ecological baselines (Arcese and Sinclair, 1997). Purposeful enhancements include habitat improvements through re-creation of fire regimes and removal of exotics (Dayer et al., 2019). More subtle factors alter predation regimes including: (1) humans as an indirect shield and (2) 'apparent competition,' which is the facilitation of a single species that changes the dynamics of another species where both are prey for a single predator (DeCesare et al., 2010). In these cases, as elaborated below, our presence and infrastructure have inadvertently altered species distributions, changed behavior, and re-structured prey–predator interactions.

Human Shields

The Human Shield Hypothesis (HSH) predicts that prey species will redistribute themselves in the absence of predation, and a commensurate shift will occur by co-association with humans and/or concomitant infrastructure, a behavior that increases avoidance of predators (Berger, 2007b; Sarmento and Berger, 2017). While it is obvious that species change occurs in consort with the degree of human threat and reward (e.g., crop raiding in elephants and elk), as protected areas are progressively fragmented into smaller pieces of disturbed landscapes, encounters with humans will only increase. In the United States, with some 420 national park units and an annual visitation of 300 million plus (Beissinger et al., 2017), only a few remote parks of large size enable functional predator–prey relations (Berger, 2017). In the lower United States, the bulk of visitation occurs, and an inevitable consequence of traffic, people, and hikers is habituation which, in turn, may shape prey vulnerabilities to predators (Geffroy et al., 2015).

Predictions of HSH have been confirmed for numerous ungulates and other mammals–Axis deer (*Axis axis*) and wildebeest avoid tigers and lions by using lawns in and around tourist lodges; the mountain nyala (*Tragelaphus buxtoni*) narrows down distance to humans to enhance protection from predation (Atickem et al., 2014), and vervet monkeys (*Chlorocebus pygerythrus*) avoid leopards by associating with researchers (Isbell, 1990). A more detailed project that spanned a decade revealed that moose used human infrastructure to avoid predation on neonates in the southern Greater Yellowstone

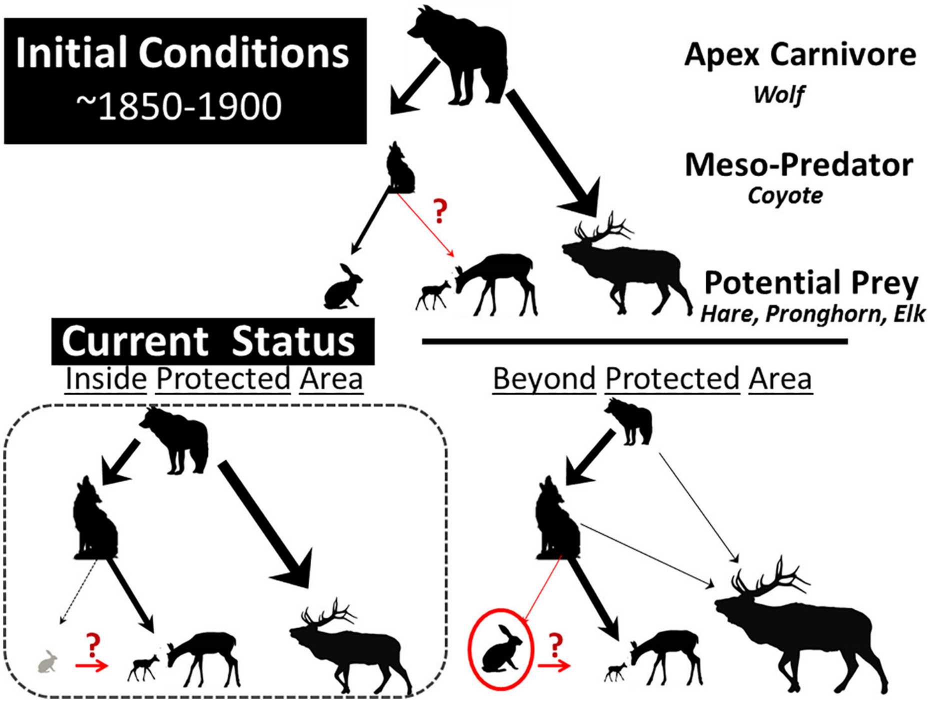

FIGURE 3 | Schematic of temporal change in a prey–predator food web in a protected area of the Greater Yellowstone Ecosystem (Wyoming) spanning about 150 years. The top illustration reflects wolf, coyote, elk, pronghorn, and white-tailed jackrabbits. The arrow width reflects the strength of predation intensity. The relative size of the icons depicts a positive or a negative relationship, and the red notation reflects uncertainty.

Ecosystem (**Figure 4**). Of two classes of adult females–pregnant and non-pregnant–in areas (i) generally lacking grizzly bears and (ii) with their increasing numbers, only pregnant females moved progressively closer to paved roads to give birth. There were no such movements by either non-pregnant females or females with calves where bears were lacking (**Figure 4**). Although grizzly bears can account for more than 75% of the mortality on neonates elsewhere, they tend to be road-averse until strongly habituated (Berger, 2007b, 2008a). Human shields have been reported from other protected areas where high human visitation dampens anti-predator responses including vigilance, grouping patterns, and/or the use of traditional refuge habitats for predator avoidance (Caro, 2005; Sarmento and Berger, 2017). Such phenomenon may be more prevalent in national parks than beyond protected boundaries since animals habituate to well-behaved people, and this sort of behavior can then result in increasing ungulate density to the point that heavy browsing affects other components of biological diversity (Hebblewhite et al., 2005).

Apparent Competition

Buffering against predation also occurs, typically as an indirect consequence when one prey species becomes either more or less abundant, a scenario that then alters predation pressure. By definition, apparent competition involves a decrement in the population growth rate of one of the species (DeCesare et al., 2010). Such patterns become of increasing concern because they frequently arise due to unintentional but broad human-mediated disturbances of natural systems. Forestry practices, roads and energy infrastructure, and habitat succession exemplify such perturbations, although others exist and involve native or alien species, sometimes both simultaneously. An example of this derives from the aforementioned case involving hares, coyotes, and pronghorn, in which the availability of hares as prey may have been affected by excessive grazing practices (Berger, 2008b). A potential consequence is that the loss of hares renders an increase in coyote predation on fawns (**Figure 3**). In a related fashion, the initiation of wolf control in parts of Alaska has possibly played a role in the inverse relationship between snowshoe hare (*Lepus americanus*) abundance and Dall sheep (*Ovis dalli*) lamb survival as mediated by coyotes (Arthur and Prugh, 2010).

Under apparent competition, both native and introduced species seem to respond comparably. Bighorn sheep (*Ovis canadensis*), for example, in the western Great Basin Desert and in New Mexico, often decline when mountain lions shift from mule deer as prey to native sheep in the absence of predator removal (Gibson, 2006; Rominger, 2018). Landscape-level disturbances such as fire and logging alter forest structure in western Canada. As moose densities increased in response, so did those of wolves; however, predation-related effects were strongest on woodland caribou whose population declined (DeCesare et al., 2010). Similar but inadvertent subsidies of one prey species by another are widespread, involving similar patterns for domestic, feral, and free-roaming alien species. In Patagonia, guanacos, the most abundant native ungulate, are shielded because domestic sheep (*Ovis aries)* (Baldi et al., 2004), European hare (*Lepus*

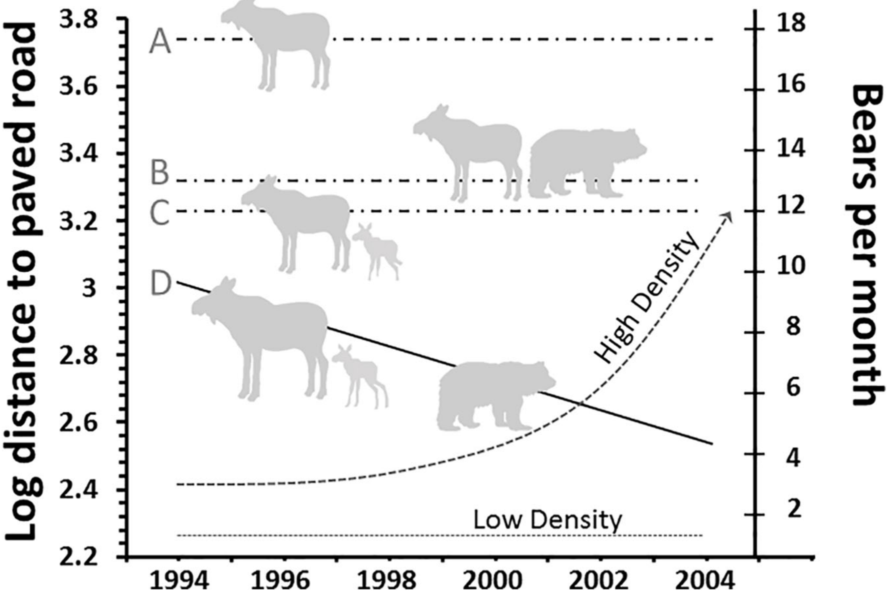

FIGURE 4 | Mean distance (10^2 m) of female moose of different reproductive status to roads during the spring parturition season. Non-pregnant females **(A)** in areas lacking and **(B)** with grizzly bears on days of median birth for conspecifics and for birthdates where bears were lacking **(C)** and present **(D)**. Modified from Berger (2008a).

europaeus), and red deer (*C. elaphus*) are the predominant prey of the native carnivore community which includes pumas (Novaro and Walker, 2005). A last example involves the endangered Przewalski's horses (*Equus przewalskii*) which were re-introduced into the relatively small (∼500 km^2) unfenced Hustai Nuruu National Park in Mongolia. Hundreds of domestic horses and livestock graze outside the protected boundaries. Although red deer colonized the park, their densities are low and wolf diet consists mostly of domestics, but foal recruitment in Przewalski horses is low because of wolf predation. A management objective is to increase the red deer numbers to buffer as alternative prey (Van Duyne et al., 2009).

The above scenarios represent just a few templates that characterize the altered states of ungulate populations and community interactions. Both the concept of human shields and the conditions by which one or more species of prey alter the demography of others emanate from initial perturbations to the system. Change is unavoidable as human populations enter into formerly non-anthropogenic landscapes. Now and far into the future, ever-increasing numbers of tourists will visit protected areas with unpredictable outcomes. Vegetation dynamics–especially bottom-up–will govern ungulate community structures and affect species abundance, degree of food overlap, and population dynamics with secondary and tertiary impacts at different trophic levels (below).

Plant–Herbivore-Mediated Tri-Tropic Interactions

Dominant species alter vegetation (Koerner and 72 members of the Grazing Exclosure Consortium, 2018). Large body size and super abundance are two, not necessarily twin, traits that affect herbivory. In particular, whereas some past continental ecosystems had especially large numbers of African elephants and North American bison, the effects can still be approximated and continue to play out at local scales (Bond, 2008; Hess et al., 2014; Moran, 2014). Elephants have been responsible for the conversion of forest and woodlands to grasslands and savanna (Owen-Smith, 1988; Sinclair et al., 2010), although precipitation, fire, soils, and ungulate density mitigate influences (Augustine and McNaughton, 2006; Pringle et al., 2007; Bond, 2008), and although in not all cases, elephant abundance does affect biodiversity. In miombo woodlands, increasing densities had little apparent effect on bat communities (Fenton et al., 1998). The impacts of other large-bodied grazers whose numbers are not controlled by predators or freed from constraints due to disease or interspecific competition (Sinclair et al., 2010) do exert a strong control of plant communities with coincident spillover effects on birds and insects (Sharam et al., 2009). Herbivory resulting from species as different in size as dik diks (*Madoqua kirkii*) and elephants have also changed the habitat use and behavior of rodents and small carnivores (Long et al., 2017) with top-down forces interacting with bottom-up ones (Louthan et al., 2019).

Most of the world's ungulates are heavily impacted by management and capably affect vegetation and other elements of biodiversity (Davidson et al., 2012; Ripple et al., 2015). For at least a million years, the hominin lineage has been associated with big game hunting; the evidence for our ancestral top-down impacts on prey species is clear in some instances, although not in others (Grayson et al., 2001; Barnosky et al., 2004).

In modern times, our trophic impacts have been modified both through direct and indirect actions. In North America, white-tailed deer have variously been estimated at up to 30 million individuals (Rooney, 2009). In eastern deciduous forests, the effects of deer are mediated through heavy browsing (Goetsch et al., 2011) and include the suppression of sapling recruitment, diminishment of shrub-nesting birds and insect-pollinated plants, and reduced caterpillars (McShea et al., 1997; McShea and Rappole, 2000; Wheatall et al., 2013). Beyond these effects, deer introduced to Anticosti Island inevitably caused the local extinction of black bear (Cote et al., 2004; Cote, 2005). The homogenization of temperate forests through excessive browsing coupled with the absence of predation has long-term consequences, suggesting a tipping point and phase shift into future grasslands (Rooney and Waller, 2003; Rooney, 2009; Ripple et al., 2019). Far to the west, mule deer, elk, and moose have secondary and tertiary effects on water nutrients, aquatic species, and amphibians depending on predation regimes (Bowyer et al., 1997; Kie et al., 2002; Ripple and Beschta, 2006). Moose, for example, where hunted, structured greater neoptropical migrant diversity through reduced browsing on willows, but in Grand Teton National Park–where protected and grizzly bears and wolves were once extirpated–several species did not occur due to excessive browsing, which resulted in habitat simplicity (Berger et al., 2001a). Elk, despite their more catholic feeding niches, also show great propensity to alter plant species diversity as well as shape bird and butterfly communities under inflated densities (Neff et al., 2007; Stewart et al., 2009; Ripple et al., 2019).

The above accounts concentrate on contemporary systems mostly without co-evolved predators and attendant effects on biodiversity beyond vegetation. Some attention has focused on past Holocene community constitution (Vrba, 1993; Ripple and Van Valkenburgh, 2010), including disarticulation and now modern reconstitution as modulated by climatic change (see below), but some 10 millennia after ungulate domestication (Clutton-Brock, 2012), a genesis that initially moved forth slowly by humans in their pursuit of bettering livelihoods now engulfs all continents (Bonacic et al., 2019). The playing fields of the past and the present are not the ones to be expected of the future despite gains in ungulate and carnivore reintroductions that re-establish varying levels of tri-trophic interaction.

DISASSEMBLY AND REASSEMBLY WHERE HUMAN ECONOMY AND CLIMATE INTERSECT

The Deserts–Africa, North America, and Asia

Ecological change across deep and short time is well appreciated. Hoofed mammals colonized new habitats during interglacial periods, when continental land bridges opened and closed, and species ranges expanded or contracted (Geist, 1978; Eisenberg, 1981; Webb, 2006). Some species adapt to changes; others fail to. A quickened pace occurs, however, as pastoralists alter the biomass of native herbivores by transforming systems in unprecedented ways which in the past (and continues today) included a profusion of alien species of domestic origin. North Africa exemplifies the first climate-driven alteration in an era with contemporary humans but lacking our current human-induced CO_2 climate-prompted footprint.

The Sahara–Losses Through Time

The planet's hottest and largest desert is the Sahara which, in size, is about that of China. During the African Humid Period from about 15,000 to 5,000 years BP, the area of present-day Egypt contained an ungulate assemblage which included hippos (*Hippopotamus amphibious*), black rhinos (*Diceros bicornis*), and elephants as well as two species of zebra (*Equus grevyi* and *Equus quagga*), one ass (*Equus asinus*), giraffe (*Giraffa camelopardalis*), and wildebeest. There were warthog (*Phacochoerus aethiopicus*), wild single-humped camels (*Camelus dromedaries*), and African Cape buffalo. Included within this realm were ibex (*Capra ibex*), Barbary sheep (*Ammotragus lervia*), and small gazelles (*Gazella leptocero* and *Gazella dorcas*). The large carnivores were spotted hyenas (*Crocuta crocuta*), lions, cheetahs (*Acinonyx jubatus*), leopards, and wild dogs (*Lycaon pictus*) (Yeakel et al., 2014).

At about 5,000–6,000 years ago, faunal collapse began as aridity increased and as modern human populations grew. The original fauna of 37 large mammal fauna lost more than 75% of its species and, for ungulates, only gazelles, ibex, and Barbary sheep persisted. The loss of marine moisture and humidity destabilized the faunal assemblage as the Serengeti-like predator–prey system shriveled (Yeakel et al., 2014; Yeakel and Dunne, 2015).

The Great Basin–a Restructured Prey–Predator System

The large mammal fauna of North America's present Great Basin Desert is far more simple than that of late Holocene. Geographically, the biome encompasses most of Nevada and western Utah and the size in total is $\sim$500,000 km^2 of temperate desert, nearly 50% larger than California. In the late Holocene, there were three species of wild equids, a tapir, three camelids, three species of pronghorn, a mastodont, a mammoth, and a gomphothere. Among the large carnivores were giant short-faced bear, sabertooth, Scimitar cat, and American cheetah (Grayson, 2011). In the late Holocene, this fauna, like that of the Sahara, diminished with complete extinction. Of the species mentioned above, only pronghorn survives there today. The causes have variously been debated (Martin and Klein, 1984; MacPhee, 2019), but it is the consequent change in food webs that is pertinent to how well future changes may be anticipated in the still dynamic Great Basin.

Based on archeological, pre-historic, and ethnographic accounts from the first European explorers in the 18th century to those a century later, the Great Basin was an admixture of grassland and shrub. Pronghorn and bighorn were the most commonly witnessed species, elk and deer were rare to non-existent, and few reports noted wolves or grizzly bears (Grayson, 2011; Lackey et al., 2013). Three species of hares occurred. By 1980, there were more than 300,000 cattle, 270,000 domestic sheep and goats, and some 30,000 feral horses (Berger, 1986); the vegetation that dominated a century earlier had been changed by excessive numbers of livestock (Young and Sparks, 2002), and differing seral phases supported irruptive mule deer populations. Subsequently, mountain lions followed, and in addition to mule deer as their primary prey, local populations of both porcupines (*Erethizon dorsatum*) and bighorn sheep were driven to near-extinction (Sweitzer et al., 1997; Gibson, 2006). Currently, cougars are widespread throughout the Great Basin, and black bears are re-colonizing this low-human-density landscape where once they had been extirpated (Malaney et al., 2018). Elk are expanding (**Figure 5**).

In this arid landscape where 150 years ago there were no indications of horses, mule deer, and cougar, all now persist. The system has changed. First, the vegetation was altered as a consequence of intense herbivory by exotics. It is now dominated by cheat-grass and expansive native shrubs (Grayson, 2011). Second, the large mammal fauna now present was likely not predictable 100 years ago.

Central Asia–the Cashmere Conundrum in Context

The planet's deserts and semi-arid grasslands support massive numbers of livestock (Batsaikhan et al., 2014), and together with humans, domestics may account for > 97% of global mammalian biomass (Bar-On et al., 2018). As drivers of terrestrial ecosystems, we have replaced apex carnivores and, through our control of predators and livestock, exerted strong direct and indirect effects on food webs by our chosen human livelihoods (Ekernas et al., 2017).

The Central Asia region, especially the Gobi Desert and the Tibetan Plateau areas of India and China, is unique in this regard for two principal reasons: first, its extant fauna is the only place remaining on Earth where the large mammal community may represent what existed in Beringia during the late Pleistocene (Guthrie, 1990); and second, domestic goats (*Capra aegagrus*) from Mongolia and China are responsible for 90% of the world's cashmere production. Italy, the United Kingdom, and Japan are the largest direct importers; most of the United States's cashmere derives from Italy. Consequently, the pairing of human social–ecological systems is easily viewed as being driven by distant fashion interests and mediated by economic incentives, notably the multi-billion garment industry (Berger et al., 2013). We describe the context below.

First, the present large mammals of central Asia include wild yak (*Bos mutus*) and wild Bactrian camels (*Camelus bactrianus*) (both endangered), chiru (*Pantholops hodgsoni*), saiga, ibex (*Capra sibirica*), blue sheep (*Pseudois nayaur*), several species of gazelles, three wild equids (khulan, kiang, and Przewalski horses), and Argali sheep (*Ovis ammon*) among others as well as dholes (*Cuon alpinus*), wolves, brown bears, and snow leopards (*Panthera uncia*) (Schaller, 1998; Harris, 2008). The high alpine steppes and deserts have, in common, ecological equivalents from the cold dry steppes of late Holocene Beringia. Instead of Alaskan bison are wild yaks, and in place of migratory caribou are chiru and saiga. Rather than Dall sheep are argali, and kiangs, khulans, and Przewalki horses fill niches putatively held by Yukon and Alaska wild equids. Although Beringia lost all of these species, including its camelids, each of the Asian surrogates inhabits some realms of the continents' deserts, mountains, or high plateaus as does an impressive assortment of domesticated ungulates–sheep, goats, and cattle as well as domestic but free-ranging Bactrian camels, yaks, and horses (Berger, 2018).

Second, the coupling of human-socio-ecological systems is evident in the presence of these domestic ungulates which, in some form, co-inhabit many of the protected areas spanning the Tibetan Plateau and the Himalayan realms of high-elevation India and China and to the Gobi Desert in Mongolia (**Figure 6**). The largest protected region–The Chang Tang National Nature Reserve–at about 330,000 km^2 is New Mexico-sized and the 3rd largest terrestrial protected area in the world. The biomass of ungulates in the Chang Tang along with that in six other protected areas comprises on average > 95% domestic species. Within these broader realms are at least eight endemic ungulates–saiga, chiru, wild Bactrian camel, khulan, kiang, takhi (*E. przewalskii*), Przewalski's gazelles (*Procapra przewalskii*), and wild yak, all formally classified as endangered. At Mongolian and Indian sites, time series data indicate that domestic goats have increased disproportionately, about four times more, than other livestock in about three decades (Berger et al., 2013). A consequence of this proliferating trend in small livestock is an increase in human–wildlife conflicts, many involving carnivores (Mishra et al., 2004, 2010) and frequently free-ranging dogs (Young et al., 2011).

Local Mongolian cashmere herders–the only realm for which we have direct data–benefit economically from foreign markets where their profit margins for cashmere have outpaced the cost of living and they reap profit margins in excess of fourfold (Berger et al., 2013). What this suggests is that there must be anticipation for fiscal rewards and, hence, not only have been flock sizes increasing but so has the proportion of goats, a trend that characterizes much of Central Asia (Namgail et al., 2010). The ecological costs of high stocking rates have been well chronicled from both short- and long-term perspectives on all continents (e.g., Du Toit et al., 2010).

Sustainable conservation requires a human face, yet across the Tibetan–Himalayan–Gobi landscapes, a system that once existed with minimal impacts to wildlife now experiences large ones (**Figure 6**). Bottom-up and top-down forces become indirect drivers of the system's food webs, but the principal driver is the western multi-billion dollar garment industry fueled through cashmere, not apex carnivores (Berger et al., 2013). Such findings are not dissimilar to the bushmeat trade in which European fishing interests indirectly govern the trade-off between African fishers and their propensity for illegal harvest of terrestrial wildlife (Brashares et al., 2004).

The World's Highest Mountains

The Himalayas and Andes each arose *via* distinct plate tectonics, and each houses a unique ungulate fauna. Both also currently experience unprecedented patterns of de-glaciation, and have been strikingly affected by human colonization, although the Himalayan region has been peopled longer (Aldenderfer, 2003). The two realms also undergo indirect modification by modern humans through climate alteration at a first tier and secondarily by direct human action. In the less densely populated Himalayas, the agents of change have been dogs, livestock, and tourism (see below). Unlike Central Asia, the southern

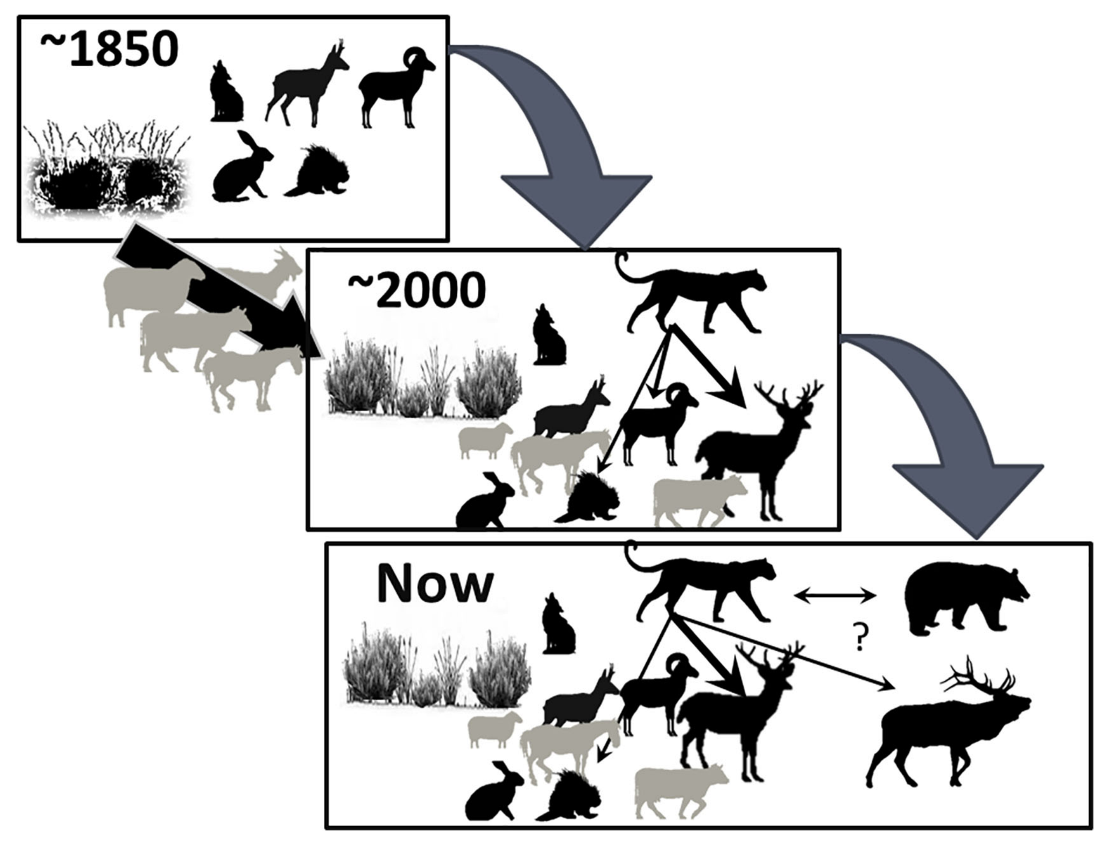

FIGURE 5 | Schematic of temporal change in a prey–predator food web in the Great Basin Desert, United States, illustrating how livestock and vegetation altered bottom-up processes to facilitate a new apex carnivore. The arrow width reflects the strength of predation intensity. The relative size of the icons depict a positive or a negative relationship, and in the lower illustration are pumas, black bear, coyotes, pronghorn, bighorn, mule deer, elk, hares, porcupines, domestic sheep, domestic horses, and cattle.

Andes abuts the ocean and disappear into the Patagonian Pacific where offshore influence modulates onshore ecosystems. These two cases offer twin but context-dependent histories, with changes to ungulates that would have been unanticipated several decades ago.

The Himalayan Front

As the Himalayas de-glaciated, wildlife and people colonized the northern reaches of India, Nepal, and Bhutan, including entry onto the Tibetan Plateau about more than 20,000 yBP (Chen et al., 2015). Along with pastoralists in what is now Bhutan are attendant domestic yaks and horses. Unlike the adjacent parts of the Tibetan Plateau where wild yaks and kiang had occurred, Bhutan has never had wild yaks or kiangs, presumably because there has been sufficient time for colonization as glacial recession has only been recent (Iwata and Narama, 2002). The initial pre-human faunas of high-elevation sites in Nepal, Bhutan, and Ladakh in India had species like takin (*Budorcas taxicolor*), goral (*Naemorhedus goral*), red deer, blue sheep, and ibex. The current de-glaciated habitats are obviously suitable–thousands of domestic horses and yaks use the high alpine grasslands and forests (Wangchuk et al., 2016).

Dogs too associate with domestic herds, sometimes with villagers and at other times with trekkers that they follow into new and less-peopled habitats where they encounter wild ungulates. India alone has ∼60 million free-ranging dogs, and in both Bhutan and Nepal, as well as Tibet and through much of Asia, dogs prey on saiga, blue sheep, Argali, chiru, kiang, goral, ibex, sambar, chital, and blackbuck (Young et al., 2011; Home et al., 2018). In Bhutan, one of us (JB) witnessed multiple predation attempts on takin and blue sheep above treeline. These included up to four dogs in 11 attacks of takin; three of nine calves were individually separated from the groups and disappeared. Their fates remained unknown, although death appeared likely (Berger, 2018). Dogs, domestic yaks, and especially horses displaced takin from mineral licks, but beyond passive displacement or active predation, modern ungulate communities are being re-altered in indirect if not direct ways through a profusion of domesticates (**Figure 7**).

Dogs can also be intermediate pathogenic hosts for zoonoses (Ministry of Agriculture and Forestry [MAGF], 2016). In Bhutan they affect yaks and may therefore indirectly influence people, and wildlife. Bhutanese high elevation dogs harbor tapeworms which, through the deposition of their eggs, are subsequently consumed from grasses by yaks. Coenurosis, a neurological

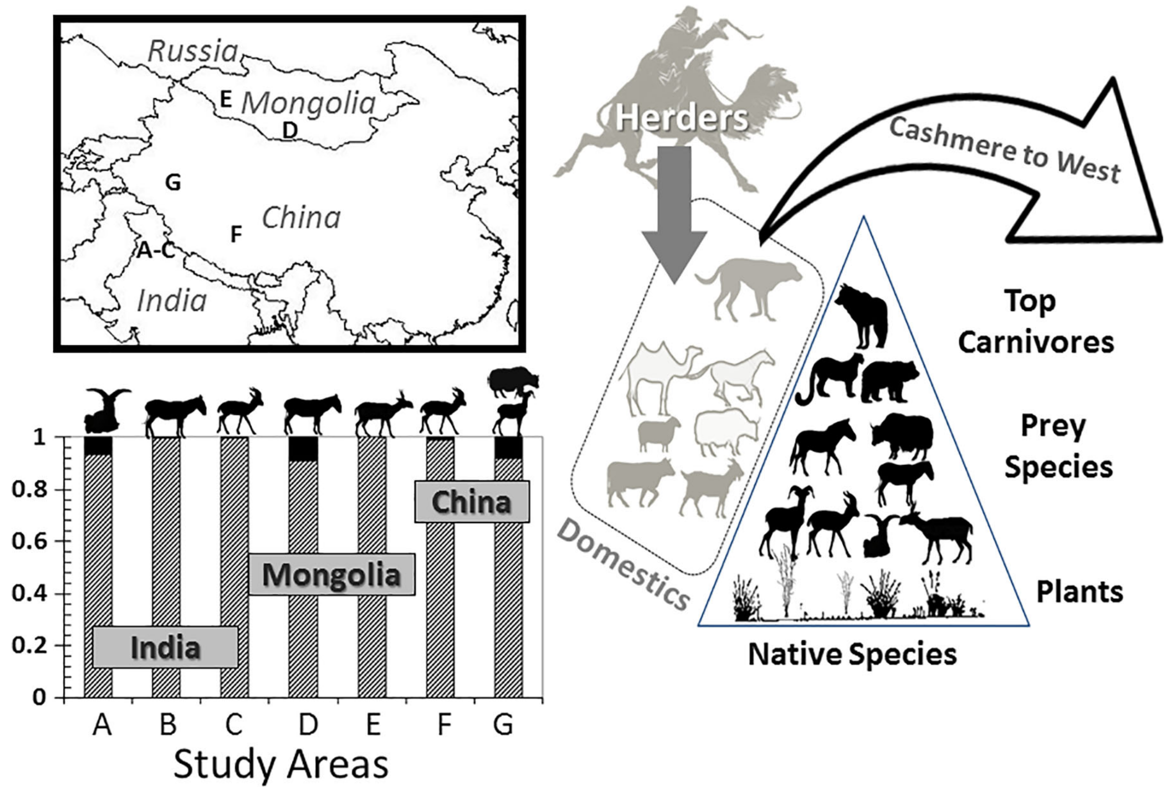

FIGURE 6 | Overview of the components of the cashmere trade to western consumers. Letters–protected areas where native (black bars) and domestic (stippled gray) ungulate biomass is expressed as a proportion of total. Icons from the left to the right are blue sheep, kiang, black-tailed gazelle, khulan, saiga, Przewalski gazelle, argali, and wild yak. The gray icons of domestics (top to bottom) are dogs, camels, horses, sheep, yaks, cattle, and goats. For native species, identified to leave are (top to bottom) wolves, snow leopards, and brown bears [specific study locales listed in Berger et al. (2013)].

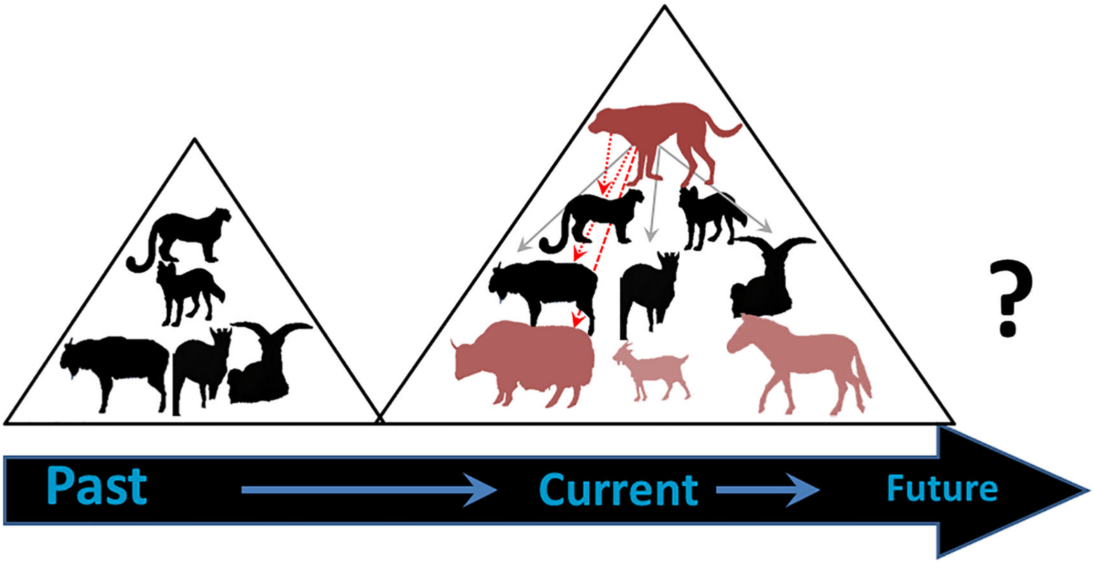

FIGURE 7 | Schematic overview of changes in a high-elevation Himalayan food web before and after pastoralism; this case study is from Bhutan's Jigme Dorji National Park (JDNP). The black icons represent native species, from top to bottom–snow leopard, dhole, takin, goral, blue sheep; the faded icons are sympatric domestics–dogs, yaks, goats*, horses. (*The goats are not in JDNP but exist in other parts of the Himalayas).

disease, affects the brain and spinal cord and may result in ∼10% mortality of young and sub-adult yaks. It is unclear the extent to which takin, snow leopards, or other wild species experience effects of coenurosis. In Nepal, and similar to other parts of the world, disease associated with dogs such as rabies, canine distemper, and others of viral origin affect wild carnivores but the extent to which, if any, impacts high elevation food webs are unstudied (Ng et al., 2019).

Aside from dogs, other indirect effects may be mediated through human activity in high-elevation Tibetan and Himalayan native grassland and alpine zones. These activities involve the seasonal relocation of Indian, Nepalese, Bhutanese, Chinese, and Tibetan agro-pastoralist to high(er) summer elevations to collect the worm fungus Cordyceps (*Ophiocordyceps sinensis*). It is used, harvested, and marketed locally and internationally for medicinal purposes (Wangchuk and Wangdi, 2015). Prior to legalization in Bhutan in 2004, these high-elevation environs experienced minimal direct human disturbance. The indirect effects now of increasing numbers of villagers, horses, domestic yaks, and dogs to collection sites for Cordyceps are unknown but likely include the illicit harvest of wild animals, displacement of native species, and potentially disease transmission through dogs or yaks (Berger, 2018) as well documented declines in grassland quality (Wangchuk and Wangdi, 2015; Shrestha et al., 2019).

In Tibetan and Himalayan highlands, the decline in volume of ∼90% of glaciers is changing the lives of people, habitat quality, and water availability and restructuring animal communities (Xu et al., 2009; Lutz et al., 2014). Ungulates are affected through changes in ice and snow, the availability of snow patches, a profusion of roads, mining, and understandable and actionable improvements of livelihoods. The impacts on native species will not abate as more people are born in, or immigrate to, these highlands. Tourism will continue in a site-dependent fashion, but due to remoteness, it is likely that change will more directly involve indirect effects on people, livestock, other alien species, and business opportunities, coupled with climate change (Schaller, 2012; Berger et al., 2015).

The Southern Andes–Hydrosphere, Harmful Algal Blooms, and Huemul

While food webs are frequently viewed within discrete ecosystems, interactions that mix species from inter-connected marine and terrestrial environments are not rare (Torben and Erlandson, 2009). Hunter–gatherers in the North Pacific, for example, have had strong impacts on ecological states–as predicted by Holling's model (**Figure 1**)–which involved human alteration in sea otter abundance and kelp forests (Simenstad et al., 1978). Reliance on near-shore food by people as generalist foragers has occurred since their arrival in the Western Hemisphere more than 12,000 years ago (Dunne et al., 2016).

In addition to people, offshore climatic events and marine subsidies each produces ecological consequences for nearby mammals on land (Polis and Hurd, 1996; Stempniewicz et al., 2017). Ungulates adjacent to coastal zones including moose, mountain goats (*Oreamnos americana*), and red deer use unusual strategies that sometimes involve consuming kelp (Clutton-Brock et al., 1982; Spaeth et al., 2001; White et al., 2018). Hippos (*Hippopotamus amphibious*) sometimes surf (Geer et al., 2016). More dramatic effects occur when low-pressure weather fronts bring heavy snow or–with warming winter temperatures–rain-on-snow winter episodes which subsequently shape life histories, vital rates, and population dynamics. Arctic reindeer and muskoxen (*Ovibos moschatus*) are reciprocally affected by Atlantic and Pacific events (Post et al., 2009, 2013; Tyler et al., 2008; Berger et al., 2018). Aside from direct and indirect bottom-up forces that impact food accessibility, other pathways exist in which offshore processes affect those onshore. Marine cyanobacteria influence food security for fishermen (Berdalet et al., 2016). Their economic well-being may result in a greater intensity of harvest on huemul, the Western Hemisphere's rarest large mammal. Ensuing terrestrial impacts stem from interactions among disease, livestock, and dogs (Ritchie et al., 2013; Doherty et al., 2017; Flueck and Smith-Flueck, 2017), all of which conflate because of humans and may indirectly and directly impact huemul.

Known as the Andean mountain deer, huemul are scattered in ∼100 small disconnected populations, are a critically endangered species, and are estimated at fewer than 2,000 individuals (Vila et al., 2010; Corti et al., 2011). As Chile's national mammal, huemul have graced its Coat of Arms (along with condors) since 1834. They once ranged to the Atlantic coast of southern Argentina where they were reported by Darwin (Diaz, 1993), but only disjunct populations remain on the east and the west slopes of the southern Andes (Povilitis, 1986, 2002). Their altitudinal range is from sea level to ∼2,000 m; abundance increases toward the distal edges of the massive Patagonia Ice Fields (Frid, 2001; Briceño et al., 2013; González and Alvarado, 2017) where the sub-Antarctic continental ice sheets undergo immense melting (Sakakibara et al., 2013; Foresta et al., 2018). The resultant periglacial zones, particularly in and around Patagonia's largest protected area, the ∼35,000-km^2 Bernardo O'Higgins National Park (**Figure 8**), appear fundamental to huemul persistence (Povilitis, 1986; Frid, 1994, 1997, 1999; Briceño et al., 2013). The Patagonian Ice Field realm is also the least peopled area of South America, in part due to foreboding weather, massive fjords, and challenges associated with life in remote areas. Consequently, knowledge of trophic dynamics and huemul demography are limited (Corti et al., 2010; Vila et al., 2010; Häussermann et al., 2017; León-Muñoz et al., 2018).

Industrial fishing in the Patagonian coastal Chile is a key driver of the national economy (Urbina, 2016) where, like in the Arctic and the sub-Arctic, oceanic warming occurs in the sub-Antarctic waters (McCabe et al., 2016). Phytoplankton communities are at times being restructured by harmful algal blooms (HABs) in both the northern and the southern Pacific (Guzman et al., 2002; Cook et al., 2015). Operationally, HABs represent situations in which mollusks and crustaceans, fish, and marine mammals are affected by toxins associated with cyanobacteria and dinoflagellates (Wells et al., 2015). While the relationships between HAB and climate are affected by many factors and not well understood, warming marine environments are often associated with HAB (Edwards and Richardson, 2004; Alheit et al., 2005).

In southern Patagonia, these events were responsible for the planet's largest baleen whale mortality event, nearly 12%

FIGURE 8 | Protected areas along the Patagonian coast in Chile (green) and the locale of its largest national park (Bernardo O'Higgins), its most visited (Torres del Paine), and the fishing village hamlet of Puerto Eden. Huemul male (top) and females (below) on re-vegetated spit with a recessing glacier backdrop.

reduction in the production of invasive salmon, and span unprecedented scales (Häussermann et al., 2017; León-Muñoz et al., 2018). As HABs proliferate, neurotoxin accumulation renders shellfish unfit for people and diseased fish–both farmed salmon and native species–diminish food security. Not only is public health a concern but also economic livelihoods reliant on fishing and crabbing industries are burdened. From a food web perspective, however, are probable indirect effects of climate-driven HABs on huemul (**Figure 9**).

Across southern Chile, HABs have concerned fishers for nearly half a century (Suarez and Guzman, 2005). Food security in remote coastal villages–whether Patagonia or elsewhere in the world–requires marine products like fish and mollusks, which at times are also buffered by the addition of a few sheep, livestock, or dogs. HABs obviate the possible consumption of marine products, and in many roadless communities, alternative foods from grocers are expensive, limited, or unavailable. One such isolated settlement is Puerto Eden, a hamlet of ∼200 people accessible only by boat (Frid, 1994, 2001; Vila et al., 2019). Situated within Bernardo O'Higgin's National Park where tidewater and other glaciers are recessing, huemul have colonized land spits between accumulated ice and vegetating moraines (**Figure 9**) up to 135 km from Puerto Eden and perhaps farther. Huemul density is inversely related to distance to human settlement (Briceño et al., 2013). If offshore events frame this relationship, four key assumptions must hold:

- Climate affects HABs with subsequent effects on human foods: The support for this tenant is generally strong as indicated from the studies referenced above. In short, the negative impacts on fisheries are modulated by warming oceanic temperatures. The climate effects on HABs are, however, complicated by contributions of glacial runoff, streams, and rivers to marine acidity, oxygen, and temperature.
- Remote coastal villagers enhance food security by accessing terrestrial-sourced nutrition: The assumption, although a truism, offers a framing to understand food and society in these distant realms. The sustainability of marine resources is of critical concern to the Chilean government given that loss or reduction of income has crucial economic consequences (Molinet et al., 2014). At a local scale, mollusks and fish are important dietary components in many fishing villages, and changes in their availability may be expected to reflect the pursuit of alternative foods. In Puerto Eden, bivalves are in frequent use as evidenced by shells piled up to 45 cm outside of homes; a small number of cattle and sheep are also maintained as additional sources

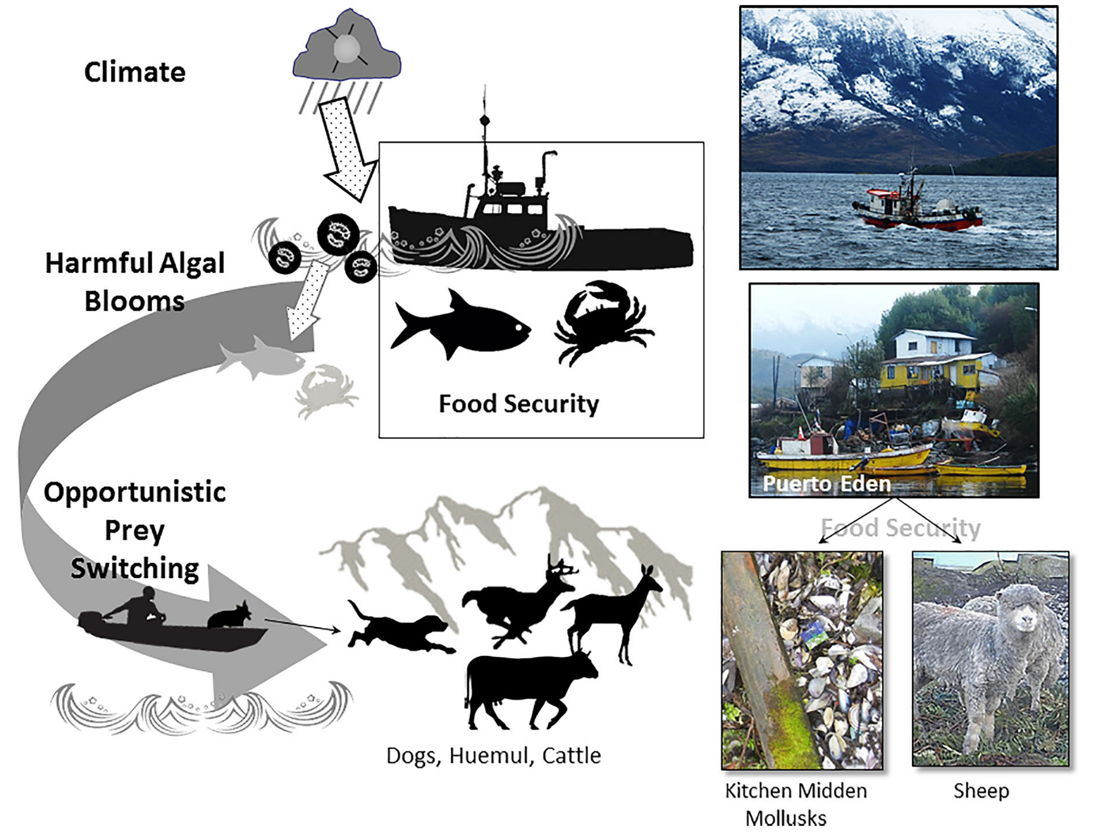

FIGURE 9 | Overview of demonstrated and hypothesized pathways by which climate and harmful algal blooms affect people and possibly huemul. Light gray fish and mollusks reflect higher-than-normal mortality and the testable proposition that HAB leads to elevated onshore foraging options. Fishing vessel (top) 30 km from Puerto Eden, bivalves outside a home, and sheep with thick wool–all photos are from Puerto Eden.

of protein (**Figure 9**). That people anywhere attempt to buffer against food shortages is unsurprising, yet to explore whether villagers experience malnourishment during HAB and subsequently alter their diets requires either time series data or spatial controls for analyses, neither of which is presently available.

- Fishermen hunt huemul during hard times: That people have always hunted is another truism. The critical issue is whether post-HAB human behavior increase huemul vulnerability to predation, a situation somewhat analogous to the harvest of bushmeat when African fisheries are no longer incentivized (Brashares et al., 2004). In deep coastal wet beech forests, huemul are difficult to find, so additional context is necessary to address the above issue.

Throughout Chile, free-ranging dogs are components of urban and rural society (Villatoro et al., 2019); they are also able predators of wild cervids (Silva-Rodríguez and Sieving, 2012), including huemul (Corti et al., 2010; Vila et al., 2010). In Puerto Eden, most artisanal fishing is by small wooden and fiberglass boats. In 2017, we noted that 19% of the 16 operational skiffs there had dogs visible. Resident communications with scientists including us reported that dogs were used to hunt huemul. When Frid (2001) studied on huemul two decades earlier, he indicated: "Hunters with dogs were present shortly before I began fieldwork (*1994*). Upon arriving at the site, we found recent tracks of humans with at least one dog. Although the Puerto Edén residents I interviewed could not estimate the hunting rate . . . one hunter claimed that he kills 10–15 huemuls a year. He always uses dogs to corner them." Clearly, fishermen supplement diets with deer meat from fjords 100 km in distance, but data to test the tenet that harvest increases as a consequence of HABs are unavailable.

In contrast, what is clear is that five of eight sites where huemul were present 15 years ago are now gone. Only at the two most remote fjords–locales where park rangers sporadically visit–and at an additional site closer to Puerto Eden where some tourist traffic occur do huemul persist. According to government authorities (internal private communications) of the Chilean National Forest Service, unfrequented realms are sites where dogs are released to hunt huemul.

- Alternative human food indirectly affects huemul persistence: Despite the maintenance of a few farm animals in Puerto Eden to enhance local cuisine and dietary options, villagers make use of terrestrial environs, presumably as an additional measure to assure food security. Beyond hunting with dogs (above), huemul are

> also indirectly affected. In 1991, 18 cattle were transported by skiff and illegally released into the remote Tempanos Fjord (Frid, 1994, 2001). Their numbers reached several hundred when removed by the government in 2004 (Frid, 1997; Briceño et al., 2013). Huemul incurred 40% mortality and 80% morbidity from 2005 to 2010 as severe clinical signs of foot disease were consistent with a parapoxvirus (Vila et al., 2019).

Coastal impacts on huemul occur through direct (e.g., illegal harvest using boat-transported dogs) and indirect (disease transmission through cattle) human-prompted actions. As throughout the world, livelihoods benefit by the use of marine resources. While its plausible that the climate–HAB connection motivates villagers in Puerto Eden to seek resources on land that subsequently encumber huemul–as speculated above–additional data on fisheries economics and the timing of subsequent behavior on land associated with huemul are needed to test the predictions.

CONCLUSION–RELUCTANT LESSONS AND COMMUNITY REASSEMBLY IN A GRAVE WORLD

Human impacts on the planet are grave and continue to downgrade natural diversity in ways that were not predictable 50 years ago (Estes et al., 2012). New pathogens affect cold-adapted mammals (Kutz et al., 2009). Feral hogs occur on all continents (except Antarctica) and in 70% of the states of the United States, where their effects at landscape levels disrupt vertebrate communities, plants, and soils (McClure et al., 2018; Lewis et al., 2019). It is nearly impossible to consider communities of large herbivores and their assembly in the absence of understanding the modern human milieu regardless of whether human population growth (Ehrlich and Holdren, 1971) is detached or coupled with globalization (Pimentel et al., 1997; Chanda, 2008). We have lost or reduced the range of many large apex predators due to fear, persecution for economic reasons, or attrition simply by habitat conversion and loss of prey (Ray et al., 2005). The sole exception from food web perspectives may be in extreme environments–the highest peaks, the bleakest deserts, or the end of land, something noted by Darwin (1859): "When we reach …. absolute deserts, the struggle for life is almost exclusively with the elements. Not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert, will competition cease." Such cases, as noted by Darwin are, however, not only far from the norm, but the world has indubitably changed.

The United States has 12 native ungulates. The national parks in the United States have more than twice that number of free-ranging non-native ungulates (Plumb et al., 2014). Relationships are interminably mixed and interactions differ from what occurred before the European occupation of those or adjacent lands.

Only a few of the 420 park units are sufficiently sized to reveal insights into ecological baselines (Colwell et al., 2012; Berger, 2017), and yet even those the size of Yellowstone, Denali, or Canada's Wood Buffalo have had serious outside influence that affected the ecological dynamics within (Nishi et al., 2006; Smith and Ferguson, 2012; Geldmann et al., 2014). Serengeti and Kruger are no different (Sinclair et al., 2010). Only for parts of the Peruvian and the Brazilian Amazon, boreal Siberia and Canada, the Arctic, unfettered Himalayas, and a few realms of wild African is it possible to allow the continuance of established prey–predator relationships (Schaller, 1998; Watson et al., 2016, 2018; Berger, 2018). Exotic ungulates and other species which affect ungulates are more the norm than exception. Wild hippos now occur in Colombia, banteng in Australia (Bradshaw et al., 2006), and gemsbok (*Oryx gazella*) and Barbary sheep in New Mexico. Burmese pythons were partly responsible for the collapse of the white-tailed deer where the former restructured the Everglades food web (Dorcas et al., 2012). Livestock and, later, cheat grass altered the habitats of the Great Basin which remain forever changed (Berger and Wehausen, 1991), and novel predator–prey relationships have emerged there (**Figures 2**, **6**). The world's 400 million free-ranging dogs–through disease, predation, and displacement–have changed the face of carnivore and ungulate communities on every continent. Although not endemic to Australia and having been introduced some 4,000–5,000 years ago, dingoes are declared 'naturalized' and continue to change the Australian food webs (Healy S., 2007; Letnic and Koch, 2010). Courts in different parts of the world deem what is native and what is not, sometimes–like wolves with dog genes–ruling for the retention of species introgressed with domestics (Anderson et al., 2009). Chernobyl has moose, red deer, roe deer, and wild boar (Deryabina et al., 2015), Korea's Demilitarized Zone has reassembled with goral, Chinese water deer (*Hydropotes inermis*), and leopards (Healy H., 2007), and the West Bank between Israel and Jordan has some 80 wolves despite a few native hoofed mammals to consume. Restoration efforts continue (Hayward M. et al., 2019; Hayward M. W. et al., 2019).

Re-assembly reoccurs in ungulate communities in odd ways. While climate forcing is prominent globally and locally, human omnipresence rapidly modifies landscapes with no indication of abatement (Berger, 2018; Bowyer et al., 2019). Disease likewise runs rampant; hemorrhagic septicemia was responsible for the largest and most rapid mass ungulate die-off ever recorded in which ∼200,000 saiga were killed in only 3 weeks (Fereidouni et al., 2019). The call-out to close 22 feed grounds that maintain thousands of elk for harvest in Wyoming has not changed across a century, although brucellosis continues and chronic wasting now enters the system where federal and state control of wildlife is still fought in the courts (Smith et al., 2004). Ceaseless tensions spill into other arenas. Advocacy groups argue for the retention of non-native species in national parks where federal rules are inconsistent. Mountain goats in Olympic National Park, for instance, were removed *via* mostly live captures in episodes spanning decades, and the shooting of them–in 2020–already occurs in Grand Teton National Park. Just to the north in Yellowstone National Park, where goats are also not native, they remain untouched. Carnivores that prey on ungulates raise other issues. The Wyoming populace opposes wolves where–like jackrabbits and porcupines–they can be shot on site when outside certain bounds. In adjacent Colorado, wolf reintroduction will be decided by popular vote–Ballot Imitative #107–in the general 2020 election, the result of 200,000 signatures by Coloradoans and announced by the Secretary of State in January 2020.

Biological interactions have shaped past and some current ungulate community structure. Far more common today are site- and species-dependent human interventions. These arise from politics, environmental and ecological disasters, war, harvest, and economics. Aldo Leopold famously said: "One of the penalties of an ecological education is that one lives alone in a world of wounds." The statement should resound loudly, yet lamenting the splendors of the past does little to better the future when unaccompanied by forethought and efforts to motivate conservation action among others. Although food webs with ungulates will not continue in the same fashion as they had in the past or even now–regardless of human presence–options to shape the future remain. These include the protection of big spaces and small species and a semblance of unencumbered habitat.

Incentives to coexist transcend the ethical as large mammals, like other species, deserve a right to be there, and public resolve should help assure that they play interactive ecological roles. Of note is that an estimated eight billion travelers visit protected areas annually (Balmford et al., 2015). Services associated with wildlife viewing are potent economic drivers in numerous African countries (World Tourism Organization, 2014), and in the United States, more than 300 million tourists per year visit national parks–a sum that collectively exceeds that for professional baseball, football, and basketball–where wildlife viewing is a goal (Beissinger et al., 2017).

During his exploration of South America in the 1830s, Darwin wrote about people, animals, plants, and even food webs (Darwin, 1859, 1889). Thirty years earlier, Alexander von Humboldt commented on the necessity to "recognize in the plant or the animal not merely an isolated species but a formed link in the chain of being to other forms" (von Humboldt, 1858), a clear allusion to the connectedness of nature whose food webs we reformat as we proliferate.

Conservation Evolves

Reintroductions continue, both of ungulates and carnivores in North America, Europe, Asia, and Africa. The issues of 19th and 20th century–overharvest, poaching, and wildlife slaughter–will not be the most pressing in the 21st century. Climate change already is, as is the direct and insidiously rapid destruction of habitat with associated changes in biodiversity. Some species rebound; others will be missed. The admixtures and loss we see today will differ yet again tomorrow. We may not embrace the change. With reluctance we must accept it, but not when or where we can make a difference to maintain what we have or restore what we have lost.

We conclude with two considerations: one is a thought exercise, the other is reality. First, it might be useful to query what would happen should the human stressors depicted in **Figure 1** be removed. Would communities reassemble back to some basal, original state? We think not. If the supposition is correct, this then has implications for our reality check which involves conservation tactics while re-enforcing the value of large protected areas. Conservation practitioners should work fiercely to continue to protect what we have while simultaneously recognizing that disturbed habitat and altered communities still offer important contributions to beta biodiversity.

Moreover, we feel that scientists need to be more involved in policy direction, in speaking out, and in outreach. We recognize that this is more likely to occur, at least for academic scientists, after tenure, but a fairly easy fix is that university departments update tenure requirements to match our societal needs. While the research is critically important and publications help maintain our scientific credibility, we must make our science matter outside a narrow journal readership. Only by demonstrating to society the real relevance of the significance of food webs, biodiversity, and community composition will we be able to shape policy, motivate politicians and elected officials, and influence state and federal agencies. What we are engaged in is not an academic pursuit. The rich biological heritage of all living things, including the ungulates, is at stake.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by all universities where authors are currently based; specific studies indicate animal cares codes and approvals.

AUTHOR CONTRIBUTIONS

JB conceived the ideas of this manuscript through prolonged conversations with TW, AV, CB, and JL. Field work and data collection were in consort with TW, AV, and CB. JL conceptualized and debated portions of this manuscript, and all authors were involved in its writing.

FUNDING

Grants for specific manuscript are listed in relevant citations to the author's manuscript. Our respective institutions – the Bhutan Foundation, the Wildlife Conservation Society, and Colorado State University and the University of Colorado – supported the writing of this manuscript.

ACKNOWLEDGMENTS

Discussions across a near lifetime with Terry Bowyer, Jim Estes, Jodi Hilty, Elaine Leslie, Reed Noss, Barbara Saveedra, Kent Redford, Michael Soule, Peter Stacey, Kevin White, and Steve Zack helped crystalize the ideas herein. Matt Hayward, Evelyn Hunter Merrill, and Stan Boutin, and this volume's editors offered helpful suggestions to improve our manuscript.

REFERENCES

Aldenderfer, M. S. (2003). Moving up in the world: archaeologists seek to understand how and when people came to occupy the Andean and Tibetan plateaus. *Amer. Sci.* 91, 542–549.

Alheit, J., Mollmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., et al. (2005). Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES J. Mar. Sci.* 62, 1205–1215. doi: 10.1016/j.icesjms.2005.04.024

Anderson, T. M., Candille, S. I., Musiani, M., Greco, C., Stahler, D. R., Smith, D. W., et al. (2009). Molecular and evolutionary history of melanism in North American gray wolves. *Science* 323, 1339–1343. doi: 10.1126/science.1165448

Arcese, P., and Sinclair, A. R. E. (1997). The role of protected areas as ecological baselines. *J.Wildl. Manag.* 61, 587–602. doi: 10.2307/3802167

Arthur, S. M., and Prugh, L. R. (2010). Predator-mediated indirect effects of snowshoe hares on Dall's sheep in Alaska. *J. Wildl. Manag.* 74, 1709–1721. doi: 10.2193/2009-322

Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., and Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* 8:e57872. doi: 10.1371/journal.pone.0057872

Atickem, A., Loe, L. E., and Stenseth, N. C. (2014). Individual heterogeneity in use of human shields by mountain Nyala. *Ethology* 120, 715–725. doi: 10.1111/eth.12242

Augustine, D., and McNaughton, S. (2006). Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9, 1242–1256. doi: 10.1007/s10021-005-0020-y

Baldi, R., Pelliza-Sbriller, A., Elston, D., and Albon, S. (2004). High potential for competition between guanacos and sheep in Patagonia. *J. Wildl. Manag.* 68, 924–938. doi: 10.2193/0022-541x(2004)068[0924:hpfcbg]2.0.co;2

Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., et al. (2015). Walk on the wild side: estimating the global magnitude of visits to protected areas. *PLoS Biol.* 13:e1002074. doi: 10.1371/journal.pbio.1002074

Barboza, P. S., and Bowyer, R. T. (2000). Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *J. Mamm.* 81, 473–489. doi: 10.1093/jmammal/81.2.473

Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L., and Shabel, A. B. (2004). Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306, 70–75. doi: 10.1126/science.1101476

Barnowe-Meyer, K. K., White, P. J., Davis, T. L., and Byers, J. A. (2009). Predator-specific mortality of pronghorn on Yellowstone's northern range. *West. N. Am. Nat.* 69, 186–194. doi: 10.3398/064.069.0207

Bar-On, Y. M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. *Proc. National Acad. Sci. U.S.A.* 115, 6506–6511. doi: 10.1073/pnas.1711842115

Batsaikhan, N., Buuveibaatar, B., Chimed, B., Enkhtuya, O., Galbrakh, D., Ganbaatar, O., et al. (2014). Conserving the world's finest grassland amidst ambitious national development. *Cons. Biol.* 28, 1736–1739. doi: 10.1111/cobi.12297

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T., et al. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci. U.S.A.* 112, 14894–14899. doi: 10.1073/pnas.1500664112

Beissinger, S. R., Ackerly, D. D., Doremus, H., and Machlis, G. E. (2017). *Science, Conservation, and National Parks*. Chicago, IL: University of Chicago Press.

Benson, J. F., and Patterson, B. R. (2013). Moose (*Alces alces*) predation by eastern coyotes (*Canis latrans*) and eastern coyote× eastern wolf (*Canis latrans× Canis lycaon*) hybrids. *Can. J. Zool.* 91, 837–841. doi: 10.1139/cjz-2013-0160

Berdalet, E., Fleming, L. E., Gowen, R., Davidson, K., Hess, P., Backer, L. C., et al. (2016). Marine harmful algal blooms, human health and wellbeing: challenges and opportunities in the 21st century. *J. Mar. Biol. Assoc. United Kingdom* 96, 61–91. doi: 10.1017/S0025315415001733

Berger, J. (1986). *Wild Horses of the Great Basin: Social Competition and Population Size*. Chicago, IL: University of Chicago Press.

Berger, J. (2005). "Hunting by carnivores and by humans: is functional redundancy possible and who really cares," in *Large carnivores and the conservation of biodiversity*, eds J. Ray, et al. (Covello: Island Press), 316–341.

Berger, J. (2007a). Carnivore repatriation and Holarctic prey: narrowing the deficit in ecological effectiveness. *Cons. Biol.* 21, 1105–1116. doi: 10.1111/j.1523-1739.2007.00729.x

Berger, J. (2007b). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* 3, 620–623. doi: 10.1098/rsbl.2007.0415

Berger, J. (2008a). *The Better to Eat You With: Fear in the Animal World*. Chicago, IL: University of Chicago Press.

Berger, J. (2008b). Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem. *USA*. *Oryx* 42, 139–142.

Berger, J. (2017). "Science and challenge to conserve large wild mammals in 21st century american protected areas. Pp, 189-208," in *Science for Parks and Parks for Science*, eds S. Beissinger, D. D. Ackerly, H. Doremus, and G. E. Machlis, (Chicago, IL: University of Chicago Press).

Berger, J. (2018). *Extreme Conservation: Life at the Edges of the World*. Chicago, IL: University of Chicago Press.

Berger, J., Buvveibaatar, B., and Mishra, C. (2013). Globalization of the cashmere market and the decline of large mammals in Central Asia. *Cons. Biol.* 27, 679–689. doi: 10.1111/cobi.12100

Berger, J., Cain, S. L., and Berger, K. M. (2006). Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biol. Lety.* 2, 528–531. doi: 10.1098/rsbl.2006.0508

Berger, J., Cheng, E., Krebs, M., Li, L., Kang, A., Schaller, G. B., et al. (2015). Legacies of past exploitation and climate affect mammalian sexes differently on the roof of the World – The Case of Wild Yaks. *Sci. Rep. Nat.* 5:8676. doi: 10.1038/srep08676

Berger, J., and Cunningham, C. (1994). *Bison: Mating and Conservation in Small Populations*. New York, NY: Columbia University Press.

Berger, J., Hartway, C., Gruzdev, A., and Johnson, M. (2018). Climate degradation and extreme icing events constrain life in cold-adapted mammals. *Sci. Rep. Nat.* 8:1156. doi: 10.1038/s41598-018-19416-9

Berger, J., Stacey, P. B., Bellis, L., and Johnson, M. P. (2001a). A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* 11, 947–960. doi: 10.1890/1051-0761(2001)011[0947:amppig]2.0.co;2

Berger, J., Swenson, J. E., and Per-Illson, I. (2001b). Re-colonizing carnivores and naive prey; conservation lessons from Pleistocene extinctions. *Science* 291, 1036–1039. doi: 10.1126/science.1056466

Berger, J., and Wehausen, J. (1991). Consequences of mammalian predator-prey disequilibrium in the Great Basin Desert. *Cons. Biol.* 5, 243–248.

Berger, K. M., and Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* 76, 1075–1085. doi: 10.1111/j.1365-2656.2007.01287.x

Berger, K. M., Gese, E. M., and Berger, J. (2008). Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* 89, 818–828. doi: 10.1890/07-0193.1

Blumstein, D. T., and Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proc. R. Soc. B: Biol. Sci.* 272, 1663–1668. doi: 10.1098/rspb.2005.3147

Boitani, L., and Linnell, J. D. (2015). *Bringing large mammals back: large carnivores in Europe. In Rewilding European Landscapes*. Cham: Springer, 67–84.

Bonacic, C., Almuna, R., and Ibarra, J. T. (2019). Biodiversity conservation requires management of feral domestic animals. *Trends Ecol. Evol.* 34, 683–686. doi: 10.1016/j.tree.2019.05.002

Bond, W. J. (2008). What limits trees in C4 grasslands and savannas? *Ann. Rev. Ecol., Evol., Syst.* 39, 641–659. doi: 10.1146/annurev.ecolsys.39.110707.173411

Bowyer, R. T., Bleich, V. C., Stewart, K. M., Whiting, J. C., and Monteith, K. L. (2014). Density dependence in ungulates: a review of causes, and concepts with some clarifications. *Calif. Fish Game* 100, 550–572.

Bowyer, R. T., Boyce, M. S., Goheen, J. R., and Rachlow, J. L. (2019). Conservation of the world's mammals: status, protected areas, community efforts, and hunting. *J. Mamm.* 100, 923–941. doi: 10.1093/jmammal/gyy180

Bowyer, R. T., Person, D. K., and Pierce, B. M. (2005). "Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity," in *Large Carnivores and the Conservation of Biodiversity*, eds J. Berger, R. Steneck, K. H. Redford, and J. C. Ray, (Covelo: Island Press), 342–361.

Bowyer, R. T., Van Ballenberghe, V., and Kie, J. G. (1997). "The role of moose in landscape processes: effects of biogeography, population dynamics, and predation," in *Wildlife and Landscape Ecology*, ed. J. A. Bissonette, (New York, NY: Springer), 265–287. doi: 10.1007/978-1-4612-1918-7_10

Bradshaw, C. J., Isagi, Y., Kaneko, S., Bowman, D. M., and Brook, B. W. (2006). Conservation value of non-native banteng in northern Australia. *Cons. Biol.* 20, 1306–1311. doi: 10.1111/j.1523-1739.2006.00428.x

Brain, C., Forge, O., and Erb, P. (1999). Lion predation on black rhinoceros (*Diceros bicornis*) in Etosha National Park. *Afr. J. Ecol.* 37, 107–109. doi: 10.1046/j.1365-2028.1999.00137.x

Brashares, J. S., Arcese, P., Sam, M. K., Coppolillo, P. B., Sinclair, A. R., and Balmford, A. (2004). Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science* 306, 1180–1183. doi: 10.1126/science.1102425

Brashares, J. S., Prugh, L. R., Stoner, C. J., and Epps, C. W. (2010). "Ecological and conservation implications of mesopredator release," in *Trophic Cascades: Predators, Prey, and the Changing Dynamics Of Nature*, eds J. Terborgh, and J. E. Estes, (Washington, DC: Island Press), 221–240.

Briceño, C., L. A. Knapp, A. Silva, J. Paredes, I. Avendaño, A. Vargas, et al. (2013). Detecting an increase in an Endangered huemul *Hippocamelus bisulcus* population following removal of cattle and cessation of poaching in coastal Patagonia, Chile. *Oryx* 47, 273–279. doi: 10.1017/S0030605312000014

Caro, T. (2005). *Antipredator Defenses in Birds and Mammals*. Chicago, IL: University of Chicago Press.

Carthey, A. J., and Blumstein, D. T. (2018). Predicting predator recognition in a changing world. *Trends Ecol. Evol.* 33, 106–115. doi: 10.1016/j.tree.2017.10.009

Chanda, N. (2008). Runaway globalization without governance. *Glob. Gov. Rev. Multilateralism Int. Org.* 14, 119–125. doi: 10.1163/19426720-01402001

Chen, F. H., Dong, G. H., Zhang, D. J., Liu, X. Y., Jia, X., An, C. B., et al. (2015). Agriculture facilitated permanent human occupation of the Tibetan Plateau after 3600 BP. *Science* 347, 248–250. doi: 10.1126/science.1259172

Ćirović, D., Teodorović, V., Vasilev, D., Marković, M., Ćosić, N., Dimitrijević, M., et al. (2015). A large-scale study of the Trichinella genus in the golden jackal (*Canis aureus*) population in Serbia. *Vet. Parasitol.* 212, 253–256. doi: 10.1016/j.vetpar.2015.07.022

Clutton-Brock, J. (2012). *Animals as Domesticates: A World View Through History*. East Lansing, MI: MSU Press.

Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. Chicago, IL: University of Chicago Press.

Colwell, R., Avery, S., Berger, J., Davis, G. E., Hamilton, H., Lovejoy, T., et al. (2012). *Revisiting Leopold: Resource Stewardship in The National Parks*. Washington, D.C: National Park System Advisory Board.

Cook, P. F., Reichmuth, C., Rouse, A. A., Libby, L. A., Dennison, S. E., Carmichael, O. T., et al. (2015). Algal toxin impairs sea lion memory and hippocampal connectivity, with implications for strandings. *Science* 350, 1545–1547. doi: 10.1126/science.aac5675

Corti, P., Shafer, A. B., Coltman, D. W., and Festa-Bianchet, M. (2011). Past bottlenecks and current population fragmentation of endangered huemul deer (*Hippocamelus bisulcus*): implications for preservation of genetic diversity. *Cons. Gen.* 12, 119–128. doi: 10.1007/s10592-009-9997-7

Corti, P., Wittmer, H. U., and Festa-Bianchet, M. (2010). Dynamics of a small population of endangered huemul deer (*Hippocamelus bisulcus*) in Chilean Patagonia. *J. Mamm.* 91, 690–697. doi: 10.1644/09-mamm-a-047.1

Cote, S. D. (2005). Extirpation of a large black bear population by introduced white-tailed deer. *Cons. Biol.* 19, 1668–1671. doi: 10.1111/j.1523-1739.2005.00252.x

Cote, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., and Waller, D. M. (2004). Ecological impacts of deer overabundance. *Ann. Rev. Ecol. Evol. Syst.* 35, 113–147. doi: 10.1146/annurev.ecolsys.35.021103.105725

Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., and Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science* 307, 1959–1961. doi: 10.1126/science.1108485

Cunningham, C., and Berger, J. (1997). *Horn of Darkness; Rhinos on the Edge*. Oxford: Oxford University Press.

Cypher, B. L., and Spencer, K. A. (1998). Competitive interactions between coyotes and San Joaquin kit foxes. *J. Mamm.* 79, 204–214. doi: 10.2307/1382855

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection. 1968 – Reprint*. London: Murray.

Darwin, C. (1889). *Journal of Researches Into the Natural History and Geology of the Countries Visited During the Voyage of HMS" Beagle" Round the World, Under the Command of Capt*. London: Ward, Lock and Company.

Davidson, A. D., Detling, J. K., and Brown, J. H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* 10:477–486. doi: 10.1890/110054

Dayer, A. A., Redford, K. H., Campbell, K. J., Dickman, C. R., Epanchin-Niell, R. S., Grosholz, E. D., et al. (2019). The unaddressed threat of invasive animals in U.S. National Parks. *Biol Invasions* 22, 177–188. doi: 10.1007/s10530-019-02128-0

DeCesare, N. J., Hebblewhite, M., Robinson, H. S., and Musiani, M. (2010). Endangered, apparently: the role of apparent competition in endangered species conservation. *Anim. Cons.* 13, 353–362. doi: 10.1111/j.1469-1795.2009.00328.x

Derocher, A. E., Wiig, Ø, and Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biol.* 23, 675–678. doi: 10.1002/ar.22555

Deryabina, T. G., Kuchmel, S. V., Nagorskaya, L. L., Hinton, T. G., Beasley, J. C., Lerebours, A., et al. (2015). Long-term census data reveal abundant wildlife populations at Chernobyl. *Cur. Biol.* 25, R824–R826.

Diaz, N. I. (1993). Changes in the range distribution of *Hippocamelus bisulcus* in Patagonia. *Zeit. fur Saugetier*. 58, 344–351.

Doak, D. F., Estes, J. A., Halpern, B. S., Jacob, U., Lindberg, D. R., Lovvorn, J., et al. (2008). Understanding and predicting ecological dynamics: are major surprises inevitable. *Ecology* 89, 952–961. doi: 10.1890/07-0965.1

Doherty, T. S., Dickman, C. R., Glen, A. S., Newsome, T. M., Nimmo, D. G., Ritchie, E. G., et al. (2017). The global impacts of domestic dogs on threatened vertebrates. *Biol. Cons.* 210, 56–59. doi: 10.1016/j.biocon.2017.04.007

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., et al. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proc. Nat. Acad. Sci. U.S.A.* 7, 2418–2422. doi: 10.1073/pnas.1115226109

Du Toit, J., Kock, R., and Deutsch, J. (eds) (2010). *Wild Rangelands: Conserving Wildlife while Maintaining Livestock in Semi-Arid Ecosystems*. Oxford: Blackwell Publishing.

Dunne, J. A., Maschner, H., Betts, M. W., Huntly, N., Russell, R., Williams, R. J., et al. (2016). The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Sci. Rep.* 6:21179. doi: 10.1038/srep21179

Edwards, M. E., and Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, 881–883.

Ehrlich, P. (1968). *The Population Bomb*. New York, NY: Buccaneer Books. Emerson.

Ehrlich, P. R., and Holdren, J. P. (1971). Impact of population growth. *Science* 171, 1212–1217.

Eisenberg, J. F. (1981). *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*. Chicago, IL: University of Chicago Press.

Eisenberg, J. F., and Redford, K. H. (1989). *Mammals of the Neotropics, Volume 2: The Southern Cone: Chile, Argentina, Uruguay, Paraguay*, Vol. 2. Chicago, IL: University of Chicago Press.

Ekernas, L. S., Sarmento, W. M., Davie, H. S., Reading, R. P., Murdoch, J., Wingard, G. J., et al. (2017). Desert pastoralists' negative and positive effects on rare wildlife in the Gobi. *Cons. Biol.* 31, 269–277. doi: 10.1111/cobi.12881

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., et al. (2012). Trophic Downgrading of Planet Earth. *Science* 333, 301–306. doi: 10.1126/science.1205106

Fenton, M. B., Cumming, D. H., Rautenbach, I. L., Cumming, G. S., Cumming, M. S., Ford, G., et al. (1998). Bats and the loss of tree canopy in African woodlands. *Cons. Biol.* 12, 399–407. doi: 10.1046/j.1523-1739.1998.96376.x

Fereidouni, S., Freimanis, G. L., Orynbayev, M., Ribeca, P., Flannery, J., King, D. P., et al. (2019). Mass die-off of saiga antelopes, Kazakhstan, 2015. *Emerg. Infect. Dis.* 25:1169. doi: 10.3201/eid2506.180990

Festa-Bianchet, M., Coulson, T., Gaillard, J. M., Hogg, J. T., and Pelletier, F. (2006). Stochastic predation events and population persistence in bighorn sheep. *Proc. Roy. Soc. Biol. Sci.* 273, 1537–1543. doi: 10.1098/rspb.2006.3467

Flueck, W. T., and Smith-Flueck, J. A. M. (2017). Troubling disease syndrome in endangered live Patagonian huemul deer (*Hippocamelus bisulcus*) from the Protected Park Shoonem: unusually high prevalence of osteopathology. *BMC Res. Notes* 10:739. doi: 10.1186/s13104-017-3052-4

Foresta, L., Gourmelen, N., Weissgerber, F., Nienow, P., Williams, J. J., Shepherd, A., et al. (2018). Heterogeneous and rapid ice loss over the Patagonian Ice Fields revealed by CryoSat-2 swath radar altimetry. *Remote Sens. Environ.* 211, 441–455. doi: 10.1016/j.rse.2018.03.041

Frid, A. (1994). Observations on habitat use and social organization of a huemul Hippocamelus bisulcus coastal population in Chile. *Biol. Conserv.* 67, 13–19. doi: 10.1016/0006-3207(94)90003-5

Frid, A. (1997). Apocalypse cow: endangered deer compete with cattle for space in Chile's fjords. *Wildl. Conserv.* 100, 52–57.

Frid, A. (1999). Huemul (*Hippocamelus bisulcus*) sociality at a periglacial site: sexual aggregation and habitat effects on group size. *Can. J. Zool.* 77, 1083–1091. doi: 10.1139/z99-078

Frid, A. (2001). Habitat use by endangered huemul (*Hippocamelus bisulcus*): cattle, snow, and the problem of multiple causes. *Biol. Cons.* 100, 261–267. doi: 10.1016/s0006-3207(01)00064-7

Fryxell, J. M., Greever, J., and Sinclair, A. R. E. (1988). Why are migratory ungulates so abundant? *Amer. Nat.* 131, 781–798. doi: 10.1086/284822

Garrott, R. A., Bruggeman, J. E., Becker, M. S., Kalinowski, S. T., and White, P. J. (2007). Evaluating prey switching in wolf–ungulate systems. *Ecol. Appl.* 17, 1588–1597. doi: 10.1890/06-1439.1

Geer, A. V. D., Anastasakis, G., and Lyras, G. A. (2016). If hippopotamuses cannot swim, how did they colonize islands: a reply to Mazza. *Lethaia* 48, 147–150. doi: 10.1111/let.12095

Geffroy, B., Samia, D. S. M., Bessa, E., and Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* 30, 755–765. doi: 10.1016/j.tree.2015.09.010

Geist, V. (1978). *Life Strategies, Human Evolution, Environmental Design: Toward A Biological Theory of Health*. Berlin: Springer-Verlag.

Geist, V. (1998). *Deer of the World: Their Evolution, Behavior and Ecology. Harrisburg*. Pennsylvania: Stackpole Books, 1998.

Geldmann, J., Joppa, L. N., and Burgess, N. D. (2014). Mapping change in human pressure globally on land and within protected areas. *Cons. Biol.* 28, 1604–1616. doi: 10.1111/cobi.12332

Gibson, L. (2006). The role of lethal control in managing the effects of apparent competition on endangered prey species. *Wildl. Soc. Bull.* 34, 1220–1224. doi: 10.2193/0091-7648(2006)34[1220:trolci]2.0.co;2

Goetsch, C., Wigg, J., Royo, A. A., Ristau, T., and Carson, W. P. (2011). Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. *J. Torrey Bot. Soc.* 138, 220–224.

Goldewijk, K. K. (2005). Three centuries of global population growth: a spatial referenced population (density) database for 1700–2000. *Pop. Environ.* 26, 343–367. doi: 10.1007/s11111-005-3346-7

González, B., and Alvarado, S. (2017). "What do we know about huemul abundance?," in *El Huemul de Aysén y Otros Rincones*, eds A. D. S. Iriarte, et al. (Aysen: Ediciones Secretaría Regional Ministerial de Agricultura de la Región de Aysén y Flora & Fauna Chile Limitada), 109–121.

Graham, R. W., and Lundelius, E. L. Jr. (1984). "Coevolutionary disequilibrium and Pleistocene extinctions," in *Quaternary Extinctions: A Prehistoric Revolution*, eds P. S. Martin, and R. G. Klein, (Tucson: University of Arizona Press), 223–249.

Grayson, D. (2011). *The Great Basin: A Natural Prehistory*. Berkeley: University of California Press.

Grayson, D. K., Alroy, J., Slaughter, R., Skulan, J., and Alroy, J. (2001). Did human hunting cause mass extinction? *Science* 294, 1459–1462.

Grovenburg, T. W., Swanson, C. C., Jacques, C. N., Klaver, R. W., Brinkman, T. J., Burris, B. M., et al. (2011). Survival of white-tailed deer neonates in Minnesota and South Dakota. *J. Wildl. Manag.* 75, 213–220. doi: 10.1371/journal.pone.0108797

Guthrie, R. D. (1990). *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe*. Chicago, IL: University of Chicago Press.

Guzman, L., Pacheco, H., Pizarro, G., and Alarcon, C. (2002). "Alexandrium catenella y veneno paralizante de los mariscos en Chile," in *Floraciones Algales Nocivas en el Cono Sur Americano*, eds E. Sar, M. Ferrario, and B. Reguera, (Madrid: Instituto Espan˜ol de Oceanografı'a), 235–255.

Harihar, A., Pandav, B., and Goyal, S. P. (2011). Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *J. Appl. Ecol.* 48, 806–814. doi: 10.1111/j.1365-2664.2011.01981.x

Harris, R. B. (2008). *Wildlife Conservation in China: Preserving the Habitat of China's Wild West: Preserving the Habitat of China's Wild West*. Abingdon: Routledge.

Häussermann, V., Gutstein, C. S., Bedington, M., Cassis, D., Olavarria, C., Dale, A. C., et al. (2017). Largest baleen whale mass mortality during strong El Niño event is likely related to harmful toxic algal bloom. *PeerJ* 5:e3123. doi: 10.7717/peerj.3123

Hayward, M., Edwards, S., Fancourt, B., Linnell, J., and Nilsen, E. (2019). "Top-down control of ecosystems and the case for rewilding: Does it all add up?," in *Rewilding*, eds N. Pettorelli, S. Durant, and J. Du Toit, (Cambridge: Cambridge University Press), 325–354. doi: 10.1017/9781108560962.016

Hayward, M. W., Scanlon, R. J., Callen, A., Howell, L. G., Klop-Toker, K. L., Di Blanco, Y., et al. (2019). Reintroducing rewilding to restoration–rejecting the search for novelty. *Biol. Conserv.* 233, 255–259. doi: 10.1016/j.biocon.2019.03.011

Healy, H. (2007). Korean demilitarized zone: peace and nature park. *Int. J. World Peace* 24, 61–83.

Healy, S. (2007). Deadly dingoes: wild or simply requiring due process'? *Soc. Stud. Sci.* 37, 443–471. doi: 10.1177/0306312706070746

Hebblewhite, M. (2005). Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *J. Anim. Ecol.* 74, 226–233. doi: 10.1111/j.1365-2656.2004.00909.x

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., et al. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144. doi: 10.1890/04-1269

Hess, A. N., Hess, R. J., Hess, J. L., Paulan, B., and Hess, J. A. (2014). American bison influences on lepidopteran and wild blue lupine distribution in an oak savanna landscape. *J. Insect Cons.* 18, 327–338. doi: 10.1007/s10841-014-9640-x

Holling, C. S. (1973). Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4, 1–23. doi: 10.1146/annurev.es.04.110173.000245

Holling, C. S. (1986). "The resilience of terrestrial ecosystems; local surprise and global change," in *Sustainable Development of the Biosphere*, eds W. C. Clark, and R. E. Munn, (Cambridge: Cambridge University Press), 292–317.

Home, C., Bhatnagar, Y. V., and Vanak, A. T. (2018). Canine Conundrum: domestic dogs as an invasive species and their impacts on wildlife in India. *Anim. Cons.* 21, 275–282. doi: 10.1111/acv.12389

Isbell, L. A. (1990). Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park. *Kenya. Am. J. Primatol.* 21, 41–52. doi: 10.1002/ajp.1350210105

Iwata, S., and Narama, C. (2002). Three Holocene and late Pleistocene glacial stages inferred from moraines in the Lingshi and Thanza village areas. Bhutan. *Q. Int.* 97, 0.69–78.

Jackson, J. B. (2008). Ecological extinction and evolution in the brave new ocean. *Proc. Nat. Acad. Sci. U.S.A.* 105(Suppl. 1), 11458–11465. doi: 10.1073/pnas.0802812105

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* 48, 215–267. doi: 10.1163/156853974x00345

Kie, J. G., Bowyer, R. T., Nicholson, M. C., Boroski, B. B., and Loft, E. R. (2002). Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83, 530–544. doi: 10.1890/0012-9658(2002)083[0530:lhadse]2.0.co;2

Koerner, S. E., and 72 members of the Grazing Exclosure Consortium, (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nat. Ecol. Evol.* 2, 1925–1932. doi: 10.1038/s41559-018-0696-y

Krausman, P. R., and Bleich, V. C. (2013). Conservation and management of ungulates in North America. *Int. J. Environ. Stud.* 70, 372–382. doi: 10.1080/00207233.2013.804748

Kutz, S. J., Jenkins, E. J., Veitch, A. M., Ducrocq, J., Polley, L., Elkin, B., et al. (2009). The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host–parasite interactions. *Vet. Parasit.* 163, 217–228. doi: 10.1016/j.vetpar.2009.06.008

Lackey, C. W., Beckmann, J. P., and Sedinger, J. (2013). Bear historical ranges revisited: Documenting the increase of a once-extirpated population in Nevada. *J. Wildl. Manag.* 77, 812–820. doi: 10.1002/jwmg.548

Laliberte, A. S., and Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *BioScience* 54, 123–138.

León-Muñoz, J., Urbina, M. A., Garreaud, R., and Iriarte, J. L. (2018). Hydroclimatic conditions trigger record harmful algal bloom in western Patagonia (summer 2016). *Sci. Rep.* 8, 1–10. doi: 10.1038/s41598-018-19461-4

Leopold, A. (1949). *A Sand County Almanac and Sketches Here and There. (Outdoor Essays & Reflections)*. Oxford: Oxford University Press.

Letnic, M., and Koch, F. (2010). Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austr. Ecol.* 35, 167–175. doi: 10.1111/j.1442-9993.2009.02022.x

Lewis, J. S., Corn, J. L., Mayer, J. J., Jordan, T. R., Farnsworth, M. L., Burdett, C. L., et al. (2019). Historical, current, and potential population size estimates of invasive wild pigs (*Sus scrofa*) in the United States. *Biol. Invas.* 21, 2373–2384. doi: 10.1007/s10530-019-01983-1

Loe, L. E., Hansen, B. B., Stien, A., Albon, S. D., Bischof, R., Carlsson, A., et al. (2016). Behavioral buffering of extreme weather events in a high-Arctic herbivore. *Ecosphere* 7:e01374.

Long, R. A., Wambua, A., Goheen, J. R., Palmer, T. M., and Pringle, R. M. (2017). Climatic variation modulates the indirect effects of large herbivores on small-mammal habitat use. *J. Animl. Ecol.* 86, 739–748. doi: 10.1111/1365-2656.12669

Louthan, A., Valencia, E., Martins, D. J., Guy, T., Goheen, J., Palmer, T., et al. (2019). Large mammals generate both top-down effects and extended trophic cascades on floral-visitor assemblages. *J. Trop. Ecol.* 35, 185–198. doi: 10.1017/s0266467419000142

Lovejoy, T. E., and Hannah, L. (eds) (2019). *Biodiversity and Climate Change: Transforming the Biosphere*. New Haven, CT: Yale University Press.

Loveridge, A. J., Hunt, J. E., Murindagomo, F., and Macdonald, D. W. (2006). Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J. Zool.* 270, 523–530. doi: 10.1111/j.1469-7998.2006.00181.x

Lutz, A. F., Immerzeel, W. W., Shrestha, A. B., and Bierkens, M. F. P. (2014). Consistent increase in High Asia's runoff due to increasing glacier melt and precipitation. *Nat. Clim. Change* 4:587. doi: 10.1038/nclimate2237

MacPhee, R. D. (2019). *End of the Megafauna*. New York, NY: W. W. Nortoon and Company.

Malaney, J. L., Lackey, C. W., Beckmann, J. P., and Matocq, M. D. (2018). Natural rewilding of the Great Basin: genetic consequences of recolonization by black bears (*Ursus americanus*). *Divers. Distrib.* 24, 168–178. doi: 10.1111/ddi.12666

Martin, P. S., and Klein, R. G. (eds) (1984). *Quaternary Extinctions: A Prehistoric Revolution*. Tuscon: University of Arizona Press.

McCabe, R. M., Hickey, B. M., Kudela, R. M., Lefebvre, K. A., Adams, N. G., Bill, B. D., et al. (2016). An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophys. Res. Lett.* 43, 10366–10376.

McClure, M. L., Burdett, C. L., Farnsworth, M. L., Sweeney, S. J., and Miller, R. S. (2018). A globally-distributed alien invasive species poses risks to United States imperiled species. *Sci. Rep.* 8:5331. doi: 10.1038/s41598-018-23657-z

McShea, W. J., and Rappole, J. H. (2000). Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conserv. Biol.* 14, 1161–1170. doi: 10.1046/j.1523-1739.2000.99210.x

McShea, W. J., Underwood, H. B., and Rappole, J. H. (eds) (1997). *The Science of Overabundance: Deer Ecology and Population Management*. Washington, DC: Smithsonian Institute Press.

Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R., and Peterson, R. O. (2012). Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J. Anim. Ecol.* 81, 553–563. doi: 10.1111/j.1365-2656.2011.01945.x

Middleton, A. D., Morrison, T. A., Fortin, J. K., Robbins, C. T., Proffitt, K. M., White, P. J., et al. (2013). Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proc. R. Soc. Biol. Sci.* 280, 20130870. doi: 10.1098/rspb.2013.0870

Milner-Gulland, E. J., Kholodova, M. V., Bekenov, A., Bukreeva, O. M., Grachev, I. A., Amgalan, L., et al. (2001). Dramatic declines in saiga antelope populations. *Oryx* 35, 340–345. doi: 10.1046/j.1365-3008.2001.00202.x

Ministry of Agriculture and Forestry [MAGF], (2016). *Bhutan. National Gid Disease Prevention and Control Plan launched*. Available at: http://www.moaf.gov.bt/national-gid-disease-prevention-and-control-plan-launched (accessed January 9, 2020).

Mishra, C., Bagchi, S., Namgail, T., and Bhatnagar, Y. V. (2010). "Multiple use of trans-Himalayan rangelands: reconciling human livelihoods with wildlife conservation," in *Wild Rangelands: Conserving Wildlife while Maintaining Livestock in Semi-arid Ecosystems*, eds J. Du Toit, R. Kock, and J. Deutsch, (Oxford: Blackwell Publishing), 291–311. doi: 10.1002/9781444317091.ch11

Mishra, C., van Wieren, S. E., Ketner, P. I, Heitkonig, M. A., and Prins, H. H. T. (2004). Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. *J. Appl. Ecol.* 41, 344–354. doi: 10.1111/j.0021-8901.2004.00885.x

Molinet, C., Niklitschek, E. J., Coper, S., Díaz, M., Díaz, P. A., Fuentealba, M., et al. (2014). Challenges for coastal zoning and sustainable development in the northern Patagonian fjords (Aysén, Chile). *Latin Am. J. Acquat. Res.* 42, 18–29. doi: 10.3856/vol42-issue1-fulltext-2

Moran, M. D. (2014). Bison grazing increases arthropod abundance and diversity in a tall grass prairie. *Environ. Entomol.* 43, 1174–1184. doi: 10.1603/en14013

Namgail, T., Van Wieren, S. E., Mishra, C., and Prins, H. H. T. (2010). Multi-spatial co-distribution of the endangered Ladakh urial and blue sheep in the arid Trans-Himalayan mountains. *J. Arid Environ.* 74, 1162–1169. doi: 10.1016/j.jaridenv.2010.04.013

Neff, P. K. K., Fettig, S. M., and VanOverbeke, D. R. (2007). Variable response of butterflies and vegetation to elk herbivory: an exclosure experiment in ponderosa pine and aspen-mixed conifer forests. *Southwest. Nat.* 52, 1–15.

Ng, D., Carver, S., Gotame, M., Karmasharya, D., Karmacharya, D., Pradhan, S. M., et al. (2019). Canine distemper in Nepal's Annapurna Conservation Area–Implications of dog husbandry and human behaviour for wildlife disease. *PLoS One* 14:e220874. doi: 10.1371/journal.pone.0220874

Nishi, J. S., Shury, T., and Elkin, B. T. (2006). Wildlife reservoirs for bovine tuberculosis (*Mycobacterium bovis*) in Canada: strategies for management and research. *Vet. Microbiol.* 112, 325–338. doi: 10.1016/j.vetmic.2005.11.013

Noss, R. F. (2012). *Forgotten Grasslands of the South: Natural History and Conservation*. Washington, DC: Island Press.

Novaro, A. J., Funes, M. C., and Jiménez, J. (2004). "Selection for introduced prey and conservation of culpeo and chilla zorros in Patagonia," in *The Biology and Conservation of Wild Canids*, eds D. W. MacDonald, and C. Sillero, (Oxford: Oxford University Press), 243–254.

Novaro, A. J., and Walker, R. S. (2005). "Human-induced changes in the effect of top carnivores on biodiversity in the Patagonian Steppe," in *Large Carnivores and the Conservation of Biodiversity*, eds J. C. Ray, et al. (Washington, DC: Island Press), 268–288.

Olson, K. A., Fuller, T. K., Schaller, G. B., Odonkhuu, D., and Murray, M. G. (2005). Estimating the population density of Mongolian gazelles Procapra gutturosa by driving long-distance transects. *Oryx* 39, 164–169. doi: 10.1017/s0030605305000402

Owen-Smith, R. N. (1988). *Megaherbivores: The Influence of Very Large Body Size on Ecology*. London: Cambridge University Press.

Peterson, R. O. (2007). *The Wolves of Isle Royale: a Broken Balance*. Ann Arbor, MI: University of Michigan Press.

Pierce, B. M., Bleich, V. C., Monteith, K. L., and Bowyer, R. T. (2012). Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *J. Mamm.* 93, 977–988. doi: 10.1644/12-mamm-a-014.1

Pimentel, D., Huang, X., Cordova, A., and Pimentel, M. (1997). Impact of population growth on food supplies and environment. *Pop. Env.* 19, 9–14.

Plumb, G., Monello, R., Resnik, J., Kahn, R., Leong, K., Decker, D., et al. (2014). *A Comprehensive Review of Ungulate Management by the National Park Service: Second Century Challenges, Opportunities, and Coherence*. Washington DC: *USDI*.

Polis, G. A., and Hurd, S. D. (1996). Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Amer. Nat.* 147, 396–423. doi: 10.1086/285858

Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., et al. (2013). Ecological consequences of sea-ice decline. *Science* 341, 519–524.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., et al. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science* 325, 1355–1358. doi: 10.1126/science.1173113

Povilitis, A. (1986). Huemuls in areas adjacent to glaciers in southern Chile. *Mountain Res. Dev.* 6, 273–275.

Povilitis, A. (2002). Current status of the huemul (*Hippocamelus bisulcus*) in central Chile. [El estado actual del huemul (*Hippocamelus bisulcus*) en Chile central]. *Gayana* 66, 59–68.

Power, J., and Compion, R. X. S. (2009). Lion predation on elephants in the Savuti, Chobe National Park, Botswana.". *Afr. Zool.* 44, 36–44.

Pringle, R. M., Young, T. P., Rubenstein, D. I., and McCauley, D. J. (2007). Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc. Natl. Acad. Sci. U.S.A.* 104, 193–197. doi: 10.1073/pnas.0609840104

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., et al. (2009). The rise of the mesopredator. *Bioscience* 59, 779–791. doi: 10.1525/bio.2009.59.9.9

Pyare, S., and Berger, J. (2003). Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. *Biol. Cons.* 113, 63–73. doi: 10.1016/s0006-3207(02)00350-6

Quintana, N. T., Ballard, W. B., Wallace, M. C., Krausman, P. R., de Vos, J., Alcumbrac, O., et al. (2016). Survival of desert mule deer fawns in central Arizona. *Southwest. Nat.* 61, 93–101.

Ray, J., Redford, K. H., Steneck, R., and Berger, J. (eds) (2005). *Large Carnivores and the Conservation of Biodiversity*. Washington, DC: Island Press.

Redford, K. H. (1992). The empty forest. *BioScience* 42, 412–422. doi: 10.2307/1311860

Ripple, W. J., and Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biol. Cons.* 133, 397–408. doi: 10.1016/j.biocon.2006.07.002

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science* 343:1241484. doi: 10.1126/science.1241484

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., et al. (2015). Collapse of the world's largest herbivores. *Sci. Adv.* 1:e1400103. doi: 10.1126/sciadv.1400103

Ripple, W. J., and Van Valkenburgh, B. (2010). Linking top-down forces to the Pleistocene megafaunal extinctions. *BioScience* 60, 16–526.

Ripple, W. J., Wolf, C., Newsome, T. M., Betts, M. G., Ceballos, G., Courchamp, F., et al. (2019). Are we eating the world's megafauna to extinction? *Conserv. Lett.* 12:12627.

Ritchie, E. G., Dickman, C. R., Letnic, M., Vanak, A. T., and Gommper, M. (2013). "Dogs as predators and trophic regulators," in *Free-ranging Dogs and Wildlife Conservation*, ed. M. E. Gommper, (New York, NY: Oxford University Press), 55–68. doi: 10.1093/acprof:osobl/9780199663217.003.0002

Rode, K. D., Robbins, C. T., Nelson, L., and Amstrup, S. C. (2015a). Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? *Front. Ecol. Environ.* 13:138–145. doi: 10.1890/140202

Rode, K. D., Wilson, R. R., Regehr, E. V., St, Martin M, Douglas, D. C., and Olson, J. (2015b). Increased land use by Chukchi Sea polar bears in relation to changing sea ice conditions. *PLoS One* 10:e142213. doi: 10.1371/journal.pone.0142213

Roemer, G. W., Gompper, M. E., and Van Valkenburgh, B. (2009). The ecological role of the mammalian mesocarnivore. *Bioscience* 59, 165–173. doi: 10.1093/jhered/esx068

Rominger, E. M. (2018). The Gordian knot of mountain lion predation and bighorn sheep. *J. Wildl. Manag.* 82, 19–31. doi: 10.1002/jwmg.21396

Rooney, T. P. (2009). High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecol.* 202, 103–111. doi: 10.1007/s11258-008-9489-8

Rooney, T. P., and Waller, D. M. (2003). Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manag.* 181, 165–176. doi: 10.1016/s0378-1127(03)00130-0

Sakakibara, D., Sugiyama, S., Sawagaki, T., Marinsek, S., and Skvarca, P. (2013). Rapid retreat, acceleration and thinning of Glaciar Upsala, Southern Patagonia Icefield, initiated in 2008. *Ann. Glaciol.* 54, 131–138. doi: 10.3189/2013aog63a236

Sanderson, E. W., Redford, K. H., Weber, B., Aune, K., Baldes, D., Berger, J., et al. (2008). The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. *Cons. Biol.* 22, 252–266. doi: 10.1111/j.1523-1739.2008.00899.x

Sarmento, W. M., and Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biol. Cons.* 212, 316–326. doi: 10.1016/j.biocon.2017.06.032

Schaller, G. B. (1998). *Wildlife of Tibetan Steppes*. Chicago, IL: University of Chicago Press.

Schaller, G. B. (2012). *Tibet Wild: A Naturalist's Journeys on the Roof of the World*. Washington, DC: Island Press.

Schwartz, C. C., and Franzmann, A. W. (1991). Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildl. Monog.* 113, 3–58.

Serrouya, R., McLellan, B. N., Boutin, S., Seip, D. R., and Nielsen, S. E. (2011). Developing a population target for an overabundant ungulate for ecosystem restoration. *J. Appl. Ecol.* 48, 935–942. doi: 10.1111/j.1365-2664.2011.01998.x

Sharam, G. J., Sinclair, A. R. E., and Turkington, R. (2009). Serengeti birds maintain forests by inhibiting seed predators. *Science* 325, 51–51. doi: 10.1126/science.1173805

Shrestha, U. B., Dhital, K. R., and Gautam, A. P. (2019). Economic dependence of mountain communities on Chinese caterpillar fungus *Ophiocordyceps sinensis* (yarsagumba): A case from western Nepal. *Oryx* 53, 256–264. doi: 10.1017/s0030605317000461

Silva-Rodríguez, E. A., and Sieving, K. E. (2012). Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. *Biol. Cons.* 150, 103–110. doi: 10.1016/j.biocon.2012.03.008

Simenstad, C. A., Estes, J. A., and Kenyon, K. W. (1978). Aleuts, sea otters, and alternate stable-state communities. *Science* 200, 403–411. doi: 10.1126/science.200.4340.403

Simpson, G. G. (1944). *Tempo and Mode in Evolution*. New York, NY: Columbia University Press.

Sinclair, A. R. E., Mduma, S., and Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature* 425, 288–290. doi: 10.1038/nature01934

Sinclair, A. R. E., Metzger, K., Brashares, J. S., Nkwabi, A., Sharam, G., and Fryxell, J. M. (2010). "Trophic cascades in African savanna: Serengeti as a case study," in *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*, eds J. Terborugh, and J. E. Estes, (Washington, DC: Island Press), 255–274.

Smith, B., Cole, E. K., and Dobkin, D. S. (2004). *An Imperfect Pasture: A Century of Change at the National Elk Refuge in Jackson Hole, Wyoming*. Wyoming: Grand Teton Natural History Association.

Smith, D., and Ferguson, G. (2012). *Decade of the Wolf: Returning the Wild to Yellowstone*. Lanham, MA: Rowman & Littlefield.

Smith, D. W., Peterson, R. O., and Houston, D. B. (2003). Yellowstone after wolves. *BioScience* 53, 330–340.

Smith, F. A., and Lyons, S. K. (eds) (2013). *Animal Body Size: Linking Pattern and Process across Space, Time and Taxonomy*. Chicago, IL: University of Chicago Press.

Smith, F. A., Tomé, C. P., Elliott Smith, E. A., Lyons, S. K., Newsome, S. D., and Stafford, T. W. (2015). (online); 2016. Unraveling the consequences of the terminal Pleistocene megafauna extinction on mammal community assembly. *Ecography* 39, 223–239. doi: 10.1111/ecog.01779

Soulé, M. E., Estes, J. A., Berger, J., and Del Rio, C. M. (2003). Ecological effectiveness: conservation goals for interactive species. *Cons. Biol.* 17, 1238–1250. doi: 10.1046/j.1523-1739.2003.01599.x

Spaeth, D. F., Hundertmark, K. J., Bowyer, R. T., Barboza, P. S., Stephenson, T. R., and Peterson, R. O. (2001). Incisor arcades of Alaskan moose: is dimorphism related to sexual segregation? *Alces* 37, 217–226.

Springer, A. M., Estes, J. A., Van Vliet, G. B., Williams, T. M., Doak, D. F., Danner, E. M., et al. (2003). Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proc. Nat. Acad. Sci. U.S.A.* 100, 12223–12228. doi: 10.1073/pnas.1635156100

Stebbins, G. L. (1981). Coevolution of grasses and herbivores. *Ann. Missouri Bot. Gard.* 68, 75–86.

Stempniewicz, L., Goc, M., Kidawa, D., Urbański, J., Hadwiczak, M., et al. (2017). Marine birds and mammals foraging in the rapidly deglaciating Arctic fjord-numbers, distribution and habitat preferences. *Clim. Change* 140, 533–548. doi: 10.1007/s10584-016-1853-4

Stewart, K. M., Bowyer, R. T., Kie, J. G., Dick, B. L., and Ruess, R. W. (2009). Population density of North American elk: effects on plant diversity. *Oecologia* 161, 303–312. doi: 10.1007/s00442-009-1376-z

Stoddart, L. C., Griffiths, R. E., and Knowlton, F. F. (2001). Coyote responses to changing jackrabbit abundance affect sheep predation. *J. Range Manag.* 54, 15–20.

Strong, D. R., Simberloff, D., Abele, L. G., and Thistle, A. B. (eds) (1984). *Ecological Communities: Conceptual Issues and the Evidence*. Princeton, NJ: Princeton Univ. Press.

Suarez, B., and Guzman, L. (2005). *Floraciones de Algas Nocivas: Mareas Rojas y Toxinas Marinas*. Santiago: Editorial Universitaria.

Sweitzer, R. A., Jenkins, S. H., and Berger, J. (1997). Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin Desert. *Cons. Biol.* 11, 1407–1417. doi: 10.1046/j.1523-1739.1997.96138.x

Terborgh, J., and Estes, J. A. (eds) (2010). *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Washington, DC: Island Press.

Thomas, C. D. (2017). *Inheritors of the Earth: How Nature is Thriving in an Age of Extinction*. London: Hachette UK.

Torben, R. C., and Erlandson, J. M. (2009). Coastal exploitation: How did ancient hunter-gatherers influence coastal environments? *Science* 352, 952–953.

Trouwborst, A., Krofel, M., and Linnell, J. D. (2015). Legal implications of range expansions in a terrestrial carnivore: the case of the golden jackal (*Canis aureus*) in Europe. *Biodiv. Conserv.* 24, 0.2593–2610.

Tyler, N. J., Forchhammer, M. C., and Øritsland, N. A. (2008). Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. *Ecology* 89, 1675–1686. doi: 10.1890/07-0416.1

United Nations, Department of Economic, and Social Affairs, Population Division, (2019). *World Population Prospects 2019: Ten Key Findings*. New York, NY: United Nations.

Urbina, M. A. (2016). Temporal variation on environmental variables and pollution indicators in marine sediments under sea Salmon farming cages in protected and exposed zones in the Chilean inland Southern Sea. *Sci. Total Environ.* 573, 841–853. doi: 10.1016/j.scitotenv.2016.08.166

Van Duyne, C. V., Ras, E., De Vos, A. E. W., De Boer, W. F., and Henkens, R. J. H. G. (2009). Wolf predation among reintroduced Przewalski horses in Hustai National Park. *Mongolia. J. Wildl. Manam.* 73, 836–843. doi: 10.2193/2008-027

Vermeij, G. J. (1993). *Evolution and Escalation: An Ecological History of Life*. Princeton, NJ: Princeton University Press.

Vila, A. R., Briceño, C., McAloose, D., Seimon, T. A., Armién, A. G., Mauldin, E. A., et al. (2019). Putative parapoxvirus-associated foot disease in the endangered huemul deer (*Hippocamelus bisulcus*) in Bernardo O'Higgins National Park. Chile. *PLoS One* 14:e0213667. doi: 10.1371/journal.pone.0213667

Vila, A. R., Lopez, R., Pastore, H., Faundez, R., and Serret, A. (2006). Current distribution and conservation of the huemul (*Hippocamelus bisulcus*) in Argentina and Chile. *Mastozool. Neotrop.* 13, 263–269. doi: 10.7717/peerj.5222

Vila, A. R., Saucedo, C., Aldridge, D., Ramilo, E., and Corti, P. (2010). "South Andean huemul *Hippocamelus bisulcus* (Molina 1782)," in *Neotropical Cervidology: Biology and Medicine of Latin American Deer*, eds J. M. Duarte, and S. González, (Brazil: Funep), 89–100.

Villatoro, F. J., Naughton-Treves, L., Sepúlveda, M. A., Stowhas, P., Mardones, F. O., and Silva-Rodríguez, E. A. (2019). When free-ranging dogs threaten wildlife: Public attitudes toward management strategies in southern Chile. *J. Environ. Manag.* 229, 67–75. doi: 10.1016/j.jenvman.2018.06.035

von Humboldt, A. (1858). *Cosmos: A Sketch of the Physical Description of the Universe*, Vol. I, trans. E. C. Otte, (Baltimore, MA: The John Hopkins Press), 1997.

Vors, L. S., and Boyce, M. S. (2009). Global declines of caribou and reindeer. *Glob. Change Biol.* 15, 2626–2633. doi: 10.1111/j.1365-2486.2009.01974.x

Vrba, E. (1993). Turnover-pulses, the Red Queen, and Related Topic. *Am. J. Sci.* 293-A, 418–452. doi: 10.2475/ajs.293.a.418

Vrba, E. S., and Schaller, G. B. (2000). *Antelopes, Deer, and Relatives*. London: Yale University Press.

Walker, S., and Novaro, A. (2010). "The World's southernmost pumas in Patagonia and the Southern Andes," in *Cougar Ecology and Conservation*, eds M. Hornocker, and S. Negri (Chicago, IL: The University of Chicago Press), 91–100.

Wallace, A. R. (1876). *The Geographical Distribution of Animals: With a Study of The Relations of Living and Extinct Faunas as Elucidating The Past Changes of The Earth's Surface*, Vol. 1. Cambridge: Cambridge University Press, 2011.

Walston, J., Karanth, K. U., and Stokes, E. (2010). *Avoiding the Unthinkable: What Will It Cost to Prevent Tigers Becoming Extinct in the Wild*. New York, NY: Wildlife Conservation Society.

Wangchuk, K., and Wangdi, J. (2015). Mountain pastoralism in transition: Consequences of legalizing Cordyceps collection on yak farming practices in Bhutan. *Pastoralism* 5:4.

Wangchuk, T. R., Wegge, P., and Sangay, T. (2016). Habitat and diet of Bhutan takin Budorcas taxicolor whitei during summer in Jigme Dorji National Park. Bhutan. *J. Nat. Hist.* 50, 759–770. doi: 10.1080/00222933.2015.1079658

Watson, J. E., Shanahan, D. F., Di Marco, M., Allan, J., Laurance, W. F., Sanderson, E. W., et al. (2016). Catastrophic declines in wilderness areas undermine global environment targets. *Cur. Biol.* 26, 2929–2934. doi: 10.1016/j.cub.2016.08.049

Watson, J. E., Venter, O., Lee, J., Jones, K. R., Robinson, J. G., Possingham, H. P., et al. (2018). Protect the last of the wild. *Nature* 563, 27–30. doi: 10.1038/d41586-018-07183-6

Webb, S. D. (2006). The great American biotic interchange: patterns and processes. *Ann. Missouri Bot. Gard.* 93, 245–258.

Webb, S. D., and Barnosky, A. D. (1989). Faunal dynamics of Pleistocene mammals. *Ann. Rev. Earth Planetary Sci.* 17, 413–436. doi: 10.1146/annurev.ea.17.050189.002213

Weber, M., and Gonzalez, S. (2003). Latin American deer diversity and conservation: a review of status and distribution. *Ecoscience* 10, 443–454. doi: 10.1080/11956860.2003.11682792

Wells, M. L., Trainer, V. L., Smayda, T. J., Karlson, B. S., Trick, C. G., Kudela, R. M., et al. (2015). Harmful algal blooms and climate change: Learning from the past and present to forecast the future. *Harmful Algae* 49, 68–93. doi: 10.1016/j.hal.2015.07.009

Wemmer, C. (ed.) (1987). *Biology and Management of the Cervidae: A Conference Held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia*. Washington, D.C: Smithsonian Institution Press.

Wheatall, L., Nuttle, T. I. M., and Yerger, E. (2013). Indirect effects of pandemic deer overabundance inferred from caterpillar-host relations. *Cons. Biol.* 27, 1107–1116. doi: 10.1111/cobi.12077

White, K. S., Barten, N. L., Crouse, S., and Crouse, J. (2014). Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology* 95, 225–237. doi: 10.1890/13-0054.1

White, K. S., Gregovich, D. P., and Levi, T. (2018). Projecting the future of an alpine ungulate under climate change scenarios. *Glob. Change Biol.* 24, 1136–1149. doi: 10.1111/gcb.13919

Wittemyer, G., Northrup, J. M., Blanc, J., Douglas-Hamilton, I., Omondi, P., and Burnham, K. P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proc. Natl. Acad. Sci. U.S.A.* 111, 13117–13121. doi: 10.1073/pnas.1403984111

Wolf, C., and Ripple, W. J. (2017). Range contractions of the world's large carnivores. *R. Soc. Open Sci.* 4:170052. doi: 10.1098/rsos.170052

Woodroffe, R., and Ginsberg, J. R. (2005). "King of the beast: evidence for guild redundancy among large mammalian carnivores," in *Large Carnivores and the Conservation of Biodiversity*, eds J. Ray, K. H. Redford, R. Steneck, and J. Berger, (Washington, DC: Island Press), 154–176.

World Tourism Organization, (2014). *Towards Measuring the Economic Value of Wildlife Watching Tourism in Africa – Briefing Paper*. Madrid: United Nations - World Tourism Organization.

Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y. U. N., et al. (2009). The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods. *Cons. Biol.* 23, 520–530. doi: 10.1111/j.1523-1739.2009.01237.x

Yeakel, J. D., and Dunne, J. A. (2015). Modern lessons from ancient food webs. *Am. Sci.* 103, 188–195.

Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., et al. (2014). Collapse of an ecological network in Ancient Egypt. *Proc. Natl. Acad. Sci. U.S.A.* 111, 14472–14477. doi: 10.1073/pnas.1408471111

Young, J. A., and Sparks, B. A. (2002). *Cattle in the Cold Desert*. Reno: University of Nevada Press.

Young, J. K., Olson, K. A., Reading, R. P., Amgalanbaatar, S., and Berger, J. (2011). Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *BioScience* 61, 125–132. doi: 10.1525/bio.2011.61.2.7

Zager, P., and Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* 17, 95–109.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 16 June 2020
doi: 10.3389/fevo.2020.00176

Metabolic and Population Effects of Winter Tick Infestations on Moose: Unique Evolutionary Circumstances?

*Peter J. Pekins**

Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, United States

Moose (*Alces alces*) have evolved to store adequate body fat to emerge from winter in adequate nutritional condition that is key to annual productivity and neonatal survival. Blood consumption by winter ticks (*Dermacentor albipictus*) affects survival and productivity of moose, often resulting in marked local and regional die-offs of calves. Concurrent with an unprecedented frequency of winter tick epizootics (>50% calf mortality) in the northeastern United States, productivity but not mortality of adult female moose also has declined because of low rates of twinning and calving. Chronic blood loss to winter ticks in late winter-early spring negatively affects pregnant cows in their energy- and protein-costly 3rd trimester of pregnancy that will eventually calve and lactate initially in an environment low in digestible energy and protein. To describe this dynamic, I calculated the endogenous fat balance of different-sized pregnant cows by developing energy-balance equations that accounted temporally for gestation, winter tick infestation, and lactation under two consumption levels. The analysis revealed the critical importance of body mass and body fat as only large cows (25% pre-winter body fat) were immune from depletion of body fat at birth in all scenarios. Mid-sized cows (20% body fat) depleted fat reserves during gestation in most scenarios, and small cows (15% body fat) in all scenarios. The infestation and forage- consumption levels influenced the predicted date of fat depletion up to several weeks, and failed calving or mortal mass loss associated with rapid loss of endogenous protein was possible in mid-sized and small cows. The continual decline in demographic parameters points to reduced body mass and body fat over time, or increased numbers of mid-sized and small cows in the population with lower reproductive potential. This regional population is confronted with a unique and sustained combination of environmental and parasitic conditions associated with a warming climate that markedly affects its survival and reproduction in quality habitat, a unique occurrence in their evolutionary history.

Keywords: body fat, climate change, energy balance, gestation, moose, body protein, productivity, winter ticks

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Brent Patterson,
Ontario Ministry of Natural Resources
and Forestry, Canada
Perry S. Barboza,
Texas A&M University, United States

***Correspondence:**
Peter J. Pekins
pete.pekins@unh.edu

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 31 January 2020
Accepted: 19 May 2020
Published: 16 June 2020

Citation:
Pekins PJ (2020) Metabolic
and Population Effects of Winter Tick
Infestations on Moose: Unique
Evolutionary Circumstances?
Front. Ecol. Evol. 8:176.
doi: 10.3389/fevo.2020.00176

INTRODUCTION

Nutritional carrying capacity of a wildlife population is typically described relative to resource availability and environmental constraints that limit that availability. In seasonal environments, ungulates balance demand and constraints relative to reproductive success (Parker et al., 2009). Although considered a "southern range" population, moose in the northeastern United States (hereafter Northeast) occupy a seasonal environment with a relatively long winter and short growing season that constrain resource availability—spring green-up typically occurs in late May-early June and leaf senescence in late September-early October. As with other moose populations, winter forage intake is inadequate to maintain body mass throughout winter (Schwartz and Renecker, 2007), and pregnant cows store and subsequently catabolize endogenous fat reserves and protein to meet the energy and protein requirements of maintenance, gestation, and lactation (Parker et al., 2009). Throughout most moose range in North America and specifically in the Northeast, the entirety of gestation and the initial 1–2 weeks of lactation occur prior to spring green-up after which forage increases in digestible protein and energy. It follows that adult cows have evolved to survive winter with adequate tissue resources to provide for the energy- and protein-costly last trimester of gestation and early lactation, and that late-winter condition and adequate fetal growth during the last trimester of gestation are related directly to neonatal survival (Keech et al., 2000; Parker et al., 2009); effectively, they are capital breeders that rely on body reserves to produce successfully.

The moose population in the Northeast United States (Maine, New Hampshire, and Vermont) irrupted during the late 1970s through early 1990s in response to extensive forest harvesting associated with a severe spruce budworm (*Choristoneura fumiferana*) epidemic (Bontaites and Gustafson, 1993; Dunfey-Ball, 2017). Although in slow decline for the past 10–15 years, it still remains the largest contiguous regional population in the lower 48 states, exceeding >50,000 animals. This decline spurred regional research and since 2014 has included >500 radio-marked cows and calves to measure pregnancy rate, calf production and survival, adult survival, and successive birthing rate of adult cows (Jones et al., 2017, 2019; Ellingwood et al., 2019). Annual measurements of harvested animals revealed that body mass of adult animals was trending down and low body mass was limiting sexual maturation of yearling cows (Adams and Pekins, 1995; Musante et al., 2010; Bergeron et al., 2013).

Current research indicates that the birthing rate of adult cows is measurably lower than the pregnancy rate, twinning is rare, and yearlings rarely breed in northern New Hampshire and western Maine (Jones et al., 2019; Powers, 2019). Further, epizootic-level calf mortality (>50%; 10-month old calves) in late March–April because of infestation of winter ticks (*Dermacentor albipictus*) is occurring with unprecedented frequency and regardless of winter severity (Ellingwood, 2018; Jones et al., 2019; Powers, 2019). Evidence that the nutritional condition of moose is not compromised by habitat quality includes: (1) forest regeneration is not affected by over-browsing (Bergeron et al., 2011; Andreozzi et al., 2014); timber harvesting creates abundant and stable optimal foraging habitat (Dunfey-Ball, 2017); and no starvation was documented with radio-marked animals in 5 years of study (Ellingwood, 2018; Jones et al., 2019; Powers, 2019). Rather, the population dynamics of much of this regional population reflects the annual and continual (5 in 6 years from 2014 to 2019) influence of parasitism by winter ticks (Ellingwood et al., 2020).

The severity of winter tick infestation is typically a function of 3 factors—moose (host) density and favorable environmental conditions for larval winter ticks (Samuel, 2007), and overlap of seasonal habitat use (Healy et al., 2018)—that manifest in severe winters that simultaneously reduce animal condition and increase the relative impact of infestations (Samuel, 2007). In contrast, the moose population in the Northeast has not experienced increased length or severity of winter in recent epizootic years. Rather, later starting winters associated with climate change are considered a unique ecological influence that extends the autumnal questing period for larval winter ticks (Jones et al., 2019; Healy et al., 2020). This longer questing period alters the direct relationship between host and parasite density, or tick abundance and infestation, while largely negating the influence of winter severity during epizootic years.

Earlier analyses identified a stark contrast between predicted calf versus adult mortality at severe infestation levels (Musante et al., 2007), and field studies corroborate that winter ticks rarely cause adult mortality in the Northeast (Jones et al., 2019) or elsewhere (Samuel, 2007). Nonetheless, these analyses also demonstrated that severe infestation by ticks measurably impacted the energy and protein balance of adult cows (Musante et al., 2007). Because productivity is declining in the Northeast (Jones et al., 2019), this analysis was designed to measure the temporal influence of winter ticks on energy and protein balance of pregnant cows to identify the potential effect of infestation on productivity in the current year, and to better understand and predict the sustained impact of high infestations. Multiple factors including body mass and composition, infestation level of winter ticks (infestation), and forage consumption were varied in energy-balance equations to illustrate a range of potential outcomes in body condition. I hypothesized that: (1) fat reserves of heavier cows would provide a buffer during the last trimester of gestation and early lactation against the energy-protein losses associated with high infestation; (2) small and mid-sized cows would lose endogenous protein (muscle mass) rapidly during the 3rd trimester of gestation at high infestation; (3) all cows would be in reasonable physical condition at birth at low infestation by ticks; and (4) low forage consumption would only influence condition at high infestation.

MATERIALS AND METHODS

The empirical data used in the analyses were collected from radio-marked moose studied in northern New Hampshire in 2014–2018 (Jones et al., 2017, 2019; Ellingwood, 2018; Powers, 2019). Animal capture and handling protocols were approved by the Institutional Animal Care and Use Committee at the University of New Hampshire (IACUC #130805). These moose occupied contiguous, commercial forestland that is a transition of the northern hardwood and boreal forest types; a thorough description is found in Jones et al. (2019). Importantly, no predator of moose exists in the study area except black bears (*Ursus americanus*) that are considered a minor predator of neonates; calf survival is high (∼70%) 60-days post-birth (Musante et al., 2010; Jones et al., 2017). The current regional moose density is estimated as 0.46 moose/km^2 (0.87 moose/km^2 in 2005), but the local density within the study area (∼1,250 km^2;

Jones et al., 2019) is considered higher; e.g., 45–50 cows and calves combined were captured annually within this area for 5 consecutive winters (January 2014–2018). Annual adult survival averaged 83% in 2014–2019 (Powers, 2019), with calf mortality concentrated in late March–April and associated with winter tick infestation (Jones et al., 2017, 2019); epizootics (61–77% mortality) documented with radio-marked calves occurred in 2014, 2015, 2016, and 2018 (Powers, 2019).

Energy balance equations were used to track cow condition (body mass and fat level) from 10 January to 23 May, a period that encompassed the second and third trimesters of gestation, feeding (blood removal) by nymphs and adult winter ticks, and 1 week of lactation. The field metabolic rate (FMR) was initially estimated as a multiple of the maintenance energy cost of a non-pregnant cow, and elevated with the estimated costs of gestation, lactation, and blood loss (replacement cost) from winter ticks; these costs were balanced against forage consumption and endogenous reserves to maintain body mass. Each variable was set relative to empirical measurements in the environment, or if a single value, to the benefit of the experimental moose.

Field Metabolic Rate (FMR)

The FMR of an adult cow was set as 1.1 times the maintenance energy requirement [603 kJ/kg body mass $(\mathrm{BM})^{0.75}$/d] as measured directly in forage consumption trials (Schwartz et al., 1988b). This value is equivalent to 1.7 × the fasting metabolic rate of moose measured by Regelin et al. (1985) as well as the average FMR measured in winter with doubly labeled water with both captive adult female white-tailed deer (*Odocoileus virginianus*) living in a 1.5 ha pen (Eckert, 2004) and free-ranging adult white-tailed deer (Pekins, 1995) that demonstrated energy-conserving behavior. In general, annual FMR of free-ranging animals is assumed to be ~2 × basal metabolic rate (Robbins, 1993). The winter FMR measured with doubly labeled water averaged ~2.1 × basal metabolic rate in free-ranging white-tailed deer fawns (Tarr and Pekins, 2002) expected to operate at higher metabolism than adults, and adult female black-tailed deer (*Odocoileus hemonius sitchensis*; Parker et al., 1999).

Body Mass (BM)

Body mass was expressed as low (325 kg), mid-sized (350 kg), and high (375 kg); these successive values differed by 5% to reflect a similar percentage difference in body fat and represent a reasonable range of winter condition (Schwartz and Renecker, 2007). I assumed that BM (including the fetus) was maintained throughout gestation and was then lowered 18 kg post-birth during the first week of lactation. This presumed a birth mass of 15 kg (Schwartz, 2007) and that the fetus represents 82% of the estimated energy deposition associated with the fetus and placenta combined (Oftedal, 1985).

Body Fat (BF)

Body fat was set at 15% (49 kg), 20% (70 kg), and 25% (94 kg) to correspond proportionally with the low, mid-sized, and high BM, respectively; at the start of winter, adult moose typically have 20–26% BF (Schwartz et al., 1988a; Schwartz and Renecker, 2007). These proportions were assumed as the initial% BF in January and converted to an energy equivalent (39.33 kJ/g) as required to meet energy balance. If BF was exhausted during gestation, endogenous protein (BP, muscle mass) was catabolized and converted with an energy equivalent (16.74 kJ/g).

Gestation

The length of gestation was assumed to be 231 days, which set the 3rd trimester at 77 days (01 March to 16 May); the annual median date of birth was 16–18 May in the study area (Jones et al., 2017). Moose delay most (90%) fetal growth (Schwartz and Hundertmark, 1993; Schwartz, 2007) until the 3rd trimester so that proportional cost was assigned to that period; 10% of the cost was assigned to the 48-day portion of the 2nd trimester from early January through February.

The peak cost of gestation is 1.8–1.9 times higher than that of non-pregnant animals with cost rising exponentially in the 3rd trimester (Schwartz and Hundertmark, 1993; Pekins et al., 1998; Schwartz, 2007). To account for the increasing rate, the 3rd trimester was broken into three periods of 25, 26, and 26 days that were assigned a cost of 1.2, 1.4, and 1.7 times the fasting metabolic rate (355.6 kJ/kgBM$^{0.75}$/d; Regelin et al., 1985). These rates represent the midpoint multiplier in each period based on the predictive equation for white-tailed deer (Pekins et al., 1998). Further, these three periods are representative stages of blood loss from adult winter ticks (see below).

Lactation

Energy cost of lactation was estimated for 7 days post-birth (16–23 May) during which daily forage consumption was assumed equal to the winter diet, or diet prior to spring green-up. The energy cost of lactation was set at 23,800 kJ/d for each cow as calculated from three factors: (1) an average energy daily intake of 1,820 kJ/kg$^{0.75}$/d by calves in their first 30 days (Reese and Robbins, 1994); (2) the energetic efficiency of milk production is 65% (Oftedal, 1985; Schwartz and Renecker, 2007); and (3) calf BM averaged 17.5 kg during the 7-day period (785 g daily increase from 15 kg birth weight; Reese and Robbins, 1994). I recognized that spring green-up could occur >1 week post-partum, or conversely, that nutritional quality of forage improves as stem and bud chemistry responds to warming prior to leaf out.

Forage Consumption

Overall, intake and forage quality were set at the upper end of values for moose. Daily forage consumption was set at two levels: 1 and 1.2% BM were used to simulate consumption at high intake or habitat quality (Schwartz and Renecker, 2007). These values correspond to multiple measurements and estimates of winter forage intake by moose, and based on a compilation of multiple studies; Schwartz and Renecker (2007) estimated that the metabolizable energy of a mixed woody browse diet as 9.2 kJ/dry g on good winter habitat (upper end of value). Although diet quality declines through winter as browse is removed, this value was used throughout the experimental period because local studies indicated that the study area contained plentiful optimal foraging habitat (Bergeron et al., 2011; Dunfey-Ball, 2017). For comparison, the 1% level was defined as low and the 1.2% level as high consumption; however, neither value is considered low on a continuum of intake.

Infestation Level

Infestation was set at two levels that represent moderate and severe infestations (30,000 and 90,000 winter ticks); these values were near the extremes (∼20,000–95,000) of infestation measured on whole hides of dead calves in the study area (Jones et al., 2019). Adult female ticks are the primary cause of blood loss in March–April and are assumed to represent ∼25% of ticks on moose (Samuel, 2004; Musante et al., 2007); however, recent measurements indicated a 50:50 sex ratio on calf hides in New Hampshire (unpublished data, Pekins). Therefore, both ratios (25 and 50% female) were used to estimate blood loss.

Blood loss was conservatively estimated as 0.5 g/engorged adult female tick in previous studies (Samuel, 2004; Musante et al., 2007) despite higher estimates of 0.6 and 0.85 g (Glines, 1983; Addison et al., 1998); the conservative value was used to account for tick loss from grooming. Nevertheless, because infestation level was measured directly on dead calves in New Hampshire (Jones et al., 2017, 2019), I used 0.75 g, which is within the range of the higher estimates. Further, these weights were multiplied by 2.5 to account for the total blood loss associated with feeding which is estimated as 2–3 × the engorged tick mass (Sonenshine, 1991). A conservative estimate of 1 g = 1 mL of blood was used to estimate blood volume loss with a replacement energy cost of 4.81 kJ/mL (Musante et al., 2007).

Engorgement by adult ticks occurs over an 8-week period and is concentrated in the middle 4 weeks of infestation (Drew and Samuel, 1989; Samuel, 2004). Therefore, proportional blood loss was established in three distinct periods of 2, 4, and 2 weeks: 01 March–15 March (10%); 16 March–15 April (80%); and 16 April–1 May (10%)—tick drop-off and calf mortality (Jones et al., 2019) are concentrated in the middle 4-week period.

Previous studies disregarded blood loss associated with nymphs and engorged adult male ticks because of the size differential relative to an engorged adult female. Feeding by nymphs occurs over >2 months in December–February (Addison et al., 1998; Samuel, 2004), effectively minimizing the daily energetic impact to replace blood loss. In contrast, adult males remove blood simultaneously with adult females during the 8-week engorgement period. Because the average weight of an engorged adult male (n = 60) in New Hampshire is 0.03 g or 4–6% of that of an adult female (unpublished data, Pekins), and for easier comparison with previous studies, the analysis did not include this blood loss; however, the additive impact is addressed in the discussion.

RESULTS

The following estimates were derived from calculations across a range of BM and condition (% BF) of adult moose cows, two forage consumption levels (1 and 1.2% BM), and a range of tick infestation (30,000–90000) and subsequent blood loss associated with the proportion of female ticks (25 and 50%). The principal physiological and bioenergetic data used to calculate energy balance and the energy impact from blood loss to winter ticks are provided in **Tables 1**, **2**.

Cost of Gestation

To best evaluate the bioenergetic relationship between gestation and nutritional condition, it is informative to consider the cost of gestation alone (without winter ticks) relative to BM and% BF, as well as the cost for non-pregnant cows. The proportional cost of gestation was similar regardless of BM, on average ∼17% above FMR for the length of gestation. At low consumption, a non-pregnant small cow (325 kg, 15% BF) experiences a minor deficit in BF (1.5 kg) on 16 May (birth date if pregnant), and mid-sized and large cows retain 17.5 and 39 kg BF, respectively. Importantly, the maximum loss in BM is only 16% for the small cow at low consumption. At high consumption, a BF surplus occurs in all non-pregnant cows ranging from 19 (small cow) to 61 kg (large cow); albeit, the small cow has highest probability of not breeding.

For pregnant cows at birth (without infestation), a small cow experiences fat deficit at low (−28.4 kg) and high consumption (−8.8 kg), the mid-sized cow at low consumption (−9.4 kg), and the large cow has a fat surplus at low (11.8 kg) and high (34.4 kg) consumption. The estimated% loss in BM (combined fat and endogenous protein) at low and high consumption was 21–35, 18–26, and 16–22% for small, mid-sized, and large cows, respectively. Of consequence to small and mid-sized cows is that the proportional cost of lactation is 1.8× higher than the maximum cost of gestation at birth. Cows with a BF deficit at birth would lose ∼0.9 kg endogenous protein/d during the single week of lactation prior to green-up, elevating the overall loss in BM an additional 3–4%.

Cost of Gestation and Winter Ticks

As predicted, the energy balance equations demonstrated that starting BM or% BF was directly related to the nutritional condition at the end of gestation and through the first week of lactation. Only the large cow (375 kg, 25% BF) had any BF (1.4 kg) at birth in the worst-case scenario (high infestation and low consumption); at high consumption the cow maintained BF through the week of lactation regardless of consumption level (**Figure 1**). Conversely, in the best scenario (low infestation and high consumption) the small cow (325 kg, 15% BF) depleted BF ∼20 days before birth; in the worst scenario, the cow depleted BF ∼01 April or 45 days before birth. The mid-sized cow (350 kg, 20% BF) was intermediate of these extremes; in the best scenario it retained 6.5 kg BF at birth and in the worst scenario had a BF deficit of 19.8 kg (**Figure 1**).

After fat depleted, I assumed that cows could no longer maintain BM and the decline in BM was equivalent to the estimated loss of endogenous protein (kg) to meet energy balance until birth. The caloric equivalent of fat is 2.3× that of protein (16.74 kJ/g) and this multiplier was used to convert the BF deficit (kg) on 16 May (birth) to an equivalent loss of endogenous protein/BM. The loss in BM associated with catabolism of endogenous protein was substantial in the small cow (range = 24–89 kg) and total loss in BM was 22–42% at birth across the two

TABLE 1 | Baseline energy estimates (kilojoules/day; kJ/d) used to calculate the winter energy balance of 3 size-classes of pregnant cow moose.

Cow	BM (kg)	BF (kg)	FMR (kJ/d)	Consumption rate (kJ/d): 1% BM	Consumption rate (kJ/d): 1.2% BM	Gestation (kJ)	Lactation (kJ/d)
Small	325	49	46,122	29,916	35,899	1,038,351	23,800
Mid-sized	350	70	48,775	32,217	38,660	1,098,076	23,800
Large	375	94	51,367	34,518	41,422	1,156,442	23,800

Values provide for body mass (BM), body fat (BF), field metabolic rate (FMR), consumption, gestation, and the first week of lactation; see Section "Materials and Methods" for allocation of temporal and proportional costs during gestation.

TABLE 2 | Baseline estimates and values used to describe the energy impact from blood loss associated with feeding by adult female winter ticks on pregnant moose.

Infestation	Female #		Blood loss (mL)		Blood loss (kJ)		BF (kg)		Daily FMR	
	25%[a]	50%	25%	50%	25%	50%	25%	50%	25%	50%
30,000	7,500	15,000	14,063	28,125	67,655	135,330	1.7	3.4	1.3–1.5	2.6–2.9
90,000	22,500	45,000	42,187	84,375	202,995	405,990	5.2	10.4	4.0–4.4	7.9–8.8

Estimates were calculated with 30 (light) and 90K (severe) infestation levels and with female:male ratios of 25:75 and 50:50 (25 and 50% female); see Section "Materials and Methods" for details. Blood loss estimates are provided relative to volume and energy, and as equivalents of body fat (BF), body protein (BP), and the daily field metabolic rate (FMR); FMR values provide the range for the body mass range (325–375 kg) used in the analyses. [a]*Denotes the proportion of adult female ticks in the infestation.*

infestation levels. The mid-sized cow was in BF deficit only at low consumption when loss of endogenous protein ranged from 25.5 to 45.3 kg and total loss in BM was 27–33% BM at birth. The large cow did not experience BF deficit at any scenario until the first week of lactation at low consumption.

One unique approach of this exercise was to evaluate the effect of infestation level (30,000–90,000 ticks) and the ratio (25–50%) of adult female ticks on a moose at two consumption rates. At the highest infestation and proportion of adult females, the maximum loss in BF was ∼8 kg for any cow (**Table 1**), or a caloric equivalent of 6–7 days of FMR. As illustrated in **Figure 2**, the energetic cost of blood loss is concentrated for 8 weeks – Periods 2 (02–24 March) and 3 (25 March–22 April) – simultaneously and proportionally increasing along with gestation. The energy cost associated with blood loss in Period 3 elevates the total cost to the equivalent at maximal cost of gestation in Period 4 when blood loss is essentially zero. Extending this elevated cost (backward) from 4 to 8 weeks long accelerates the date of BF depletion and increases the days of rapid loss in BM associated with catabolism of endogenous protein, both of most consequence to the small cow. At low consumption, blood loss elevates total cost by 14% (small cow) to 12.5% (large cow) in Periods 2 and 3 (**Figure 2**), and slightly exceeds the cost of gestation in Period 2 for all cows.

Forage-consumption rates produced temporal differences in condition of all sized cows as illustrated in **Figure 2**. At high consumption, a measurable BF deficit occurs in Period 4 (post-ticks) for the small cow and during the 1-week lactation (Period 5) for mid-sized cow; the large cow does not experience a BF deficit through Period 5. In contrast, at low consumption all cows experienced measurable BF deficit one period earlier, with the small cow largely dependent on endogenous protein for most of the 3rd trimester of gestation. The small and mid-sized cows met the cost of lactation entirely with endogenous protein at both consumption rates.

DISCUSSION

This exercise used a number of energetic estimates and assumptions that were simplified to more easily illustrate the relative influences of body mass, nutritional condition, and infestation level of winter ticks on pregnant cow moose; importantly, conservative estimates were used to benefit the nutritional condition of the cow. For example, FMR was set low relative to maintenance energy requirements, high estimates of forage value were applied throughout winter and "low consumption" was relative to that, only a single week of lactation was assumed prior to green-up, and catabolism of fat and muscle would not yield 100% of their energetic value as applied in the equations. Although blood-loss estimates assumed that the entire adult female infestation removed blood, this assumption ignored physical removal of ticks via shaking, grooming, and rubbing throughout the engorgement period (Addison et al., 2019). Conversely, negative behavioral, physical, and physiological responses to high tick loads including reduced forage consumption, increased grooming, and skin ailments were ignored (Samuel and Welch, 1991; Addison and McLaughlin, 1993; Mooring and Samuel, 1998; Addison et al., 2019), as was blood loss associated with all nymphs and adult male ticks. Nonetheless, because the infestation levels reflected the wide range of infestation measured on hides of dead calves through mid-April (∼20,000–95,000 ticks; Jones et al., 2019), the exercise arguably included a reasonable range of infestation and blood loss. All together, these analyses should be viewed in an evaluative context and conservative relative to the additive impact of winter tick infestation on individual productivity and population response of moose.

Paramount to the interpretation of such impact is that prior to spring green-up, moose have evolved to sustain adequate endogenous energy to complete gestation and 1–2 weeks of lactation. Pre-winter BM and condition are key to winter survival

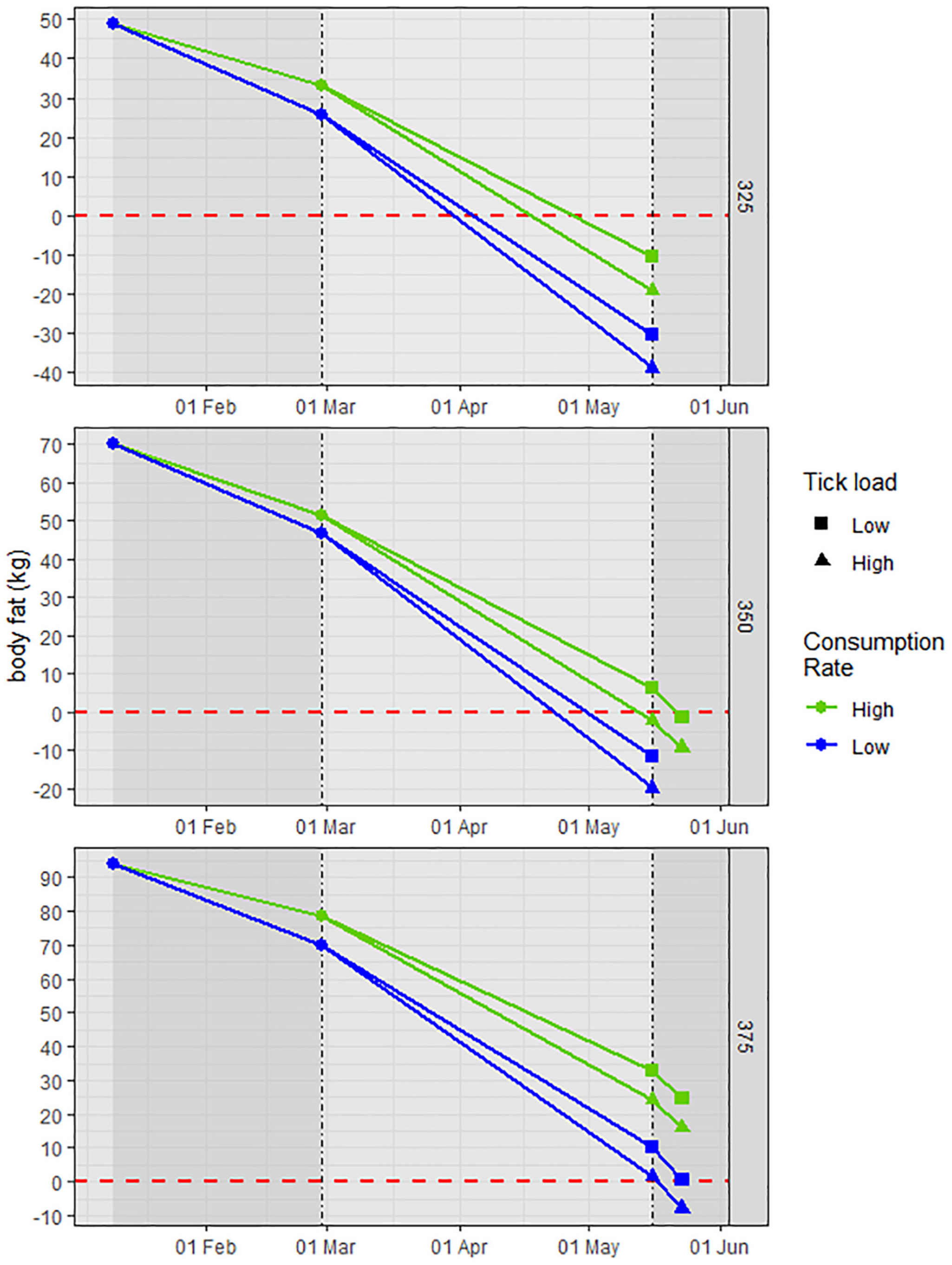

FIGURE 1 | An illustration of the temporal loss of endogenous body fat (BF; kg) in adult cow moose of different starting body mass (325, 350, and 375 kg) and% BF (15, 20, and 25%) from 10 January through 16 May, a period encompassing part of the 2nd trimester and the 3rd trimester of gestation, and 1 week of lactation. The inflection points on 01 March and 16 May denote the 77-day period (01 March–16 May) of the 3rd trimester and 1 week of lactation (17–23 May). Consumption rate was varied as 1 and 1.2% body mass, and infestation was based on 90,000 ticks at two ratios of adult females – 25 and 50%. An energy balance equation was used to calculate the BF (kg) required to meet the energy deficit from the difference between the total daily energy cost (field metabolic rate, gestation, blood loss to ticks, and lactation) and consumption (kJ/d); the BF value on any given day represents the remaining endogenous BF (kg).

and productivity because moose cannot meet their energy or protein requirements from natural winter forage (Schwartz and Renecker, 2007; Parker et al., 2009), and like other northern ungulates, moose employ an overall energy conservation strategy to conserve endogenous resources. Declines in BM and condition are expected, and delayed fetal growth concentrating 90% of gestational cost in the 3rd and last trimester (Schwartz and Hundertmark, 1993; Schwartz, 2007) is considered an

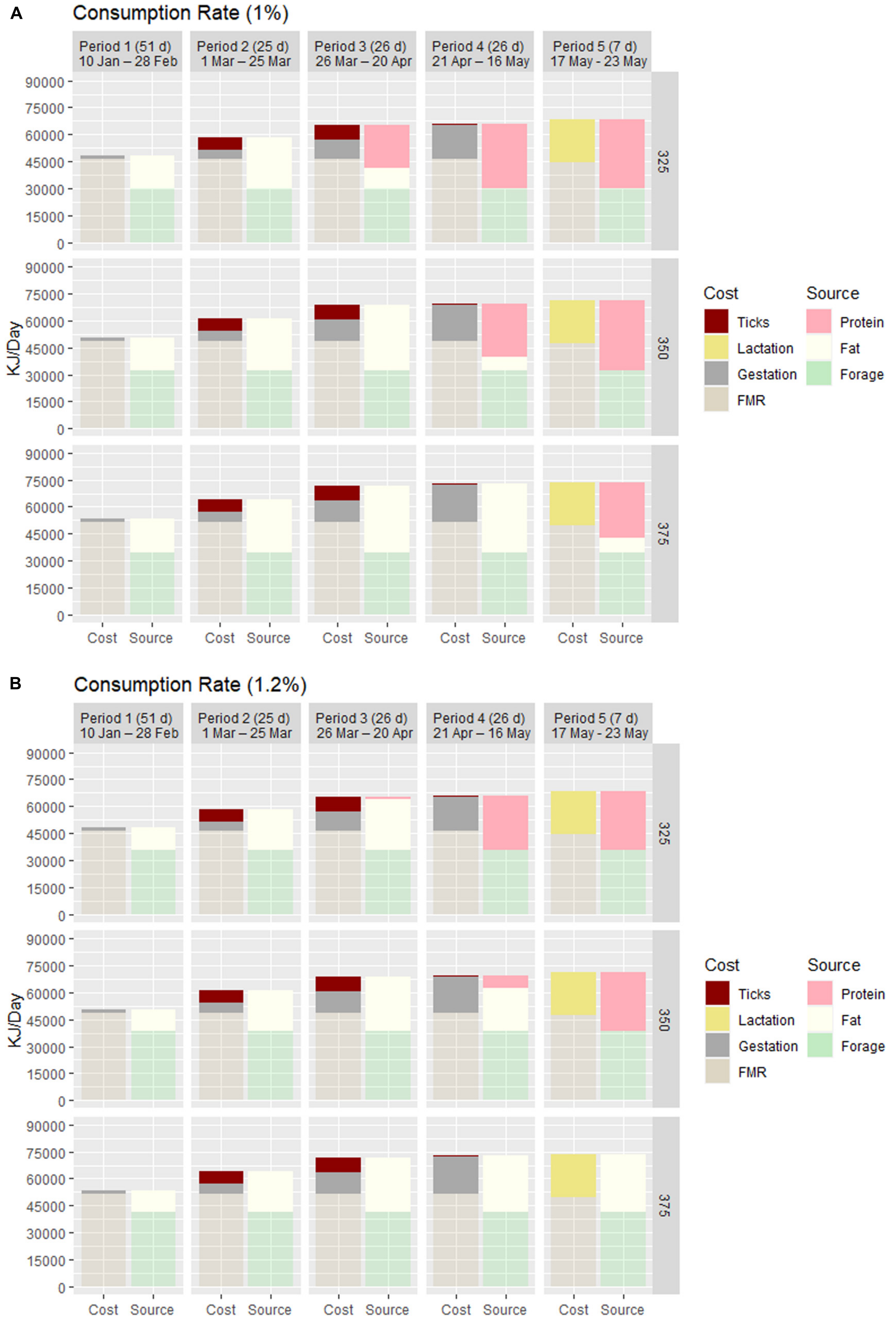

FIGURE 2 | The proportional cost and source of the daily energy budget of adult cow moose of different starting body mass (325, 350, and 375 kg) and body fat (15, 20, and 25%) in five distinct periods from 10 January through 16 May. Period 1 was the latter part of the 2nd trimester of gestation (50 days), Periods 2–4 represented distinct periods (25, 26, and 26 days) of exponentially increasing cost of gestation with Periods 2 and 3 accounting for the concentrated blood loss to winter ticks, and Period 5 was lactation (7 days). The bars indicate how cost (field metabolic rate, gestation, blood loss, and lactation) was met relative to source (forage, BF, and BP) and the time frame at which a BF deficit occurs and BP is used. Consumption was varied as 1% **(A)** and 1.2% body mass **(B)** to illustrate its relative impact on energy balance.

evolutionary strategy to confront the lack of digestible protein in winter browse (Robbins, 1993).

The difference in nutritional condition on 16 May (birth) between the small (325 kg) and large (375 kg) cows was evident, with or without tick infestation, and provides stark evidence of this evolutionary strategy (**Figure 2**). Even at high consumption rate and regardless of infestation level, the small cow depleted its BF by 22 April (end of Period 3, **Figure 2**; 3–4 weeks pre-birth), whereas, the large cow had surplus BF after the first week of lactation (**Figures 1**, **2**). For the small cow, the rapid loss in BM associated with its catabolism of endogenous protein alone through late gestation and early lactation is likely not sustainable – total loss in BM would exceed 30%. The consequence is either mortal mass loss or failed pregnancy; given minimal adult mortality (Jones et al., 2019), the animal presumably copes through failed pregnancy (i.e., underdeveloped fetus and compromised neonate). For mid-sized cows, BM provides critical plasticity to meet the costs of late gestation and early lactation through the combined use of BF and BP without realizing mortal loss of BM (i.e., >30% BM). Although BF is paramount in the overall strategy, the importance of BP in late gestation and early lactation is clear and likely most important in longer winters when green-up is delayed (Parker et al., 2009).

It is not coincidental that pregnancy (∼80% annually; Jones et al., 2017) and birthing rates differ in the study population, and that abandoned, compromised, and still-born calves are located each year in the peak birthing period (Ellingwood, 2018). This difference is not uncommon in moose populations and reflects compromised body condition of pregnant cows as early as November–December (Testa and Adams, 1998) and/or late winter (Schwartz and Hundertmark, 1993). The low successive birthing rate in the population (Jones et al., 2019; Powers, 2019) indicates that a measurable proportion of cows are annually constrained by their pre-winter condition/BM. Although BM in autumn has been suggested as not predictive of productivity of moose in Norway (Milner et al., 2013), the pre-winter BM reflects relative condition, and this exercise illustrates that adequate BF is required to meet the combined cost of gestation and winter ticks in the critical 3rd trimester.

Unproductive cows are presumably compromised by inadequate compensatory growth in the previous summer-autumn from either the combined cost of gestation and infestation (325 kg cow) or raising a calf through summer (350 kg cow). Numerous studies have identified the relationship between condition and productivity in moose (e.g., Franzmann and Schwartz, 1985; Keech et al., 2000) and this exercise demonstrates the necessity of adequate BF to successfully reproduce. Of most consequence is that the cost of gestation is focused nearly entirely (90%) in the last trimester at end of winter, that the entirety of gestation and early lactation occur prior to spring green-up, and that decline in BM is rapid (2.3×) after depletion of BF. The near complete failure of surviving female calves to ovulate/breed as yearlings similarly reflects inadequate compensatory growth in their second summer to overcome low post-winter BM; the threshold yearling BM (field-dressed) associated with ovulation is 200 kg (Adams and Pekins, 1995).

Variability in successive calving rate was high in the current study (2015–2019). Equal proportions of adult cows calved 2 years in succession, and every other year; few calved 3–5 years continuously, and some were unsuccessful for 2 consecutive years—calving success was defined as multiple observations (imperfect) of a live calf in summer (Powers, 2019). Cows failing to produce a viable or surviving calf avoid the cost of lactation and benefit most from compensatory growth during summer-autumn to produce the following year (Parker et al., 2009; Shively et al., 2019); further, non-pregnant cows avoid the cost of both gestation and lactation, although the annual pregnancy rate was ∼80% (Powers, 2019). Examples of constraining winters causing lag in population recovery of ungulates in North America include white-tailed deer (Patterson and Power, 2002; Garroway and Broders, 2007), moose (Heard et al., 1997; Testa and Adams, 1998), and caribou (*Rangifer tarandus*; Cameron, 1994; Allaye Chan-McLeod et al., 1999). Arguably, winter ticks act in an analogous manner with moose in the Northeast via direct mortality and reduced productivity, except epizootics can occur regardless of winter conditions (Musante et al., 2010; Jones et al., 2019). Although the "selfish cow" theory suggests that an adult cow might pause pregnancy for self-maintenance in severe environmental conditions (Russell et al., 1998, 2005; Morano et al., 2013) and delaying reproduction could lead to higher lifetime production (Festa-Bianchet and Cote, 2008 in Parker et al., 2009), this advantage is unlikely during continuous and long-term parasitism by winter ticks.

The difference between the pregnancy and calving rates, and that dead and under-developed neonates are located in the field (Ellingwood, 2018), points to an imbalance between endogenous resources and the cost of gestation. Rapid loss in BM associated with catabolism of BP should not occur prior to the 3rd trimester (01 March) unless BF is depleted; in no scenario did that occur, and even the small cow retained BF into early April at low consumption and high infestation (Period 3, **Figure 2**). Therefore, rapid loss in BM prior to the 3rd trimester would require extremely poor condition (i.e., without BF) in mid-winter. Although perinatal mortality on poor winter habitat was proposed in a Norwegian study (Milner et al., 2013), the probability of such would be rare based on this analysis, and it is counter to the evolutionary strategy to delay the cost of gestation until the 3rd trimester. The analyses point to all cows reaching the 3rd trimester with some BF, and that successful calving will be most influenced by subsequent balance of endogenous fat and protein against the exponentially increasing cost of gestation and the concentrated blood loss to winter ticks. All cows could sustain these costs for multiple days with BP alone, and it is more likely that failed calving involves an underdeveloped fetus, compromised calf, or predisposed predation versus absorption.

Although this analysis identifies adequate BF as a prerequisite for successful reproduction, BP is undeniably critical in meeting the cost of fetal growth, particularly during the 3rd trimester when >80% of growth occurs. The 15 kg newborn/18 kg conceptus mass (15–18% protein in related species; Robbins and Moen, 1975; Oftedal, 1985) is roughly equivalent to the loss (use) in lean BM (25% protein); importantly, this loss occurs simultaneously and prior to depletion of BF. Blood loss associated with winter ticks in late March–April represents an additional loss of BP during the 3rd trimester. At moderate-high infestation (30,000–70,000 ticks), blood loss was estimated as 28–42% of the daily maintenance protein requirement of a 360 kg non-pregnant cow, a proportional impact exceeding that associated with the daily energy requirement (Musante et al., 2007). Relative to that maintenance protein requirement (Schwartz et al., 1987; Schwartz and Renecker, 2007), blood loss at infestations of 30,000 and 90,000 ticks requires 2.8–16.9 kg protein (**Table 2**), or an equivalent loss of 11–68 kg of lean BM; ∼3 to 20% of BM from lowest to highest infestation. Similarly, DelGiudice et al. (1997) estimated daily loss of 0.5–0.8 kg lean BM/d in a 400 kg moose at infestation of ∼30,000 ticks in a nutritionally restricted population on Isle Royale. Extrapolation across 8 weeks of feeding by adult female ticks equals ∼36 kg of lean BM, assuming a constant rate of loss. Critical to moose is that the winter diet is protein-deficient relative to the daily requirement, hence, winter ticks accelerate the use of BP and BM loss to address the additive cost of blood loss. Importantly, this specific loss in lean BM was not captured in the energy balance equation. But it is substantial and mostly disadvantages small and mid-sized cows by further reducing the probability of successful calving. Not coincidentally, mortality of 10-month old calves is ultimately a consequence of acute anemia as BP and lean BM deplete in face of concentrated blood loss that can exceed the total blood volume in 3–4 weeks at infestations of 30,000+ ticks (Musante et al., 2007; Jones et al., 2019).

With regard to compensatory growth in summer, the nutritional importance and availability of summer forage, specifically dietary protein, is paramount to the autumnal condition (BM and BF) of cows. Surprisingly, forage intake rates of lactating and non-lactating cows in Alaska were similar to each other and to predicted maximum rates, or that all animals maximized intake in summer (Shively et al., 2019). Thus, lactating cows were necessarily smaller, averaging 32 kg less than their unproductive counterparts in autumn; presumably, this difference would be largely reflected in lower BF. The impact of winter ticks (relative to the infestation level) would be to lower nutritional condition in both these groups entering summer, ultimately reducing pre-winter BM and BF of all animals with highest penalty for lactating cows. Arguably, the study population reflects the annual interactions of multiple factors in the face of continually high, annual infestation of winter ticks —body condition and energy balance, protein balance and requirements as influenced by late-term gestation and blood loss to winter ticks, and differential compensatory growth relative to the cost of lactation and setting pre-winter condition —with productivity the annual population response.

Low reproductive rate and BM is associated with resource constraints in a traditional assessment of nutritional carrying capacity; however, resource and habitat constraints are presumed minimal for moose in the Northeast that is characterized as excellent moose habitat (Scarpitti et al., 2005; Dunfey-Ball, 2017). Typically, these physiological outcomes are relieved either through improved environmental conditions (e.g., habitat quality and winter conditions) or lower population density (direct or indirect), with only the latter of near-term consequence in the Northeast. A density-dependent relationship presumably exists between moose and winter ticks relative to annual infestation and moose mortality, and Samuel (2007) posits densities of <1 and $>\sim3$ moose/km^2 in Ontario as respective thresholds for minimal and epizootic-level impacts by winter ticks. In comparison, during the recent period of frequent epizootics since the mid-2000s, the density estimate in New Hampshire has declined from 0.87 to 0.46 moose/km^2. Assuming these density estimates are relatively accurate, this lower density is sustaining sufficient abundance of winter ticks to cause frequent epizootics and reduced productivity in the study area. Given that density estimates are typically regional in nature, it is important to recognize that density and impacts could be higher at the local scale, and that patterns in forest harvesting and foraging behavior are related directly to and influence moose and tick abundance (Healy et al., 2018, 2020; Powers and Pekins, 2020). In common throughout the Northeast are broad-scale commercial forest harvesting that promotes optimal moose habitat and warming temperatures that increase the autumnal questing period of winter ticks and subsequent infestation of moose. Further study is warranted to better understand and predict the influence of these interrelationships that are principal factors in the population dynamics of moose in the Northeast.

In more northern regions, substantial increases in moose populations are typically associated with major environmental perturbations (e.g., fire) that result in long-term population cycles (see Peek, 2007); further, predation often plays an important role in the dynamics of northern populations (Ballard and Van Ballenberghe, 2007). Similarly, the rapid moose expansion that occurred in the Northeast originated from extensive harvest of a large swathe of contiguous forestland across three states in only 15–20 years (Chen et al., 2017). The temporal difference in these two situations is that commercial forest harvesting continues to maintain high availability of optimal foraging habitat in the Northeast (15–20% of forestland; Dunfey-Ball, 2017). Given the density-dependent relationship between moose and winter ticks, it is intriguing to consider whether predation might act as an ameliorating factor against build-up of winter ticks given epizootics were relatively uncommon historically, and whether winter ticks slowly act as a "*de facto*" predator in the Northeast; albeit, all animals are potentially "harmed" by winter ticks.

It follows that winter tick density grew with increasing moose density, and by the mid-2000s the first epizootic was identified (Musante et al., 2010), with epizootics suspected or directly measured with unprecedented frequency since (Ellingwood et al., 2020). Surprisingly, a single year of "low" calf mortality (still 30%) occurred in 2017 when infestation was the lowest measured in the study, presumably due to the effect of September drought on larval survival and abundance (Dunfey-Ball, 2017; Ellingwood et al., 2019). This reprieve, however, was short-lived as the autumnal abundance of winter ticks was enough to induce an epizootic in spring 2018 (Ellingwood et al., 2020). Again, the unprecedented frequency and persistence of these population impacts illustrate that a unique moose-winter tick relationship operates in the Northeast and that shorter winters and warming temperatures in autumn and spring are directly beneficial to winter ticks and subsequently detrimental to moose.

I note that both the rapid geographic expansion and growth, and current slow decline of this very large regional population (>50,000 animals) occurred since the 1980s. This time frame provides little support for the idea of thermal stress in moose operating at the individual or population level or in the Northeast; how could growth in this regional population occur while others decline in similar environmental conditions? As raised by Montgomery et al. (2019), this relationship is invariably correlative when presented (e.g., Lenarz et al., 2009) and simplified by comparing ambient temperature to the upper critical temperature (UCT) reported by Renecker and Hudson (1986); obvious physical and productivity data (e.g., BM and twinning rate) that contradict such a conclusion are oftentimes ignored. Further, thermoregulatory data or predictions based on air temperature alone are not applicable to a free-ranging animal, and with regard to the most regularly cited study (Renecker and Hudson, 1986), data are both minimal (two animals) and highly variable in summer; those researchers would agree that caution should be used in any extrapolation. Although individual animals obviously experience thermal stress and adjust to it behaviorally (e.g., Lowe et al., 2010; Montgomery et al., 2019), it should be noted that extrapolation of the summer UCT (Renecker and Hudson, 1986) places nearly all moose under constant "thermal stress" throughout the productive summer season, a physiological impossibility and primary evidence to refrain from such simplistic correlations.

Climate change affects winter length at both ends (Williams et al., 2015), and length (days) of severe winter conditions, not the conditions *per se*, best predicts weather-associated population impacts; for example, winter severity indices for white-tailed deer typically total the number of "severe days" (Nelson, 1995). Because warming temperatures should induce earlier spring green-up, there is irony relative to the negative influence caused by extended questing of winter ticks in autumn versus the positive influence realized from an improved spring diet during late gestation and early lactation. It is important to recognize that ungulates occupying seasonal environments may be positively (Tape et al., 2016) or negatively (Monteith et al., 2015) affected by measurable change in vegetation/habitat, and might also benefit, or not, from subtle changes within an annual seasonal cycle. For example, a 2-week earlier green-up would measurably reduce endogenous tissue loss, provide a higher quality diet prior to conception, and aid in early compensatory growth. Conversely, a 2-week extension of the autumnal questing season of winter ticks represents a potential 20+% increase of infestation assuming a questing period of 9 weeks (September through early November). No empirical data exist to evaluate the relative influence of winter tick parasitism versus diet improvement from an earlier spring, but an earlier spring would also provide advantageous ground conditions for maximum survival of adult females and larvae (Drew and Samuel, 1986; Addison et al., 1998; Yoder et al., 2016; Holmes et al., 2018). Considering that the physiological impact of winter ticks is directly related to infestation level that affects survival of 10-month old calves, subsequent productivity in surviving yearlings (Musante et al., 2007; Jones et al., 2019), condition during and after gestation and lactation, and that epizootics occur regardless of winter conditions in the Northeast (Musante et al., 2010; Jones et al., 2019), a warming climate should be considered a constant negative to moose in the Northeast at this time.

The moose-winter tick relationship provides a prime example of how the influence of warming temperatures occurs most commonly and directly at the insect, parasite, and disease levels that are directly impacted by minimal change in ambient temperature (Leighton et al., 2012), and indirectly on medium-sized and large mammals like moose that regularly practice thermoregulatory behavior (e.g., Wattles et al., 2018; Montgomery et al., 2019). Previous research has identified the negative impact of sustained high abundance of winter ticks on survival and productivity of moose in the Northeast, and this analysis identifies the relationship between declining condition of adult cows and productivity (Keech et al., 2000) as influenced by the correlation between BM and BF (Sand et al., 1995). Further, the low successive birthing rate reflects that individual condition and annual productivity are influenced by reproductive success the previous year in this system.

Exposed to frequent high infestation of winter ticks, it follows that this population has higher than normal proportions of small and mid-sized cows most vulnerable to depletion of BF during gestation and lactation, and ultimately, unsuccessful calving. The long-term trend is decline in field-dressed weights and corpora lutea counts in yearling and adult cows from 1999–2009 to 2005–2009 (Bergeron et al., 2013). Because yearlings are unproductive in the study area (Jones et al., 2017, 2019), surviving female calves are compromised relative to their potential lifetime productivity (Gaillard et al., 2003). Use of demographic data from the mid-2000s and 2014–2019 in population models (Ellingwood et al., 2020) reveals the stark impact on population trajectory at the current high frequency of epizootics (high infestation), with potential halving of the population in as few as 10 years. Although this conservative analysis likely underestimates individual impact, because adequate if not optimal habitat is available, the moose population should respond rapidly upon release from high infestation. Interestingly, the single year (2017) of low infestation had 15% higher calving success than the 6-year average (2014–2019; Powers, 2019).

Relative to weather and climate, further study is warranted to better interpret the dynamic interactions and relationships between and among moose and tick densities, habitat use and infestation of moose, and ground conditions and winter tick abundance. Use of empirical data from the Northeast in a predictive, agent-based model has yielded insights about a self-sustaining, habitat use-infestation relationship (Healy et al., 2020), and subsequent field estimates of larval tick abundance (Powers and Pekins, 2020) provide supporting evidence at the micro-site level. Further, population modeling indicates that population stability in the Northeast occurs at an epizootic frequency of 1 in 4 years (Ellingwood et al., 2020), yet the current rate is 5 in 6 and 7 in the past 10 years. Clearly, moose are confronted with an historically unique combination of environmental and parasitic conditions associated with a warming climate that markedly affects their survival and productivity; in effect, winter tick parasitism represents the major constraint in the nutritional carrying capacity of moose in the Northeast.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

FUNDING

Funding for this project was provided in part through Wildlife Restoration Program grant No. F13AF01123 (NH W-104-R-1) to New Hampshire Fish and Game Department from the United States Fish and Wildlife Service, Division of Wildlife and Sport Fish Restoration with matching funds provided by the University of New Hampshire.

ACKNOWLEDGMENTS

Many "moose" grads collected the bulk of the empirical data used in the analysis – A. Musante, D. Scarpitti, M. Eckert, D. Bergeron, H. Andreozzi, H. Jones, N. Fortin, K. Dunfey-Ball, D. Ellingwood, C. Healy, and B. Powers supervised tens of undergraduate students including the most reliable J. DeBow and T. Soucy. A. Siren constructed the figures and provided endless editing, improvements, and ideas. I am thankful to work with such motivated and talented students.

REFERENCES

Adams, K. P., and Pekins, P. J. (1995). Growth patterns of New England moose: yearlings as indicators of population status. *Alces* 31, 53–59.

Addison, E. M., Fraser, D. J. H., and McLaughlin, R. F. (2019). Grooming and rubbing behavior by moose experimentally infested with winter ticks (*Dermacentor albipictus*). *Alces* 55, 23–35.

Addison, E. M., Joachim, D. G., McLaughlin, R. F., and Fraser, D. J. H. (1998). Ovipositional development and fecundity of *Dermacentor albipictus* (Acari: Ixodidae) from moose. *Alces* 34, 165–172.

Addison, E. M., and McLaughlin, R. F. (1993). Seasonal variation and effects of winter ticks (Dermacentor albipictus) on consumption of food by captive moose (*Alces alces*) calves. *Alces* 29, 219–224.

Allaye Chan-McLeod, A. C., White, R. G., and Russell, D. E. (1999). Comparative body composition strategies of breeding and nonbreeding female caribou. *Can. J. Zool.* 77, 1901–1907. doi: 10.1139/z99-169

Andreozzi, H. A., Pekins, P. J., and Langlais, M. L. (2014). Impact of moose browsing on forest regeneration in Northeast vermont. *Alces* 50, 67–79.

Ballard, W. B., and Van Ballenberghe, V. (2007). "Predator/Prey relationships," in *Ecology and Management of the North American Moose*, eds A. W. Franzmann and C. C. Schwartz (Boulder, CO: University Press of Colorado), 247–273.

Bergeron, D. H., Pekins, P. J., Jones, H. F., and Leak, W. B. (2011). Moose browsing and forest regeneration: a case study. *Alces* 47, 39–51.

Bergeron, D. H., Pekins, P. J., and Rines, K. (2013). Temporal assessment of physical characteristics and reproductive status of moose in New Hampshire. *Alces* 49, 39–48.

Bontaites, K. M., and Gustafson, K. (1993). The history and status of moose management in New Hampshire. *Alces* 29, 163–167.

Cameron, R. D. (1994). Reproductive pauses by female caribou. *J. Mammal.* 75, 10–13. doi: 10.2307/1382230

Chen, C., Weiskittel, A., Bataineh, M., and MacLean, D. A. (2017). Evaluating the influence of varying levels of spruce budworm defoliation on annualized individual tree growth and mortality in Maine, USA and New Brunswick, Canada. *For. Ecol. Manage.* 396, 184–194. doi: 10.1016/j.foreco.2017.03.026

DelGiudice, G. D., Peterson, R. O., and Samuel, W. M. (1997). Trends of winter nutritional restriction, ticks, and numbers of moose in Isle Royale. *J. Wildl. Manage.* 61, 895–903.

Drew, M. L., and Samuel, W. M. (1986). Reproduction of the winter tick, *Dermacentor albipictus*, under field conditions in Alberta, Canada. *Can. J. Zool.* 64, 714–721. doi: 10.1139/z86-105

Drew, M. L., and Samuel, W. M. (1989). Instar development and disengagement rate of engorged female winter ticks, Dermacentor albipictus (Acari: Ixodidae), following single- and trickle-exposure of moose (*Alces alces*). *Exp. Appl. Acarol.* 6, 189–196. doi: 10.1007/BF01193979

Dunfey-Ball, K. R. (2017). *Moose Density, Habitat, and Winter Tick Epizootics in a Changing Climate*. Master's Thesis, University of New Hampshire, Durham, NH.

Eckert, M. D. (2004). *Estimating Field Metabolic Rate of Captive Deer in Winter: A Comparison of Three Methods*. Master's Thesis, University of New Hampshire, Durham, NH.

Ellingwood, D. (2018). *Assessing the Impact of Winter Tick Epizootics on Moose Condition and Population Dynamics in Northern New Hampshire*. Master's Thesis, University of New Hampshire, Durham, NH.

Ellingwood, D., Pekins, P. J., and Jones, H. (2019). Using snow urine samples to assess the impact of winter ticks on moose calf condition and survival. *Alces* 55, 13–21.

Ellingwood, D., Pekins, P. J., Jones, H., and Musante, A. R. (2020). Evaluating moose (*Alces alces*) population response to infestation level of winter ticks (*Dermacentor albipictus*). *Wildl. Biol.* doi: 10.2981/wlb.00619

Festa-Bianchet, M., and Cote, S. D. (2008). *Mountain Goats: Ecology, Behavior, and Conservation of an Alpine Ungulate*. Washington, D.C: Island Press.

Franzmann, A. W., and Schwartz, C. C. (1985). Moose twinning rates: a possible population condition assessment. *J. Wildl. Manage.* 49, 394–396. doi: 10.2307/3801540

Gaillard, J.-M., Loison, A., Toigo, C., Delmore, D., and Van Laere, G. (2003). Cohort effects and deer population dynamics. *Ecoscience* 10, 412–420. doi: 10.1080/11956860.2003.11682789

Garroway, C. J., and Broders, H. G. (2007). Adjustment of reproductive investment and offspring sex ratio in whiote-taileed deer (*Odocoileus virginianus*) in Nova Scotia. *Can. J. Mammal.* 88, 1305–1311. doi: 10.1644/06-mamm-a-212r2.1

Glines, M. V. (1983). *The Winter Tick, Dermacentor Albipictus (Packard, 1869): Its Life History, Development at Constant Temperatures and Physiological Effects On Moose, Alces Alces* L. Master's thesis, University of Alberta, Edmonton.

Healy, C., Pekins, P. J., Attallah, S., and Congalton, R. G. (2020). Using agent-based models to inform the dynamics of winter tick parasitism of moose. *Ecol. Complex* 41:100813. doi: 10.1016/j.ecocom.2020.100813

Healy, C., Pekins, P. J., Kantar, L., Congalton, R. G., and Atallah, S. (2018). Selective habitat use by moose during critical periods in the winter tick life cycle. *Alces* 54, 85–100.

Heard, D., Barry, S., Watts, G., and Child, K. (1997). Fertility of female moose (*Alces alces*) in relation to age and body condition. *Alces* 33, 165–176.

Holmes, C. J., Dobrotka, C. J., Farrow, D. W., Rosendale, A. J., Benoit, J. B., Pekins, P. J., et al. (2018). Low and high thermal tolerance characteristics for unfed larvae of the winter tick *Dermacentor albipictus* (Acari: Ixodidae) with special reference to moose. *Ticks Tick. Borne. Dis.* 9, 25–30. doi: 10.1016/j.ttbdis.2017.10.013

Jones, H., Pekins, P., Kantar, L., Sidor, I., Ellingwood, D., Lichtenwalner, A., et al. (2019). Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacentor albipictus*) epizootics in New Hampshire and Maine (USA). *Can. J. Zool.* 97, 22–30. doi: 10.1139/cjz-2018-0140

Jones, H., Pekins, P. J., Kantar, L. E., and Ellingwood, D. (2017). Fecundity and summer calf survival of moose during 3 successive years of winter tick epizootics. *Alces* 53, 85–98.

Keech, M. A., Bowyer, R. T., Hoef, J. M., Ver Boertje, R. D., Dale, B. W., and Stephenson, T. R. (2000). Life-history consequences of maternal condition in alaskan moose. *J. Wildl. Manage.* 64, 450–462. doi: 10.2307/3803243

Leighton, P. A., Koffi, J. K., Pelcat, Y., Lindsay, L. R., and Ogden, N. H. (2012). Predicting the speed of tick invasion: an empirical model of range expansion for the lyme disease vector *Ixodes scapularis* in Canada. *J. Appl. Ecol.* 49, 457–464. doi: 10.1111/j.1365-2664.2012.02112.x

Lenarz, M. S., Nelson, M. E., Schrage, M. W., and Edwards, A. J. (2009). Temperature mediated moose survival in northeastern Minnesota. *J. Wildl. Manage.* 73, 503–510. doi: 10.2193/2008-265

Lowe, S. J., Patterson, B. R., and Schaefer, J. A. (2010). Lack of behavioral responses of moose (*Alces alces*) to high ambient temperatures near the southern periphery of their range. *Can. J. Zool.* 88, 1032–1041. doi: 10.1139/Z10-071

Milner, J. M., van Beest, F. M., Solberg, E. J., and Storaas, T. (2013). Reproductive success and failure: the role of winter body mass in reproductive allocation in Norwegian moose. *Oecologia* 172, 995–1005. doi: 10.1007/s00442-01202547-x

Monteith, K. L., Klaver, R. W., Hersey, K. R., Holland, A. A., Thomas, T. P., and Kauffman, M. J. (2015). Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia* 178, 1137–1148. doi: 10.1007/s00442-015-3296-4

Montgomery, R. A., Redilla, K. M., Moll, R. J., Van Moorter, B., Rolandsen, C. M., Millspaugh, J. J., et al. (2019). Movement modeling reveals the complex nature of the response of moose to ambient temperatures during summer. *J. Mammal.* 100, 169–177. doi: 10.1093/jmammal/gyy185

Mooring, M. S., and Samuel, W. M. (1998). The biological basis of grooming in moose: programmed versus stimulus-driven grooming. *Anim.Behav.* 56, 1561–1570. doi: 10.1006/anbe.1998.0915

Morano, S., Stewart, K. M., Sedinger, J. S., Nicolai, C. A., and Vavra, M. (2013). Life-history strategies of North American elk: trade-offs associated with reproduction and survival. *J. Mammal.* 94, 162–172. doi: 10.1644/12-mamm-a-074.1

Musante, A., Pekins, P., and Scarpitti, D. (2007). Metabolic impacts of winter tick infestations on calf moose. *Alces* 43, 101–110.

Musante, A. R., Pekins, P. J., and Scarpitti, D. L. (2010). Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. *Wildl. Biol.* 16, 185–204. doi: 10.2981/09-014

Nelson, M. E. (1995). Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Can. J. Zool.* 73, 1069–1076. doi: 10.1139/z95-127

Oftedal, O. T. (1985). "Pregnancy and lactation," in *Bioenergetics of Wild Herbivores*, eds R. J. Hudson and R. G. White (Boca Raton, FL: CRC Press), 216–238.

Parker, K. L., Barboza, P. S., and Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* 23, 57–69. doi: 10.1111/j.1365-2435.2009.01528.x

Parker, K. L., Gillingham, M. P., Hanley, T. A., and Robbins, C. T. (1999). Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildl. Monogr.* 143, 1–48.

Patterson, B. R., and Power, V. A. (2002). Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia* 13, 62–71. doi: 10.1007/s004420100783

Peek, J. M. (2007). "Habitat relationships," in *Ecology and Management of the North American Moose*, eds A. W. Franzmann and C. C. Schwartz (Boulder, CO: University Press of Colorado), 351–375.

Pekins, P. J. (1995). *Winter Energy and Activity Budgets of Free-Ranging Deer in Northern New Hampshire*. Final Report. Pittman-Robertson Grant W-12-R. Concord, NH: New Hampshire Fish and Game Department.

Pekins, P. J., Smith, K. S., and Mautz, W. W. (1998). The energy cost of gestation in white-tailed deer. *Can. J. Zool.* 76, 1091–1097. doi: 10.1139/z98-032

Powers, B. L. (2019). *Assessing the Relationships of Winter Ticks, Weather and A Declining Moose Population in Northern New Hampshire*. Master's Thesis, University of New Hampshire, Durham.

Powers, B. L., and Pekins, P. J. (2020). Abundance of winter ticks (*Dermacentor albipictus)* in two regenerating forest habitats in New Hampshire, USA. *Alces* 56, 1–13.

Reese, E. O., and Robbins, C. T. (1994). Characteristics of moose lactation and neonatal growth. *Can. J. Zool.* 72, 953–957. doi: 10.1139/z94-130

Regelin, W. L., Schwartz, C. C., and Franzmann, A. W. (1985). Seasonal energy metabolism of adult moose. *J. Wildl. Manage.* 49, 394–396. doi: 10.2307/3801539

Renecker, L. A., and Hudson, R. J. (1986). Seasonal energy expenditures and thermoregulatory responses of moose. *Can. J. Zool.* 64, 322–327. doi: 10.1139/z86-052

Robbins, C. T. (1993). *Wildlife Feeding and Nutrition*. San Diego, CA: Academic Press.

Robbins, C. T., and Moen, A. N. (1975). Uterine compositin and growth in pregnant white-tailed deer. *J. Wildl. Manage.* 39, 684–691.

Russell, D. E., Gerhart, K. L., White, R. G., and Van De Wetering, D. (1998). Detection of early pregnancy in caribou: evidence for embryonic mortality. *J. Wildl. Manage.* 62, 1966–1975. doi: 10.2307/3802559

Russell, D. E., White, R. G., and Daniel, C. J. (2005). *Energetics of the Porcupine Caribou Herd: A Computer Simulation Model*. Ottawa: Canadian Wildlife Service.

Samuel, W. M. (2004). *White as A Ghost: Winter Ticks and Moose. Natural History Series*. Edmonton: Federation of Alberta Naturalists.

Samuel, W. M. (2007). Factors affecting epizootics of winter ticks and mortality of moose. *Alces* 43, 39–48.

Samuel, W. M., and Welch, D. A. (1991). Winter ticks on moose and other ungulates: factors influencing their population size. *Alces* 27, 169–182.

Sand, H., Cederlund, G., and Danell, K. (1995). Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose (*Alces alces*). *Oecologia* 102, 433–442. doi: 10.1007/BF00341355

Scarpitti, D., Habeck, C., Musante, A. R., and Pekins, P. J. (2005). Integrating habitat use and population dynamics of moose in northern New Hampshire. *Alces* 41, 25–35.

Schwartz, C. C. (2007). "Reproduction, natality and growth," in *Ecology and Management of the North American Moose*, eds A. W. Franzmann and C. C. Schwartz (Boulder, CO: University Press of Colorado), 141–171.

Schwartz, C. C., Hubbert, M. E., and Franzmann, A. W. (1988a). Changes in body composition of moose during winter. Energy requirements of adult moose for winter maintenance. *Alces* 24, 178–187.

Schwartz, C. C., Hubbert, M. E., and Franzmann, A. W. (1988b). Energy requirements of adult moose for winter maintenance. *J. Wildl. Manage.* 52, 26–33. doi: 10.2307/3801052

Schwartz, C. C., and Hundertmark, K. J. (1993). Reproductive characteristics of Alaskan moose. *J. Wildl. Manage.* 57, 454–468. doi: 10.2307/3809270

Schwartz, C. C., Regelin, W. L., and Franzmann, A. W. (1987). Protein digestion in moose. *J. Wildl. Manage.* 55, 352–357.

Schwartz, C. C., and Renecker, L. A. (2007). "Nutrition and energetics," in *Ecology and Management of the North American Moose*, eds A. W. Franzmann and C. C. Schwartz (Boulder, CO: University Press of Colorado), 441–478.

Shively, R. D., Crouse, J. A., Thompson, D. P., and Barboza, P. S. (2019). Is summer food intake a limiting factor for boreal browsers? Diet, temperature, and reproduction as drivers of consumption in female moose. *PLoS One* 14:e0223617. doi: 10.1371/journal.pone.0223617

Sonenshine, D. E. (1991). *Biology of Ticks*. New York, NY: Oxford University Press.

Tape, K. D., Gustine, D. D., Ruess, R. W., Adams, L. G., and Clark, J. A. (2016). Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. *PLoS One* 11:e0152636. doi: 10.1371/journal.pone.0152636

Tarr, M. D., and Pekins, P. J. (2002). Influences of winter supplemental feeding on the energy balance of white-tailed deer fawns in New Hampshire, U.S.A. *Can. J. Zool.* 80, 6–15. doi: 10.1139/z01-200

Testa, J. W., and Adams, G. P. (1998). Body condition and adjustments to reproductive effort in female moose (*Alces alces*). *J. Mammal.* 79, 1345–1354. doi: 10.2307/1383026

Wattles, D. W., Zeller, K. A., and DeStefano, S. (2018). Range expansion in unfavorable environments through behavioral responses to microclimatic conditions: moose (*Alces americanus*) as the model. *Mamm. Biol.* 93, 189–197. doi: 10.1016/j.mambio.2018.05.009

Williams, C. M., Henry, H. A. L., and Sinclair, B. J. (2015). Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biol. Rev.* 90, 214–235. doi: 10.1111/brv.12105

Yoder, J. A., Pekins, P. J., Jones, H. F., Nelson, B. W., Lorenz, A. L., and Jajack, A. J. (2016). Water balance attributes for off-host survival in larvae of the winter tick (*Dermacentor albipictus*; Acari: Ixodidae) from wild moose. *Int. J. Acarol.* 42, 26–33. doi: 10.1080/01647954.2015.1113310

Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

BRIEF RESEARCH REPORT
published: 16 June 2020
doi: 10.3389/fevo.2020.00160

Conserving African Ungulates Under Climate Change: Do Communal and Private Conservancies Fill Gaps in the Protected Area Network Effectively?

Benjamin Luke Payne*† and Jakob Bro-Jørgensen**

Mammalian Behaviour and Evolution Group, Department of Evolution, Ecology and Behaviour, Institute of Integrative Biology, University of Liverpool, Neston, United Kingdom

OPEN ACCESS

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Jacob Goheen,
University of Wyoming, United States
Robin Naidoo,
World Wildlife Fund, United States

****Correspondence:***
Jakob Bro-Jørgensen
bro@liv.ac.uk

†Present address:
Benjamin Luke Payne,
Natural England, York,
United Kingdom

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *20 December 2019*
Accepted: *07 May 2020*
Published: *16 June 2020*

Citation:
Payne BL and Bro-Jørgensen J (2020) Conserving African Ungulates Under Climate Change: Do Communal and Private Conservancies Fill Gaps in the Protected Area Network Effectively? Front. Ecol. Evol. 8:160. doi: 10.3389/fevo.2020.00160

Throughout Africa, conservancies under community and private management are becoming increasingly important as a complement to the protection offered by the established core network of protected areas (PAs), which are largely under national management. However, opportunities for creating new conservation areas are restricted by increasing demand on land use by growing human populations, and it is unclear how effectively the current protected area network captures spatial priorities for conservation. Taking into account climate-induced range-shifts, we first identified spatial priorities for antelope conservation in Africa by gap analysis of the network of PAs listed with an IUCN category in the World Database for Protected Areas. For three countries from which information were available, we then assessed to what extent the gaps identified were covered by PAs not listed with an IUCN category, for the latter making a distinction between whether management was referred to as community-based or not. The results showed limited overlap, suggesting that the success of community-based and privately managed PAs in covering spatial priorities from a continent-wide perspective could be increased by more strategic land use planning at the national level.

Keywords: conservation management, species distribution modeling, national parks, community-based conservation, Bovidae

INTRODUCTION

Protected areas (PAs) constitute a cornerstone in conservation. Currently around 15% of the Earth's land surface is under protection (UNEP-WCMC et al., 2019), not far off the 17% Aichi target set for 2020 set by the UN Convention on Biological Diversity (UNEP, 2010). However, whether this coverage is sufficient to effectively preserve biodiversity is the subject of debate, especially following E.O. Wilson's call for half the Earth be set aside for wildlife conservation (Larsen et al., 2015;

Wilson, 2016). A major factor influencing the proportion of land surface requiring protection is whether PAs are placed strategically.

Historically, the core networks of national parks and reserves were not designed with the sole aim of covering the areas of highest conservation priority systematically; rather, conservation often had to contend with marginal lands that were of limited use for other human activities (Joppa and Pfaff, 2009). Ideally, the more recently established PAs supplementing the core networks would fill their gaps, but because creation of PAs is often opportunistic, and the underlying motivation varies, the extent to which they do so is unclear. Here we focus on three countries in sub-Saharan Africa for which data were available, i.e., Kenya, Tanzania and Namibia, to explore whether communal and private conservancies as a whole are strategically located within the PA network.

Regardless of the answer to this question, the important contribution of communal and private conservancies to conservation in recent years is indisputable (Dudley et al., 2018). In Kenya, a boom in communal and private conservancies over the past two decades involves the Northern Rangeland Trust and the Maasai Mara Wildlife Conservancies Association as key players (Nelson and Cooney, 2018). Over the same timeframe, Tanzania has promoted the establishment of Wildlife Management Areas to engage local communities in conservation (Bluwstein et al., 2018). This policy transfers wildlife user rights to committees of village representatives that negotiate contracts with private investors, with the national government and conservation organizations as advisors. Positive conservation impacts of Wildlife Management Areas are evident despite some challenges in their implementation, notably relating to the role of the government and the level of taxation (Lee, 2018; Nelson and Cooney, 2018). In Namibia, the legislative framework has since the mid-1990s allowed conditional rights to manage and benefit from natural resources to be transferred by creation of communal conservancies where local communities enter into joint ventures or lease arrangements with tourism or trophy hunting enterprises (Naidoo et al., 2016; Nelson and Cooney, 2018).

But has the proliferation of communal and private conservancies covered spatial priorities from a continental perspective effectively? Pinpointing optimal locations for PAs is complicated by the threat posed by climate change. Even PA networks that protect biodiversity well at present may not necessarily do so in the future because of the climate-induced range-shifts expected for many species (Payne and Bro-Jørgensen, 2016b; Keeley et al., 2018). This is especially the case if habitat fragmentation prevents wildlife from moving between PAs, whether because of natural barriers or human land-uses, infrastructural development and fencing (Payne and Bro-Jørgensen, 2016a; Wilson et al., 2016). Identifying the localities that preserve biodiversity most effectively long-term thus requires consideration not only of how changes in climate are likely to affect habitat suitability for wildlife, but also whether connectivity in the landscape will allow animals to track habitat changes. Here we use species distribution modeling to accommodate the expected consequences of climate-change (Guisan et al., 2017).

Ungulates are well suited as indicator taxa to assess how effectively PA networks cover areas of high biodiversity value because of their species richness and ubiquity (Bro-Jørgensen, 2016). Ungulates are often keystone species integral to ecosystem functioning, be it as prey for carnivores (Hopcraft et al., 2010), dispersers of seeds (Feer, 1995), architects of habitats (Prins and van der Jeugd, 1993; Augustine and McNaughton, 2004; Bond, 2008) or contributors to nutrient cycling (McNaughton and Georgiadis, 1986). In Africa, the extraordinary radiation of antelopes makes bovids particularly useful as a barometer of ecosystem health and its response to environmental change (Veldhuis et al., 2019), and in this study, we use bovids as our indicator taxon. Antelope conservation also demands increased attention in its own right as shown by around a third of the species being listed as threatened, and two-thirds with declining population sizes, on the global IUCN Red List (IUCN, 2020).

Taking into account predicted range-shifts because of climate change, we first identified the key priority areas for antelope conservation outside the core PA network in Africa. We then assessed how well community-based and privately managed PAs in the three focal countries captured these spatial priorities by testing their locations relative to locations selected at random. Our results indicate that the success is mixed and that several species are of urgent concern. The findings suggest that that PA network design can be improved by (i) strategic support for locally managed PAs in priority areas, which in turn highlights the need to mainstream conservation priorities into land-use planning at national level, and (ii) enhanced collaboration across national borders.

METHODS

Species Distribution Models

We rasterized ESRI shape files of the species distributions maps for 72 African antelope species from the IUCN Red List[1] to a 10' grid scale. Using data on climatic conditions between 1950 and 2000 from WorldClim (Hijmans et al., 2005), we then modeled "presence or absence" as a function of annual precipitation (log), and hottest and coldest monthly temperature using quadratic generalized linear models (GLMs) in the R package BIOMOD (Thuiller et al., 2009); selection of the three predictive variables was based on a principal component analysis and variable importance assessment (Thuiller et al., 2010) of 34 environmental variables describing climate, soil, elevation, evapotranspiration and land cover. We evaluated AIC-selected species distribution models derived from 70% of the data against the remaining 30% by quantifying the area-under-the-curve (AUC), sensitivity, and specificity (Swets, 1988) and noted model accuracy to range from "high" (AUC > 0.9; 69 species) to "useful" (AUC > 0.7; 3 species). Subsequently, we predicted future ranges by informing the species distribution models by climate projections according to three Atmosphere-Ocean Global Circulation Models (AOGCMs), i.e., UKMO HADCM3, NCAR

---

[1] http://www.iucnredlist.org

CCSM3, and BCCR BCM2. We then produced multi-climate-model ensemble forecasts of species distributions by requiring that predictions agreed under at least two of the three AOGCMs climate models, thereby minimizing the effect of inconsistencies in the climate models. Since the IUCN distribution maps are alpha shapes indicating the Extent of Occurrence (EOO) rather than the Area of Occupancy (AOO), we followed Thuiller et al. (2006) in applying a weighted "Human Footprint" filter in the simulations to decrease the probability of species populating human-affected areas. The "Human Footprint" incorporates human population density, land transformation, human access, and power infrastructure (Sanderson et al., 2002). Note that the human footprint was modeled as a static filter since projections were not available. The forecasts were based on the balanced A1B greenhouse gas emission storyline (Akçakaya et al., 2014).

We used two alternative approaches to predict the effect of climate change on species distributions by 2080. The first, conservative approach aims to reflect a future where species are prevented from dispersing outside their current ranges because of widespread human land-use; here we only included projected distributions that fell within the current distribution. The second approach aims to reflect what the species distribution might be without human interference; here we modeled the future bioclimatic envelope, i.e., the area projected to be climatically suitable and which is connected spatiotemporally to the current bioclimatic envelope, defined as the area of climatically suitable habitat connected to the current range. Intermediate time steps for assessing connectivity were 2030 and 2050.

Gap Analysis

We used the Marxan software (Ball et al., 2009) to conduct gap analyses of the PA network in Africa based on the forecasts for 2080 produced by the species distribution models; separate analyses were conducted for the conservative and envelope approaches. Marxan selects the set of planning units that best represents specified biodiversity features and allows users to define the total area of the set, the desired emphasis on spatial clustering of units, and the presence of any PAs that are mandatory in the final solution. Data on the PA network came from the UNEP-WCMC/IUCN World Database on Protected Areas (WDPA) (UNEP-WCMC, 2012). We set all PAs listed with an IUCN PA category as mandatory in the final solution; assuming these are generally more consolidated, we henceforth refer to these as "core PAs" and PAs listed without an IUCN PA category as "supplementary PAs." For species with a range below 20,000 km^2, we set protection of the entire range as mandatory because this limit defines the threshold for the extent of occurrence (EOO) below which a species qualifies as "vulnerable" on the IUCN Red List. For other species, we followed Ball et al. (2009) in setting the proportion of the range of species *x* requiring protection by relating it to a theoretical species *y*, which requires either 20% (low protection) or 30% (high protection) protection of its 1,000 cell range (∼34,400 km^2) using the formula: $(x_p/y_p) \approx (x_t/y_t)^{0.5}$, where *p* is the area protected, and *t* is the total range-size (Ardron et al., 2010). We set the boundary length modifier to reflect a high cost (10,000) to prioritize fewer, larger PAs and thereby promote the connectivity required under climate change. Each species was assigned a penalty factor whereby threatened species were considered more important to the solution (critically endangered 5,000, endangered 4,000, vulnerable 3,000, near threatened 2,000, least concern 1,000; the silver dik-dik [*Madoqua piacentinii*], which has no threat status, was set as 3,000 because of a similar size range to other vulnerable species). Because of computational restrictions associated with the large dataset, we conducted 1,000 repetitions using simulated annealing and the final solution identified priority areas where at least 750 repetitions agreed (Ardron et al., 2010).

Overlap Between Marxan Priority Areas and Supplementary PAs

For the analysis, we focused on the only three African countries for which the PA descriptions in WDPA included extensive references to community management, i.e., Kenya, Tanzania and Namibia. For these countries, we considered PAs as "community-managed" if either the designation, government type or management authority referred to them as such; none of these community-managed PAs were listed with an IUCN PA category. The PAs which were neither listed with an IUCN PA category nor qualified as "community-managed" are referred to as "supplementary PAs under other management."

To test whether the overlap between supplementary PAs and Marxan solutions differed from random, we generated randomized values by (i) creating a set of points to represent all cells in a country except the core PA cells; (ii) taking a random selection of those points to represent the number of cells in the Marxan solution for the country; (iii) taking another random selection of cells equal to the number of supplementary PA cells in the country; (iv) determining the number of cells that overlap with the selections created under (ii) and (iii); (v) repeating steps (iii) and (iv) 10,000 times; and (vi) comparing the actual values to the average of the randomizations generated under (v) using X^2-tests. Using a similar approach, we also compared the overlap between the Marxan solution and the supplementary PAs according to their management type separately; in this instance, fewer points were included in the sets created under step (i) to exclude cells of the alternative management type. All statistical analyses were conducted in R (R Development Core Team, 2019).

We found only minor differences between the results relating to the high and low protection scenarios, and for simplicity, we therefore display only the former and refer to discrepancies in the text.

RESULTS

Gap Analysis for Africa

The priority areas for antelope conservation identified by the gap analyses of the core PA network in Africa are shown together with the extent of the core PA network and supplementary PAs in the WDPA in **Figure 1**; separate solutions are illustrated for the bioclimatic envelope approach (**Figure 1A**), and the conservative approach where species are unable to disperse (**Figure 1B**).

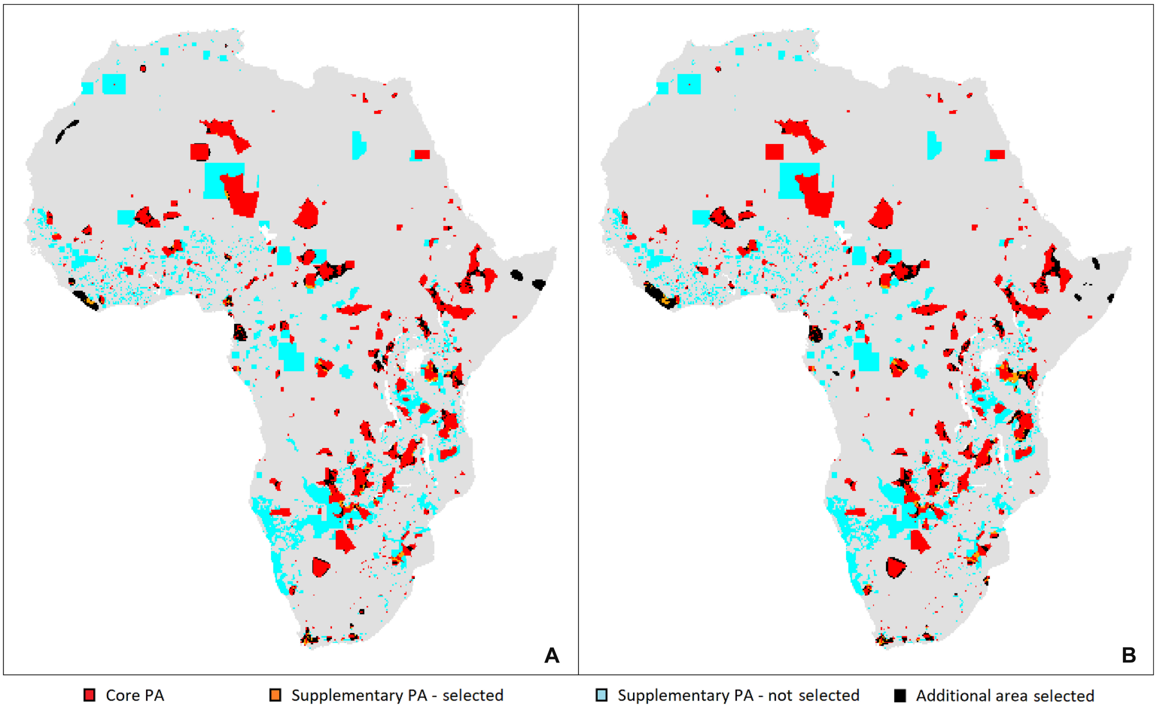

FIGURE 1 | Priority areas for antelope conservation in Africa under climate change. Gaps in the core protected area network identified by Marxan are shown in relation to current protection, where "selected" refers to Marxan priority areas. **(A)** Solution under the bioclimatic envelope approach. **(B)** Solution under the conservative approach where species are unable to disperse.

Kenya

Predicted Local Extinctions and Colonizations

Projected patterns in antelope biodiversity in Kenya by 2080 are shown in **Figure 2**, which indicates both the predicted overlap in bioclimatic envelopes and species richness predicted under the conservative approach. Of the 35 bovid species currently in the country, the hirola (*Beatragus hunteri*) is forecast to have no suitable area remaining by 2080 when modeling the spatiotemporally connected bioclimatic envelope. When adopting the conservative approach, assuming that dispersal from their current distribution is not possible, this forecast is shared by three additional species, i.e., sable antelope (*Hippotragus niger*), Ader's duiker (*Cephalophus adersi*) and bongo (*Tragelaphus eurycerus*). The bioclimatic envelope of seven antelope species not currently recorded as extant in the country are forecast to extend into Kenya by 2080, i.e., Soemmering's gazelle (*Nanger soemmerringii*), which has been recorded as a vagrant species in the north until recently (Kingdon, 1982), kob (*Kobus kob*), formerly present in the west of the country (Kingdon, 1982), southern reedbuck (*Redunca arundinum*), red-flanked duiker (*Cephalophus rufilatus*), bay duiker (*Cephalophus dorsalis*), natal red duiker (*Cephalophus natalensis*), and Sharpe's grysbok (*Raphicerus sharpei*).

Gap Analysis for the Core PA Network

Of the priority areas identified by Marxan to supplement the core network of PAs in Africa, those in Kenya include an area improving the connectivity between Tsavo East and West national parks (NPs) in the south as well as an area connecting Tsavo and Amboseli NPs, resulting in a large transfrontier park between Kenya and Tanzania (**Figure 3**). In the north of the country, a priority area expands Sibiloi NP on the east bank of Lake Turkana to the east and north to join Murle NP and Chelbi Wildlife Sanctuary across the Ethiopian border. Under the high protection scenario only, a priority area in the west of the country connects to the Amudat Community Wildlife Area across the border in Uganda. Finally, priority areas expand the existing core PAs in the center of the country.

Do Supplementary PAs Fill Gaps Effectively?

The supplementary PAs in Kenya were not more likely to cover the African-wide priority areas for antelope conservation located in the country than if they had been situated at random; this was the case whether supplementary PAs was considered as a whole or divided by their type of management (**Table 1**).

Tanzania

Predicted Local Extinctions and Colonizations

Projected patterns in antelope biodiversity by 2080 in Tanzania, the country with the highest species richness, are shown in **Figure 2**, which indicates both the predicted overlap in bioclimatic envelopes and species richness predicted under the conservative approach. Of 37 bovid species currently in the country, the Ader's duiker is forecast to have no

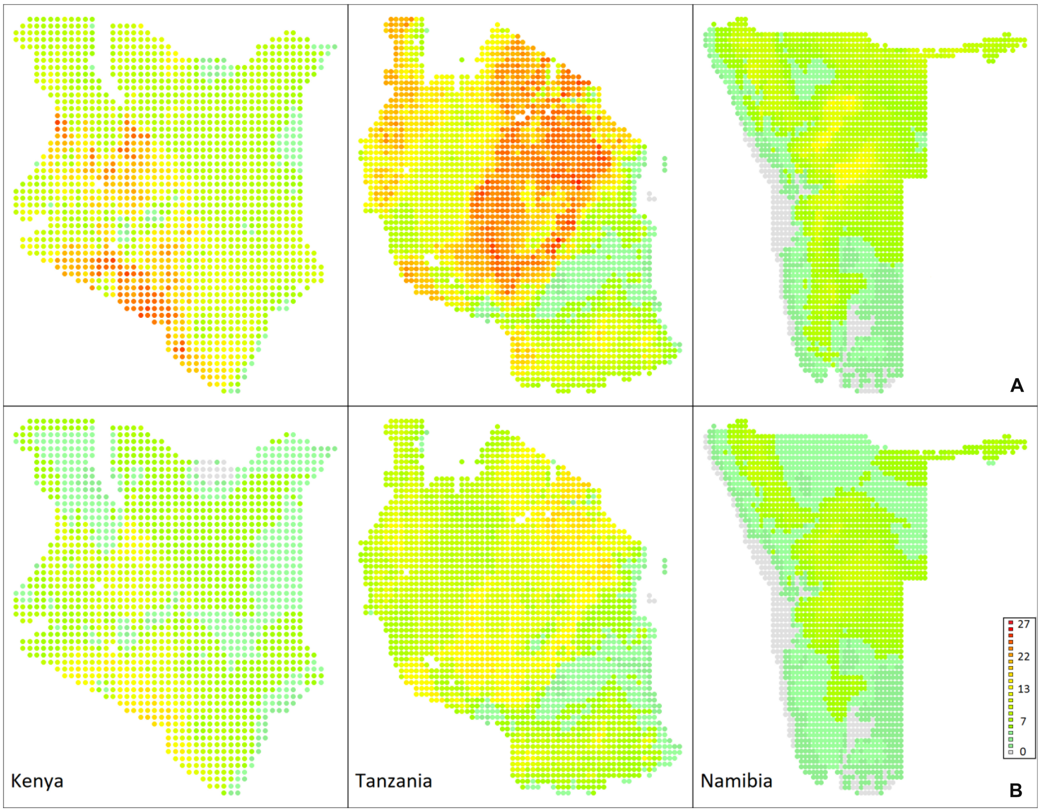

FIGURE 2 | Antelope biodiversity forecasts for 2080 in three sub-Saharan countries. **(A)** Heat map of the number of species for which bioclimatic envelopes overlap at a site. **(B)** Heat map of the species richness predicted under the conservative approach where species are unable to disperse.

suitable area remaining by 2080, both when modeling the spatiotemporally connected bioclimatic envelope and when assuming that dispersal from their current distribution is not possible. The bioclimatic envelope of five antelope species not currently present in Tanzania are forecast to extend into the country by 2080, i.e., the black-fronted duiker (*Cephalophus nigrifrons*), yellow-backed duiker (*Cephalophus silvicultor*), bay duiker, Salt's dikdik (*Madoqua saltiana*), and Günther's dikdik (*Madoqua guentheri*).

Gap Analysis for the Core PA Network

Priority areas identified by Marxan expand Kilimanjaro and Mikomazi NPs in the northeast to form the large transfrontier park with Kenya mentioned previously. Priority areas also extend Ngorongoro Conservation Area and Serengeti NP and in the high protection scenario using the conservative approach (without dispersal), the transfrontier park covers a contiguous area from Tsavo NPs in Kenya to Lake Victoria in Tanzania (**Figure 3**). In the southeast of the country, priority areas expand the Selous Game Reserve to the northwest, connecting to the Mufindi Scarp and Kigogo Forest Reserve in the high protection scenario without dispersal; in the scenario without dispersal, Selous Game Reserve also is expanded to the south to connect with community PAs such as Tunduru.

Do Supplementary PAs Fill Gaps Effectively?

As a whole, the supplementary PAs in Tanzania were significantly more likely to cover the African-wide priority areas for antelope conservation located in the country than if they had been situated at random (**Table 1**). Under the conservative approach only, this also held for community-managed supplementary PAs taken separately; for supplementary PAs under other management, there was a tendency to capture antelope priority areas both under the conservative and envelope approaches (**Table 1**).

Namibia

Predicted Local Extinctions and Colonizations

Projected patterns in antelope biodiversity in Namibia by 2080 are shown in **Figure 2**, which indicates both the predicted overlap in bioclimatic envelopes and species richness predicted under the conservative approach. All the 20 bovid species currently in the country retain a spatiotemporally connected bioclimatic envelope within the country by 2080, however, six species are forecast to have no suitable area remaining if dispersal from their current distribution is not possible, i.e., the African buffalo (*Syncerus caffer*), sitatunga (*Tragelaphus spekii*), sable antelope, southern lechwe (*Kobus leche*), southern reedbuck and Sharpe's grysbok. The bioclimatic envelope of four antelope species not currently present in the country are forecast to extend into Namibia by 2080, i.e., Cape grysbok (*Raphicerus melanotis*), gray

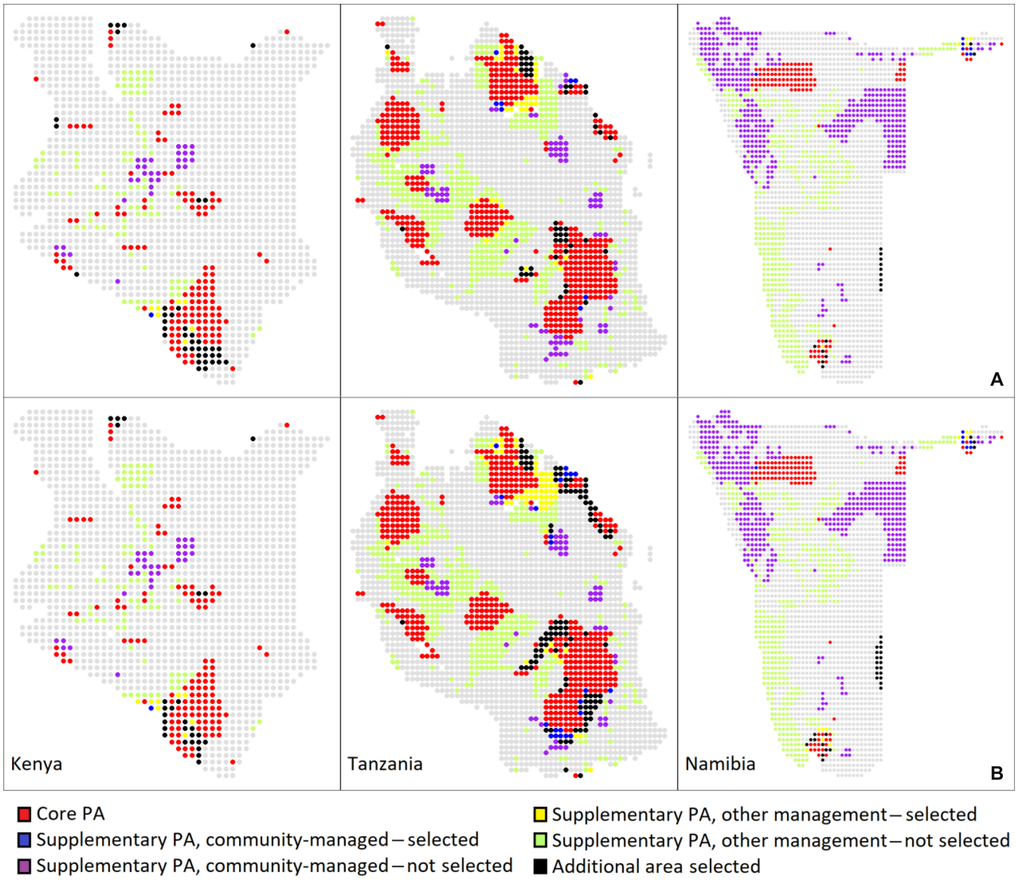

FIGURE 3 | PA networks and priority areas in three sub-Saharan countries. Areas selected for protection to complement the core PA network in a continent-wide gap analysis are shown in relation to the current PA network from WDPA. **(A)** Solutions under the bioclimatic envelope approach. **(B)** Solutions under the conservative approach where species are unable to disperse.

rhebok (*Pelea capreolus*), bohor reedbuck (*Redunca redunca*), and lowland nyala (*Tragelaphus angasi*).

Gap Analysis for the Core PA Network

Priority areas identified by Marxan expand the Ai-Ais Hot Springs NP in the south of the country, and on the eastern border, priority areas connect to the Kgalagadi Transfrontier Park in neighboring Botswana and South Africa (except in the low protection envelope scenario) (**Figure 3**). In the northeast of the country, priority areas are identified adjacent to Mudumu and Nkasa Rupara NPs in the Zambezi Region, which would strengthen the Kavango-Zambezi Transfrontier Conservation Area linking PAs in Angola, Botswana, Zambia, and Zimbabwe.

Do Supplementary PAs Fill Gaps Effectively?

The supplementary PAs in Namibia were not more likely to cover the African-wide priority areas for antelope conservation located in the country than if they had been situated at random; this held whether supplementary PAs were considered as a whole or divided by their type of management (**Table 1**).

DISCUSSION

According to our analysis, the PAs supplementing the core PA network in Tanzania are well-placed to capture priorities in antelope conservation at a continental scale, whereas in Kenya and Namibia no significant association appeared. These findings suggest that whereas the supplementary PAs make a valuable contribution to antelope conservation in all three countries, strategic support for conservation initiatives in priority areas may improve the design of PA networks. Our gap analysis recommends expansion of current PAs and increased interconnectivity, which will benefit a wide range of antelopes that qualify as landscape-species in that their requirements reflect more general conservation priorities at the ecosystem level. These taxa include migrating species such as the blue wildebeest (*Connochaetes taurinus*) and the gazelles, nomadic species such as the common eland (*Tragelaphus oryx*) and oryxes, and the many species that move seasonally between dry season concentration areas and wet season dispersal areas, e.g., hartebeest (*Alcelaphus buselaphus*) and the African buffalo (Lamprey, 1963). Several of the priority

TABLE 1 | Protected area coverage according to WDPA (UNEP-WCMC 2012) and spatial priority areas for antelope conservation in three African countries (**P* < 0.05; ***P* < 0.01).

Country	Area, total	PA, total	Core PA network	Supplementary PAs			Spatial priority areas outside the core PA network							
							Conservative approach (without dispersal)				Bioclimatic envelope approach			
				Total	Community-managed	Other management	Overlap with supplementary PAs			Outside supplementary PAs	Overlap with supplementary PAs			Outside supplementary PAs
							Total	Community-managed	Other management		Total	Community-managed	Other management	
Kenya														
Cells	1654	255	123	132	32	100	9	1	8	27	8	1	7	39
Proportion of country		15.4%	7.4%	8.0%	1.9%	6.0%	0.5%	0.1%	0.5%	1.6%	0.5%	0.1%	0.4%	2.4%
Deviation from random							Cells, random = 3.1; $X^2 = 3.14$; *P* = 0.208	Cells, random = 0.6: $X^2 < 0.01$; *P* = 0.999	Cells, random = 2.3: $X^2 = 3.77$; *P* = 0.152		Cells, random = 4.1; $X^2 = 1.40$; *P* = 0.498	Cells, random = 0.9; $X^2 < 0.01$; *P* = 1.000	Cells, random = 3.1; $X^2 = 1.68$; *P* = 0.432	
Tanzania														
Cells	2590	985	433	552	87	465	81	22	59	104	46	8	38	50
Proportion of country		38.0%	16.7%	21.3%	3.4%	18.0%	3.1%	0.8%	2.3%	4.0%	1.8%	0.3%	1.5%	1.9%
Deviation from random							Cells, random = 47.3; $X^2 = 10.20$; *P* = 0.006**	Cells, random = 6.5; $X^2 = 10.80$; *P* = 0.004**	Cells, random = 36.6; $X^2 = 5.64$; *P* = 0.060		Cells, random = 24.6; $X^2 = 6.66$; *P* = 0.036*	Cells, random = 3.0; $X^2 = 2.43$; *P* = 0.297	Cells, random = 19.7; $X^2 = 5.97$; *P* = 0.051	
Namibia														
Cells	2600	1046	112	934	472	462	17	7	10	31	12	7	5	17
Proportion of country		40.2%	4.3%	35.9%	18.2%	17.8%	0.7%	0.3%	0.4%	1.2%	0.5%	0.3%	0.2%	0.7%
Deviation from random							Cells, random = 18.0; $X^2 = 0.03$; *P* = 0.986	Cells, random = 8.9; $X^2 = 0.25$; *P* = 0.881	Cells, random = 9.4; $X^2 = 0.05$; *P* = 0.974		Cells, random = 10.8; $X^2 = 0.04$; *P* = 0.978	Cells, random = 5.5; $X^2 = 0.08$; *P* = 0.961	Cells, random = 5.1; $X^2 < 0.01$; *P* = 1.000	

areas connect PAs across national borders, which underlines the importance of international collaborative networks to establish and manage transfrontier parks.

Our study also identifies particular species which should be afforded special attention in PA design and management because either global or local extinction is predicted. The bioclimatic envelope for the critically endangered hirola, which is extant in Kenya only, is projected to have disappeared by 2080, calling for careful ecological monitoring as well as the establishment of an *ex situ* population. Recent research supports habitat degradation as a major cause underlying the species' decline (Ali et al., 2017). If confined to its current distribution, global extinction is also projected for the critically endangered Ader's duiker, which is extant in Kenya and Tanzania only, however, a spatiotemporally connected bioclimatic envelope remains in Kenya, indicating PAs adjacent to its current distribution as a management priority. In addition, two subspecies of conservation concern are forecast to disappear from Kenya by 2080 if restricted to their current range, i.e., the critically endangered mountain bongo (*T. e. isaaci*), which occurs in Kenya only, and Roosevelt's sable antelope (*H. n. roosevelti*), which is considered critically endangered at the national level. Spatiotemporally connected bioclimatic envelopes remain for both species, again highlighting that PAs adjoining their current distribution may be essential to allow dispersal. The range of the sable antelope, which is now restricted to Shimba Hills National Reserve, previously extended to Tsavo and Malindi (Kock and Goss, 1995), pointing to dispersal corridors and possibly translocation as priorities. For the mountain bongo, the island characteristics of its montane forest habitat present a challenge for protecting a sufficiently interconnected network of reserves to allow dispersal in what is a densely populated part of the country. In Namibia, local extinction is projected for several humid-adapted species, all classified as "least concern" on the IUCN Red List and limited to the extreme northeast of the country where their distributions constitute only a small fraction of their global ranges.

The partial overlap between locally managed PAs and gaps in the core network of primarily nationally managed PAs demonstrates the value of local conservation initiatives to achieve strategic goals. Nonetheless, our study also indicates that many priority areas remain without any protection, bringing the importance of strengthening strategic land-use planning at the national and multinational levels to the fore. Mainstreaming of the conservation agenda into policy-making is an Aichi strategic goal (UNEP, 2010), and at national levels, we recommend a wider application of multi-sector zoning approaches to land-use mapping to promote the allocation of land according to its underlying potential. A priority in this context is also the formulation of explicit fencing policies (Durant et al., 2015). For NGOs providing support for community conservation initiatives, our findings likewise underscore the importance of taking wider spatial priorities into account to maximize beneficial effects.

In the study, we used WDPA to explore gaps in PA networks. WDPA is a valuable resource as the most comprehensive database for PAs available, however, as it relies on data entered by a diverse set of users, ensuring that the same standards are uniformly applied is a challenge which WDPA are making commendable efforts to address. Still, we came across several inconsistencies and omissions in the database. In particular, a few countries have yet to categorize important national parks by IUCN management type, and not all communal and private conservancies are in the database, in spite of the best practice guidelines from the IUCN (Dudley, 2008; Dudley et al., 2014). In line with the advice in the WDPA guidelines, we therefore stress that the present results are to be taken as indicative of general issues, and suggestive of particular concerns worth further investigation, rather than as the basis for firm conclusions.

In closing, we note that although the success of PAs in averting threats to wildlife varies (Leverington et al., 2010; Geldmann et al., 2019), rates of declines in biodiversity are typically far lower inside than outside PAs (Gray et al., 2016), and strengthening both the design and management of PAs remains of paramount importance for conservation. For this purpose, our analysis illustrates how mapping of continent-wide conservation priorities can inform land-use planning and guide policies at national level. A pressing need is now to ensure that data on PA networks are reported in a more consistent manner across the globe to improve the quality of such analyses.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

BP and JB-J conceived and designed the study. BP performed the analyses. JB-J wrote the manuscript with input from BP.

FUNDING

Funding was provided by the Duncan Norman Trust.

ACKNOWLEDGMENTS

We thank M. Baylis, J. Hurst, N. Pettorelli, and I. Saccheri, W. Thuiller and two reviewers for comments.

REFERENCES

Akçakaya, H. R., Butchart, S. H. M., Watson, J. E. M., and Pearson, R. G. (2014). Preventing species extinctions resulting from climate change. *Nat. Clim. Change* 4, 1048–1049. doi: 10.1038/nclimate2455

Ali, A. H., Ford, A. T., Evans, J. S., Mallon, D. P., Hayes, M. M., King, J., et al. (2017). Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. *J. Appl. Ecol.* 54, 1720–1729. doi: 10.1111/1365-2664.12856

Ardron, J. A., Possingham, H. P., and Klein, C. J. (2010). *Marxan Good Practices*, 2nd Edn, Victoria: Pacific Marine Analysis and Research Association.

Augustine, D. J., and McNaughton, S. J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J. Appl. Ecol.* 41, 45–58. doi: 10.1111/j.1365-2664.2004.00864.x

Ball, I. R., Possingham, H. P., and Watts, M. (2009). "Marxan and relatives: software for spatial conservation prioritisation," in *Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools*, eds A. Moilanen, K. A. Wilson, and H. P. Possingham (Oxford: Oxford University Press), 185–195.

Bluwstein, J., Homewood, K., Lund, J. F., Nielsen, M. R., Burgess, N., Msuha, M., et al. (2018). A quasi-experimental study of impacts of Tanzania's wildlife management areas on rural livelihoods and wealth. *Sci. Data* 5:180087. doi: 10.1038/sdata.2018.87

Bond, W. J. (2008). What limits trees in C4 grasslands and savannas? *Annu. Rev. Ecol. Evol. Syst.* 39, 641–659. doi: 10.1146/annurev.ecolsys.39.110707.173411

Bro-Jørgensen, J. (2016). "Our antelope heritage – why the fuss?," in *Antelope Conservation: from Diagnosis to Action. Conservation Science and Practice Series*, eds J. Bro-Jørgensen, and D. Mallon (Oxford: Wiley-Blackwell), 1–10. doi: 10.1002/9781118409572.ch1

Dudley, N. (ed.) (2008). *Guidelines for Applying Protected Area Management Categories*. Gland: IUCN.

Dudley, N., Groves, C., Redford, K. H., and Stolton, S. (2014) Where now for protected areas? Setting the stage for the 2014 World Parks Congress. *Oryx* 48, 496–503.

Dudley, N., Jonas, H., Nelson, F., Parrish, J., Pyhala, A., Stolton, S., et al. (2018). The essential role of other effective area-based conservation measures in achieving big bold conservation targets. *Glob. Ecol. Conserv.* 15:e00424. doi: 10.1016/j.gecco.2018.e00424

Durant, S. M., Becker, M. S., Creel, S., Bashir, S., Dickman, A. J., Beudels-Jamar, R. C., et al. (2015). Developing fencing policies for dryland ecosystems. *J. Appl. Ecol.* 52, 544–551.

Feer, F. (1995). Seed dispersal in African forest ruminants. *J. Trop. Ecol.* 11, 683–689. doi: 10.1017/s0266467400009238

Geldmann, J., Manica, A., Burgess, N. D., Coad, L., and Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc. Natl. Acad. Sci. U.S.A.* 116, 23209–23215. doi: 10.1073/pnas.1908221116

Gray, C. L., Hill, S. L. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., et al. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nat. Commun.* 7:12306. doi: 10.1038/ncomms12306

Guisan, A., Thuiller, W., and Zimmermann, N. E. (2017). *Habitat Suitability And Distribution Models: With Applications in R*. Cambridge: Cambridge University Press.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Intern. J. Climatol.* 25, 1965–1978. doi: 10.1002/joc.1276

Hopcraft, J. G. C., Olff, H., and Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends Ecol. Evol.* 25, 119–128. doi: 10.1016/j.tree.2009.08.001

IUCN (2020). *The IUCN Red List of Threatened Species*. Available at: http://www.iucnredlist.org (accessed April 15, 2020).

Joppa, L. N., and Pfaff, A. (2009). High and far: biases in the location of protected areas. *PLoS One* 14:e8273. doi: 10.1371/journal.pone.008273

Keeley, A. T. H., Ackerly, D. D., Cameron, D. R., Heller, N. E., Huber, P. R., Schloss, C. A., et al. (2018). New concepts, models, and assessments of climate-wise connectivity. *Environ. Res. Lett.* 13:073002. doi: 10.1088/1748-9326/aacb85

Kingdon, J. (1982). *East African Mammals, An Atlas of Evolution in Africa. Vol. IIIC (Bovids)*. New York, NY: Academic Press.

Kock, R. A., and Goss, T. (1995). Sable sighting in Tsavo East National Park. *J. East Afr. Nat. Hist.* 84, 19–23. doi: 10.2982/0012-8317(1995)84[19:ssiten]2.0.co;2

Lamprey, H. F. (1963). Ecological separation of the large mammal species in the tarangire game reserve, Tanganyika. *Afr. J. Ecol.* 1, 63–92. doi: 10.1111/j.1365-2028.1963.tb00179.x

Larsen, F. W., Turner, W. R., and Mittermeier, R. A. (2015). Will protection of 17% of land by 2020 be enough to safeguard biodiversity and critical ecosystem services? *Oryx* 49, 74–79. doi: 10.1017/s0030605313001348

Lee, D. E. (2018). Evaluating conservation effectiveness in a Tanzanian community wildlife management area. *J. Wildlife Manag.* 82, 1767–1774. doi: 10.1002/jwmg.21549

Leverington, F., Costa, K. L., Pavese, H., Lisle, A., and Hockings, M. (2010). A global analysis of protected area management effectiveness. *Environ. Manag.* 46, 685–698. doi: 10.1007/s00267-010-9564-5

McNaughton, S. J., and Georgiadis, N. J. (1986). Ecology of African grazing and browsing animals. *Annu. Rev. Ecol. Syst.* 17, 39–65.

Naidoo, R., Weaver, L. C., Diggle, R. W., Matongo, G., Stuart-Hill, G., and Thouless, C. (2016). Complementary benefits of tourism and hunting to communal conservancies in Namibia. *Conserv. Biol.* 30, 628–638. doi: 10.1111/cobi.12643

Nelson, F., and Cooney, R. (2018). *Communities Hold The Key To Expanding Conservation Impact In Africa*. Available at: https://www.iucn.org/crossroads-blog/201810/communities-hold-key-expanding-conservation-impact-africa (accessed April 18, 2020).

Payne, B., and Bro-Jørgensen, J. (2016a). A framework for prioritizing conservation translocations to mimic natural ecological processes under climate change: a case study with African antelopes. *Biol. Conserv.* 201, 230–236. doi: 10.1016/j.biocon.2016.07.018

Payne, B., and Bro-Jørgensen, J. (2016b). Disproportionate climate-induced range loss forecast for the most threatened antelopes. *Curr. Biol.* 26, 1200–1205. doi: 10.1016/j.cub.2016.02.067

Prins, H. H. T., and van der Jeugd, H. P. (1993). Herbivore population crashes and woodland structure in East Africa. *J. Ecol.* 81, 305–314.

R Development Core Team (2019). *R: A Language And Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing*. Available at: http://www.R-project.org (accessed December 10, 2019).

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., and Woolmer, G. (2002). The human footprint and the last of the wild. *Bioscience* 52, 891–904.

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293. doi: 10.1126/science.3287615

Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J. R. M., Midgley, G. F., and Corsi, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob. Change Biol.* 12, 424–440. doi: 10.1111/j.1365-2486.2006.01115.x

Thuiller, W., Lafourcade, B., and Araújo, M. (2010). *Presentation Manual for BIOMOD*. Grenoble: Université Joseph Fourier.

Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M. B. (2009). BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373. doi: 10.1111/j.1600-0587.2008.05742.x

UNEP (2010). *Convention on Biological Diversity, Decision X/2: Strategic Plan for Biodiversity 2011-2020*. Available at: https://www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf (accessed December 20, 2019).

UNEP-WCMC (2012). *Data Standards for the World Database on Protected Areas*. Cambridge: UNEP-WCMC.

UNEP-WCMC, IUCN, and NGS, (2019). *Protected Planet Live Report 2019*. Cambridge: UNEP-WCMC, IUCN & NGS.

Veldhuis, M. P., Ritchie, M. E., Ogutu, J. O., Morrison, T. A., Beale, C. M., Estes, A. B., et al. (2019). Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science* 363, 1424–1428. doi: 10.1126/science.aav0564

Wilson, E. O. (2016). *Half Earth: Our Planet's Fight for Life*. New York, NY: W.W. Norton.

Wilson, M. C., Chen, X., Corlett, R. T., Didham, R. K., Ding, P., Holt, R. D., et al. (2016). Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landsc. Ecol.* 31, 219–227. doi: 10.1007/s10980-015-0312-3

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 18 June 2020
doi: 10.3389/fevo.2020.00163

Balancing Current and Future Reproductive Investment: Variation in Resource Selection During Stages of Reproduction in a Long-Lived Herbivore

Levi J. Heffelfinger[1†], *Kelley M. Stewart*[1*], *Kevin T. Shoemaker*[1], *Neal W. Darby*[2] *and Vernon C. Bleich*[1,3]

[1] *Department of Natural Resources and Environmental Science, University of Nevada, Reno, Reno, NV, United States,* [2] *Mojave National Preserve, National Park Service, Barstow, CA, United States,* [3] *Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, Bishop, CA, United States*

OPEN ACCESS

Edited by:
Andrew James Jonathan MacIntosh,
Kyoto University, Japan

Reviewed by:
Heiko U. Wittmer,
Victoria University of Wellington, New Zealand
Chuck Anderson,
Colorado Parks and Wildlife, United States

***Correspondence:**
Kelley M. Stewart
KelleyS@unr.edu;
kstewart@cabnr.unr.edu

†Present address:
Levi J. Heffelfinger,
Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX, United States

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *20 December 2019*
Accepted: *11 May 2020*
Published: *18 June 2020*

Citation:
Heffelfinger LJ, Stewart KM, Shoemaker KT, Darby NW and Bleich VC (2020) Balancing Current and Future Reproductive Investment: Variation in Resource Selection During Stages of Reproduction in a Long-Lived Herbivore. Front. Ecol. Evol. 8:163. doi: 10.3389/fevo.2020.00163

Large herbivores exhibit relatively slow-paced life histories, and allocate resources toward maintaining high rates of adult survival, while juvenile survival has greater variability. Maternal females make decisions throughout life stages of reproduction to meet their nutritional demands while simultaneously ensuring survival and recruitment of young to maximize fitness. We investigated tradeoffs associated with resource selection by mule deer (*Odocoileus hemionus*) surrounding stages of reproduction in Mojave National Preserve, CA, United States. To understand potential tradeoffs associated with offspring survival and maternal nutritional condition, we measured differences in patterns of resource selection among pre-parturient females, females provisioning young, and females following the loss of young. The third trimester of gestation and lactation are considered the most nutritionally demanding stages of reproduction. We hypothesized that energetic costs would change rapidly throughout those stages of reproduction, especially after the loss of an offspring. Further, we hypothesized that lactating females would balance the acquisition of nutritional sources with safety of young. We used radio-collar and randomly generated locations to model resource selection in a hierarchical approach utilizing machine learning algorithms and traditional resource selection functions (RSFs). We also monitored recruitment of young born to GPS-collared females using VHF radio-collars equipped with mortality indicators. During all three stages of reproduction, adult females selected greater NDVI, less rugged terrain, areas close to water (especially while provisioning offspring), and higher elevations. Selection for greater levels of NDVI was stronger pre-parturition and following the loss of offspring compared to when females were provisioning offspring. We also observed high variation toward the selection of NDVI among individual females while provisioning young, which was less pronounced during the other reproductive stages. Offspring survival during our study was positively associated with females that selected greater levels of NDVI. Further, we were not able to detect a tradeoff between safety of young (ruggedness) and nutrient acquisition (NDVI). Perhaps predation risk and nutritional resources are not mutually exclusive in this ecosystem; and, females may be able to balance reproductive investment with the ability to select for water and nutrition while simultaneously ensuring lower risk of predation for themselves and their offspring.

Keywords: fitness, *Odocoileus hemionus*, machine learning, Mojave desert, life history, mule deer, random forest, resource selection

INTRODUCTION

Life-history strategies and associated decisions are tightly linked with survival and reproductive success, which are directly linked to population performance (Clutton-Brock and Sheldon, 2010; Bonte and Dahirel, 2017). Variation in life-history strategies among species result from selective pressures caused by a variety of factors including: climatic stochasticity, predation, disease, or food availability (Ricklefs and Wikelski, 2002). Animals exhibit variation in pace of their life-histories; specifically, the amount of investment to the care of young versus survival or future reproduction during the reproductive cycle (Clutton-Brock and Sheldon, 2010). Species with fast-paced life histories typically invest time and energy into producing many young in a short lifetime (Promislow and Harvey, 1990). In contrast, species that exhibit a slow-paced life history typically invest a larger proportion of resources into longer gestation, greater investment in individual offspring, and successful recruitment of young over a longer lifetime (Van Noordwijk and de Jong, 1986).

Animals are commonly forced to make tradeoffs to maximize certain demographic parameters to enhance overall fitness (Ricklefs, 1994). Whether or not individuals are forced to make those reproductive tradeoffs is often driven by somatic reserves or availability of nutritional resources on the landscape. When a large amount of maternal time and effort is allocated to producing and recruiting young, somatic reserves can be greatly diminished, and availability of resources on the landscape may determine if reproduction will be successful (Stearns, 1989). If females are in a poor nutritional state with limited opportunity to successfully reproduce, species with fast-paced life histories may be forced to trade off their own survival for reproduction. Conversely, species that exhibit slow-pace of life strategies are more likely to tradeoff current for future reproductive effort rather than trading survival. Both strategies have the goal of maximizing reproductive fitness over their lifetime (Williams, 1966; Stearns, 1989; Gaillard et al., 1998, 2000).

Large, herbivorous mammals exhibit a slow pace of life strategy, and individuals in poor nutritional condition may tradeoff investment in current reproduction for future reproductive success (Clutton-Brock et al., 1983). Nevertheless, maternal females that consistently maintain a higher nutritional plane between breeding seasons rarely exhibit signs of reproductive costs and limitations on opportunities for future reproduction (Hamel et al., 2009). Conversely, females occupying nutritionally limiting environments, or individuals unable to maintain a continuous high plane of nutrition are often tightly linked to environmental stochasticity, especially relative to forage availability to drive year-to-year reproductive success (Therrien et al., 2008; Monteith et al., 2014; Heffelfinger et al., 2018). Even in instances where females are not nutritionally limited, an additional cost to reproduction is keeping young safe from predation by maintaining vigilance and using areas that are safer for young (White and Berger, 2001). Thus, in areas where current and future reproductive costs may be more dependent on landscape level or environmental attributes (arid environments, harsh winters, etc.), maternal females may be faced with decisions about selection or use of resources that directly affect their ability to care and provision young, while attempting to maintain a high enough plane of nutrition to invest in future reproduction.

Animal location data can be used to investigate patterns of resource use on the landscape at both the individual and population levels (Johnson, 1980; Manly et al., 2007). Those patterns can, in turn, reflect behavioral influence on acquisition and allocation of resources toward survival and reproductive success. Selection of high-quality resources can directly result in higher fitness for an animal regardless of their life-history strategy. Therefore investigation into selection of resources is assumed to be tied directly to reproductive fitness (Kawecki and Stearns, 1993; Aldridge and Boyce, 2007; Dzialak et al., 2011). The stages of reproduction, however, induce different limitations and requirements on the nutritional state or potential to increase fitness of individuals (Barboza et al., 2009). For example, adults may select habitats with lower quality food resources if the habitat affords offspring increased protection from predators (White and Berger, 2001; Hebblewhite and Merrill, 2009). Conversely, late-gestation and lactation are the most energetically and nutritionally demanding periods throughout the life-cycle of females, and selection of resources should be directed toward those with the greatest nutrition (Barboza et al., 2009). Therefore, understanding resource selection during reproductive stages such as gestation, early provisioning of young (lactation), and post-provisioning (following juvenile mortality), may prove to be important in understanding potential tradeoffs throughout the reproductive cycle (McLoughlin et al., 2006). A sudden shift to a non-provisioning state from the energetically costly state of lactation (via loss of offspring) may result in a shift in behavior and resource use. With the loss of an offspring, females likely shift to a strategy of resource selection that maximizes body condition to recover from the high demands of lactation prior to the start of the next reproductive cycle. Further, adult females must also maintain vigilance to mitigate predation risk among variable nutritional constraints throughout the reproductive life stages (Cristescu et al., 2019). Few studies, however, have explored differences in resource selection associated with specific stages of reproduction using location data (Barten et al., 2001; Long et al., 2009; Shuman et al., 2018). Even fewer studies have attempted to assess the fitness consequences (e.g., individual probability of successful recruitment of young into the population) resulting from variation in selection of resources between reproductive stages.

Large, herbivorous mammals typically exhibit high and relatively stable survival rates of adults throughout their geographical range (Bishop et al., 2009; Hurley et al., 2011; Bender et al., 2012; Monteith et al., 2014). Therefore, population performance of ungulates is most often regulated by successful reproduction and recruitment of young (Gaillard et al., 1998, 2000). We used a non-migratory population of mule deer (*Odocoileus hemionus*) as a representative species of large herbivores to test how selection of resources varies during different stages of reproduction as a result of tradeoffs between nutritional requirements for the mother and safety of offspring. Our objective was to identify factors that influence space use of individual females and selection of resources within their annual home range, indicated by landscape characteristics, during three stages of reproduction, (1) late gestation and just prior to parturition, (2) while the maternal female is provisioning young (i.e., during lactation), and (3) after an abrupt halt in allocating resources to young (i.e., following mortality of offspring). Further, we seek to evaluate how selection of resources by females while provisioning young may influence the chance of successfully recruiting their young into the population. Previous work in our study area indicates that individuals select landscape features, including areas close to water and at high elevations, typical for mule deer populations occupying arid environments prior to parturition (McKee et al., 2015). We hypothesized that female mule deer trade off high-quality resources for safety of offspring, by selecting areas within their annual home range that are more conducive to survival and recruitment of offspring. Therefore, we predicted that females with dependent young select and occupy areas more suitable to the safety of young compared to selection of resources prior to parturition. Further, we hypothesized that after a sudden transition to a non-reproductive state following loss of offspring, mule deer selected resources suitable for recovery of nutrient stores to improve nutritional condition prior to the next reproductive cycle.

MATERIALS AND METHODS

Study Site

Mojave National Preserve is located in San Bernardino County, in southeastern California, United States (35° 00′ N 115° 28′ W). Mojave National Preserve covers nearly 650,000 ha of extensive bajadas and playas in the valley floors between rugged mountain ranges of granite, basalt, and igneous rock (McKee et al., 2015). Elevation ranges from 270 m in the valleys to 2417 m at the peak of Clark Mountain. Vegetative communities in Mojave National Preserve vary by elevation and with temperature and precipitation (National Park Service, 2017). Vegetative assemblages represent typical Mojave Desert ecosystems with small influences of Great Basin and Sonoran Desert vegetation in transition zones (McKee et al., 2015; National Park Service, 2017).

Mojave National Preserve has high temperatures during the summer months and the precipitation pattern is bi-modal, with peaks during summer and winter (McKee et al., 2015). Mean annual precipitation at mid- to upper elevations is 18 cm (*SD* = 26; 1992-present, Meso West Weather Station, Operated by the University of Utah, Salt Lake City) and 9.3 cm (*SD* = 12) at low elevations (1980-present, Soda Springs, northern Mojave National Preserve). Mean maximum temperatures during the winter are 19 and 13°C, and 40.5 and 33°C during the summer at low and high elevations respectively.

We established three study sites that best characterized suitable habitat based on movements of adult female mule deer from a previous study (**Figure 1**; McKee et al., 2015). The New York Mountains study site is 27,195 ha and has four permanent water sources. The New York Mountains study site consists of steep, rocky pinyon-juniper woodland (*Pinus monophylla* and *Juniperus osteosperma*) in the upper elevations, a scrub live oak (*Quercus turbinella*) and bitterbrush (*Purshia glandulosa*) shrubland in mid-elevations, and yucca (*Yucca schidigera*) and creosote (*Larrea tridentata*) in desert shrublands at lower elevations. The Midhills study site consists of 39,368 ha with 19 water sources, and experienced an extensive wildfire in 2005. The burned portion of the study site is currently dominated by globemallow (*Sphaeralcea* spp.), bitterbrush, and desert almond (*Prunus fasciculata*) within the rolling hills but still has patches of unburned Great Basin sagebrush (*Artemisia tridentata*) and pinyon-juniper woodland in the upper elevations (McKee et al., 2015). Cima Dome, the third study area, consists of 40,404 ha, has seven permanent water sources with little elevation change, and is dominated by Joshua tree (*Yucca brevifolia*) woodland, blackbrush (*Coleogyne ramosissima*), bitterbrush, creosote bush, and sparse patches of juniper (**Figure 1**; McKee et al., 2015).

Field Data Collection

In late February or early March from 2013 to 2016, we captured adult female mule deer via net gun from a helicopter (Krausman et al., 1985). Only one female was captured from each observed social group encountered to maintain independence of sampling. Each deer was brought to a central processing station where they were marked with uniquely colored and numbered ear tags and fitted with GPS radio collars programmed to collect one location every 90 min (collar model G2110D, Advanced Telemetry Systems, Isanti, MN, United States). After each adult female was processed we released them from the central processing station. Movement data were censored for the first 2 weeks following capture to discount the effects of handling. We programmed radio collars to drop off about 1 year after deployment; collars also had a mortality switch with a Very High Frequency (VHF) transmitter so ground crews could locate collars following a mortality event or after the collar was dropped.

We used ultrasonography to determine pregnancy status for each adult female (Stephenson et al., 1995, 2002). A vaginal implant transmitter (VIT, model M3930L, Advanced Telemetry Systems, Isanti, MN, United States) was inserted into the birth

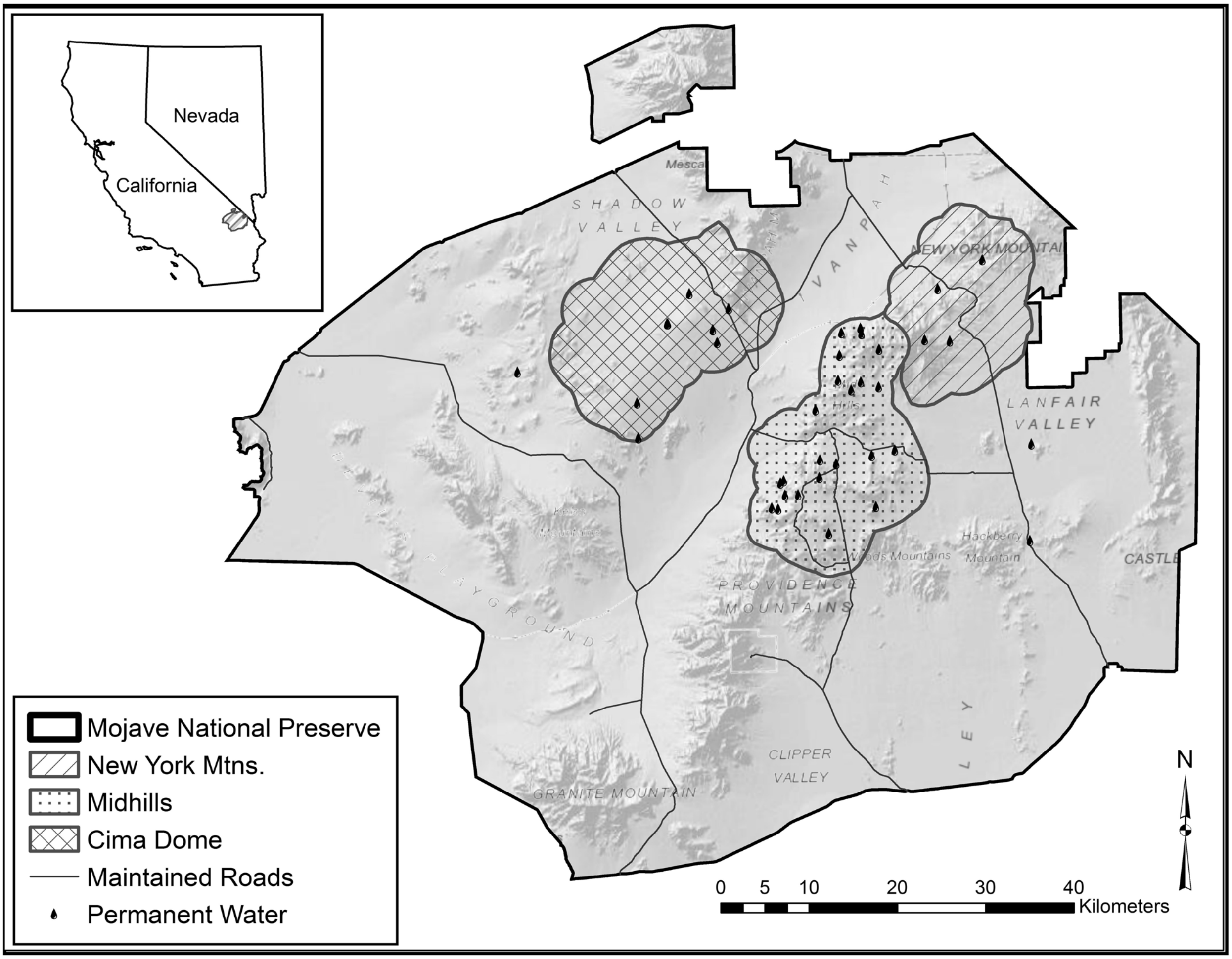

FIGURE 1 | Map of the Mojave National Preserve, CA, United States, with study area delineations and permanent water occurrences exhibited in the Mojave Desert. Inset map shows location relative to Nevada and California, United States (shaded). Figure recreated from McKee et al. (2015).

canal of all females that were pregnant (Bishop et al., 2007). We used modified VITs described by Bishop et al. (2011) that were also equipped with a temperature sensor, a photo sensor, and Precise Event Timing (PET) as described by Carstensen et al. (2003), Bishop et al. (2007), and Heffelfinger et al. (2018). When data collection was completed, individuals were then released from the central processing station, or if moved more than 4 km from the capture site, were returned to the original capture location and released.

Concurrent with this study, juvenile survival was investigated with 110 neonates that were captured, collared, and monitored every 1–3 days for survival (see Heffelfinger et al., 2018 for a more detailed description of neonate handling methodology). Using the PET coding from each VIT, used to capture a neonate, timing of parturition for the mother was known. For those juveniles caught in instances where the PET coding failed ($n = 44$), parturition date was estimated using at least two of the following indices: neonate's hoof condition, behavior, umbilicus condition, size, and date the mother was last known to be pregnant (Haugen and Speake, 1958; Haskell et al., 2007; Monteith et al., 2014). Juveniles were monitored via telemetry following capture. Thus, the date of mortality for each neonate was known and was then linked with GPS data for the associated maternal female.

All procedures were approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno (IACUC Protocol #: 00538) and were in keeping with guidelines established by the American Society of Mammologists for research on wild mammals (Sikes, 2016). We also complied with capture and handling procedures developed by the California Department of Fish and Wildlife.

Dataset Preparation

Our ability to assess resource selection during various stages of reproduction was dependent on capturing and monitoring neonates from collared adults. Thus, for this analysis, we used locations of collared females with associated captured and marked neonates from 2013 to 2016. We eliminated any major outlying points associated with short-term, exploratory movements by visually evaluating locations in

ArcGIS (Moen et al., 1997; ArcGIS 10.3, Environmental Systems Research Institute, Redlands, CA, United States). We calculated annual kernel density estimates with a 99.9% isopleth using Geospatial Modeling Environment (Beyer, 2015). Those annual home ranges were used to quantify availability of resources within the home range (i.e., 3rd order selection, Johnson, 1980). We buffered the estimated kernel by the average movement between points from marked individuals (200 m; *SD* = 196.63) to prevent exclusion of space that was available to study animals beyond the outermost used locations in the 99.9% kernel. This method of defining the available space familiar to females resulted in a mean kernel estimate of availability of 24.34 km^2 (*SD* = 16.48; **Supplementary Figure S1**). Spatial familiarity regarding resources within an animal's annual home range can influence demographic parameters (Forrester et al., 2015; Gehr et al., 2020). Thus, we used those estimates of annual home ranges as our designation for availability in order to draw inference in how maternal females select areas for reproduction from a spatial area in which they are familiar. Thus, our goal was to understand what features in individual home ranges influenced resource selection throughout phases of reproduction.

We separated locations from each individual into time periods associated with pre-parturition, provisioning of young, and for some individuals, post-juvenile mortality. We classified locations using the following criteria. For pre-parturition, we included locations 30 days prior to the date of parturition for each individual from which we had captured a neonate. We expected that individuals would most likely exhibit behaviors associated with the preparation of giving birth during this timeframe that could be compared with the subsequent periods of interest. For the timeframe of provisioning young, locations were included from parturition to either the time of juvenile mortality or through 30 days of provisioning young. We used 30 days post-parturition, because the quantity of milk produced and frequency of nursing drastically diminishes after 30 days, and resource requirements for the mother decline substantially (Sadlier, 1980; Gauthier and Barrette, 1985). Thus, to compare the change from extreme provisioning of resources to no longer allocating resources to offspring, we only included individuals who had lost young prior to 30 days post-parturition for our post-juvenile mortality period. Inherently, our strict rule of only including females who lost young within the first 30 days resulted in a lower sample size of individuals, but the first 30 days is when female investment in provisioning young is greatest and most appropriate to test our hypothesis.

Our movement data set consisted of many unique maternal females throughout the 4 years of the study within reproductive timeframes (pre-parturition, provisioning young, and post-juvenile mortality). We obtained movement data during the pre-parturition timeframe for 12 females in 2013, 15 females in 2014, 19 females in 2015, and 22 females in 2016 (n = 68; 32,297 locations). During the provisioning young timeframe, we obtained movement data for 12 females in 2013, 15 females in 2014, 18 females in 2015, and 22 females in 2016 (n = 67; 26,655 locations). Lastly, during the post-juvenile mortality timeframe we gathered location data for 7 females in 2013, 8 females in 2014, 3 females in 2015, and 2 females in 2016 (n = 20; 9,214 locations).

We included multiple landscape characteristics, shown to be important in selection of resources by mule deer (McKee et al., 2015), as covariates to identify patterns of resource selection during the three time periods (**Table 1**). Those covariates included distance to the nearest water source (m), elevation (m), slope (%), tree cover (%), and shrub cover (%) using LANDFIRE remote imagery products (Landfire, 2014). We also estimated a measure of ruggedness with the vector ruggedness metric (VRM; Sappington et al., 2007) and a transformation of aspect by cosine (north-south) and sine function (east-west), which was calculated from a Digital Elevation Model (DEM) of the study area (Landfire, 2014).

We retrieved monthly Normalized Difference Vegetation Index (NDVI) values for the duration of the study from Landsat 8 imagery to include as a covariate to assess selection based on vegetation phenology (Climate Engine, 2017). The Mojave National Preserve has very little hardwood canopy cover. Thus, NDVI is a relative measure of both shrub and annual forb "greenness." Finally, we retrieved land cover data to assign dominant vegetative communities throughout the study area using the United States Geological Survey (USGS) Central Mojave Vegetation Database derived in 2011 and amended in 2014 (Thomas et al., 2004; McKee et al., 2015). Dominant vegetation types were divided into the following categories: juniper wooded shrubland, Joshua tree wooded shrubland, pinyon wooded shrubland, Mojave yucca shrubland, desert wash, low elevation blackbrush-creosote shrubland, big-sagebrush shrubland, and burn area from the Hackberry Complex fire in 2005. Collinearity was assessed for all predictor variables using a correlation matrix in R (3.3.2, R Core Team) and we did not include any variables in the same model if highly correlated ($|r| > 0.65$ with one another; Stewart et al., 2002; Long et al., 2014).

We determined the number of 'available' points to sample randomly within the complete home range for each deer following the sensitivity analysis approach suggested by Renner et al. (2015), which is designed to ensure an appropriate sample size of background points such that resource selection coefficients derived from logistic regression (e.g., generalized linear mixed-effects model; Gillies et al., 2006) matches the 'selection intensity' coefficients derived from a point-process modeling approach (Warton and Shepherd, 2010; Renner et al., 2015). Specifically, we first fitted down-weighted Poisson regression (DWPR) models for each individual deer using the full set continuous and categorical covariates hypothesized to influence resource selection (see below) to a wide range of alternative background point densities ('glm' function in R). We varied background point densities from 50 to 2500 points per km^2, repeating the sampling and fitting algorithm 25 times across 8 different background point densities. We then identified the approximate threshold beyond which model performance (log likelihood) became insensitive to the specific set of background points sampled ('likelihood convergence'; Renner et al., 2015). Using this method, we found that an average density of 500 random background points per km^2 was sufficient for characterizing the distribution of environmental conditions available to each deer in our study (**Supplementary Figure S2**). Therefore, we constructed our resource selection models (both Random Forest and GLMM;

TABLE 1 | Descriptive statistics (mean ± SD) of available (random) and used (mule deer locations) data points for individuals in each reproductive time period on the Mojave National Preserve, California, United States, 2013–2016.

Variable	Pre-Parturition *n* = 68		Provisioning Young *n* = 67		Post-Juvenile Mortality *n* = 20	
	Used	Available	Used	Available	Used	Available
NDVI	0.1824 ± 0.0390	0.1640 ± 0.0352	0.1849 ± 0.0473	0.1606 ± 0.0340	0.1704 ± 0.0364	0.1523 ± 0.0270
Distance to Water (m)	2048 ± 1112	2364 ± 1531	1899 ± 1014	2427 ± 1614	1953 ± 837	2118 ± 1144
Elevation (m)	1585 ± 125	1520 ± 150	1590 ± 104	1518 ± 150	1584 ± 127	1506 ± 151
Ruggedness (VRM)	0.0022 ± 0.0023	0.0018 ± 0.0022	0.0028 ± 0.0025	0.0017 ± 0.0022	0.0022 ± 0.0022	0.0014 ± 0.0020
North – South Aspect	1.12 ± 0.68	1.00 ± 0.68	1.05 ± 0.69	1.00 ± 0.67	1.10 ± 0.67	0.95 ± 0.67
East – West Aspect	1.08 ± 0.70	0.97 ± 0.72	1.04 ± 0.69	0.96 ± 0.72	1.10 ± 0.71	0.97 ± 0.71
Slope (%)	8.39 ± 7.36	7.49 ± 7.60	9.71 ± 7.91	7.34 ± 7.55	8.75 ± 7.25	6.49 ± 6.87
Shrub Cover (%)	2.96 ± 2.06	3.41 ± 1.80	3.05 ±2.09	3.43 ± 1.78	3.00 ± 1.97	3.59 ± 1.62
Tree Cover (%)	2.37 ± 5.75	1.05 ± 4.08	2.99 ± 6.55	1.00 ± 4.00	2.35 ± 5.62	0.80 ± 3.51

Aspect variables were transformed using the cosine and sine functions on a scale of 0 – 2 (2 being North and East respectively). Shrub cover was scaled 0 – 10 (1 = 10% shrub cover, 2 = 20% shrub cover, etc.). NDVI is Normalized Difference Vegetation Index.

see below) such that each unique deer/status combination was paired with an appropriate number of random background points (500 per km^2).

Identifying Variables for Resource Selection by Reproductive Stage

We used Random Forest, a machine learning approach (Breiman, 2001; Cutler et al., 2007; Shoemaker et al., 2018, implemented in the 'ranger' package in R), to identify those features on the landscape that were most important in explaining resource selection across our population of female mule deer for each reproductive stage. Those features identified as important by the Random Forest algorithm were used to fit a generalized linear mixed-effects model (GLMM) designed to test for differences among reproductive timeframes (see below). RF is a machine-learning algorithm commonly used by ecologists to perform feature elimination and to discover relationships between a response variable and numerous predictor variables without imposing constraints such as linear responses and interactions (Cutler et al., 2007; Shoemaker et al., 2018). Our RF models (one model for each reproductive status) were fitted using 1000 trees, with each splitting criterion chosen from a sample of 5 (out of 9) predictor variables (we removed the 'slope' variable prior to model fitting due to high correlation with 'ruggedness'). The RF settings were optimized via cross-validation using the 'caret' package in R (Kuhn, 2019). We computed the relative importance (RI) of predictor variables as the average degree to which out-of-bag prediction error increased when information about each predictor variable was removed from the analysis (Cutler et al., 2007). Importance rankings therefore account for both the main influence of the predictor on selection as well as inclusion of the variables in identified interactions (Shoemaker et al., 2018). For ease of interpretation we rescaled the reported relative importance values by normalizing them from 0 (least) to 1 (most) important variables. We generated partial dependence plots to visualize univariate relationships for those variables with the highest importance indices (Shoemaker et al., 2018). Finally, we used cross-validation to evaluate how well our RF model built at the individual level would predict resource use at a population scale; instead of the traditional method where each "fold" (*n* = 3) represented a random subset of the entire dataset (De'ath and Fabricius, 2000), we generated each fold as a subset of individuals from the study.

Testing Differences in Resource Selection by Reproductive Stage

After characterizing important variables and general trends in resource selection across our population via our RF modeling process, we used a generalized linear mixed-effect modeling framework (GLMM, for which we assumed a binomial error distribution and a logit link) to test for differences in resource selection patterns among reproductive stages. To ensure that selection coefficients and interactions terms were generalizable to the population and not an artifact of individual variation in selection patterns (Gillies et al., 2006; Aarts et al., 2013), we included random intercept and slope terms for each unique individual. Specifically, variation in resource selection patterns among individuals was modeled with a random-intercept term and random coefficients for each main effect and interaction term in the full model (Gillies et al., 2006) (analogous to 3rd order selection; Johnson, 1980). The full model included main effect terms for each of the top four environmental gradients identified in the RF analysis (NDVI, elevation, ruggedness, and distance to water; see "*Results*" section), a main effect term for reproductive stage, and interaction terms for each of these environmental gradients with reproductive stage (testing differences in resource selection patterns by reproductive stage). To ensure resource selection coefficient estimates were unbiased and analogous to coefficients derived from a point-process model (PPM; Warton and Shepherd, 2010), we fixed the random intercept term with a high variance and "infinitely weighted" available vs. used points following Muff et al. (2019).

Effects of Resource Selection on Reproductive Output

After identifying population level patterns in selection of resource (RF modeling) and differences in reproductive timeframes at the individual scale (GLMM tests), we sought to identify a potential tradeoff between juvenile safety (rugged terrain) and nutrition acquisition (NDVI). We tested for a linear relationship between an individual's selection for ruggedness (individually based selection coefficients (from our GLMM exercise) and the available NDVI within a female's home range to potentially illustrate a tradeoff. Additionally, we sought to assess influences of habitat selection on increasing an individual's reproductive output (i.e., successful juvenile recruitment). To test for a relationship between habitat characteristics and reproductive success (juvenile recruitment), we conducted a known-fate analysis using juvenile recruitment data derived from telemetry data which was censored after the first 120 days of life (DeCesare et al., 2016). We summarized the data in a capture history format, with each row representing a unique juvenile and each column representing whether each juvenile was known to be alive or dead during each 1-week interval. Weekly juvenile survival probability was modeled as a logit-linear function of the maternal female's use of the top three environmental gradients identified in the RF analysis (see above), NDVI, and a logit-normal random intercept term for year. We fitted known-fate models in a Bayesian framework using JAGS (Plummer, 2003), which was called from R using the "jagsUI" package (Kellner, 2019).

RESULTS

Identifying Variables for Resource Selection by Reproductive Stage

In all three reproductive periods, the RF model indicated a clear top four variables that explain resource selection patterns within our system. In order of importance, mule deer tended to select greater values of NDVI, a variation in rugged terrain, areas closer to water sources, and higher elevations, than were available (**Figure 2**). The order and magnitude of these four variables switched slightly among time periods (**Figure 3**), with distance to water becoming more important than ruggedness for the provisioning period. Using these identified important variables, directed tests for differences between reproductive timeframes are outlined in our GLMM procedure (below). Predictor variables that did not prove to be especially important in explaining resource selection during our reproductive timeframes included vegetation type, North-South aspect, East-West Aspect, shrub cover, and tree cover (**Figure 3**). Cross-validation of our RF models resulted in AUC values of 0.65, 0.65, and 0.63 for pre-parturition, provisioning, and post-juvenile mortality stages, respectively (0.96, 0.97, and 0.97 when cross-validated with standard threefold cross-validation). Low cross-validation performance when folds were comprised of entire deer likely reflects substantial variation in resource selection patterns among individuals in our study population (also detected in our GLMM models; **Figure 4**).

Testing Differences in Resource Selection by Reproductive Stage

Our GLMM models further confirmed our important variable identification (RF modeling) by demonstrating a selection for greater values of NDVI, less rugged terrain, areas closer to water sources, and higher elevations, than were available (**Table 2** and **Figure 4**). Our test of differences between reproductive stages also indicated that selection coefficients moderately differed by reproductive status along resource gradients (**Table 2**). Interestingly, the GLMM models suggested a less prominent role for NDVI as a predictor of resource selection while females were provisioning young, though, population level inference indicates general selection for higher NDVI (**Table 2** and **Figure 4**). Our GLMM results also indicate a stronger selection for areas closer to permanent water sources while females were provisioning young (**Table 2**). Additionally, our GLMM modeling results highlighted the high individual heterogeneity in selection coefficients within our study (**Figure 4**), which generally exceeded variation by reproductive status (with the exception of NDVI and distance to water). Estimated among-individual heterogeneity in selection, reported as standard deviations on the logit scale, was 0.40 for NDVI, 1.54 for ruggedness, 1.34 elevation, and 1.53 for distance to water.

Effects of Resource Selection on Reproductive Output

Our test whether females traded off nutritional acquisition for juvenile safety indicated no statistical relationship between an individual's selection for ruggedness and available NDVI (**Figure 5**). Our known-fate survival analyses indicated that juvenile recruitment was positively influenced by the maternal females use of areas with greater NDVI while provisioning (mean = 0.56, 95% CI 0.09 to 1.04; **Figure 6**). We also noted a weak effect of elevation on juvenile survival, with higher elevations corresponding to lower recruitment success (mean = −0.27, 95% CI −0.72 to 0.13; **Figure 6**). The use of other environmental gradients (terrain ruggedness and distance to water) by maternal females had no detectable effect on juvenile recruitment (ruggedness: mean = −0.13, 95% CI −0.5 to 0.23; distance to water: mean = −0.03, 95% CI −0.39 to 0.34; **Figure 6**).

DISCUSSION

Our hypothesis that female mule deer in the Mojave National Preserve would trade off nutritional intake for selection of areas to increase safety of young by shifting to a risk averse strategy was not well supported. In fact, we observed few instances where patterns of selection differed substantially among reproductive stages, primarily because of the large amount of individual variation in selection among our study animals. Overall, there were four main variables that explained the majority of resources selected by mule deer within this population across reproductive stages; vegetation greenness (NDVI), terrain ruggedness, distance to water, and elevation. Females that were provisioning young appeared to select lower values of NDVI relative to other reproductive timeframes (albeit with much more individual heterogeneity), but also selected areas close to sources of water. Though selection for more rugged terrain seemed to vary between our population level modeling (RF) and individual based procedure (GLMM) analyses, there were

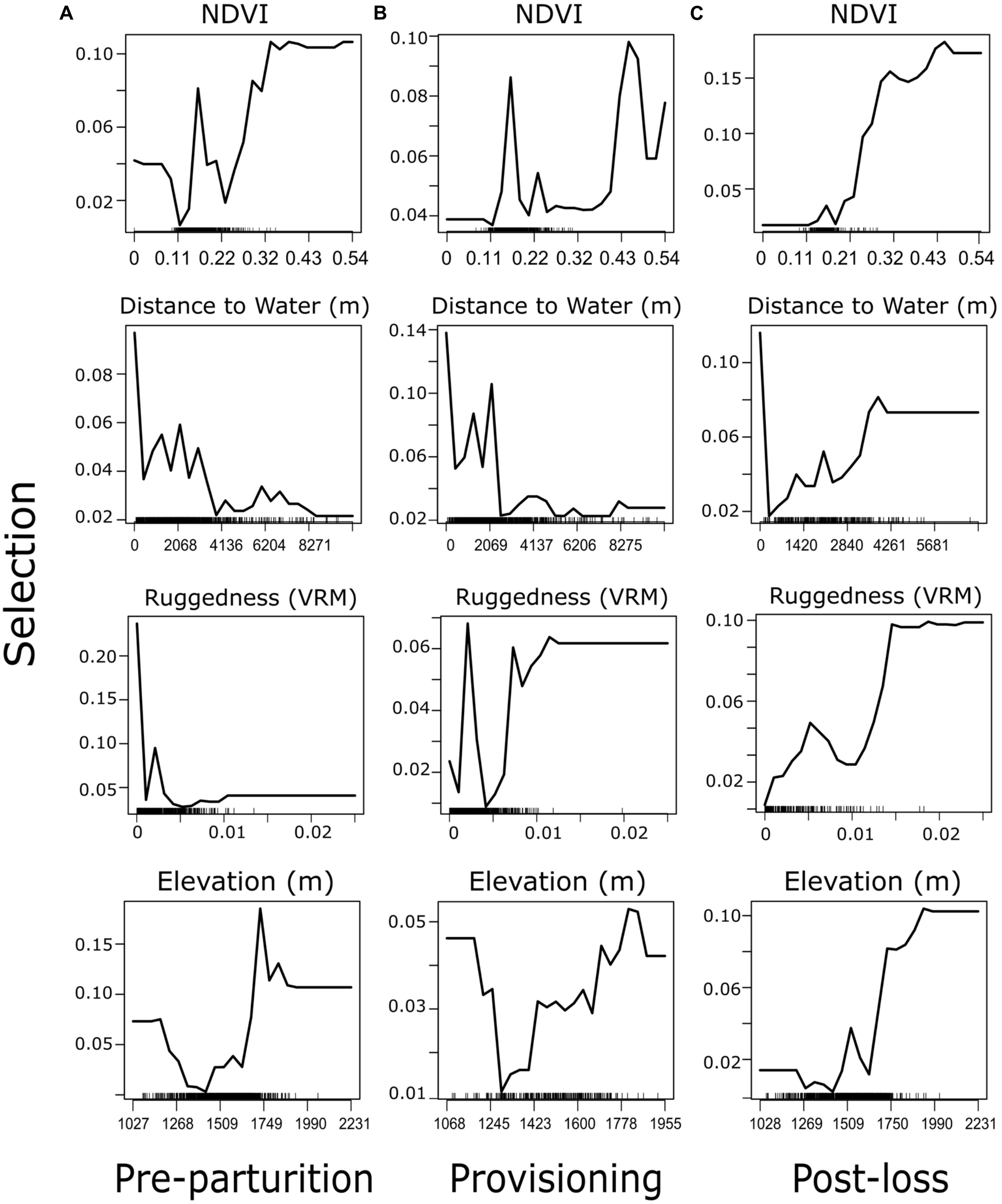

FIGURE 2 | Partial dependence plots of the top four variables explaining resource selection from random forest analysis of female mule deer during **(A)** pre-parturition (*n* = 68), **(B)** while provisioning offspring (*n* = 67), and **(C)** post-juvenile mortality (*n* = 20) on the Mojave National Preserve, California, United States, 2013 – 2016. Selection represents the density of expected occurrences associated with a point on the landscape at the respective value with a point process model (analogous to the probability of being a used location).

no significant shifts in selection between reproductive stages. Further, our tests of a direct tradeoff between nutritional intake (NDVI) and safety of young (rugged terrain) was not well supported. Selection of rugged terrain, however, did not decrease while females were provisioning young. Thus, females may have reduced concentration on nutrient acquisition (NDVI), while staying close to water and maintaining a minimum threshold level of safety for young through moderate use of rugged terrain among other landscape features.

Our GLMM results suggest that females tended to select spatial areas to maximize nutritional intake (selecting habitat with higher NDVI) during all reproductive stages. Though, there was a shift in selection toward lower values of NDVI while females were provisioning young, the overall population

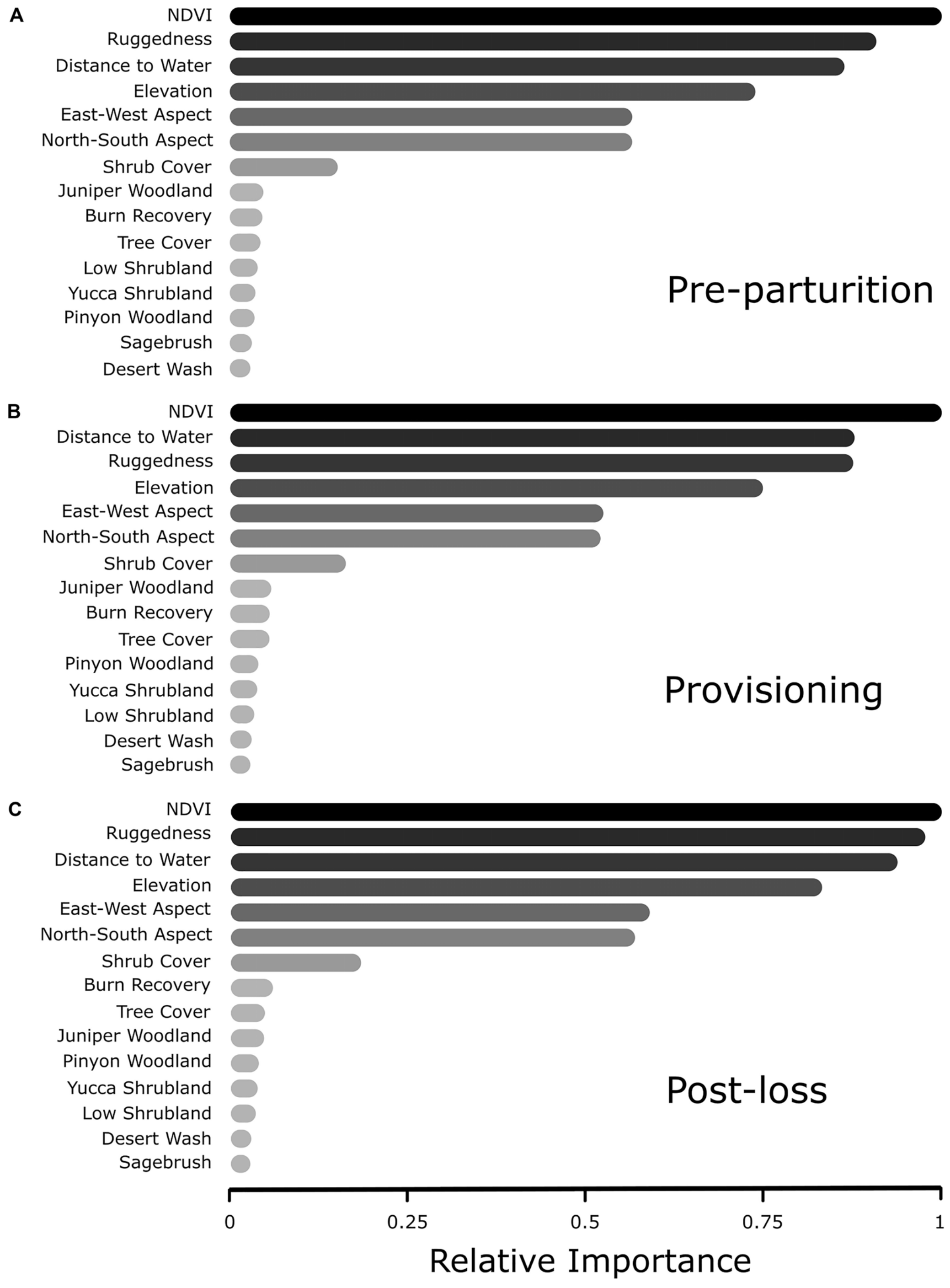

FIGURE 3 | Relative importance rankings of resource selection from random forest analysis of female mule deer during **(A)** pre-parturition (n = 68), **(B)** while provisioning offspring (n = 67), and **(C)** post-juvenile mortality (n = 20) on the Mojave National Preserve, California, United States, 2013 – 2016. Relative importance illustrates the influence of the predictor on resource selection estimated through rigorous conditional inference trees via a random forest algorithm.

level effect remained positive. We also demonstrated that terrain ruggedness and NDVI were positively correlated in our study area suggesting that females were able to select areas that were relatively safe for offspring while also allowing provisioning mothers to meet their nutritional and water demands. This observation is consistent with our result that successful recruitment of young, indicated by survival to 120 days after parturition, was highest in habitats with higher NDVI. Those results suggest that the nutritional value of habitat areas with relatively high NDVI, were not especially risky for

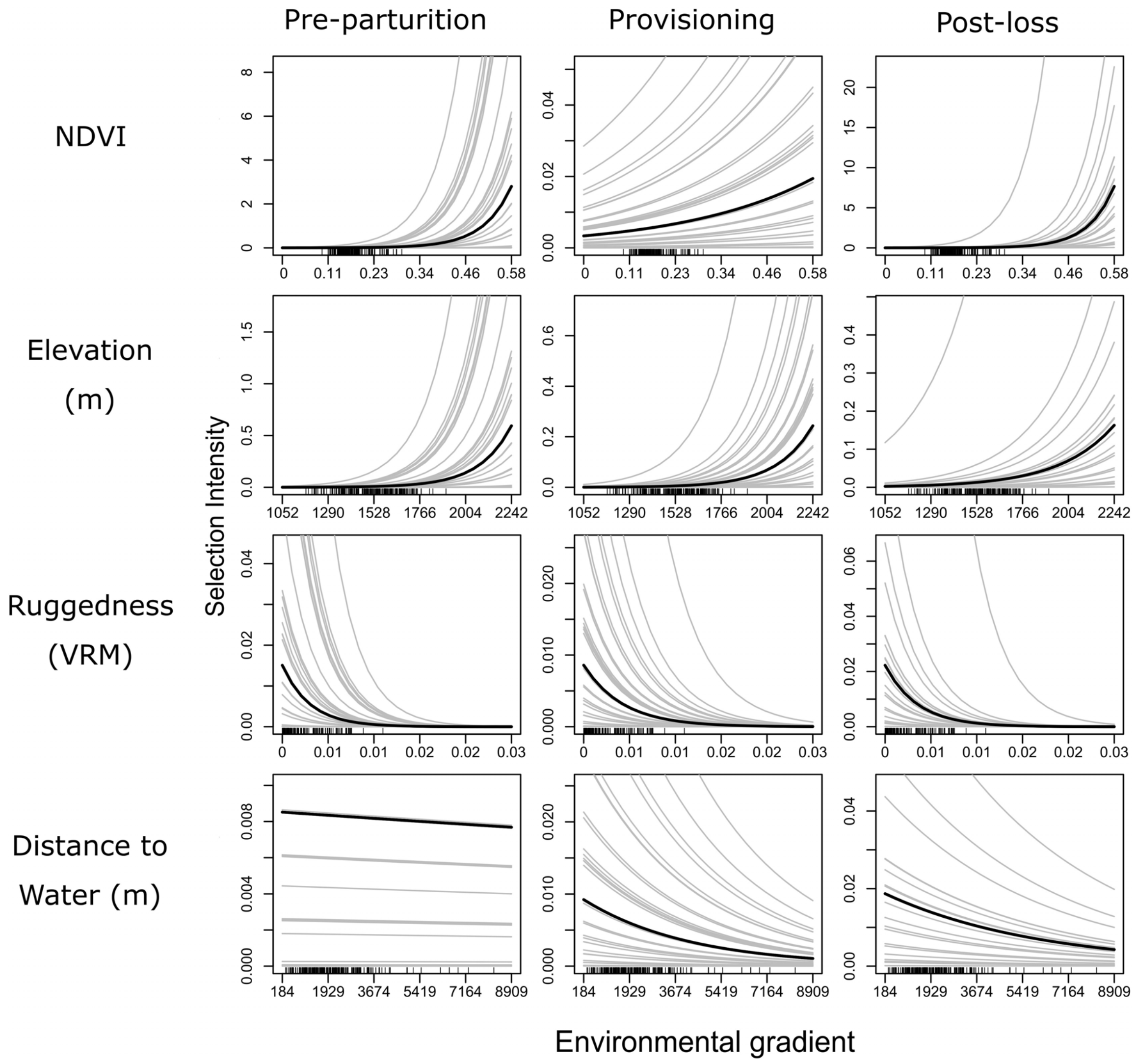

FIGURE 4 | Partial dependence plots illustrating the expected influence of each of four environmental gradients (rows of panel grid) on relative resource selection of female mule deer during pre-parturition (*n* = 68), while provisioning young (*n* = 67), and post-juvenile mortality (*n* = 20) on the Mojave National Preserve, California, United States, 2013 – 2016. Solid black lines indicate population level patterns, while gray lines represent patterns of selection for individual mule deer. All predictions were derived from a GLMM model fitted to GPS collar data, with random intercepts and slope terms fitted to individual deer. This figure illustrates the extreme variation in patterns of selection among individuals and the varying degree of differences in patterns of resource selection among reproductive states.

mothers with dependent young. A more effective test for a tradeoff between personal nutrition acquisition and offspring safety would require a study site where patches of high value for resource acquisition and offspring protection were mutually exclusive.

We expected female mule deer to use shrub and tree cover in addition to rugged terrain to increase safety of young, but those variables were not selected strongly by females while provisioning young; in fact, shrub and tree cover were not meaningful predictors of habitat use during any reproductive stage. Interestingly, mule deer are known to defend their young from small or mid-sized predators (Lingle et al., 2005). Potentially for this reason, mule deer typically prefer habitats with high visibility, in addition to a lower perceived risk of predation while foraging or resting (Altendorf et al., 2001; Esparza-Carlos et al., 2016; Bose et al., 2018). Our GLMM analyses did not confirm a shift to stronger selection for offspring safety while provisioning young, indeed; the overall population level effect for selection of rugged terrain was negative. Further, we observed constant selection of higher elevations in addition to lesser degrees of ruggedness, all of which could be assumed to enhance the ability for maternal vigilance toward predation risk. Our survival analysis, however, failed to confirm that ruggedness or elevation was positively correlated with offspring survival at our study site, and even indicated a trend toward lower recruitment success at higher elevations.

Forage quality, as indicated by higher NDVI, had a strong positive effect on the probability of successfully recruiting young

TABLE 2 | Coefficients from a generalized linear mixed model in which resource selection was modeled as a function of (standardized) NDVI, elevation, ruggedness, and distance to water.

	Estimate	CI, lower	CI, upper	
NDVI	0.528	0.361	0.695	*
NDVI*Post-mort	0.049	−0.258	0.355	
NDVI*Provisioning	−0.416	−0.61	−0.221	*
Elevation	0.898	0.514	1.282	*
Elevation*Post-mort	−0.372	−0.868	0.123	
Elevation*Provisioning	−0.106	−0.411	0.198	
Ruggedness	−0.759	−1.167	−0.351	*
Ruggedness*Post-mort	0.108	−0.284	0.499	
Ruggedness*Provisioning	0.224	−0.014	0.462	
Distance to Water	−0.015	−0.429	0.399	
Distance to Water*Post-mort	−0.2	−0.652	0.251	
Distance to Water*Provisioning	−0.301	−0.576	−0.025	*
Provisioning	−0.387	−0.431	−0.342	*
Post mort	0.475	0.406	0.544	*

*Coefficients were allowed to vary by reproductive status. Interactions between the reproductive state and main effects indicate the shift of selection or avoidance of that variable compared specifically to the reproductive stage of reference (in this case the provisioning state). *Significant at α = 0.05.*

into the population, while the effect of other environmental characteristics (e.g., ruggedness and distance to water) was much weaker. Indeed, NDVI has been directly linked to availability of high-quality forage for large herbivores (Marshal et al., 2005; Pettorelli et al., 2005; Creech et al., 2016). Additionally, lactation is nutritionally demanding for females (Oftedal, 2000; Barboza et al., 2009), and the month immediately following parturition is when quantity of milk and the number of suckling bouts by the neonate are greatest (Sadlier, 1980; Gauthier and Barrette, 1985). When rich nutritional sources are available to a female while provisioning offspring, the quality and quantity of milk increases and she is able to invest those resources in her young (Scornavacca et al., 2016). In addition to nutrient acquisition to support lactation, the increased requirements for water during lactation is paramount to successfully supply milk to young (Barboza et al., 2009). Throughout all reproductive timeframes, females selected areas closer to permanent water sources, however, we observed stronger selection for areas closer to water while females were provisioning young. Water resources are essential for preparation for parturition and meeting the physiological demands of late gestation and lactation (Barboza et al., 2009; Bleich et al., 2010; McKee et al., 2015). Both nutrient acquisition (via areas of greater NDVI) and access to water sources are important to maintain quality and quantity of milk for growth and survival of young. Thus, the nutritional quality of the landscape (through accessibility to forage and water) is directly linked to investment in offspring by maternal females (Scornavacca et al., 2016). Therefore, the ability of a female to keep her young safe while acquiring quality nutrients and then investing them in offspring directly affects her fitness and also population performance through survival and recruitment of young (Heffelfinger et al., 2018). Therefore, the ability of large herbivores to provision nutritious milk to their young (i.e., current investment), while maintaining the mother's nutritional plane during lactation for future reproductive effort and survival (i.e., future investment) is likely to be an optimum strategy in instances where females are not forced to make tradeoffs between nutrition and safety of young.

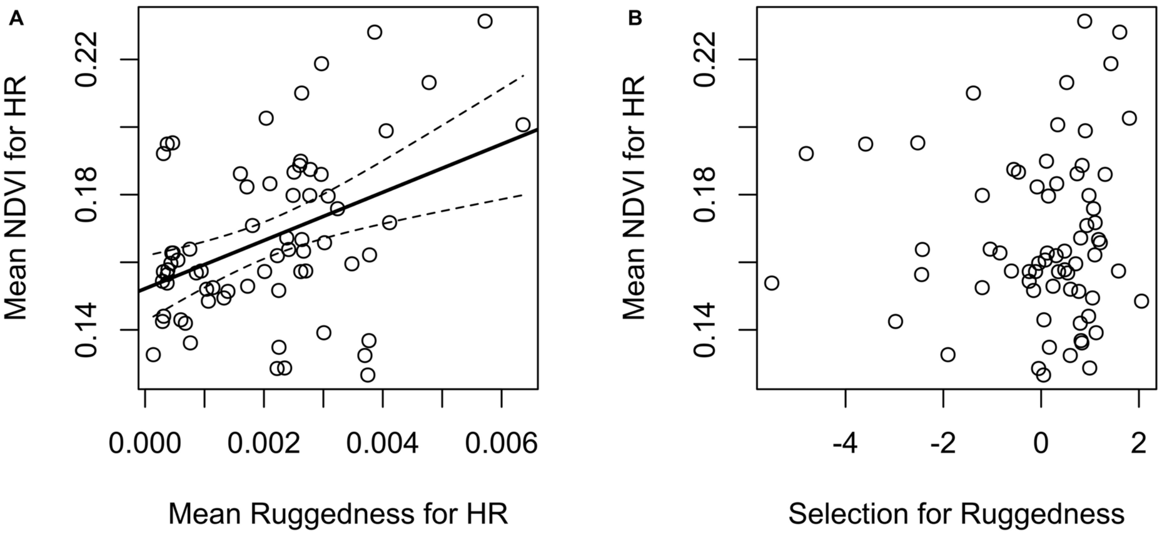

FIGURE 5 | Potential trade-offs (or lack thereof) between nutritional resources and offspring safety for female mule deer on the Mojave National Preserve (2013–2016) while provisioning young ($n = 67$). **(A)** The left figure reveals a general positive relationship between habitat regions likely to confer offspring safety (topographic ruggedness, averaged across individual home ranges) and the availability of nutritional resources (NDVI, averaged across individual home ranges). Black solid line and dashed curve were derived from ordinary linear regression, and represent a fitted regression line and 95% confidence interval, respectively. **(B)** The right figure illustrates the relationship between individual-level selection coefficients for rugged terrain (logit-scale, derived from a generalized linear mixed-effects model of resource selection) vs. the availability of nutritional resources (NDVI), averaged across individual home ranges (no statistical relationship was detected).

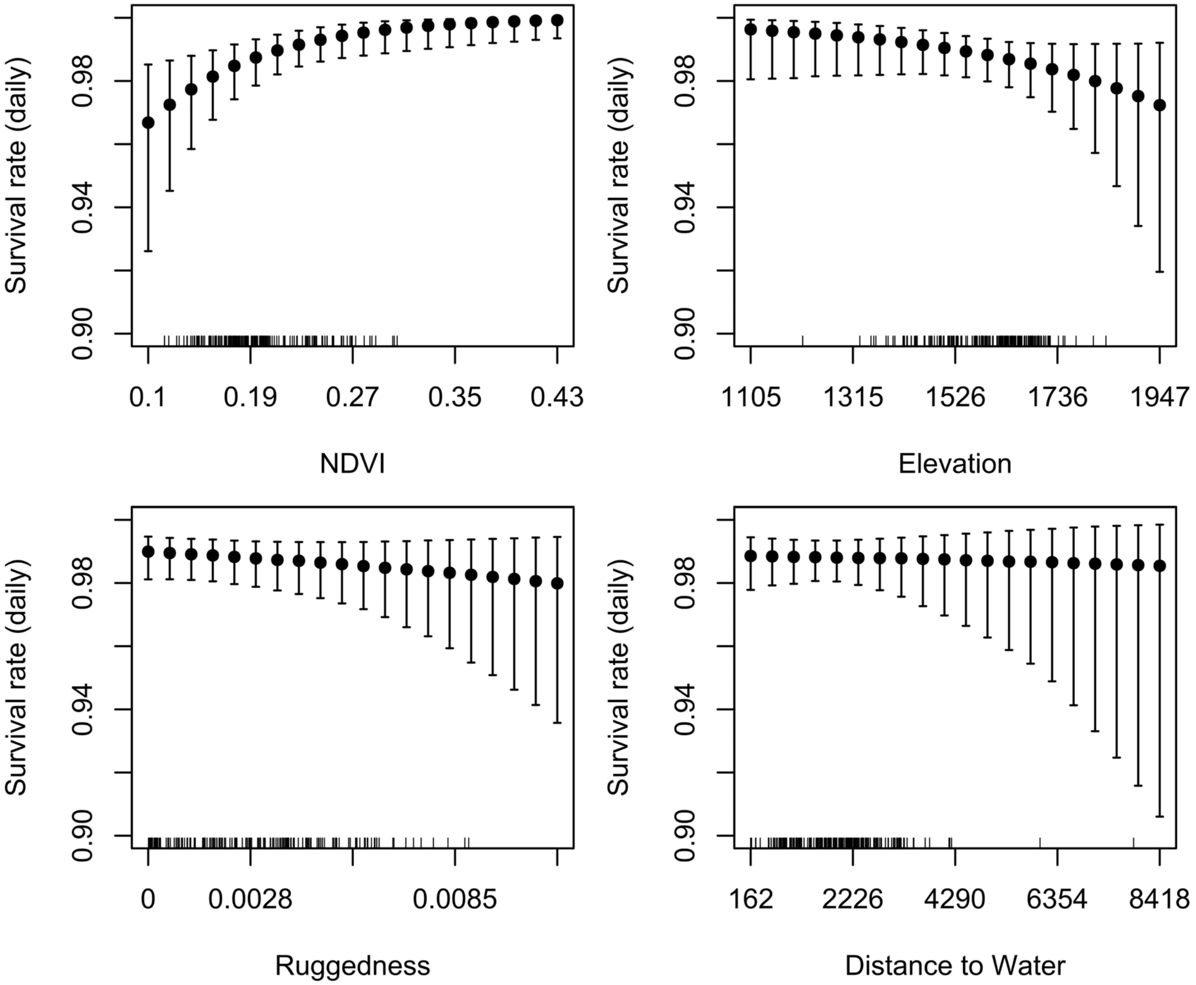

FIGURE 6 | Partial dependence plots illustrating the relationship between daily offspring survival rate and corresponding mean environmental attributes (extracted from 30 m rasters) of habitats used by maternal female mule deer while provisioning young (*n* = 67 fitted with GPS collars) on the Mojave National Preserve (2013–2016), determined on the basis of a Bayesian known-fate survival analysis. Models were fit using data from up to 120 days post-parturition; after 120 days offspring were considered to be successfully recruited. There was strong evidence for a positive effect of NDVI on offspring survival, weak evidence for a negative effect of elevation, and little to no evidence for effects of terrain ruggedness or distance to water.

Our prediction that females would prioritize resource acquisition (i.e., NDVI) over other landscape characteristics after loss of their offspring was mildly supported by our results. Indeed, females selected for greater values of NDVI in all reproductive timeframes. However, our GLMM models indicated stronger selection for areas of greater NDVI following mortality of juveniles compared to the period when females were provisioning young. Those females that lost young immediately shifted to strong selection for higher nutritional sources likely to recover body condition following peak lactation. The ability to recover from the reproductive effort may be crucial to rebuild resources for the upcoming reproductive period. Therefore, change in selection of resources between provisioning young and recovery to a higher nutritional state may enable females to restore lost energy reserves and be more likely to successfully rear offspring to recruitment the following year. Nevertheless, our observation of increased selection for high NDVI habitats after offspring loss was either a result of release from the need to protect offspring or an increased need to replenish somatic reserves after the nutritional demands of lactation to further future investment in reproduction the following year.

Selection for NDVI was strong and consistent before parturition and following the loss of young compared to when females were provisioning young. Further, individual heterogeneity was greater while females were provisioning. Caring for young imposes many constraints on individual behavior for maternal mule deer. They must obtain nutritional resources, access sources of free-standing water, and maintain vigilance and defense of young from predation. The suite of constraints imposed on maternal females may result in many short term tradeoffs in resource use that are difficult to detect at a longer temporal scale. Heterogeneity among individuals that we observed during the provisioning stage, however, may indicate that individuals exhibited varying behaviors based on their individual needs, differences in nutritional condition, and the requirements of their young. Indeed, we demonstrated that among the high heterogeneity for selection of NDVI during this timeframe, females that successfully utilized areas of greater NDVI were more successful at recruiting young into the population. Therefore, weak selection of resources at the population level toward greater values of NDVI during the provisioning stage may be indicative of a high variance of differing short-term behaviors exhibited by maternal females rather than an indication of nutritional tradeoffs to increase survival of young. Furthermore, the lack of high variance in selection of NDVI pre-parturition and following the loss of young may indicate that females are no longer making short term behavioral decisions toward caring for young and avoiding predators of young, and therefore shift to more risk prone strategies to directly provision themselves to recover from the nutritional constraints of late gestation and lactation.

There are very few studies investigating tradeoffs associated with selection of resources during different periods of the reproductive cycle, and how potentially differing needs of individuals affected overall selection of resources to enhance individual fitness (Barten et al., 2001; Long et al., 2009; Shuman et al., 2018). Long et al. (2009) investigated selection of resources and movements of female mule deer before and after parturition in a montane environment. Compared to our findings, they observed a varying relationship before and after estimated parturition in respect to the selection of distance to water sources. During pre-parturition, Long et al. (2009) reported that mule deer selected locations further from water compared to post-parturition. Nevertheless, they investigated movement patterns of mule deer without information on survival of young in a temperate forest region of northeastern Oregon, United States (Long et al., 2009). Mule deer are known to be more closely tied to water in arid environments than in cooler, wetter environments, but plants in the montane environment generally have lower preformed water content than many of the succulent plants in our study (Hervert and Krausman, 1986; McKee et al., 2015). Therefore, availability of water, both temporally and spatially, may differ too much to directly compare our results to Long et al. (2009). Barten et al. (2001) investigated habitat selection by caribou before and after parturition. They reported that caribou mothers switched habitat types when transitioning from pre-parturition to provisioning of young, whereas females that did not reproduce did not exhibit habitat switching. They also reported that females with young preferred high-elevation terrain, similar to our results and likely indicating selection of areas that balance nutrient acquisition and safety of young. Their study area also had more efficient, larger-bodied predators [e.g., wolves (*Canis lupus*) and brown bears (*Ursus arctos*)] than occur in our study area, which consist of coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and occasionally cougars (*Puma concolor*). Finally, Shuman et al. (2018) evaluated resource selection of female white-tailed deer (*Odocoileus virginianus*) during both pre-parturition and while provisioning young collectively. Their findings are counterintuitive in that females selected regions generally closer to nutritional sources (agriculture) to give birth while avoiding those same resources given availability within the region. Further, they conclude that females may be balancing both nutrition acquisition and care for young via predator avoidance, similar to the heterogeneity we observed during the provisioning time period. Although our investigation compared to Barten et al. (2001); Long et al. (2009), and Shuman et al. (2018) occurred in dramatically different ecosystems, the evidence that large, female herbivores select habitats to increase safety of young while acquiring resources for nutritional maintenance during the reproductive cycle is compelling (Bleich et al., 1997; Bowyer, 2004). Depending on habitat quality and resources available, ungulates must constantly balance reproductive output via protection and safety of young with maintenance of their own nutritional needs for future investment in offspring to maximize their reproductive fitness.

We utilized RF as a means of feature selection and to identify potential differences in resource selection across reproductive timeframes. Because the RF models did not account for autocorrelation of observations within individuals, these models were prone to overfitting and therefore we only interpreted broad resource selection patterns and we caution against interpreting any fine-scale patterns identified by these models (**Figure 2**). Performance of our RF models for resource selection, measured via a rigorous cross-validation whereby we sequentially withheld all data associated with individual deer from model-fitting, was generally poor (AUC of 0.65 for pre-parturition, 0.65 while provisioning young, and 0.63 following mortality of young). This unimpressive relationship, though better than random performance (Hernandez et al., 2006), likely resulted from high among-individual variation in patterns of resource selection, which we also detected via our GLMM modeling approach when modeled at the individual scale (3rd order selection; Johnson, 1980). Indeed, when we compare univariate relationships between our RF models (**Figure 2**) and our GLMM models (**Figure 4**) several key differences are apparent. Both modeling approaches suggest a strong and positive effect of NDVI on resource selection propensity by females across all reproductive stages and a general tendency to select habitat areas nearer to water and higher in elevation. However, the GLMM models suggest a general tendency to avoid rugged habitats whereas the RF models suggest (albeit weakly) a tendency toward selection of habitats with high or intermediate ruggedness during provisioning and after loss of offspring. In general, these differences could be due to the ability of RF models to capture non-linear relationships, the fact that RF models implicitly incorporate complex (potentially over fitted) interactions that can cloud the interpretation of partial dependence plots, or due simply to increased overfitting tendency of RF and other machine learning methods. Overall, our study underscores the benefits of coupling exploratory machine-learning methods (e.g., RF) with model-based inference (e.g., GLMM) to make inferences about selection of resources in wild populations (Shoemaker et al., 2018).

In our study and in future studies evaluating tradeoffs in resource selection around reproduction, a potential difficulty is the lower number of individuals that are included in the reproductive timeframe following the loss of an offspring. Indeed, we imposed a strict rule to only include females that had lost young within the first 30 days, because our objectives were to evaluate shifts in resource selection following a sudden shift in nutritional requirements (e.g., cessation of lactation). Energetic demands of lactation via quantity of milk produced to provide for dependent young is greatest during the first 30 days post-parturition (Sadlier, 1980; Gauthier and Barrette, 1985). Thus, by imposing a strict rule of including females that lost young in the first 30 days, we had greater potential to identify shifts in resource selection as a result in life-history stage changes. Indeed, loss of young is not a desired outcome, but understanding how maternal females shift from investment in current to future reproduction to maximize lifetime fitness is also important. Likely the only way to overcome the low sample size of this reproductive stage without an experiment to remove young from maternal females is to maximize the initial sample size of maternal females at capture. Nevertheless, we observed less variation among individuals after the loss of young so perhaps landscape scale movement and resource selection is more predictable and can be understood with lower sample sizes than understanding variation among individuals in selection of resources while provisioning young. Thus, the lower sample size during this timeframe may still result in reasonable inferences. Further research is needed toward examining tradeoffs surrounding reproductive stages in large herbivores. Additionally, monitoring individuals for greater than a single year to understand longitudinal shifts in reproductive strategies over time also would be beneficial (Festa-Bianchet et al., 2017). Our study was limited to 1 year of location data per unique individual. Incorporating multi-year movement data for individuals may shed additional light on how reproductive strategies shift temporally.

In many ecosystems, maternal females are faced with potentially conflicting decisions to maintain their nutritional condition, care for young, and recover from the costly life-history stages of reproduction. We show that females invest energy in selection of habitats that cater to the survivorship of their young, thereby investing in current reproduction. Further, the assumption that females may have to trade safety of offspring for nutritional requirements may not always be necessary. If females are able to select resources that allow for safety of offspring, usually a risk averse strategy, and also allow for females to obtain resources that support their nutritional needs (usually a risk prone strategy), they may not be forced to make those reproductive tradeoffs. Our study area appears to have areas where safety of young and availability of nutritional resources are not mutually exclusive. Indeed, we observed that females selected areas of higher NDVI, indicating green forage, while caring for and provisioning young, likely a strategy to increase individual fitness. However, there was a large amount of individual variation toward the selection of NDVI while provisioning young. We show that among this variation, those females that select greater levels of NDVI were more successful at recruiting young into the population. Further, after a transition to a non-provisioning state (i.e., post-juvenile mortality), females still shifted selection to areas with even higher quality forage to recover from the rearing of young, and likely to begin replenishing energetic stores necessary for reproduction the next year. Expanding our knowledge of factors that influence behavioral decisions during reproduction will prove to be of high importance moving forward. As environments fluctuate and landscape dynamics shift, understanding strategies of reproductive investment at the individual level that animals make to increase fitness, and then how those decisions relate to population performance, will further our understanding of large mammal ecology.

DATA AVAILABILITY STATEMENT

Code and data for all analyses presented in this paper are available on GitHub: https://github.com/kevintshoemaker/desert_deer_rsf. The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno Protocol # 00538 and were in keeping with guidelines established by the American Society of Mammologists for research on wild mammals (Sikes, 2016).

AUTHOR CONTRIBUTIONS

LH was a graduate student and KMS was the graduate advisor on this project. KMS and VB obtained the funding for the project and designed the study with input from ND. KTS and LH performed the statistical analyses with input from KMS. All authors contributed to writing the manuscript.

FUNDING

We appreciate the financial and technical support provided by the Safari Club International Foundation (Grant # 1321-153-523F), the Golden Gate Chapter of Safari Club International (Grant #1321-153-52VY), the California Department of Fish and Wildlife (in-kind support), National Park Service (1320-153-52XV), and the Boone and Crockett Club. The research presented here was supported by a Hatch Grant from the Agricultural Experiment Station at the University of Nevada, Reno.

ACKNOWLEDGMENTS

We received invaluable assistance with adult animal capture and handling from B. Gonzalez, B. Pierce, L. Konde, J. Villipique, A. Adams, M. Blum, J. Merrell, D. Huggins, N. Jackson, B. Regan, T. Allen, and all others who helped with data collection for this manuscript. We graciously thank J. Sedinger, B. Sedinger, and A. Foley for their guidance in improving our manuscript, and A. Bush for his exhaustive help with field methodologies and collecting some of the data used herein. This is Professional Paper 122 from the Eastern Sierra Center for Applied Population Ecology.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00163/full#supplementary-material

FIGURE S1 | Distribution of buffered annual home range sizes used for quantifying availability across reproductive time frames for 68 (pre-parturition), 67 (provisioning young), and 20 (post juvenile mortality), female mule deer on the Mojave National Preserve, California, United States from 2013–2016. Home ranges were estimated with 99.9% isopleths from a kernel density estimate (KDE) and then buffered by mean step length (200 m) to account for available space on the outer edge of the home range.

FIGURE S2 | Representative results from our 'likelihood convergence' procedure for ensuring that GLMM models were supplied with a sufficient density of background points to capture the full range of environmental variation. Specifically, we fitted down-weighted Poisson regression (DWPR) models (fitted as a standard GLM in R using the full set of continuous and categorical covariates) to a wide range of alternative background point densities for each individual, and identified the minimum threshold beyond which model performance become largely independent of the specific set of background points sampled. Using this technique, we found that 500 random background points per km^2 was sufficient for our purposes.

REFERENCES

Aarts, G., Fieberg, J. Brasseur, S., and Matthiopoulos, J. (2013). Quantifying the effect of habitat availability on species distributions. *J. Animal Ecol.* 82, 1135–1145. doi: 10.1111/1365-2656.12061

Aldridge, C. L., and Boyce, M. S. (2007). Linking occurrence and fitness to persistence: habitat—based approach for endangered greater sage—grouse. *Ecol. Appl.* 17, 508–526. doi: 10.1890/05-1871

Altendorf, K. B., Laundré, J. W., López González, C. A., and Brown, J. S. (2001). Assessing effects of predation risk on foraging behavior of mule deer. *J. Mammal.* 82, 430–439. doi: 10.1093/jmammal/82.2.430

Barboza, P., Parker, K., and Hume, I. (2009). *Integrative Wildlife Nutrition*. Berlin: Springer.

Barten, N. L., Bowyer, R. T., and Jenkins, K. J. (2001). Habitat use by female caribou: tradeoffs associated with parturition. *J. Wildl. Manag.* 65, 77–92.

Bender, L. C., Hoenes, B. D., and Rodden, C. L. (2012). Factors influencing survival of desert mule deer in the greater San Andres Mountains, New Mexico. *Hum. Wildl. Interact.* 6, 245–260.

Beyer, H. L. (2015). *Geospatial Modelling Environment (Version 0.7.4.0). (Software)*. Available online at: http://www.spatialecology.com/gme (accessed March 3, 2017).

Bishop, C. J., Anderson, C. R., Walsh, D. P., Bergman, E. J., Kuechle, P., and Roth, J. (2011). Effectiveness of a redesigned vaginal implant transmitter in mule deer. *J. Wildl. Manag.* 75, 1797–1806. doi: 10.1002/jwmg.229

Bishop, C. J., Freddy, D. J., White, G. C., Watkins, B. E., Stephenson, T. R., and Wolfe, L. L. (2007). Using vaginal implant transmitters to aid in capture of mule deer neonates. *J. Wildl. Manag.* 71, 945–954. doi: 10.2193/2006-123

Bishop, C. J., White, G. C., Freddy, D. J., Watkins, B. E., and Stephenson, T. R. (2009). Effect of enhanced nutrition on mule deer population rate of change. *Wildl. Monogr.* 172, 1–28. doi: 10.2193/2008-107

Bleich, V. C., Bowyer, R. T., and Wehausen, J. D. (1997). Sexual segregation in mountain sheep: resources or predation? *Wildl. Monogr.* 97, 1–50.

Bleich, V. C., Marshal, J. P., and Andrew, N. G. (2010). Habitat use by a desert ungulate: predicting effects of water availability on mountain sheep. *J. Arid Environ.* 74, 638–645. doi: 10.1016/j.jaridenv.2009.10.019

Bonte, D., and Dahirel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos* 126, 472–479. doi: 10.1111/oik.03801

Bose, S., Forrester, T. D., Cassady, D. S., and Wittmer, H. U. (2018). Effect of activity states on habitat selection by black-tailed deer. *J. Wildlife Manag.* 82, 1711–1724. doi: 10.1002/jwmg.21529

Bowyer, R. T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *J. Mammal.* 85, 1039–1052. doi: 10.1644/bbl-002.1

Breiman, L. (2001). Random forests. *Mach. Learn.* 45, 5–32.

Carstensen, M., DelGiudice, G. D., and Sampson, B. A. (2003). Using doe behavior and vaginal-implant transmitters to capture neonate white-tailed deer in north-central Minnesota. *Wild. Soc. Bull.* 31, 634–641.

Climate Engine. (2017). *Desert Research Institute and University of Idaho*. Available online at: http://climateengine.org (accessed March 3, 2017)

Clutton-Brock, T., and Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* 25, 562–573. doi: 10.1016/j.tree.2010.08.002

Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1983). The costs of reproduction to red deer hinds. *J. Anim. Ecol.* 52, 367–383.

Creech, T. G., Epps, C. W., Monello, R. J., and Wehausen, J. D. (2016). Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI. *J. Arid Environ.* 127, 160–170. doi: 10.1016/j.jaridenv.2015.11.011

Cristescu, B., Bose, S., Elbroch, L. M., Allen, M. L., and Wittmer, H. U. (2019). Habitat selection when killing primary versus alternative prey species supports prey specialisation in an apex predator. *J. Zool.* 309, 259–268. doi: 10.1111/jzo.12718

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., et al. (2007). Random forests for classification in ecology. *Ecology* 88, 2783–2792. doi: 10.1890/07-0539.1

De'ath, G., and Fabricius, K. E. (2000). Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178–3192. doi: 10.1890/0012-9658(2000)081[3178:cartap]2.0.co;2

DeCesare, N. J., Hebblewhite, M., Lukacs, P. M., and Hervieux, D. (2016). Evaluating sources of censoring and truncation in telemetry—based survival data. *J. Wildl. Manag.* 80, 138–148. doi: 10.1002/jwmg.991

Dzialak, M. R., Harju, S. M., Osborn, R. G., Wondzell, J. J., Hayden-Wing, L. D., Winstead, J. B., et al. (2011). Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PLoS One* 6:14597.

Esparza-Carlos, J. P., Laundré, J. W., Hernández, L., and Íñiguez-Dávalos, L. I. (2016). Apprehension affecting foraging patterns and landscape use of mule deer in arid environments. *Mammal. Biol.* 81, 543–550. doi: 10.1016/j.mambio.2016.07.006

Festa-Bianchet, M., Douhard, M., Gaillard, J. M., and Pelletier, F. (2017). Success and challenges of long-term field studies of marked ungulates. *J. Mammalo.* 98, 612–620. doi: 10.1093/jmammal/gyw227

Forrester, T. D., Casady, D. S., and Wittmer, H. U. (2015). Home sweet home: fitness consequences of site familiarity in female black-tailed deer. *Behav. Ecol. Sociobiol.* 69, 603–612. doi: 10.1007/s00265-014-1871-z

Gaillard, J. M., Festa-Bianchet, M., and Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* 13, 58–63. doi: 10.1016/s0169-5347(97)01237-8

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Ann. Rev. Ecol. Syst.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gauthier, D., and Barrette, C. (1985). Suckling and weaning in captive white-tailed and fallow deer. *Behaviour* 94, 128–149. doi: 10.1163/156853985x00307

Gehr, B., Bonnot, N. C., Heurich, M., Cagnacci, F., Ciuti, S., Hewison, A. M., et al. (2020). Stay home, stay safe—Site familiarity reduces predation risk in a large herbivore in two contrasting study sites. *J. Anim. Ecol.* . doi: 10.1111/1365-2656.13202

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898. doi: 10.1111/j.1365-2656.2006.01106.x

Hamel, S., Côté, S. D., Gaillard, J. M., and Festa−Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: high−quality females always do better. *J. Anim. Ecol.* 78, 143–151. doi: 10.1111/j.1365-2656.2008.01459.x

Haskell, S. P., Ballard, W. B., Butler, D. A., Tatman, N. M., Wallace, M. C., Kochanny, C. O., et al. (2007). Observations on capturing and aging deer fawns. *J. Mammal.* 88, 1482–1487. doi: 10.1644/07-mamm-a-004r.1

Haugen, A. O., and Speake, D. W. (1958). Determining age of young fawn white-tailed deer. *J. Wildl. Manag.* 22, 319–321.

Hebblewhite, M., and Merrill, E. H. (2009). Trade−offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90, 3445–3454. doi: 10.1890/08-2090.1

Heffelfinger, L. J., Stewart, K. M., Bush, A. P., Sedinger, J. S., Darby, N. W., and Bleich, V. C. (2018). Timing of precipitation in arid environments: effects on population performance of a large herbivore. *Ecol. Evol.* 8, 3354–3366. doi: 10.1002/ece3.3718

Hernandez, P. A., Graham, C. H., Master, L. L., and Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785. doi: 10.1111/j.0906-7590.2006.04700.x

Hervert, J. J., and Krausman, P. R. (1986). Desert mule deer use of water developments in Arizona. *J. Wildl. Manag.* 50, 670–676.

Hurley, M. A., Unsworth, J. W., Zager, P., Hebblewhite, M., Garton, E. O., Montgomery, D. M., et al. (2011). Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildl. Monogr.* 178, 1–33. doi: 10.1002/wmon.4

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. doi: 10.2307/1937156

Kawecki, T. J., and Stearns, S. C. (1993). The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. *Evol. Ecol.* 7, 155–174. doi: 10.1007/bf01239386

Kellner, K. (2019). *jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses. R Package Version 1.5.1.* Available online at: https://CRAN.R-project.org/package=jagsUI (accessed July 30, 2019).

Krausman, P. R., Hervert, J. J., and Ordway, L. L. (1985). Capturing deer and mountain sheep with a net-gun. *Wildl. Soc. Bull.* 13, 71–73.

Kuhn, M. (2019). *caret: Classification and Regression Training. R Package Version 6.0-82.*. Available online at: https://CRAN.R-project.org/package=caret (accessed April 22, 2020).

Landfire. (2014). *Existing Vegetation Type Layer, LANDFIRE 1.1.0, U.S. Department of the Interior, Geological Survey*. Available online at: https://www.landfire.gov/vegetation.php (accessed February 28, 2017)

Lingle, S., Pellis, S. M., and Wilson, W. F. (2005). Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white−tailed deer fawns early in life. *J. Anim. Ecol.* 74, 1140–1149. doi: 10.1111/j.1365-2656.2005.01014.x

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., and Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol. Monogr.* 84, 513–532. doi: 10.1890/13-1273.1

Long, R. A., Kie, J. G., Bowyer, R. T., and Hurley, M. A. (2009). Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. *Wildl. Biol.* 15, 288–298. doi: 10.2981/09-003

Manly, B. F. J., McDonald, L., Thomas, D., McDonald, T. L., and Erickson, W. P. (2007). *Resource Selection By Animals: Statistical Design And Analysis For Field Studies*. Berlin: Springer Science & Business Media.

Marshal, J. P., Krausman, P. R., and Bleich, V. C. (2005). Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. *Rangel. Ecol. Manag.* 58, 360–365. doi: 10.2111/1551-5028(2005)058[0360:rtafda]2.0.co;2

McKee, C. J., Stewart, K. M., Sedinger, J. S., Bush, A. P., Darby, N. W., Hughson, D. L., et al. (2015). Spatial distributions and resource selection by mule deer in an arid environment: Responses to provision of water. *J. Arid Environ.* 22, 76–84. doi: 10.1016/j.jaridenv.2015.06.008

McLoughlin, P. D., Boyce, M. S., Coulson, T., and Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proc. R. Soc. B Biol. Sci.* 273, 1449–1454. doi: 10.1098/rspb.2006.3486

Moen, R. A., Pastor, J., and Cohen, Y. (1997). Accuracy of GPS telemetry collar locations with differential correction. *J. Wildl. Manag.* 61, 530–539.

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2014). Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildl. Monogr.* 186, 1–62. doi: 10.1002/wmon.1011

Muff, S., Signer, J., and Fieberg, J. (2019). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *J. Anim. Ecol.* 19, 1–13.

National Park Service (2017). *Nature and Science of Mojave National Preserve*. Available online at: <http://www.nps.gov/moja/naturescience/index.htm> (accessed March 3, 2017)

Oftedal, O. T. (2000). Use of maternal reserves as a lactation strategy in large mammals. *Proc. Nutr. Soc.* 59, 99–106. doi: 10.1017/s0029665100000124

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., and Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20, 503–510. doi: 10.1016/j.tree.2005.05.011

Plummer, M. (2003). "JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling," in *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vol. 124, Vienna, 10.

Promislow, D. E., and Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life−history variation among mammals. *J. Zool.* 220, 417–437. doi: 10.1111/j.1469-7998.1990.tb04316.x

Renner, I. W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S. J., et al. (2015). Point process models for presence−only analysis. *Methods Ecol. Evol.* 6, 366–379. doi: 10.1111/2041-210x.12352

Ricklefs, R. E. (1994). Life history invariants: some explorations of symmetry in evolutionary biology. *Science* 264, 116–118.

Ricklefs, R. E., and Wikelski, M. (2002). The physiology/life-history nexus. *Trends Ecol. Evol.* 17, 462–468. doi: 10.1016/s0169-5347(02)02578-8

Sadlier, R. (1980). Milk-yield of black-tailed deer. *J. Wildl. Manag.* 44, 472–478.

Sappington, J. M., Longshore, K. M., and Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in theMojave Desert. *J. Wildl. Manag.* 71, 1419–1426. doi: 10.2193/2005-723

Scornavacca, D., Lovari, S., Cotza, A., Bernardini, S., Brunetti, C., Pietrocini, V., et al. (2016). Pasture quality affects juvenile survival through reduced maternal care in a mountain−dwelling ungulate. *Ethology* 122, 807–817. doi: 10.1111/eth.12530

Shoemaker, K. T., Heffelfinger, L. J., Jackson, N. J., Blum, M. E., Wasley, T., and Stewart, K. M. (2018). A machine-learning approach for extending classical wildlife resource selection analyses. *Ecol. Evol.* 8, 3556–3569. doi: 10.1002/ece3.3936

Shuman, R. M., Cherry, M. J., Dutoit, E. A., Simoneaux, T. N., Miller, K. V., and Chamberlain, M. J. (2018). Resource selection by parturient and postparturient white-tailed deer and their fawns. *J. South. Assoc. Fish Wildl. Agen.* 5, 78–84.

Sikes, R. S. (2016). Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688. doi: 10.1093/jmammal/gyw078

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Funct. Ecol.* 3, 259–268.

Stephenson, T. R., Bleich, V. C., Pierce, B. M., and Mulcahy, G. P. (2002). Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. *Wildl. Soc. Bull.* 30, 557–564.

Stephenson, T. R., Ward Testa, J., Adams, G. P., Garth Sasser, R., Schwartz, C. C., and Hundertmark, K. J. (1995). Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. *Alces* 31, 167–172.

Stewart, K. M., Bowyer, R. T., Kie, J. G., Cimon, N. J., and Johnson, B. K. (2002). Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J. Mammalo.* 83, 229–244. doi: 10.1644/1545-1542(2002)083<0229:tdoemd>2.0.co;2

Therrien, J. F., Côté, S. D., Festa-Bianchet, M., and Ouellet, J. P. (2008). Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction. *Anim. Behav.* 75, 235–243. doi: 10.1016/j.anbehav.2007.04.030

Thomas, K., Keeler-Wolf, T., and Stine, P. (2004). *Mojave Desert Ecosystem Program: Central Mojave Vegetation Database. USGS Final Report for Mojave Desert Ecosystem Program*. Sacramento, CA: USGS.

Van Noordwijk, A. J., and de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128, 137–142. doi: 10.1086/284547

Warton, D. I., and Shepherd, L. C. (2010). Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. *Ann. Appl. Stat.* 4, 1383–1402. doi: 10.1214/10-aoas331

White, K. S., and Berger, J. (2001). Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canad. J. Zool.* 79, 2055–2062. doi: 10.1139/z01-170

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100, 687–690. doi: 10.1086/282461

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 24 June 2020
doi: 10.3389/fevo.2020.00154

Untangling Effects of Human Disturbance and Natural Factors on Mortality Risk of Migratory Caribou

Sabrina Plante[1,2]*, Christian Dussault[1,3], Julien H. Richard[1,2], Mathieu Garel[4] and Steeve D. Côté[1,2]

[1] Caribou Ungava, Département de Biologie, Université Laval, Québec, QC, Canada, [2] Département de Biologie, Centre d'Études Nordiques, Université Laval, Québec, QC, Canada, [3] Ministère des Forêts, de la Faune et des Parcs, Direction de l'Expertise sur la Faune Terrestre, l'Herpétofaune et l'Avifaune, Québec, QC, Canada, [4] ONCFS – Unité Ongulés Sauvages, Gières, France

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Katherine Parker,
University of Northern British
Columbia, Canada
Robert Weladji,
Concordia University, Canada

***Correspondence:**
Sabrina Plante
Sabrina.plante.6@ulaval.ca

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *19 December 2019*
Accepted: *05 May 2020*
Published: *24 June 2020*

Citation:
Plante S, Dussault C, Richard JH,
Garel M and Côté SD (2020)
Untangling Effects of Human
Disturbance and Natural Factors on
Mortality Risk of Migratory Caribou.
Front. Ecol. Evol. 8:154.
doi: 10.3389/fevo.2020.00154

Human disturbances are rapidly increasing in northern and Arctic regions, raising concerns about the recovery and persistence of declining caribou (*Rangifer tarandus*) populations. Yet, the consequences of behavioral responses toward human disturbances on vital rates rarely have been investigated. Herein, we assessed the cumulative and instantaneous effects of human disturbances (roads, human settlements, mines and mining exploration) at different temporal scales on the mortality risk of 254 GPS- collared migratory caribou monitored in two herds, the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds, in northern Québec and Labrador, Canada. We also assessed the relative importance of human disturbances on caribou mortality risk compared with non-anthropogenic factors, including habitat use by caribou, predation risk by gray wolves (*Canis lupus*), and local weather conditions. Human disturbances alone, exclusive of hunting, had a limited impact on mortality risk of caribou. Repeated exposure to disturbances did not have detectable effects on mortality risk during the early life period (1—7 years old), but more abundant precipitation (RFH) or the use of areas with a higher predation risk (RGH) did so. At the seasonal scale, non-anthropogenic factors, particularly the use of highly selected habitat by caribou and air temperature, had a greater effect than anthropogenic factors on the mortality risk in the RFH. Caribou of the RFH using more frequently higlhy selected habitats decreased their chance of mortality during winter, whereas individuals using warmer areas during summer faced a higher risk of mortality. At the daily scale, we observed that anthropogenic and non-anthropogenic factors generally had either no effect on the daily risk of mortality, or their effects were undistinguishable from the effect of latitude, with which they were highly correlated. The only exception was for the RFH in winter, for which the daily risk of mortality increased 10 folds for each 10-km increment closer to industrial disturbances. Although the impacts of human disturbances on caribou survival were limited to specific regions and areas, we nevertheless detected a negative effect on survival on the RFH, even at the currently low level of human development. Our study highlights the importance of assessing effects of human disturbances at various spatiotemporal scales, and of considering the relative influence of other non-anthropogenic factors to fully understand drives of wildlife populations.

Keywords: habitat use, human disturbance, migratory caribou, mortality risk, predation risk, weather conditions

INTRODUCTION

In the last decades, the human footprint has increased rapidly, including >70% of ecoregions around the world (Venter et al., 2016). The increased human pressure on ecosystems has been identified as the main cause of species extinction and biodiversity loss (Brooks et al., 2002; Davies et al., 2006; Fahrig and Rytwinski, 2009). Effects of human disturbances on wildlife vary from short-term modifications in behavior, activity budgets and nutrition (Dussault et al., 2007; Benhaiem et al., 2008; Marchand et al., 2014), to processes occurring at larger spatiotemporal scales, such as resources and range use (Moreau et al., 2012), distribution (Shackelford et al., 2018), population dynamics (Sorensen et al., 2008), and species interactions (Courbin et al., 2009).

Quantifying impacts of human disturbances on vital rates of wildlife is of particular interest in ecology because it can help determine if and how individual responses to disturbances translate into consequences at the population level. Human disturbances can directly effect survival, including mortality caused by collision with vehicles (Forman and Alexander, 1998; Lodé, 2000) or when species vulnerability to hunting increases because of human development (Lebel et al., 2012; Plante et al., 2017). Most effects of disturbance, however, are not directly lethal for wildlife, but include energetic and lost-opportunity costs (Frid and Dill, 2002). These costs can accumulate over time and space, and ultimately translate into long-term consequences on individual performance and vital rates (Bradshaw et al., 1998; Johnson and St-Laurent, 2011). Over time, the consequences of these indirect effects on population dynamics and trophic interactions can exceed those from direct sources of mortality (Creel and Christianson, 2008). Nevertheless, many studies still focus on single development projects and short-term behavioral responses toward disturbances, without further investigating the potential cumulative effects over broad spatiotemporal scales, and perhaps more importantly, without considering the consequences on vital rates (Weladji and Forbes, 2002; Tablado and Jenni, 2017).

Multiple natural factors may also act simultaneously with human disturbances to further effect vital rates in wildlife populations (Yamasaki et al., 2008; Tablado and Jenni, 2017; Ramey et al., 2018). Consequently, the study of relationships between habitat use and animal performance is an effective tool to assess the relative importance of multiple limiting factors acting simultaneously (Gaillard et al., 2010; DeCesare et al., 2014; Uboni et al., 2017). Patterns of habitat use often are assumed to represent an aggregated response to multiple factors acting at different spatiotemporal scales, and should reflect priorities or trade-offs among competing needs (Senft et al., 1987; Rettie and Messier, 2000). Linking habitat use to vital rates may thus help to reveal the relative importance of multiple natural and anthropogenic factors for wildlife populations (McLoughlin et al., 2010).

Animals may not be able to minimize the effect of one or multiple limiting factors without compromising their performance to face other factors. In risky environments for example, individuals can fail to reduce predation risk sufficiently through habitat use (DeCesare et al., 2014). Alteration of the environment also can create discrepancies between perceived and true habitat suitability (Schlaepfer et al., 2002). If poor or risky habitats are used or become attractive to individuals despite reduced quality, those habitats become ecological traps where individuals are attracted despite their reduced chance of survival (Battin, 2004). Such non-ideal or maladaptive behaviors have mostly been reported in rapidly changing environments (e.g., human-altered landscapes) where modifications of the habitat occur at a much faster rate than the potential adaptation rate of animals (Battin, 2004; Robertson and Hutto, 2006).

In past decades, northern and Arctic regions have witnessed a drastic increase in human disturbances, and serious concerns have been raised regarding the ability of individuals to adapt, or populations to persist in these newly modified landscapes (United Nation Environmental Programme [UNEP], 2001). Caribou and reindeer (*Rangifer tarandus*; hereafter caribou) are at the very heart of these considerations because they represent a key species both ecologically and culturally (Bergerud et al., 2008). Although caribou populations have fluctuated in the past, the current decline of most caribou populations worldwide indicates that large-scale modifications induced by the development of human activities may contribute to this situation (Vors and Boyce, 2009; Festa-Bianchet et al., 2011). Caribou could be particularly sensitive to human disturbances because they occupy broad ranges and have a limited intrinsic capacity of population growth because of their low productivity (Cardillo et al., 2005; Fahrig and Rytwinski, 2009). Numerous studies have also reported strong behavioral responses of caribou toward human disturbances (Vistnes and Nellemann, 2008), such as the avoidance of infrastructures over several kilometers (e.g., Boulanger et al., 2012; Johnson and Russell, 2014). Until recently, human development has been relatively limited in the ranges of the migratory tundra caribou compared with what has been experienced by boreal caribou populations. Yet, very few studies have assessed effects of human disturbance on vital rates of migratory caribou (i.e., reproductive rate only; Nellemann et al., 2003; Cameron et al., 2005). As human development continues in the north, it is crucial to assess the impacts of human disturbances on the vital rates and demography of migratory tundra caribou before levels of development occur that would impede population persistence and recovery (Festa-Bianchet et al., 2011).

To assess effects of human disturbances on the survival of wide-ranging animals such as migratory caribou, we need to consider natural limiting factors acting independently or simultaneously with human disturbances. Climate, predation, parasites, insect harassment, and diseases are natural factors known to reduce survival that may also ultimately contribute to the decline of caribou populations (Festa-Bianchet et al., 2011; Mallory and Boyce, 2018). Although warmer temperatures during summer have been positively associated with the growth of some caribou herds (Mallory and Boyce, 2018), those temperatures also can increase insect harassment, parasite load, and heat stress (Soppela et al., 1986; Weladji et al., 2003), all entailing physiological costs and energy expenditures that deteriorate body condition (Toupin et al., 1996; Pachkowski et al., 2013). Warmer temperatures can advance melt-down and delay freeze-up of water bodies, which could dramatically increase movement costs for caribou (Leblond et al., 2016), or lead to death when caribou try to cross over thin ice (Poole et al., 2010). Warmer temperatures during winter can also increase the frequency and intensity of rain-on-snow events, which limit access to food resources and may lead to major mortality events (Forbes et al., 2016; Berger et al., 2018). Climate warming is also increasing the frequency and intensity of fires in the tundra and boreal forest, thus shrinking the available habitat for caribou (Rupp et al., 2006; Joly et al., 2011; Skatter et al., 2017).

Although caribou have cohabited with natural predators for centuries and have evolved efficient antipredator tactics (e.g., long-distance migrations; Seip, 1991; Bergerud et al., 2008), human disturbances could modify predator-prey relationships and further increase the impact of predation (Latham et al., 2011; Dussault et al., 2012; Newton et al., 2017; DeMars and Boutin, 2018). For example, linear infrastructures can facilitate gray wolf (*Canis lupus*) movements and access to certain areas of caribou ranges, which further increases effects of predation on population dynamics (James and Stuart-Smith, 2000; DeMars and Boutin, 2018).

Our overarching hypothesis was that effects of human disturbances on the mortality risk of eastern migratory caribou as well as the relative importance of such disturbances compared with natural factors known to affect survival, including habitat use by caribou, predation risk by wolves and local weather conditions (i.e air temperature and precipitation) were driving caribou abundance. We focused on two caribou herds located in northern Québec and Labrador, Canada, the Rivière-aux-Feuilles (RFH) and the Rivière-George herds (RGH), between 2009 and 2016. Over the last decades, these two herds, which are part of the eastern migratory caribou designatable unit, have declined to a point where they have been recommended to be listed as Endangered in COSEWIC (2017). Simultaneously with these declines, the region has experienced a moderate increase in human activity, owing mainly to an expansion of the mining (MRNF, 2012). Previous research showed that caribou of these herds avoided human disturbances over distances up to 23 km, which can cause substantial habitat loss within their range (Plante et al., 2018). Despite this avoidance, caribou remain more vulnerable to harvest near human infrastructures (Plante et al., 2017). Thus, there is a need to better understand and quantify the interactions between human disturbances and the mortality risk of caribou.

We assessed the cumulative and instantaneous effects of human disturbances on mortality risk in the two caribou herds by considering three temporal scales: early life, seasonal, and daily scales. We first evaluated whether repeated exposure to disturbances increased mortality risk during the early period of caribou life (1−7 years old) and at the seasonal scale (winter and summer). We also evaluated whether daily exposure to disturbances increased daily mortality risk of individuals. Secondly, we used a conceptual framework inspired by DeCesare et al. (2014) to compare the relative importance of human disturbances and non-anthropogenic factors on mortality risk of caribou. We first considered a habitat use hypothesis, where mortality risk of caribou is mostly affected by the proportion of time spent in highly selected habitats (H1; **Figure 1A**). We expected that caribou spending less time in habitats that are strongly selected at the population level would face a higher risk of mortality because of the potentially lower quality of these habitats or to the marginality of their behavior (e.g., bolder personalities), which could increase predation risk (Lesmerises et al., 2019). Alternatively, the use of highly selected habitats could be a "non-ideal" behavior, being inefficient at reducing the mortality risk associated with one or more factors. We thus considered the two alternative hypotheses where, regardless of the use of highly selected habitats, most variation in the mortality risk would be explained by exposure to anthropogenic or other non-anthropogenic factors. Accordingly, we considered the disturbance risk and predation risk hypotheses, where individuals more exposed to disturbances (H2; **Figure 1B**), or predation risk (H3; **Figure 1C**), respectively, have a higher mortality risk. We also considered a weather hypothesis, where adverse temperature and precipitation conditions encountered by individuals during winter (e.g., heavy snow) and summer (e.g., warm temperature) increase mortality risk (H4; **Figure 1D**). We also tested the hypothesis of additive effects of habitat use and other anthropogenic or natural factors on survival (H5; **Figure 1E**). Finally, we considered the hypothesis of maladaptive habitat use (Battin, 2004; Robertson and Hutto, 2006), where spending more time in highly selected habitats could increase exposure to disturbances or predation risk and consequently reduce survival (H6; **Figure 1F**).

MATERIALS AND METHODS

Study Area

The RFH and RGH have both experienced steep declines in the last decades. The RFH has peaked at >500,000 individuals around 2001 (Couturier et al., 2004), and decreased to an estimated population size of 199,000 (CI 90% = 183,080−214,920) in Taillon et al. (2016). The RGH has experienced a more drastic decline, with an estimated population peak at 823,375 (CI 90% = 721,375−925,375) individuals around 1993 (Couturier et al., 2004), 74,000 (CI 90%=60,680-87,320) in 2010, and an estimated population of <8,900 individuals (CI 90% = 8,232−9,568) in MFFP and NLFLR (2016, unpubl. data).

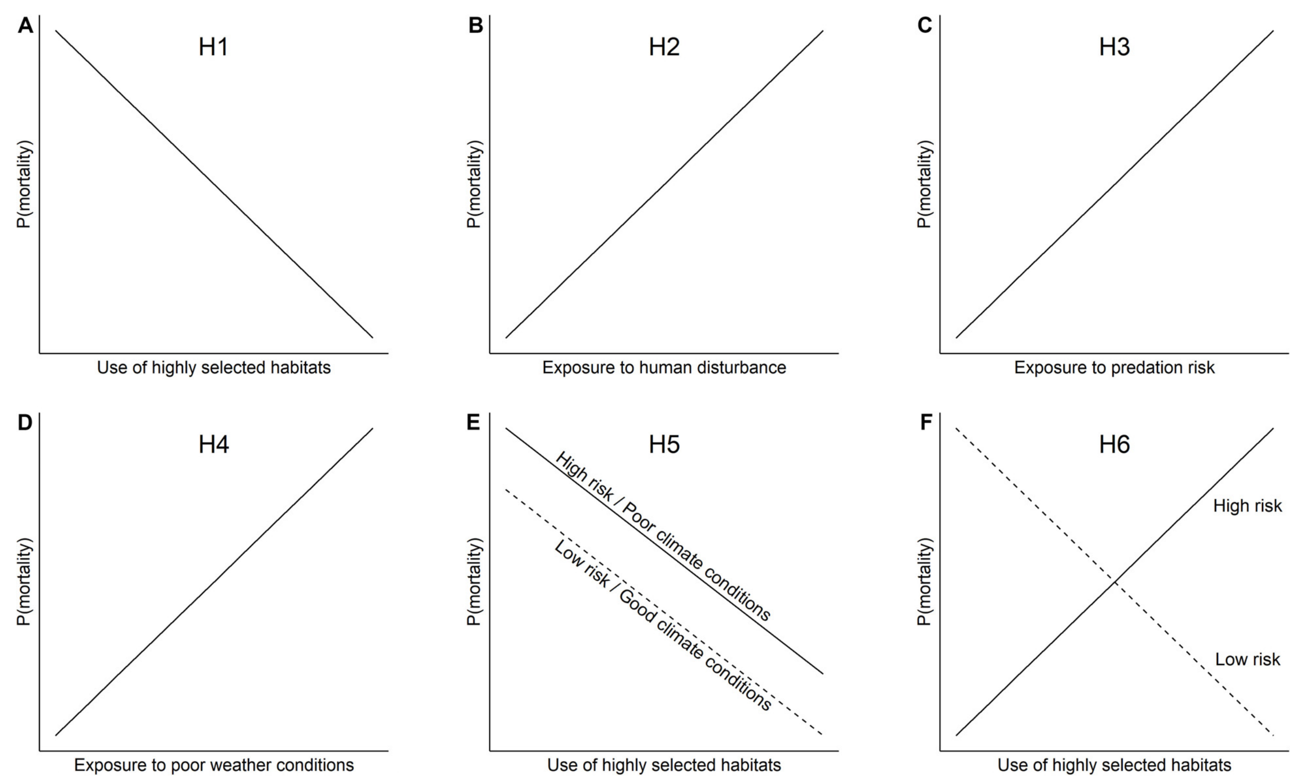

FIGURE 1 | Hypotheses and predictions tested to explain variations in the risk of mortality of eastern migratory caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George herds (RGH), northern Québec and Labrador, Canada (2009–2016). Competing hypotheses H1 through H6 (as given in the text) included **(A)** the use of highly selected habitats (% of individual locations in highly selected habitats), **(B)** exposure to disturbance risk, **(C)** exposure to predation risk, **(D)** exposure to poor weather conditions, **(E)** additive effects, and **(F)** maladaptive habitat use.

Numerous factors are suspected to have contributed to these declines, including resource limitation and density-dependent effects, climate, hunting and predation (Côté et al., 2010).

The RFH and RGH range over more than 1,000,000 km^2 north of the 51st parallel in northern Québec and Labrador, mostly within the Nunavik and Nunatsiavut regions of Canada (**Figure 2**). The area is characterized by subarctic and arctic climates, with short and cool summers (1981−2010; 9.7°C on average for the warmest trimesters) followed by long and cold winters (−19.5°C on average for the coldest trimesters; Berteaux et al., 2018). Precipitation averages 898 mm·year^{-1}, mostly falling as snow between October and March. The RFH and RGH ranges are characterized by numerous lakes and rolling hills with more rugged terrain in the northeast portion of the RGH range.

In April, caribou of the RFH undertake a northward migration from their winter range, located in the boreal-taiga forests, to their calving ground and summer range, in the Arctic tundra (mean distance [2000−2011] = 615 km; Le Corre et al., 2017). Vegetation on the RFH summer range is mainly composed of shrubs (*Betula* sp. and *Salix* sp.), grasses, herbaceous plants and lichens (Latifovic et al., 2017). In autumn, the RFH migrates south and returns to its winter range in the taiga forest, which is dominated by black spruce (*Picea mariana*) and tamarack (*Larix larcina*) interspersed with lakes and open areas covered by shrubs and lichens. Caribou of the RGH used to undertake similar but shorter migrations between summer and winter ranges (mean distance from 2000 to2011 = 350 km; Le Corre et al., 2017). Migration paths have continued to shorten in recent years (Caribou Ungava, *unpublished results*), resulting in great overlap between summer and winter ranges for the 2009−2016 period. Summer range was composed mainly of grasses and shrubs, with conifer forest in the southern portion and in valleys. Winter range had a similar composition, but with a higher proportion of conifer forest because the range extended further south of the tree line.

Caribou of the RFH and RGH cohabit with two large predators: the gray wolf and the black bear (*Ursus americanus*). Wolves are known to predate both adults and calves (Bergerud et al., 2008), whereas black bears mainly predate calves opportunistically (Zager and Beecham, 2006; Dussault et al., 2012). Other large ungulates such as moose (*Alces alces*) and muskox (*Ovibos moschatus*) occur at low densities in the area. Caribou of the RFH and RGH are the main large prey available year-round for wolves on these ranges (M. Bonin, *unpublished results*).

Humans represent both a direct and an indirect risk of mortality for caribou of the RFH and RGH. Caribou are an important subsistence food for northern communities (Bergerud et al., 2008). On the RGH, sport hunting was discontinued in 2012, and ban on all hunting in Labrador was enacted in

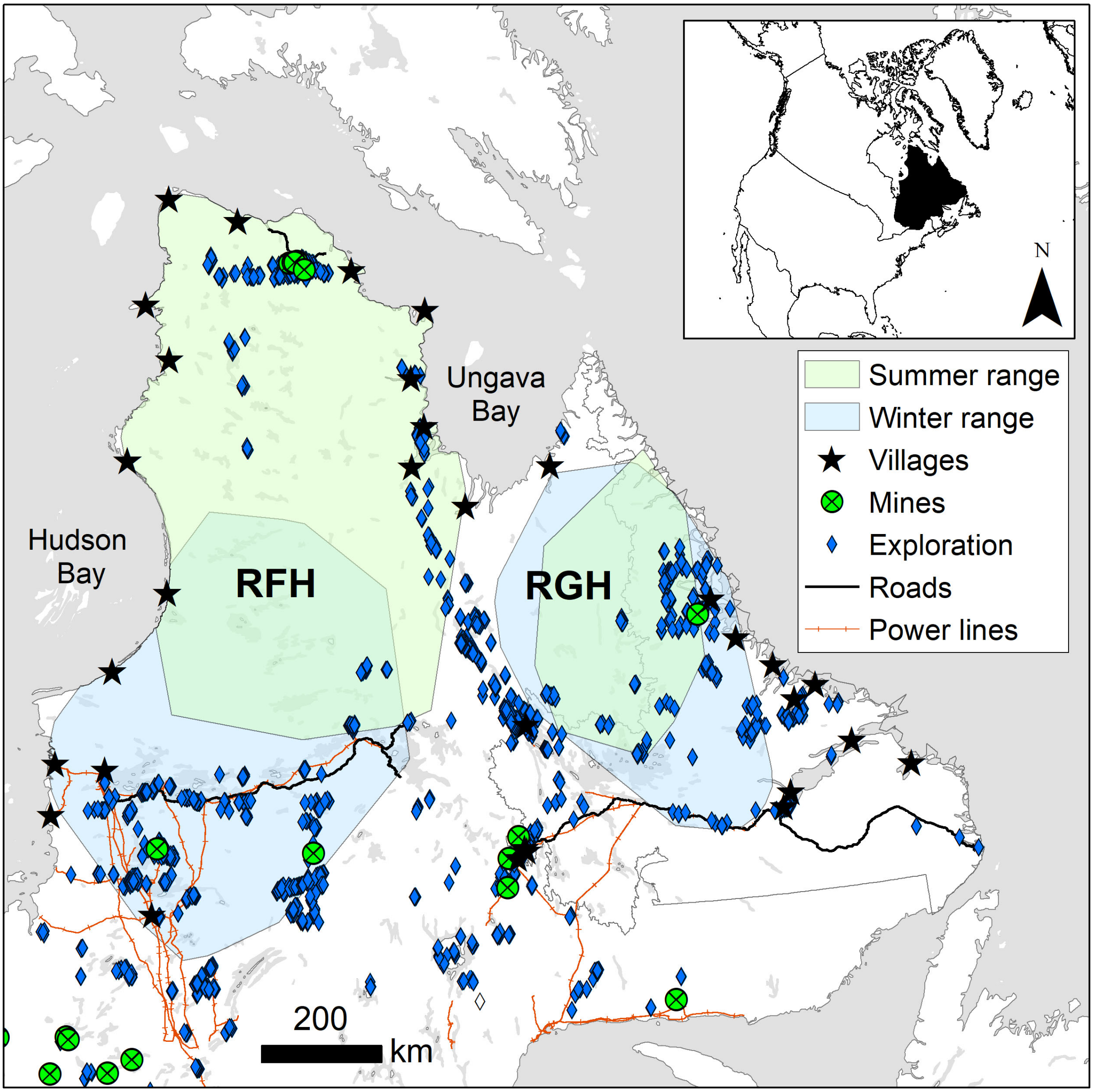

FIGURE 2 | Winter and summer ranges of eastern migratory caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George herds (RGH) and distribution of human disturbances in northern Québec and Labrador, Canada (2009–2016).

2013. Despite this, subsistence harvesting continued through the remainder of the study period. Hunting is known to have been a predominant source of mortality for the RGH through the study period and to the present (Department of Fisheries and Land Resources, Newfoundland, unpubl. data). On the RFH, autumn and winter sport hunting and subsistence harvest occurred throughout the study period. Indirectly, human disturbances could affect caribou survival through habitat loss and cumulative costs associated with the behavioral and physiological responses of avoiding infrastructures. Human disturbances include human settlements, mostly located along the coast, mining operations and exploration (mostly drilling sites), three major roads stretching outside settlements, and hydroelectric infrastructures (power lines, reservoirs and dams; **Figure 2**). Winter ranges are more disturbed than summer ranges, but human disturbances remain at relatively low density across the area (**Table 1**).

Capture and Monitoring of Caribou

We focused on the mortality risk of adult female caribou because population dynamics are highly sensitive to small variation in the survival of adult females (Gaillard et al., 2000). Between 2009 and 2016, we captured 254 yearling and adult females (RFH = 119; RGH = 135) using a net gun fired from a helicopter, and we equipped them with GPS collars (GPS Iridium and Globalstar, Vectronic Aerospace GmbH) programmed to record locations every 1 to 13 h (MFFP, NLFLR and Caribou Ungava,

TABLE 1 | Total area (km^2) of caribou seasonal ranges and density of human disturbances (per 1000 km^2) in the ranges of the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds in northern Québec and Labrador, Canada, 2009−2016.

			Disturbance density/(1000 km^2)			
Herd	**Range**	**Total area (km^2)**	**Mining exploration**	**Mines**	**Villages**	**Roads (km)**
RFH	Winter	286,803	3.84	0.003	0.01	7.80
	Summer	291,596	2.15	0.02	0.03	0.61
RGH	Winter	164,218	2.15	0.01	0.01	2.08
	Summer	105,152	1.68	0.00	0.00	0.00

All mining and exploration projects occurring between 2009 and 2016 were included in the reported densities, even if they were active for a shorter period of time. The density of villages and roads did not change during the 2009−2016 period.

unpubl. data). We determined environmental characteristics used by caribou and the survival status of individuals (alive or dead) using the information provided by GPS collars. We considered individuals as dead when we received a mortality signal or, in cases where mortality sensors failed, when caribou stopped moving permanently. In many instances (one-half of the individuals; **Table 2**), the cause of death was difficult to determine because we could visit carcasses only several months after death. We thus pooled all mortality causes in analyses.

Human Disturbance Effects on Mortality Risk

We first assessed the effects of human disturbances on caribou mortality risk at three temporal scales: early life (1−7 years old), seasonal, and daily scales. This allowed us to distinguish cumulative effects of disturbances (effects detectable over a season or a critical part of the lifetime) from instantaneous effects (effects observed within a day). We defined human disturbances as infrastructures and their potential associated human presence or activity. We had no information on the nature or level of activity associated with each infrastructure, but assumed that the effects of infrastructures on caribou behavior include the human activity occurring at, or around, infrastructures. For all scales of analysis, we quantified caribou exposure to a combination of all types of disturbances, which included mines, mining exploration, villages and roads. We excluded hydroelectric infrastructures because they were located at the southern limit of winter ranges of both herds. Caribou exposure to this type of disturbance was thus limited and previous research indicated a limited impact of this disturbance on caribou behavior (Plante et al., 2018). We also quantified exposure to industrial (mines and mining exploration) and non-industrial disturbances (villages and roads) separately. We expected non-industrial disturbances to have both instantaneous (e.g., higher risk of harvest near villages and roads) and cumulative effects on survival (e.g., stress and avoidance costs), whereas we mainly expected cumulative effects for industrial disturbances, because there is no harvest near exploration and mining sites. We restricted our assessment to disturbances located within 100 km of caribou locations. We considered caribou as exposed to disturbance within this radius because it included the largest zones of influence of disturbances reported for these herds (max = 23 km; Plante et al., 2018), and it encompassed the area where the risk of harvest by sport and subsistence hunters was the highest (90% of harvest occurred within <100 km of an infrastructure).

Early Life Risk of Mortality

We first quantified the effect of repeated exposure to human disturbances on the mortality risk during the early life of caribou (1−7 years old). We wanted to evaluate the possibility that the costs of repeated exposure to disturbance over the first 1−7 years-of- life could accumulate over time to a point where it would impact survival. We suspected that, if disturbance effects on survival were mostly observed through cumulative effects over time, smaller scales (one season or day) would not be enough to detect such effects. We modeled early life mortality risk of 112 female caribou (RFH = 62; RGH = 50) captured as yearling and monitored continuously until their death or the end of the study. We limited our analysis to caribou captured as yearling to avoid

TABLE 2 | Descriptive statistics of migratory caribou mortalities during summer and winter of 2009−2016 for the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds in northern Québec and Labrador, Canada.

					Causes of mortality			
Herd	**Season**	**% of time in year**	**% of total mortality**	**N mortality**	**Hunting**	**Predation**	**Natural**	**Unknown**
RFH	Summer	16−30%	35%	14	0	3	1	10
	Winter	31−45%	40%	16	3	4	0	9
RGH	Summer	16−32%	26%	18	1	6	0	11
	Winter	31−45%	43%	30	11	3	1	15

Statistics include the proportion of days covered by the summer and winter seasons per year (minimum and maximum% across years), the proportion and the total number of mortalities occurring within each season, as well as the cause of mortality when available. Some mortality events were removed from the survival analysis because they did not meet statistical assumptions.

uncertainty in age estimation (aging for individuals captured at >1 year was based on tooth wear). Among this sub-sample, 40 caribou died during the study (RFH = 17; RGH = 23). The age at death was calculated as the difference in days between estimated birth date (set at June 15th the year before capture for all individuals; Taillon et al., 2016) and date of death. Because our study extended from 2009 to 2016, individuals that survived throughout the study period reached a maximum of 7 years old. This is near the upper limit of the prime-age age class for most large herbivores and explains why we considered our study to target the early life of migratory caribou (Gaillard et al., 2000). We quantified early life exposure to disturbances by computing the proportion of locations within 100 km of a disturbance during the complete monitoring period of each individual. We tested effects of human exposure on early life rate of mortality using Cox proportional hazard models (function *coxph* in *Survival* package, R 3.5.1 Software, R Core Team, 2018). We verified the assumption of proportional hazard over time (function *cox.zph*), and excluded models for which the assumption was violated. We assessed the mortality risk using the hazard ratio (HR; exponential of β), that is the ratio between hazard rates of one unit of the factors tested. As such, mortality risk increased when HR > 1, decreased when HR < 1 and was not significantly influenced by the tested variable when the 95% CI included 1. We quantified the proportion of variance in mortality risk explained by human disturbances using the Nagelkerke's adjusted R^2 (function *r.squaredLR* in package *MuMIn*), and we verified model performance compared with the null model using a likelihood ratio test (in *coxph* output; Hosmer and Lemeshow, 2000).

Seasonal Mortality Risk

At the seasonal scale, we compared exposure to human disturbances for individuals that survived throughout our study, and individuals that died within a given season. We focused on summer and winter seasons because most mortalities occurred during these seasons and mortality events were too rare in other biological seasons to perform the survival analysis (**Table 2**). Summer and winter seasons were temporally delineated using First Passage Times that identify variations in caribou movements between seasons (Le Corre et al., 2014). We used the mean date of initiation and completion of migrations for all individuals to define each season on a yearly basis. Depending on the year, summer season started between mid-June and mid-July (RFH: 30 June – 10 July; RGH: 19 June – 8 July) and ended between the end of August and mid-October (RFH: 31 August– 20 October). Winter season started between mid-November and the end of December (RFH: 20 November – 11 December; RGH: 9 November – 31 December) and ended between the end of March and the beginning of May (RFH: 27 March – 27 April; RGH: 9 April – 5 May).

We used 465 individual-seasons to model summer mortality risk (RFH = 233 with 14 mortalities; RGH = 232 with 18 mortalities), and 329 individual-seasons to model winter mortality risk (RFH = 147 with 14 mortalities; RGH = 1 82 with 25 mortalities). We quantified repeated exposure of caribou to disturbances by calculating the proportion of seasonal locations within a 100-km radius of any disturbances, and types of industrial and non-industrial disturbances separately. We statistically tested the relationship between exposure to disturbances and mortality risk using mixed-effects Cox proportional hazard models (*coxme*, package *Survival* in R). We set the year as a random effect to account for the annual variations in exposure to disturbances, in the number of active industrial activities, and in the length of summer or winter seasons across years (**Table 2**). We determined the proportion of variance explained by disturbances and the performance of the model compared with a null model using the same approach as for the early life scale.

Daily Mortality Risk

As for the seasonal analysis, we focused the daily survival analysis on mortalities occurring during summer and winter. We used 858 individual-days during summer (RFH = 5 57 with 14 mortalities; RGH = 301 with 18 mortalities), and 636 individual-days during winter (RFH = 394 with 14 mortalities; RGH = 2 42 with 25 mortalities). We assessed the effect of human disturbances on daily mortality risk by comparing distance to disturbances of individuals that would eventually die and of individuals that survived during the 24 h before the death occurred. We created statistical clusters, which included the locations of an individual during the 24 h before it died and the locations of all caribou that were alive during the same period. For each caribou location, we calculated the Euclidian distance to the nearest disturbance of any type, and to the nearest industrial and non-industrial disturbances. We truncated distance values at 100 km, and averaged them over the 24-h period. To facilitate the interpretation of the coefficients associated with daily risk of mortality and make that value comparable to the analyses performed at other scales, we multiplied distance values by −1. By doing so, higher coefficients represented greater exposure to disturbances, as for the other scales. We used conditional logistic regressions (*clogit*, package *Survival* in R). We could not assess model performance compared to the null model using a likelihood ratio test because the calculation of R^2 was not possible for this type of model.

Relative Importance of Human Disturbances and Natural Factors

Use of Highly Selected Habitats by Caribou

We compared the relative impact of human disturbances on caribou mortality to that of natural factors at the three temporal scales of analysis. Following our hypotheses, we evaluated the role of habitat use by caribou on mortality risk (H1, **Figure 1A**). The observed patterns of habitat use were considered as aggregate responses of caribou toward multiple factors. These responses were described using Resource Selection Functions (RSFs; Manly et al., 2002) on 334 female caribou (RFH = 168; RGH = 166). The RSF was performed at the herd level, for each season separately (see **Supplementary Appendix 1** for details). The RSF included 5 to 6 vegetation cover types, the Normalized Difference Vegetation Index (NDVI; 250 m 16-day composite VI from the MODIS MOD13Q1 product; Didan, 2015) as an index of vegetation productivity, the elevation and the proximity to water. We assessed the predictive performance of RSF models with a k-fold cross-validation (Boyce et al., 2002). When predictive performance was good ($r_{spearman} > 0.70$), we used the selection coefficients to predict the relative probability of occurrence of caribou on seasonal ranges.

We then described the individual patterns of use of highly selected habitats relative to the population RSF to assess how individual variations affected mortality. We first extracted the RSF score of the population model under each caribou location. We then defined highly selected habitats as the highest 25% of RSF scores among those for caribou locations. For the early life and seasonal scales, we quantified the use of highly selected habitats by calculating the proportion of caribou locations in these habitats. For the daily scale, we directly compared the RSF score at caribou locations for individuals that died and individuals that survived during the 24 h preceding death.

Predation Risk by Wolves

We determined whether caribou more exposed to predation risk by wolves faced an increased risk of mortality (H3; **Figure 1C**). The predation risk was defined based on RSF models of 42 wolves equipped with GPS collars in the caribou seasonal ranges (RFH = 28; RGH = 14; see **Supplementary Appendix 1** for details). We included the same variables we used for caribou RSFs, i.e., vegetation cover type, NDVI, elevation and proximity to water in the wolf RSF models. We also used the same seasonal areas and periods for describing habitat selection by wolves that we used for caribou. We avoided including indices of caribou use in habitat selection-models for wolves because we aimed at identifying habitat characteristics associated with higher wolf occurrence, independently of caribou use. We extracted the relative probability of wolf occurrence at each caribou location and we defined risky habitats as those having a RSF score $\geq$ 75th percentiles among RSF scores occurring at caribou locations. We calculated the proportion of locations of each caribou in risky habitats when assessing the effect on early life and seasonal mortality risk, and used RSF scores of wolves to make predictions at caribou locations when assessing daily mortality risk.

Weather Conditions

For weather conditions (H4; **Figure 1D**), we extracted the mean daily temperature (°C) and total daily amount of precipitation (kg/m^2) at each caribou location (National Oceanic and Atmospheric Administration [NOAA], 2017 climatic data; 35 km × 35 km-resolution). To ensure that weather conditions were comparable among individuals. even if they had different monitoring periods, we calculated the daily differences between temperatures and precipitations at locations of an individual and the mean values of these variables for all other individuals monitored during the same day. Therefore, we used weather conditions indices that contrasted the conditions faced by an individual compared to average conditions faced by all monitored individuals during a given day. We chose to model differences in the meteorological conditions encountered by individuals versus the mean value instead of actual local values because caribou in both herds spread over a large area within a given season, resulting in large differences in conditions encountered by individuals. This approach allowed us to test the effect of encountered conditions on survival, while keeping a certain amount of variability among individuals. It also limited the effect of extreme values on survival output, i.e., when individuals were far from the main groups.

Finally, we tested the hypotheses of additive effects of habitat use and human disturbances, predation or weather (H5; **Figure 1E**) by including different combinations of these factors in the models. We also tested the hypothesis of maladaptive habitat use in regards to human disturbances or predation risk (H6; **Figure 1F**) by including the interaction between the use of highly selected habitats and caribou exposure to human disturbances or predation risk by wolves in other candidate models.

Model Selection

We used the Akaike Information Criterion (AIC; Burnham and Anderson, 2002) to compare the relative fit of the models derived from our hypotheses. For nested models with $\Delta AIC \leq 2$, we retained the model with fewer variables because additional covariates were considered uninformative (Arnold, 2010). Otherwise, we interpreted all non-nested models with $\Delta AIC \leq 2$. We also compared our candidate models to a null model to verify that covariates included in models improved model fit (Mac Nally et al., 2018). We relied on the likelihood ratio test to assess the performance of best models compared with null models. At the daily scale, we could not test models including only the intercept with conditional logistic functions. We thus compared model performance to a model including only the latitude as a covariate (see next section for details). We verified multicollinearity among variables included in the same model with the variance inflation factor (VIF). We assumed no multicollinearity when VIF scores were <5 (Zuur et al., 2010).

Correlations and Confounding Effects

We also examined the correlations between all variables considered in the candidate models using Pearson's paired tests of correlations (*cor.test* in R, **Supplementary Appendix 2**). This was done prior to the modeling step for two reasons. First, some factors could not be tested in the same model because of over-parametrization issues due to the low number of mortalities (King and Zeng, 2001). Thus, the collinearity of these variables could not be assessed with multicollinearity tests. Yet, their correlation would indicate some redundancy among factors used to explain variation in mortality risk of caribou, potentially affecting the interpretation of results. Variables that were weakly correlated (<0.50) were tested in the same set of candidate models. When correlation was >0.50, we retained the variable providing the best fit according to the model selection process. Secondly, we suspected that exposure of caribou to human disturbances and predation risk, as well as the effect of weather conditions on survival, could vary substantially with latitude. Caribou are highly mobile, even outside migration periods, which could make exposure to anthropogenic and non-anthropogenic factors highly variable across individuals, or over time, even within a single season. For example, during summer caribou of the RFH were more exposed to disturbances when they reached the northern tip of the Ungava peninsula because of the aggregation of infrastructures in this confined area. Exposure to disturbances, and their effects on the mortality risk of caribou could thus be correlated with latitude. We could not directly test the effect of latitude on early life and seasonal survival because latitudes used by individuals varied markedly during these periods. To ensure that effects could be attributed to the tested variable and not the confounding effect of latitude, we explored the potential correlation between the variables and latitude. When the correlation with latitude was >0.50, we tested the effect of the variable on mortality risk despite potential confounding effects of latitude, but we interpreted the results accordingly. At the daily scale, we could better test the effect of latitude on mortality risk by including a latitude model in the candidate set to assess whether other variables explained more variability in mortality risk than latitude alone. Model performance at this scale of analysis could not be assessed with a likelihood ratio test based on a null model (see above). Instead, we used latitude as the null model for comparison.

RESULTS

Human Disturbance Effects

Early Life Mortality Risk

For the early life period (1−7 years old), all models except the one including all disturbance types for the RGH satisfied the assumption of proportional hazards. In all cases, models indicated no effect of human disturbances on the mortality risk of caribou over the early life period, for both the RFH and RGH (**Figure 3A** and **Table 3**).

Seasonal Mortality Risk

At the seasonal scale, we documented significant effects of human disturbance on caribou mortality risk, which differed across herds and seasons. For the RFH, repeated exposure to human disturbances had no effect on the mortality risk of caribou during summer (**Figure 3B** and **Table 3**). During winter, we observed that a greater exposure to industrial disturbances increased the risk of mortality. The risk of dying was 10 times higher for individuals exposed to industrial disturbances throughout winter than for individuals never exposed (Hazard Ratio, HR = 10.3, 95% CI = 1.3−79.8). Caribou exposure to industrial disturbances explained a small proportion of the variation observed in caribou mortality risk ($R^2 = 0.06$) and the uncertainty around the estimate was large. During winter, caribou exposure to disturbances was correlated with latitude ($r = 0.58$), with caribou more exposed to disturbances at lower latitudes.

For the RGH, the model testing the effect of non-industrial disturbances on summer mortality risk was discarded because it did not converge and the condition of proportional hazard was not met. The other models for the RGH indicated that caribou more exposed to human disturbances in general, or to industrial disturbances in particular, faced a lower risk of mortality during summer (**Figure 3B**). Caribou exposed to disturbance throughout summer were 1.4 to 1.7 time more likely to die for each 10% decrease in exposure for all disturbances or industrial disturbances only, respectively (all disturbances: HR for a 10% increment in exposure = 0.69, 95% CI = 0.54−0.88; industrial disturbances: HR for a 10% increment in exposure = 0.60, 95% CI = 0.44−0.82). Exposure to these disturbances explained a limited proportion of the variation in caribou mortality risk ($R^2_{all} = 0.11$, $R^2_{industrial} = 0.13$). The correlation between the distance of caribou to human disturbances and latitude was significant ($r = 0.52$), but weak for industrial disturbances only ($r = 0.19$). During winter, our results indicated that the human disturbance factors we assessed did not affect caribou mortality risk in this herd.

Daily Mortality Risk

On the RFH, daily mortality risk of caribou during summer was not affected by human disturbance (**Figure 3C** and **Table 3**). During winter, we noted that caribou closer to industrial disturbances faced an increased risk of mortality. The mortality risk of caribou was 11 times higher for each 10-km increment toward industrial disturbances (HR for a 10-km increment = 10.7, 95% CI = 10.2−11.3).

On the RGH, we determined that proximity to disturbances in general, and of non-industrial disturbances in particular, increased the daily mortality risk during summer (**Figure 3C**). Mortality risk was, on average, 11 times higher for each 10-km increment toward disturbances (HR for a 10-km increment: all disturbances = 11.2; 95% CI = 10.2−12.1; non-industrial = 11.3; 95% CI = 10.1−12.6). The correlation between proximity to disturbances and latitude was significant ($R_{alldisturbances} = 0.52$, $R_{non-industrial} = 0.62$), indicating that caribou were more exposed to disturbance in the southern portion of their summer range. Yet, caribou died on average 200 km south of where caribou that survived were during the same day. Thus, we cannot distinguish effects of latitude and human disturbances on daily survival during summer for this herd and season. During winter, we observed no effect of human disturbances on daily survival for the RGH (**Figure 3C**).

Relative Importance of Human Disturbances and Natural Factors

Early Life Mortality Risk

Human disturbance was not the most influential factor on early life mortality risk of caribou of the RFH and RGH (**Table 1** of **Supplementary Appendix 3** and **Table 4**). On the RFH, the predation risk and precipitation models received equivalent support. Caribou using areas which received more precipitations faced a higher risk of mortality during the early life period. The precipitation model predicted that the mortality risk of caribou was 68 times higher for each increase of 100 g/m^2 in precipitation ($R^2 = 0.46$). Surprisingly, caribou using riskier areas in terms of predation by wolves more frequently had a better chance of surviving throughout the first 7 years-of-life ($R^2 = 0.44$). The predation model predicted that mortality

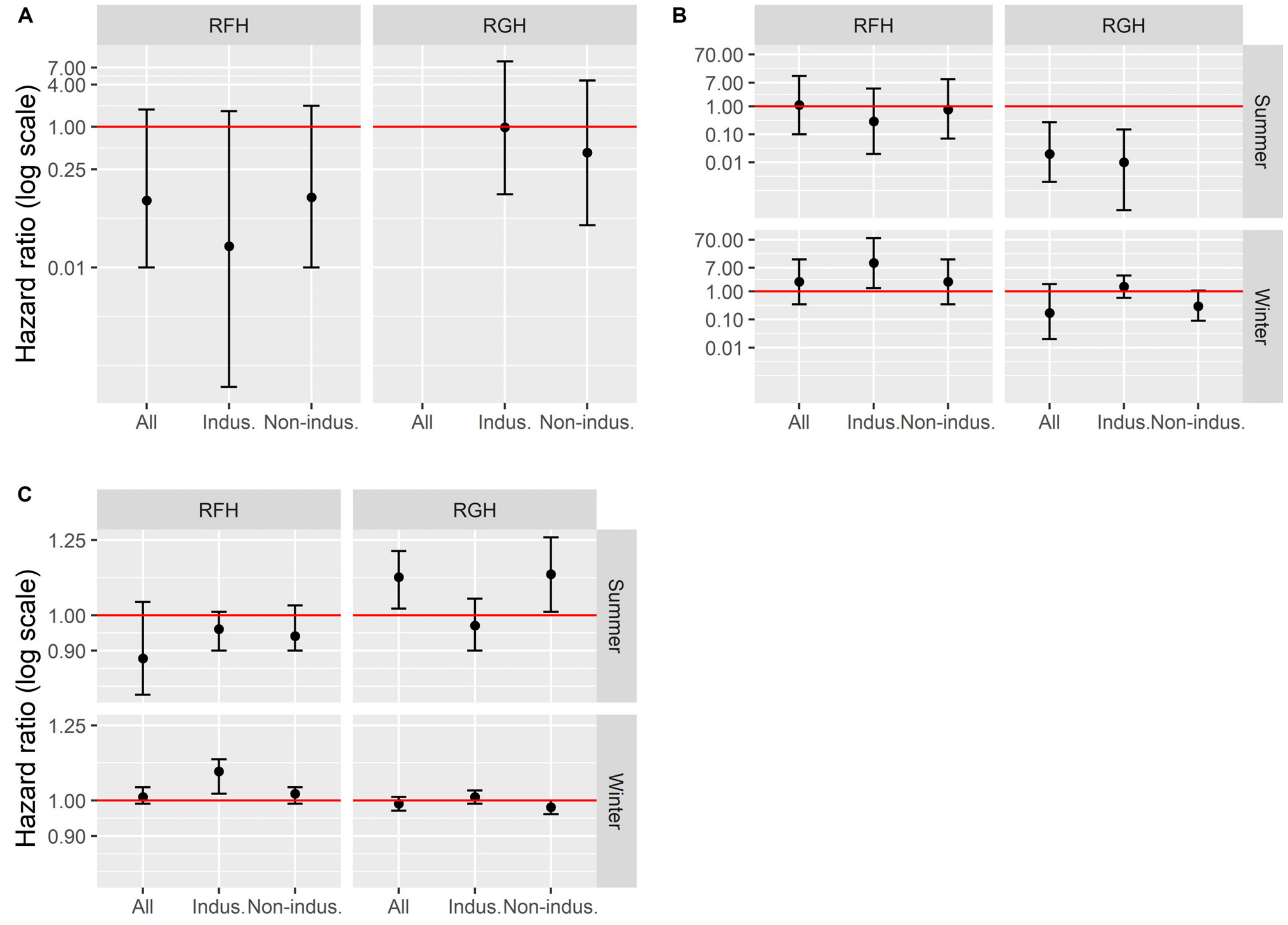

FIGURE 3 | Human disturbance effects [hazard ratio (HR), represented on a log scale] on caribou mortality risk at three temporal scales, early-life 1–7 years old; **(A)**, seasonal **(B)** and daily **(C)** mortality risk, and 95% confidence intervals, on the Rivière-aux-Feuilles (RFH) and Rivière-George herd (RGH), northern Québec, Canada, 2009–2016. A hazard ratio < 1 indicates that exposure to disturbances decreased mortality risk, whereas a hazard ratio >1 indicates that exposure to disturbances increased mortality risk (red line = hazard ratio of 1). Disturbances tested included all disturbance types (mines, mining exploration, roads, and human settlements), industrial disturbances only (indus.; mine and mining exploration) and non-industrial disturbances only (non-indus.; roads and human settlements).

risk of caribou was 1.76 time higher for each 10% decrease in predation risk exposure (HR for 10% increment in predation risk exposure = 0.57; 95% CI = 0.40—0.80). We note that for this herd, predation risk and habitat highly selected by caribou were strongly correlated during winter ($r = 0.82$), but not during summer ($r = 0.13$). For the RGH, we also found support for the predation risk hypothesis, but contrary to the RFH, caribou frequently using riskier areas in terms of predation risk faced an increased risk of mortality during the early-life period (HR for 10% increment in predation risk exposure = 1.48, 95% CI = 1.12—1.96; $R^2 = 0.25$).

Seasonal Mortality Risk

At the seasonal scale, the effect of human disturbances on the mortality risk were limited compared with those of non-anthropogenic factors. For the RFH, model selection for summer mortality risk indicated support for the temperature model (**Table 2** of **Supplementary Appendix 3** and **Table 4**). The risk of mortality was higher for caribou using areas relatively warmer than those used by other caribou during the same day. The risk of mortality was 6.5 times higher for each increase of 1°C in the difference of temperature between the area used by a caribou and the population mean (HR = 6.49, 95% CI = 3.0—14.4; $R^2 = 0.25$).

During winter, model selection for the RFH supported the habitat use hypothesis. Individuals spending more time in highly selected habitats faced a lower risk of mortality during winter. Caribou were 2 times more likely to die for each 10% decrease in the use of highly selected habitat (HR for 10% increment in use = 0.47, 95% CI = 0.27—0.84; $R^2 = 0.17$).

On the RGH, summer survival was mainly explained by exposure to disturbances (**Supplementary Appendix 3** and **Table 4**). The best model indicated that caribou more exposed to disturbances had a lower chance of dying during summer, as mentioned previously (**Figure 3**). None of the models including only non-anthropic factors outperformed the null model (H_0 with $\Delta AIC \leq 2$). During winter, none of our hypotheses outperformed the null model (H_0 with $\Delta AIC \leq 2$).

TABLE 3 | Summary of the effects of human disturbances (based on Cox-proportional hazard analyses) on early-life, seasonal and daily mortality risk of migratory caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George herds (RGH), northern Québec and Labrador, Canada, 2009−2016.

Scale	Herd	Season	Factor	Effect on mortality risk	Comments
Early-life	RFH	—	All disturbances	No effect	—
		—	Industrial	No effect	—
		—	Non-industrial	No effect	—
	RGH	—	All disturbances	—	Assumption not met
		—	Industrial	No effect	—
		—	Non-industrial	No effect	—
Seasonal	RFH	Summer	All disturbances	No effect	—
			Industrial	No effect	—
			Non-industrial	No effect	—
		Winter	All disturbances	No effect	—
			Industrial	Increased mortality risk	Small proportion of variance explained by this factor (R^2 = 0.06)
			Non-industrial	No effect	—
	RGH	Summer	All disturbances	Decreased mortality risk	Small proportion of variance explained by this factor (R^2 = 0.11), Correlation with latitude: cannot distinguish anthropogenic and latitudinal effects
			Industrial	Decreased mortality risk	Small proportion of variance explained by this factor (R^2 = 0.13)
			Non-industrial	—	Assumption not met
		Winter	All disturbances	No effect	—
			Industrial	No effect	—
			Non-industrial	No effect	—
Daily	RFH	Summer	All disturbances	No effect	—
			Industrial	No effect	—
			Non-industrial	No effect	—
		Winter	All disturbances	No effect	—
			Industrial	Increased mortality risk	
			Non-industrial	No effect	—
	RGH	Summer	All disturbances	Increased mortality risk	Correlation with latitude: cannot distinguish anthropogenic and latitudinal effects
			Industrial	No effect	—
			Non-industrial	Increased mortality risk	Correlation with latitude: cannot distinguish anthropogenic and latitudinal effects
		Winter	All disturbances	No effect	—
			Industrial	No effect	—
			Non-industrial	No effect	—

Daily Mortality Risk

At the daily scale, human disturbances had negligible effects compared to non-anthropogenic factors. On the RFH, the latitude model outperformed all other models for both summer and winter seasons (H_0 with $\Delta AIC \leq 2$; **Table 2** of **Supplementary Appendix 3** and **Table 4**). During summer, caribou mainly died at lower latitudes (HR for increment of 1 km = 0.98, 95% C I = 0.97−0.99), whereas during winter, caribou mainly died at higher latitudes (HR for increment of 1 km = 1.01, 95% CI = 1.00−1.02).

On the RGH, model selection for summer indicated strong support for the latitude model. This model predicted that individuals died on average 200 km south of where individuals that survived were on the same day (HR for increment of 1 km = 0.98, 95% CI = 0.97−0.99). During winter, we found support for the habitat use model, where individuals using highly selected habitat at the population level experienced lower mortality risk. The mortality risk was 1.7 times higher for each 10% decrease in the use of highly selected habitat (HR for 10% increment in use = 0.57, 95% CI = 0.37, 0.84).

DISCUSSION

Caribou and reindeer populations are declining across their circumarctic distribution, and long-term widespread changes in the landscape resulting from climate change and human development are likely contributing to these declines (Vors and Boyce, 2009; Festa-Bianchet et al., 2011; Environment Canada, 2012). Although industrial development is relatively recent in migratory caribou ranges of northern Québec and Labrador,

TABLE 4 | Summary of the effects of the most important factors affecting early-life, seasonal and daily mortality risk of migratory caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George herds (RGH), northern Québec and Labrador, Canada, 2009−2016.

Scale	Herd	Season	Factor	Effect on mortality risk	Comments
Early-life	RFH	—	Precipitations	Increased	—
		—	Predation risk	Decreased	Small effect size
	RGH	—	Predation risk	Increased	—
Seasonal	RFH	Summer	Temperature	Decreased	
		Winter	Habitat use	Decreased	Small effect size
	RGH	Summer	Human disturbances	Decreased	Small effect size; small proportion of variance explained by this factor (R^2 = 0.11)
		Winter	—	—	None of the model outperformed the null model
Daily	RFH	Summer	Latitude	Decreased	—
		Winter	Latitude	Increased	—
	RGH	Summer	Latitude	Decreased	—
		Winter	Habitat use	Decreased	Small effect size

we previously reported strong behavioral responses toward human disturbances, which translated into significant functional habitat loss (Plante et al., 2018). Yet, the consequences of these modifications in behavior and habitat use on animal performance and population trends had yet to be investigated.

We demonstrated that human disturbances can impact caribou survival, but the direction and magnitude of those effects varied greatly across the herds and the three considered temporal scales. Our results indicate both positive and negative impacts of human disturbances on caribou survival. Yet, the interpretation of these effects requires caution because they either explained little variation in mortality risk or their effect were indistinguishable from that of latitude. In addition, we suggest that, in most instances, disturbances were not the dominant or unique factor explaining survival of caribou from the RFH and RGH. Indeed, effects of natural factors on caribou survival prevailed over those of anthropogenic ones. None of the six hypotheses presented in our conceptual framework received consistent support across temporal scales.

Early Life Mortality Risk

Our results first indicate that human disturbances did not have detectable cumulative impacts on caribou survival in the long-term (early life period; 1−7 years old) at the current level of development in the RFH and RGH ranges. This result does not support the conclusions of a growing number of empirical results revealing the existence of long-term cumulative impacts of human disturbances on *Rangifer* vital rates (Sorensen et al., 2008; Environment Canada, 2011; Johnson et al., 2015). We believe that this discrepancy is attributable to the relatively low level of human development on the RFH and RGH ranges compared with those evaluated in other studies on boreal caribou. For the boreal caribou ecotype, reductions in population size have been tightly linked to the cumulative habitat loss caused by habitat alteration through forestry operations and avoidance of infrastructures (Sorensen et al., 2008; Environment Canada, 2011; Johnson et al., 2015). Moreover, disturbance densities have reached critical levels in annual ranges of many boreal caribou populations (Environment Canada, 2011), making the avoidance of disturbances almost impossible because of the lack of suitable alternative habitat (Gill et al., 2001). This habitat alteration is also causing an increase in predation risk for caribou through numerical responses of alternative prey and predators, and increased access and efficiency of predators in modified landscapes (Environment Canada, 2011). This outcome is unlikely for migratory caribou of the RFH and RGH because the mechanisms through which human disturbances may impact these caribou are likely different from other herds. Undisturbed habitat is still readily available for migratory caribou of the RFH and RGH (**Figure 2**), and individuals may avoid disturbances over large distances (Plante et al., 2018).

Early life survival of migratory caribou was mainly affected by patterns of habitat use in relation to predation risk (RFH and RGH) and climatic conditions (precipitation; RFH). We documented contrasting effects of the use of habitats with high predation risk for the two herds. In the RFH, using risky areas more often appeared to increase survival. For this herd, caribou and wolves mainly occurred in forested habitats during winter (selected by both species, **Supplementary Appendix 1**). The winter season covers 31−45% of the year, and patterns observed during this season could have a great influence on the results at the early life scale. Because caribou and wolves used the same habitats during a large portion of the year, we suspect that the positive effect of using risky habitats on caribou survival may be partly related to the positive outcomes of the tactic of habitat use by caribou. In the RGH, increased exposure to risky habitats decreased caribou survival. It is known that, in addition to harvesting, predation is a significant cause of mortality for caribou in northern Québec and Labrador, wolves being responsible for at least 10−33% of mortalities (see also **Table 2**). This discrepancy in the effect of predation risk between the two herds may arise from our predation risk index not considering the population size of predators, variable spatio-temporal access of predators to caribou, rates of encounters, and success of predation events. It is also possible that limiting factors during the study period could have differed between the two herds, with a stronger effect of predation risk for the RGH compared to the RFH. In addition, we could not test the hypothesis that wolves avoided or selected proximity to infrastructures because of the low sample size of marked wolves and their distribution on caribou ranges.

Our long-term assessment of anthropogenic and natural factors may not have adequately portray the conditions encountered by caribou throughout the early life period, or that survival was mainly impacted by the accumulation of immediate factors acting at shorter temporal scales than the one we investigated. For example, caribou may be highly sensitive to a specific factor during a given season, but could compensate for its negative effects in the following season (Darling and Côté, 2008), which would limit our ability to detect its influence over the first 7 years of their adult life. Many of the factors we tested may have also acted simultaneously in the population, but affected early life survival of each individual differently. In addition, we could not consider intrinsic factors, such as body condition, that are often identified as major determinants of survival in long-lived mammals (Gaillard et al., 2003).

Seasonal Mortality Risk

At the seasonal scale, repeated exposure to industrial disturbances reduced survival of the RFH during winter. The RFH winter range bears the highest density of disturbances across our study areas. This seasonal effect on survival may be a consequence of cumulative costs of short-term behavioral responses toward disturbances, such as avoidance (Plante et al., 2018), increased stress level (Wasser et al., 2011), movement rate (Dussault et al., 2007), or vigilance (Benhaiem et al., 2008). To test this hypothesis, future work should concentrate on quantifying physiological responses to human disturbances at different temporal scales, to determine whether chronic stress responses can influence survival (Wasser et al., 2011). The seasonal effect we observed on survival also could be the result of cumulative risk exposure to direct mortality sources such as hunting. Whether caribou faced chronic stress or increased risk of harvest near infrastructures, the consequence was the same for the RFH, and resulted from the accumulation of exposure to human disturbance over time and space. We note that exposure of caribou from the RFH to industrial disturbances was correlated with latitude, with individuals more exposed in the southern portion of their winter range. Hence, we cannot confirm that the negative effects on caribou survival is entirely attributable to industrial disturbances. In addition, industrial disturbances explained only a small portion of the variability in winter mortality risk (6%), indicating that other factors are driving caribou survival during this period.

Our model revealed that repeated exposure to human disturbance was beneficial for survival of the RGH caribou during summer. These effects are likely the consequences of the correlation between caribou exposure to human disturbance and latitude. Indeed, human disturbances were not randomly distributed in caribou seasonal ranges, especially in summer range. This, combined with the highly mobile nature of caribou during summer, created strong temporal and latitudinal variations in exposure to human disturbances. This result implies that summer mortality risk in the RGH was probably not influenced by human disturbances, but rather by other factors correlated with latitude for example, vegetation composition, vegetation productivity, or abundance of predators.

Overall, seasonal survival of migratory caribou was mainly driven by the use of highly selected habitats (RFH) and climatic conditions (RFH; temperature). Caribou of the RFH using habitats similarly to the rest of the population, i.e., spending more time in strongly selected habitat at the population level, faced a lower risk of mortality during winter. Conversely, caribou exhibiting marginal behaviors compared with the population had a higher risk of mortality. Marginal individuals can face a higher risk of mortality because they are not as good at avoiding or defending themselves against predators when isolated from most of the population. These caribou also might have bolder personalities, which may place them in riskier situations (Lesmerises et al., 2019). Alternatively, habitats strongly selected by the population are presumably high-quality habitats that may contribute to maintain or improve body condition, and ultimately survival. Previous research indicates a strong influence of habitat productivity on the body condition of calves and females in the RFH and RGH (Couturier et al., 2009a,b), which could in turn affect survival. Density-dependent effects of food availability on nutrition, body condition, and survival, may have decreased in the last decades, especially for the RGH, which strongly declined during our study period. This may explain why we did not identify habitat quality as an influent factor for the survival of caribou of the RGH.

We documented that using sites with warmer temperatures during summer increased the seasonal mortality risk of caribou of the RFH herd. Although caribou are believed to be tolerant to warm temperatures (Hagemoen and Reimers, 2002), they could suffer from high thermoregulatory costs and heat stress during warm summer days (Soppela et al., 1986). More importantly, warm temperatures in arctic summers are associated with increased insect activity and harassment (Weladji et al., 2003). In periods of intense insect harassment, caribou reduce their food intake, shorten their resting periods and increase their movements (Toupin et al., 1996; Mörschel and Klein, 1997; Hagemoen and Reimers, 2002). These alterations of activity entail energetic costs that could compromise body condition and eventually survival (Helle and Tarvainen, 1984; Weladji et al., 2003), especially if caribou do not subsequently compensate for lost feeding opportunities (Colman et al., 2003).

Daily Mortality Risk

At a shorter time scale, we observed contrasting results regarding effects of human disturbances on daily survival, but those effects were undistinguishable from latitudinal effects. On the RFH, the models indicated that caribou benefited from being closer to human disturbances during summer, but again, this relationship likely originated from differential range-use patterns by individuals, not from disturbance. Caribou that died during summer generally remained further south, whereas exposure to human disturbances mainly occurred in the north. Perhaps individuals in poorer body condition were unable to reach the northern part of their summer range and died at southern locations. In the RGH range, however, proximity to villages and roads reduced daily survival during summer, but again, latitudinal effects prevailed over anthropogenic ones. These results underline the complexity of testing the effect of punctual or permanent infrastructures on highly mobile species such as migratory caribou.

Behavioral vs. Fitness Consequences of Human Disturbances

Our study underpins the importance of not relying exclusively on behavioral responses to draw conclusions on the impacts of human disturbance on wildlife populations. Although strong behavioral responses toward disturbances were reported for the RFH and RGH (Plante et al., 2018), effects on survival, although detectable, were limited. Behavioral responses toward disturbances could be the mechanism through which caribou could minimize the negative impacts of disturbance on their condition and survival. Our study thus exemplifies a non-linear relationship between behavioral responses and consequences on fitness (Gill et al., 2001). We also highlight the importance of considering cumulative effects of human development over an array of spatiotemporal scales. We acknowledge, however, that cumulative effects on migratory caribou survival appear to be limited by the currently low levels of human disturbances. Nonetheless, reporting an effect over a season is significant considering the potential antagonist or compensatory processes occurring over time, which could have weakened the anthropogenic effects we observed.

Management Implications

Empirical evidences of the negative impacts of habitat loss and fragmentation resulting from human development are abundant for boreal caribou populations, indicating that cumulative effects are likely the ultimate factor responsible for their decline in Canada (Sorensen et al., 2008; Environment Canada, 2011). In the RFH and RGH ranges, human development is relatively recent and the human footprint is still limited by remoteness and harsh conditions. Yet, the accelerated and projected development in recent years (MRNF, 2012) raises multiple questions regarding the conservation and management of these declining herds. Our results document that effects of human disturbance (exclusive of hunting) on survival are not predominant and widespread at the current level of development in northern Québec and Labrador. Nevertheless, we observed meaningful impacts even considering the low level of development compared to that experienced by most boreal caribou populations. Predicting the level at which development and human disturbance would induce more significant impacts on caribou survival is difficult, but our results imply that the impact would increase with the density of disturbances within caribou ranges. Yet, this context offers a great opportunity to anticipate the consequences of various development scenarios instead of juggling with the consequences retrospectively.

More importantly, effects of human disturbances on population dynamics need to be further investigated for these herds to clarify their role in the current population declines. Although human development *per se* was not the primary driver of survival in the RFH and RGH, development may contribute as one of many factors generating population declines. Management and conservation guidelines established for boreal caribou may not apply to migratory ecotypes for many reasons, including the marked difference in range use and movements. Wide-ranging caribou could be particularly vulnerable to human development, because of the large area they need to fulfill vital activities such as foraging and predator avoidance. Further development could increase the risk of disrupting migration behavior, with unknown consequences on population persistence. Yet, the current plans of development in the north still relies on the impact assessment of individual projects. Migratory caribou are also facing the increasing threat of climate change. Warmer climate and more frequent extreme weather events are and will likely negatively affect migratory caribou populations through multiple complex processes. Yet, the impacts of climate change on wildlife populations are arduously manageable. Restricting human development could improve caribou survival in certain areas and periods, and this could constitute the only possible action to help compensate for the negative impacts expected from unmanageable threats such as climate change.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Migratory caribou data in Quebec are considered sensitive, and are protected by a sharing agreement with the Ministry of Forests, Wildlife and Parks (Ministère des Forêts, de la Faune et des Parcs). Requests to access these datasets should be directed to Joëlle Taillon, Ph.D., researcher, Ministère des Forêts, de la Faune et des Parcs, Québec, Québec, G1S 4X4, joelle.taillon@mffp.gouv.qc.ca.

ETHICS STATEMENT

The animal study was reviewed and approved by the Animal Care Committee of Laval University.

AUTHOR CONTRIBUTIONS

SP designed the study with the help of CD, JR, and SC. SP realized the analyses and wrote the first draft of the manuscript. CD, JR, MG, and SC helped with the analyses and commented the manuscript before submission.

FUNDING

Caribou Ungava was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC RDCPJ

46512-14). SP was supported by the Fonds de Recherche Québécois pour la Nature et les Technologies (FRQNT 183343) and Caribou Ungava.

ACKNOWLEDGMENTS

We are grateful to Caribou Ungava partners (in alphabetical order): Air Inuit, ArcticNet, Azimut Exploration, Centre d'Études Nordiques, Grand Council of Crees, Exploration Osisko, Canada Foundation for Innovation, GlenCore-Mine Raglan, Hydro-Québec, Makivik Corporation, Government of Newfoundland-Labrador – Wildlife Division, Government of Québec – Ministère des Forêts de la Faune et des Parcs, TataSteel Minerals Canada Limited, and the Torngat Wildlife Plants and Fisheries Secretariat. We are especially grateful to V. Brodeur, D. Grenier, C. Jutras, J. Pisapio, S. Rivard, J. Taillon, and N. Trudel for their contribution to fieldwork and data collection. We also thank S. Biondo, F. Huot, and M. Le Corre for sharing data, and S. Hamel for statistical advices.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00154/full#supplementary-material

REFERENCES

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *J. Wildl. Manage.* 74, 1175–1178. doi: 10.1371/journal.pone.0206711

Battin, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* 18, 1482–1491. doi: 10.1111/j.1523-1739.2004.00417.x

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. J. M., et al. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Anim. Behav.* 76, 611–618. doi: 10.1016/j.anbehav.2008.03.012

Berger, J., Hartway, C., Gruzdev, A., and Johnson, M. (2018). Climate degradation and extreme icing events constrain life in cold-adapted mammals. *Sci. Rep.* 8:1156. doi: 10.1038/s41598-018-19416-9

Bergerud, A. T., Luttich, S. N., and Camps, L. (2008). *The Return of Caribou to Ungava*. Montreal: McGill-Queen's University Press.

Berteaux, D., Casajus, N., and Ropars, P. (2018). *Portrait du Climat du Nord du Québec et du Labrador Pour la Période 1981-2010*. Rimouski, QC: Université du Québec à Rimouski.

Boulanger, J., Poole, K. G., Gunn, A., and Wierzchowski, J. (2012). Estimating the zone of influence of industrial developments on wildlife: a migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. *Wildl. Biol.* 18, 164–179. doi: 10.2981/11-045

Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecol. Model.* 157, 281–300. doi: 10.1016/s0304-3800(02)00200-4

Bradshaw, C. J. A., Boutin, S., and Hebert, D. M. (1998). Energetic implications of disturbance caused by petroleum exploration to woodland caribou. *Can. J. Zool.* 76, 1319–1324. doi: 10.1139/z98-076

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. D., Rylands, A. B., Konstant, W. R., et al. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16, 909–923. doi: 10.1046/j.1523-1739.2002.00530.x

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd Edn. New York, NY: Springer.

Cameron, R. D., Smith, W. T., White, R. G., and Griffith, B. (2005). Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic* 58, 1–9.

Cardillo, M., Mace, G., Jones, K., Bielby, J., Bininda-Emonds, O., Sechrest, W., et al. (2005). Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241. doi: 10.1126/science.1116030

Colman, J. E., Pedersen, C., Hjermann, D. Ø., Holand, Ø., Moe, S. R., and Reimers, E. (2003). Do wild reindeer exhibit grazing compensation during insect harassment? *J. Wildl. Manage.* 67, 11–19.

COSEWIC (2017). *Committee on the Status of Endangered Wildlife in Canada*. Ottawa: COSEWIC.

Côté, S., Festa-Bianchet, M., Dussault, C., Tremblay, J.-P., Brodeur, V., Simard, M., et al. (2010). "Caribou herd dynamics: Impacts of climate change on traditional and sport harvesting," in *Nunavik and Nunatsiavit: From Science to Policy – An Integrated Regional Impact Study (IRIS) of Climate Change and Modernization*, eds M. Allard and M. Lemay (Québec: ArcticNet), 249–269.

Courbin, N., Fortin, D., Dussault, C., and Courtois, R. (2009). Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landsc. Ecol.* 24, 1375–1388. doi: 10.1007/s10980-009-9389-x

Couturier, S., Côté, S. D., Huot, J., and Otto, R. (2009a). Body-condition dynamics in a northern ungulate gaining fat in winter. *Can. J. Zool.* 87, 367–378. doi: 10.1139/z09-020

Couturier, S., Côté, S. D., Otto, R. D., Weladji, R. B., and Huot, J. (2009b). Variation in calf body mass in migratory caribou: the role of habitat, climate and movements. *J. Mammal.* 90, 442–452. doi: 10.1644/07-mamm-a-279.1

Couturier, S., Otto, J. R., and Rivard, S. (2004). *Demography of the Migratory Tundra Caribou (Rangifer tarandus) of the Nord-du-Québec Region and Labrador*. Québec: Ministère des Ressources naturelles.

Creel, S., and Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol. Evol.* 23, 194–201. doi: 10.1016/j.tree.2007.12.004

Darling, E. S., and Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecol. Lett.* 11, 1278–1286. doi: 10.1111/j.1461-0248.2008.01243.x

Davies, R. G., Orme, C. D. L., Olson, V., Thomas, G. H., Ross, S. G., Ding, T.-S., et al. (2006). Human impacts and the global distribution of extinction risk. *Proc. Biol. Sci.* 273, 2127–2133.

DeCesare, N. J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., and Musiani, M. (2014). Linking habitat selection and predation risk to spatial variation in survival. *J. Anim. Ecol.* 83, 343–352. doi: 10.1111/1365-2656.12144

DeMars, C. A., and Boutin, S. (2018). Nowhere to hide: effects of linear features on predator–prey dynamics in a large mammal system. *J. Anim. Ecol.* 87, 274–284. doi: 10.1111/1365-2656.12760

Didan, K. (2015). Data From MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC. Available online at: https://doi.org/10.5067/MODIS/MOD13Q1.006 (accessed September 28, 2017).

Dussault, C., Ouellet, J.-P., Laurian, C., Courtois, R., Poulin, M., and Breton, L. (2007). Moose movement rates along highways and crossing probability models. *J. Wildl. Manage.* 71, 2338–2345.

Dussault, C., Pinard, V., Ouellet, J.-P., Courtois, R., and Fortin, D. (2012). Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Proc. Natl. Acad. Sci. Biol. U.S.A.* 279, 4481–4488. doi: 10.1098/rspb.2012.1700

Environment Canada (2011). *Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada: 2011 Update*. Ottawa: Environment Canada.

Environment Canada (2012). *Recovery Stategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada. Species at Risk Act Recovery Strategy Series*. Ottawa: Environment Canada.

Fahrig, L., and Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecol. Soc.* 14:20.

Festa-Bianchet, M., Ray, J. C., Boutin, S., Côté, S., and Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Can. J. Zool.* 89, 419–434. doi: 10.1371/journal.pone.0136933

Forbes, B. C., Kumpula, T., Meschtyb, N., Laptander, R., Macias-Fauria, M., Zetterberg, P., et al. (2016). Sea ice, rain-on-snow and tundra reindeer nomadism in arctic Russia. *Biol. Lett.* 12:20160466. doi: 10.1098/rsbl.2016.0466

Forman, R. T. T., and Alexander, L. E. (1998). "Roads and their major ecological effects," in *Annual Review of Ecology and Systematics*, ed. D. G. Fautin (Palo Alto, CA: Annual Review Inc), 207–232.

Frid, A., and Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6:11.

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., et al. (2010). Habitat–performance relationships: finding the right metric at a given spatial scale. *Philos. Trans. R. Soc. B.* 365, 2255–2265. doi: 10.1098/rstb.2010.0085

Gaillard, J.-M., Loison, A., Festa-Bianchet, M., Yoccoz, N., and Solberg, E. J. (2003). "Ecological correlates of life span in populations of large herbivorous mammals," in *Evolutionary, Ecological, and Demographic Perspectives*, eds J. R. Carey and S. Tuljapurkar (New York, NY: Population Council), 39–56.

Gill, J. A., Norris, K., and Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biol. Conserv.* 97, 265–268. doi: 10.1016/s0006-3207(00)00002-1

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol*. 75, 887–898. doi: 10.1111/j.1365-2656.2006.01106.x

Hagemoen, R. I. M., and Reimers, E. (2002). Reindeer summer activity pattern in relation to weather and insect harassment. *J. Anim. Ecol.* 71, 883–892. doi: 10.1046/j.1365-2656.2002.00654.x

Helle, T., and Tarvainen, L. (1984). Effects of insect harassment on weight gain and survival in reindeer calves. *Rangifer* 4, 24–27.

Hosmer, D. W., and Lemeshow, S. (2000). *Applied Logistic Regression*. New York, NY: Wiley.

James, A. R. C., and Stuart-Smith, A. K. (2000). Distribution of caribou and wolves in relation to linear corridors. *J. Wildl. Manage.* 64, 154–159.

Johnson, C. J., Ehlers, L. P. W., and Seip, D. R. (2015). Witnessing extinction: cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biol. Conserv.* 186, 176–186. doi: 10.1016/j.biocon.2015.03.012

Johnson, C. J., and Russell, D. E. (2014). Long-term distribution responses of a migratory caribou herd to human disturbance. *Biol. Conserv.* 177, 52–63. doi: 10.1016/j.biocon.2014.06.007

Johnson, C. J., and St-Laurent, M.-H. (2011). "Unifying framework for understanding impacts of human developments on wildlife," in *Energy Development and Wildlife Conservation in Western North America*, ed. D. Naugle (Washington, DC: Island Press), 27–54. doi: 10.5822/978-1-61091-022-4_3

Joly, K., Klein, D. R., Verbyla, D. L., Rupp, T., and Chapin, F. S. (2011). Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography* 34, 345–352. doi: 10.1111/j.1600-0587.2010.06377.x

King, G., and Zeng, L. (2001). Logistic regression in rare events data. *Polit. Anal.* 9, 137–163. doi: 10.1093/oxfordjournals.pan.a004868

Klaczek, M. R., Johnson, C. J., and Cluff, H. D. (2015). Den site selection of wolves (*Canis lupus*) in response to declining caribou (*Rangifer tarandus groenlandicus*) density in the central Canadian Arctic. *Polar Biol.* 38, 2007–2019. doi: 10.1007/s00300-015-1759-z

Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecol. Appl.* 21, 2854–2865. doi: 10.1890/11-0666.1

Latifovic, R., and Pouliot, D. (2005). Multitemporal land cover mapping for Canada: methodology and products. *Can. Aeronaut. Space. J.* 31, 347–363.

Latifovic, R., Pouliot, D., and Olthof, I. (2017). Circa 2010 land cover of Canada: local optimization methodology and product development. *Remote Sens.* 9:1098. doi: 10.3390/rs9111098

Le Corre, M., Dussault, C., and Côté, S. D. (2014). Detecting changes in the annual movements of terrestrial migratory species: using the first-passage time to document the spring migration of caribou. *Mov. Ecol.* 2:19. doi: 10.1186/s40462-014-0019-0

Le Corre, M., Dussault, C., and Côté, S. D. (2017). Weather conditions and variation in timing of spring and fall migrations of migratory caribou. *J. Mammal.* 98, 260–271.

Lebel, F., Dussault, C., Massé, A., and Côté, S. D. (2012). Influence of habitat features and hunter behavior on white-tailed deer harvest. *J. Wildl. Manage.* 76, 1431–1440. doi: 10.1002/jwmg.377

Leblond, M., St-Laurent, M.-H., and Côté, S. D. (2016). Caribou, water and ice - Fine-scale movements of a migratory arctic ungulate in the context of climate change. *Mov. Ecol.* 4:14. doi: 10.1186/s40462-016-0079-4

Lesmerises, F., Dussault, C., and St-Laurent, M.-H. (2019). Effect of behavioral marginality on survival of an alpine ungulate. *Ecosphere* 10:e02806.

Lodé, T. (2000). Effect of a motorway on mortality and isolation of wildlife populations. *AMBIO* 29, 163–166. doi: 10.1579/0044-7447-29.3.163

Mac Nally, R., Duncan, R. P., Thomson, J. R., and Yen, J. D. L. (2018). Model selection using information criteria, but is the "best" model any good? *J. Appl. Ecol.* 55, 1441–1444. doi: 10.1111/1365-2664.13060

Mallory, C. D., and Boyce, M. S. (2018). Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environ. Rev.* 26, 13–25. doi: 10.1139/er-2017-0032

Manly, B. F., Thomas, D. L., McDonald, T. L., and Erickson, W. P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Berlin: Springer.

Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D., and Loison, A. (2014). Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biol. Conserv.* 177, 1–11. doi: 10.1016/j.biocon.2014.05.022

McLoughlin, P. D., Boyce, M. S., Coulson, T., and Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proc. R. Soc. B.* 273, 1449–1454. doi: 10.1098/rspb.2006.3486

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., and Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *J. Anim. Ecol.* 79, 4–12. doi: 10.1111/j.1365-2656.2009.01613.x

Moreau, G., Fortin, D., Couturier, S., and Duchesne, T. (2012). Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. *J. Appl. Ecol.* 49, 611–620. doi: 10.1111/j.1365-2664.2012.02134.x

Mörschel, F. M., and Klein, D. R. (1997). Effects of weather and parasitic insects on behavior and group dynamics of caribou of the Delta herd, Alaska. *Can. J. Zool.* 75, 1659–1670. doi: 10.1139/z97-793

MRNF (2012). *Rapport sur Les Activités Minières au Québec*. Québec: MRNF.

NASA (2016). *Land Processes Ditributed Active Archive Center (LPDAAC), USGS Earth Resources Observation and Science (EROS) Center*. Sioux Falls: Vegetation Indices 16-Day L3 Global 250 m - MOD13Q1.

National Oceanic and Atmospheric Administration [NOAA] (2017). *Climate Dataset: North American Regional Reanalysis (NARR)*. Boulder, CO: Physical Sciences Laboratory.

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., and Newton, A. (2003). Progressive impact of piecemeal infrastructure development on wild reindeer. *Biol. Conserv.* 113, 307–317. doi: 10.1016/s0006-3207(03)00048-x

Newton, E. J., Patterson, B. R., Anderson, M. L., Rodgers, A. R., Vander, Vennen, L. M., and Fryxell, J. M. (2017). Compensatory selection for roads over natural linear features by wolves in northern Ontario: implications for caribou conservation. *PLoS One* 12:e0186525. doi: 10.1371/journal.pone.0186525

Pachkowski, M., Côté, S. D., and Festa-Bianchet, M. (2013). Spring-loaded reproduction: effects of body condition and population size on fertility in migratory caribou (*Rangifer tarandus*). *Can. J. Zool.* 91, 473–479. doi: 10.1139/cjz-2012-0334

Pettorelli, N. (2013). *The Normalized Difference Vegetation Index*. Oxford, UK: Oxford University Press.

Plante, S., Dussault, C., and Côté, S. D. (2017). Landscape attributes explain migratory caribou vulnerability to sport hunting. *J. Wildl. Manage.* 81, 238–247. doi: 10.1002/jwmg.21203

Plante, S., Dussault, C., Richard, J. H., and Côté, S. D. (2018). Human disturbance effects and cumulative habitat loss in endangered migratory caribou. *Biol. Conserv.* 224, 129–143. doi: 10.1016/j.biocon.2018.05.022

Poole, K. G., Gunn, A., Patterson, B. R., and Dumond, M. (2010). Sea ice and migration of the Dolphin and Union caribou herd in the Canadian Arctic: an uncertain future. *Arctic* 63, 414–428.

R Core Team (2018). *R: A language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: https://www.R-project.org/

Ramey, R. R., Thorley, J. L., and Ivey, A. S. (2018). Local and population-level responses of Greater sage-grouse to oil and gas development and climatic variation in Wyoming. *PeerJ* 6:e5417. doi: 10.7717/peerj.5417

Rettie, W. J., and Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23, 466–478. doi: 10.1034/j.1600-0587.2000.230409.x

Robertson, B. A., and Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87, 1075–1085. doi: 10.1890/0012-9658(2006)87[1075:affuet]2.0.co;2

Rupp, T. S., Olson, M., Adams, L. G., Dale, B. W., Joly, K., Henkelman, J., et al. (2006). Simulating the influences of various fire regimes on caribou winter habitat. *Ecol. Appl.* 16, 1730–1743. doi: 10.1890/1051-0761(2006)016[1730:stiovf]2.0.co;2

Schlaepfer, M. A., Runge, M. C., and Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends Ecol. Evol.* 17, 474–480. doi: 10.1016/s0169-5347(02)02580-6

Seip, D. R. (1991). Predation and caribou populations. *Rangifer* 7, 46–52.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. *Bioscience* 37, 789–799. doi: 10.1111/mec.14842

Shackelford, N., Standish, R. J., Ripple, W., and Starzomski, B. M. (2018). Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conserv. Biol.* 32, 672–684. doi: 10.1111/cobi.13036

Skatter, H. G., Charlebois, M. L., Eftestøl, S., Tsegaye, D., Colman, J. E., Kansas, J. L., et al. (2017). Living in a burned landscape: Woodland caribou (*Rangifer tarandus caribou*) use of postfire residual patches for calving in a high fire – low anthropogenic Boreal Shield ecozone. *Can. J. Zool.* 95, 975–984. doi: 10.1139/cjz-2016-0307

Soppela, P., Nieminen, M., and Timisjärvi, J. (1986). Thermoregulation in reindeer. *Rangifer* 1, 273–278.

Sorensen, T., McLoughlin, P. D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., et al. (2008). Determining sustainable levels of cumulative effects for boreal caribou. *J. Wildl. Manage.* 72, 900–905. doi: 10.2193/2007-079

Tablado, Z., and Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance. *Biol. Rev.* 92, 216–233. doi: 10.1111/brv.12224

Taillon, J., Brodeur, V., and Rivard, S. (2016). *). Biological Status of Migratory Caribou, Leaf River Herd*. Québec: Ministère des Forêts.

Toupin, B., Huot, J., and Manseau, M. (1996). Effect of insect harassment on the behaviour of the Rivière George caribou. *Arctic* 49, 375–382.

Uboni, A., Smith, D. W., Stahler, D. R., and Vucetich, J. A. (2017). Selecting habitat to what purpose? The advantage of exploring the habitat–fitness relationship. *Ecosphere* 8:e01705. doi: 10.1002/ecs2.1705

United Nation Environmental Programme [UNEP] (2001). *GLOBIO-Global Methodology for Mapping Human Impacts on the Biosphere*, eds C. Nellemann, L. Kullerud, I. Vistnes, B. C. Forbes, G. P. Kofinas, B. P. Kaltenborn, et al. (Nairobi: UNEP).

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., et al. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7:12558. doi: 10.1038/ncomms12558

Vistnes, I., and Nellemann, C. (2008). The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biol.* 31, 399–407. doi: 10.1007/s00300-007-0377-9

Vors, L. S., and Boyce, M. S. (2009). Global declines of caribou and reindeer. *Glob. Change Biol.* 15, 2626–2633. doi: 10.1111/j.1365-2486.2009.01974.x

Wasser, S. K., Keim, J. L., Taper, M. L., and Lele, S. R. (2011). The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Front. Ecol. Environ.* 9, 546–551. doi: 10.2307/41479958

Weladji, R. B., and Forbes, B. C. (2002). Disturbance effects of human activities on *Rangifer tarandus* habitat: implications for life history and population dynamics. *Polar Geogr.* 26, 171–186. doi: 10.1080/789610191

Weladji, R. B., Holand, Ø., and Almøy, T. (2003). Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. *J. Zool.* 260, 79–85. doi: 10.1017/s0952836903003510

Yamasaki, S. H., Duchesneau, R., Doyon, F., Russell, J. S., and Gooding, T. (2008). Making the case for cumulative impacts assessment: modelling the potential impacts of climate change, harvesting, oil and gas, and fire. *For. Chron.* 84, 349–368. doi: 10.5558/tfc84349-3

Zager, P., and Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* 17, 95–108. doi: 10.2192/1537-6176(2006)17[95:troabb]2.0.co;2

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. doi: 10.1111/j.2041-210x.2009.00001.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

REVIEW
published: 30 June 2020
doi: 10.3389/fevo.2020.00211

Modeling Landscape Use for Ungulates: Forgotten Tenets of Ecology, Management, and Inference

Michael J. Wisdom[1]*, Ryan M. Nielson[2], Mary M. Rowland[1] and Kelly M. Proffitt[3]

[1] US Forest Service Pacific Northwest Research Station, La Grande, OR, United States, [2] Eagle Environmental, Incorporated, Fort Collins, CO, United States, [3] Montana Fish, Wildlife & Parks, Bozeman, MT, United States

Modeling landscape use (i.e., estimating the probability or relative probability of use, occurrence, or selection in a given area and time) by ungulates is an increasingly common and important practice in research and management. Models of occupancy, distribution, movement, habitat use, and resource selection are formal approaches by which landscape use has been characterized and results published for a myriad of ungulate species. Understanding landscape use has benefited from a growing volume of data on animal locations and model covariates, and the ease of modeling with automated software. These models are particularly noteworthy in their potential to estimate use at multiple scales, characterize individual and population distributions, and predict spatiotemporal responses to environmental change. Despite these advantages, ecological processes can be secondary or forgotten. Models without a strong ecological foundation may perform well in case studies but fail to advance our understanding of a species' habitat requirements and response to habitat change across a broad inference space. In response, we describe criteria, synthesized from the ecological literature, of direct relevance to modeling landscape use for advancing the ecological understanding and effective management of ungulates. Criteria include (1) a knowledge coproduction framework for scientist-manager collaborations; (2) an explicit inference space with supporting replication for broad inference; (3) process covariates and their ecological scaling to address habitat requirements; (4) ecologically plausible sets of competing models; (5) model evaluation to address objectives and hypotheses of ecological importance; (6) assessment of relationships with animal and population performance; and (7) reliable interpretations for ecological understanding and management uses. Contemporary modeling of landscape use has been challenged by large, disparate data sources and an emphasis on statistical methods. However, advances in knowledge and conservation of ungulates based on tenets of ecology, management, and inference are achievable with careful consideration of these criteria.

Keywords: habitat use, model development, covariates, evaluation, inference space, occupancy modeling, resource selection, ungulate management

Edited by:
Paul Richard Krausman,
University of Arizona, United States

Reviewed by:
Stan Boutin,
University of Alberta, Canada
John Alfred Bissonette,
Utah State University, United States

****Correspondence:***
Michael J. Wisdom
michael.wisdom@usda.gov

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *01 February 2020*
Accepted: *08 June 2020*
Published: *30 June 2020*

Citation:
Wisdom MJ, Nielson RM, Rowland MM and Proffitt KM (2020) Modeling Landscape Use for Ungulates: Forgotten Tenets of Ecology, Management, and Inference. Front. Ecol. Evol. 8:211. doi: 10.3389/fevo.2020.00211

INTRODUCTION

Modeling landscape use, based on estimates of occupancy (Royle et al., 2012), distributions (Jarnevich et al., 2015), movement (Horne et al., 2007), frequency of use (Nielson and Sawyer, 2013), or resource selection (Boyce et al., 2002), is a common practice in contemporary ungulate research and management. While statistical assumptions and intended applications vary, models of landscape use estimate the probability or relative probability of species use, occurrence, or selection of a given area and time (per details by Lele et al., 2013), and provide valuable knowledge about animal behavior that presumably reflects a species' habitat needs (Gaillard et al., 2010). These models are particularly appealing because they are highly flexible, employing a multivariate framework of potential covariates and interactions that can include predation, nutrition, human disturbance, vegetation, climate, weather, topography, and myriad other biotic and abiotic factors (Boyce et al., 2016). Well-designed models of landscape use provide a means to evaluate and predict how populations respond to habitat change from a variety of anthropogenic activities, management strategies, and ecological processes (e.g., Sawyer et al., 2006, 2019; White et al., 2018; Briscoe et al., 2019; Reinking et al., 2019).

Spatial data readily available from geographic information systems (GIS) provide continuous coverage, open-source layers for deriving many covariates (Turner et al., 2015), and current technologies provide voluminous data on animal use across large areas (Hebblewhite and Haydon, 2010; Burton et al., 2015; Middleton et al., 2019). Development and evaluation of landscape-use models can now be accomplished efficiently with canned statistical analysis routines in freely available software packages.

Landscape-use modeling, however, often is focused on statistical methods rather than on ecological processes (Wisdom et al., 2018a,b; Briscoe et al., 2019). Without a strong ecological framework, critics have argued that models of landscape use are not process-based (Morris, 2003; Gaillard et al., 2010), not developed with ecological rationale (McLoughlin et al., 2010; Laforge et al., 2015), fail to identify a clear inference space with appropriate replication (Nielsen et al., 2010; Wisdom et al., 2018a,b; Briscoe et al., 2019), not evaluated with independent data (Roberts et al., 2017) of ecological importance (Rykiel, 1996; Johnson, 2001), and lack connections with demographic consequences (Gaillard et al., 2010; Matthiopoulos et al., 2015, 2019). Without considering these issues, it has been argued that patterns of landscape use simply reflect animal behavior (Garshelis, 2000). And, if patterns of landscape use are not replicated over large areas and long time periods, robust predictions to variation in space and time are unknown.

Critics have voiced particular concerns about the use of model covariates that may not reflect ecological processes (Morris, 2003). Covariates often are assumed to index specific processes or habitat requirements (i.e., surrogate variables), but evidence for linkages to processes often is absent or unclear (Nielsen et al., 2010). Many vegetation and abiotic covariates, for example, are readily available in open-source formats world-wide (Chen et al., 2015; Shean et al., 2016). By contrast, covariates of nutrition, predation, and human disturbance, which explicitly reflect processes of energy acquisition and loss, typically require extensive field sampling (e.g., Cook et al., 2016; Proffitt et al., 2016, 2019). Consequently these process covariates are less likely to be considered (Wisdom et al., 2018a), in contrast to more available "convenience covariates" requiring little or no fieldwork. Uncritical use of convenience covariates for modeling, akin to "convenience sampling" in ecological studies, poses hidden problems that can unknowingly bias or inhibit knowledge gain (Anderson, 2001).

Ecological scaling of covariates to match scales of different life-history characteristics also is frequently ignored during model development and selection (McGarigal et al., 2016), and can result in models that are ecologically misleading or irrelevant (Mateo Sánchez et al., 2014). Explicit rationale for how covariates of energy acquisition (e.g., nutrition) and energy loss (e.g., human disturbance, predation, climatic stressors) are considered in modeling often is unstated or secondary to statistical paradigms that conventionally govern model development and selection (e.g., Burnham and Anderson, 2002; Hooten and Hobbs, 2015).

Finally, the level of spatial and temporal replication used to develop and evaluate models dictates an explicit inference space, yet often is undefined or not quantified for mapping (Yates et al., 2018). Most landscape-use models are based on case studies (one place, one time) with limited inference (Johnson, 2002; Yates et al., 2018). A growing suite of large but disparate datasets on ungulate landscape use, however, provides new opportunities for model replication across multiple study areas and time periods as a form of ecological meta-analysis (Gurevitch et al., 2018). Opportunistic use of disparate data sources poses new challenges for modeling because data are not collected under an *a priori*, unified sampling design, and problematic sources of variability must be addressed (Gurevitch et al., 2018).

These are daunting challenges for species with broad distributions, seasonal habitat needs, and diverse behavioral and evolutionary strategies, combined with complex management issues. These challenges necessitate modeling landscape use with a variety of covariates that address multiple spatiotemporal scales, ecological processes, and land uses (Apollonio et al., 2017). Many ungulates are migratory (Bolger et al., 2008; Sawyer et al., 2009; Barker et al., 2019), for example, requiring models that address seasonal ranges and multiple land ownerships. Their relatively large body size and dietary preferences also have led to human–wildlife conflicts (Gill, 1992; Sekhar, 1998; Ward et al., 2004), warranting models that accurately predict occurrence. Ungulates often are hunted, and harvest regulations depend on knowledge of landscape use (Krausman and Bleich, 2013). Many ungulates also respond negatively to anthropogenic disturbance by increasing movement rates (Spitz et al., 2019), shifting distributions (Sawyer et al., 2006), or even abandoning ranges (Hebblewhite, 2008). Models of landscape use that include covariates of human disturbance thus are essential to land-use planning (Proffitt et al., 2010; Dwinnell et al., 2019).

In response, we describe a landscape-use modeling framework for ungulates and other species that explicitly considers ecological and management criteria to frame and guide model design, development, and utility. We do not delve into statistical methods of modeling landscape use, which have been reviewed extensively (Boyce and McDonald, 1999; Boyce et al., 2002; Gillies et al., 2006; Lele et al., 2013; Muff et al., 2019). Instead, we provide ecological and management justification for modeling criteria, describe benefits of their consideration, and highlight examples of their use for ungulates, with obvious relevance to other vertebrate taxa.

ECOLOGICAL AND MANAGEMENT CRITERIA FOR MODELING LANDSCAPE USE

We identified seven criteria from the literature as tenets for modeling landscape use by ungulates (**Table 1** and **Figure 1**). Similar criteria have been broadly described in the literature on sampling and experimental design for ecological and management studies, but have not been synthesized for modeling applications for ungulates or other vertebrates in one comprehensive source. We considered this need and integrated research and management considerations in each criterion.

We present the criteria as a linear process for modeling in three phases: (1) design, (2) development; and (3) utility (**Figure 1**). Model design includes all aspects of planning: establishing and using effective partnerships among scientists, managers, and stakeholders to define model purpose, objectives, and ecological hypotheses and expectations for testing (see the section "Knowledge Coproduction Framework"); and identifying the targeted geographic area, environmental conditions, and populations for inference (see the section "Explicit Inference Space with Supporting Replication"). Model development builds on design to address how covariates representing ecological relationships and habitat requirements are identified and scaled to match targeted life-history and seasonal-use activities (see the section "Process Covariates and Their Ecological Scaling"); and using these covariates in ecologically plausible, competing models that reflect life-history traits, habitat requirements, and evolutionary behavior (see the section "Ecological Model Development and Selection"). Model utility encompasses the final, critical phase that provides measures and interpretations of the ecological and management worth of a selected model. Criteria also include the evaluation of a model in relation to *a priori* hypotheses and expectations (see the section "Model Evaluation to Address Objectives"); identifying whether model predictions or components further relate to demographic performance of targeted populations (see the section "Relationships With Animal and Population Performance"); and the interpretations and uses of a model that provide essential context and direction for how results can advance ecological understanding and benefit management (see the section "Reliable Interpretations and Uses").

The relevance of each criterion depends on objectives and associated hypotheses. Models developed for ecological understanding but not for explicit management applications, for example, do not require a large investment in knowledge coproduction with managers. Other models may have narrowly defined objectives for management, such as characterizing ungulate distributions by land ownership, without resources or need to expand inference space, formally evaluate the model, or relate predictions to demography. In that context, we consider the criteria as aspirational standards by which modelers of landscape use could evaluate the ecological and management worth of their work, not edicts to blindly follow. We offer the criteria to complement the well-developed and justified focus on statistically based modeling, to improve ecological understanding and management utility.

Knowledge Coproduction Framework

Knowledge coproduction is defined as the "process of producing usable, or actionable, science through collaboration between scientists and those that use science to make policy and management decisions" (Meadow et al., 2015). Coproduction is highly relevant to landscape-use modeling for meeting the dual purpose of improving ecological understanding of a species' habitat requirements and using this knowledge to meet societal needs. Models created with this dual purpose are most effective when designed and implemented collaboratively among scientists, managers, and stakeholders (Irvine et al., 2009; Canfield et al., 2013; Wisdom et al., 2018b).

For ungulates, these collaborations are particularly important because complex management issues, potential for property damage and human conflicts, and important recreational values require scientists and managers to work closely with a diversity of stakeholders. Coproduction is a natural extension of the types of interactions among scientists, managers, and stakeholders on issues of harvest management, which are relevant to a high percentage of ungulates that are hunted (Heffelfinger et al., 2013; Krausman and Bleich, 2013).

Examples of effective coproduction modeling in ecology are growing (e.g., Davies and White, 2012; Reyers et al., 2015; Nel et al., 2016) but not currently standard practice (Addison et al., 2013; Meadow et al., 2015). The benefits of formal adoption of coproduction methods for modeling include: (1) better articulation of knowledge gaps impeding ecological understanding and management; (2) improved communication of modeling results, inference space, and proper application; and (3) increased acceptance and use of models in management. Coproduction as applied to landscape-use modeling involves collaboration in all phases of the scientific process: defining objectives and inference space, describing ecological and management hypotheses for testing, identifying analysis scales and potential covariates, developing and implementing appropriate modeling methods, interpreting results, and careful inference (**Table 1** and **Figure 1**).

While deceptively simple, coproduction can be daunting and time-consuming (Voinov et al., 2016), requiring more resources than traditional research. However, by establishing a formal process of collaboration among scientists, managers, and stakeholders, ownership in the process and successful outcomes become more likely compared to traditional approaches led by scientists (Voinov et al., 2016; Merkle et al., 2019). Coproduction requires both researchers and managers to make a genuine, long-term commitment to thoughtfully consider each other's viewpoints and objectives, and to work collaboratively for mutual benefit.

TABLE 1 | Criteria to frame and guide the design, development, utility of landscape-use models for ungulates, and associated description and rationale with example supporting citations.

Criteria	Description and rationale	Example supporting citations
Knowledge coproduction framework	A shared modeling process among scientists, managers, and stakeholders to meet mutually established objectives will ensure effective model uses that are scientifically credible and of high management utility.	Canfield et al. (2013), Wisdom et al. (2018a)
Explicit inference space with supporting replication	Quantifying and mapping the conditions in which inferences from model predictions can be reliably made defines the ecological interpretations and management applications that are possible. Models developed from multiple areas and time periods provide inferences that are robust to environmental variation in the associated space and time.	Rowland et al. (2018a), Salas et al. (2018), Briscoe et al. (2019), Lula et al. (2020)
Process covariates and their ecological scaling	Model covariates that embody ecological relationships and associated habitat requirements, scaled to match life-history traits and seasonal activities of interest, provide clear ecological understanding and predictable characterization of landscape use for management.	Laforge et al. (2015), Wisdom et al. (2018b), Briscoe et al. (2019)
Ecological model development and selection	Model development and selection based on ecological rationale, such as with model suites composed of covariates related to energy gain, conservation, or loss, explicitly addresses habitat requirements of a species, providing a causal basis for patterns of landscape use and credible uses in management.	Long et al. (2014), Rowland et al. (2018b), Eckrich et al. (2019), Lula et al. (2020)
Model evaluation to address objectives	Models can be evaluated with a variety of methods identified as part of objectives and *a priori* hypotheses and expectations. Conventional methods that correlate predictions of landscape use with observed use are ideally based on independent data. Conclusions are limited to the environmental variation modeled.	Rykiel (1996), Johnson (2001), Roberts et al. (2017), Rowland et al. (2018b)
Relationships with animal and population performance	Predictions from models of landscape use - or specific habitat components - that are correlated with animal or population performance reflect the fitness consequences of landscape use, and thus extend utility beyond traditional predictions of use.	Nilsen et al. (2004), Gaillard et al. (2010), Losier et al. (2015), Matthiopoulos et al. (2015, 2019)
Reliable interpretations and uses	Results from modeling require interpretation to determine how well findings support objectives, hypotheses, inference space, and intended uses. Results that do not support expected model utility can inform new studies and modeling to address model deficiencies through adaptive management.	Walters (1986), Yates et al. (2018)

Examples

A long-term collaboration to model elk (*Cervus canadensis*) habitat used principles of knowledge coproduction from development (Canfield et al., 2013) to application (Ranglack et al., 2017; DeVoe et al., 2019; Lowrey et al., 2020). Following a series of stakeholder and legal challenges to elk habitat management in western Montana, wildlife scientists and managers from the U.S. Forest Service and Montana Fish, Wildlife and Parks formed a committee to discuss and compile recommendations for collective improvement of elk habitat. The committee spent 3 years sharing knowledge, discussing uncertainties in current science, and identifying modeling needed to improve elk habitat management in the region.

The resulting recommendations (Canfield et al., 2013) prompted a series of research and modeling projects to address management needs of both agencies. Ranglack et al. (2017) evaluated attributes of security areas used by nine elk populations and developed new management definitions for optimal canopy cover and distance from motorized routes that substantially improved elk security. Definitions are now used to inform management of vegetation and motorized access during archery and rifle elk seasons on public lands.

DeVoe et al. (2019) built on these definitions to evaluate the nutritional consequences of archery hunting on elk. Results included recommendations to integrate management of forage and security (i.e., canopy cover and motorized routes) to improve habitat and encourage elk to remain on public lands throughout the rifle season, the traditional period and method of population management. Lowrey et al. (2020) addressed an additional knowledge gap regarding elk responses to dramatic changes in forest structure and elk security brought about by severe infestations of mountain pine beetle (*Dendroctonus ponderosae*). Authors used their findings to define management thresholds for canopy cover and distance from motorized routes to maintain elk use during hunting seasons in areas experiencing severe conifer mortality from beetle infestations. Results are being used to inform management of elk security on public forests impacted by beetle-kill.

Explicit Inference Space With Supporting Replication

Clearly defining an inference space during model design ensures that sampling replication is appropriate for inference across the selected spatial and temporal extents (Hobbs, 2003). We define "inference space," also referred to as the "target system" (Yates et al., 2018), as the geographic area and associated environmental conditions and their temporal variability to which interpretations, conclusions, and predictions of landscape use or other ecological relationships are made (also see Garton et al., 2001; Morrison, 2001, 2012). In spite of the importance of a clearly defined inference space, we noted few cases in the ecological literature where a target system was purposely identified and quantified for model applications (Yates et al., 2018). And yet, every model has its predictive limits, which have been well-defined for statistical inference (Chatfield,

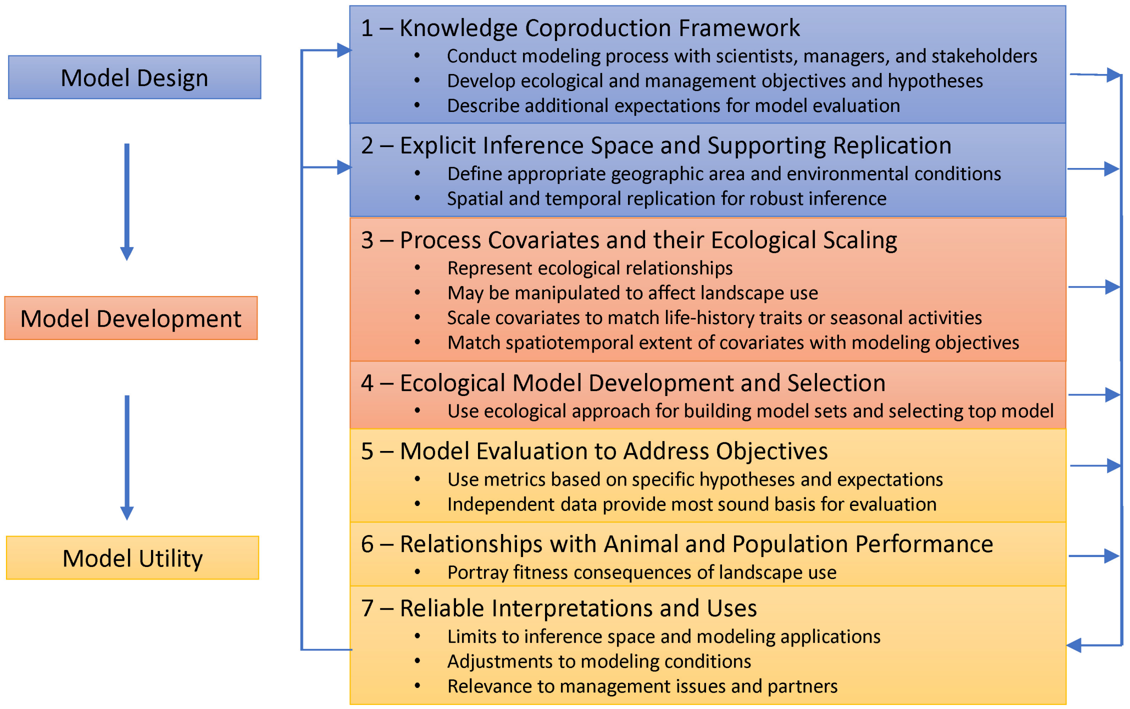

FIGURE 1 | Modeling phases (left boxes) and associated design criteria (right boxes) that outline an ecological and management process (downward arrows) for model design, development, evaluation, and interpretation of landscape use models for ungulates. The primary feedback loop (upward arrows) is generated from interpretation of results from model development, selection, and evaluation, and relationships to performance to determine how well findings support objectives, hypotheses, inference space, and intended uses. Results that do not support model expectations can guide additional studies and modeling to address model deficiencies, using concepts of adaptive management (Walters, 1986).

1995). Understanding inferential limits from ecological and management perspectives reduces misapplication of the model (Garton et al., 2001).

A challenge in addressing inference space is the reliance on models of landscape use developed and evaluated with data from one study area as a case study lacking replication. By definition, case studies are based on local conditions, which limit knowledge gain and management utility to those specific conditions. As the number of study areas or similar units of spatial replication increases, the inference space for model predictions expands to an area larger than the replicates themselves (Yates et al., 2018). Inference space then represents conditions across the larger landscape, encompassing like variation among study areas. Broad scales of inference are possible, such as to habitats within an entire ecoregion or biome for widely distributed ungulate species [e.g., Acevedo et al., 2011 for landscape-use modeling of wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), Iberian wild goat (*Capra pyrenaica*), and roe deer (*Capreolus capreolus*) in Spain; and Kanagaraj et al., 2019 for the sub-ungulate Asian elephant (*Elephas maximus*) in India and Nepal].

Inference space for modeling landscape use can be done in two ways, *a priori* or *a posteriori*. In the first, an explicit target system is identified when developing modeling objectives and hypotheses for testing. A formal sampling design is developed, with focus on the spatial and temporal replication needed for desired inference. If objectives call for development and validation of a landscape-use model across an extensive area, such as an ecoregion [e.g., Salas et al., 2018 for Marco Polo Sheep (*Ovis ammon polii*) across 4.1 million ha in eastern Tajikistan], the geographic extent of sample replicates needed for modeling will be substantially larger than those for a local population [e.g., Lula et al., 2020 for bighorn sheep (*Ovis canadensis*) restoration in the Madison Range of southwest Montana, United States]. The number and type of replicates needed will largely depend on the environmental variation considered in modeling (**Figure 2**), and classic methods of sampling design can be used to allocate units of replication to address the environmental variation in the defined inference space (Krebs, 1989).

Explicitly defining the inference space and units of replication before data collection and modeling under an *a priori* design can help avoid the "Modifiable Areal Unit Problem" (MAUP; Openshaw, 1984), in which the size and distribution of sampling (replication) units, and their aggregation, can lead to different results depending on how the units are combined for analysis (Jelinski and Wu, 1996; Bissonette, 2017). Study areas or other spatial replicates (polygons) are modifiable and setting arbitrary study extents based on mapping boundaries (e.g., ownership) can dramatically affect response variables. Thus, establishing spatial extents of these areas *a priori* to encompass variation of interest helps avoid the MAUP (Bissonette, 2017).

The *a posteriori* approach involves modeling landscape use opportunistically with available data and adapts inference space

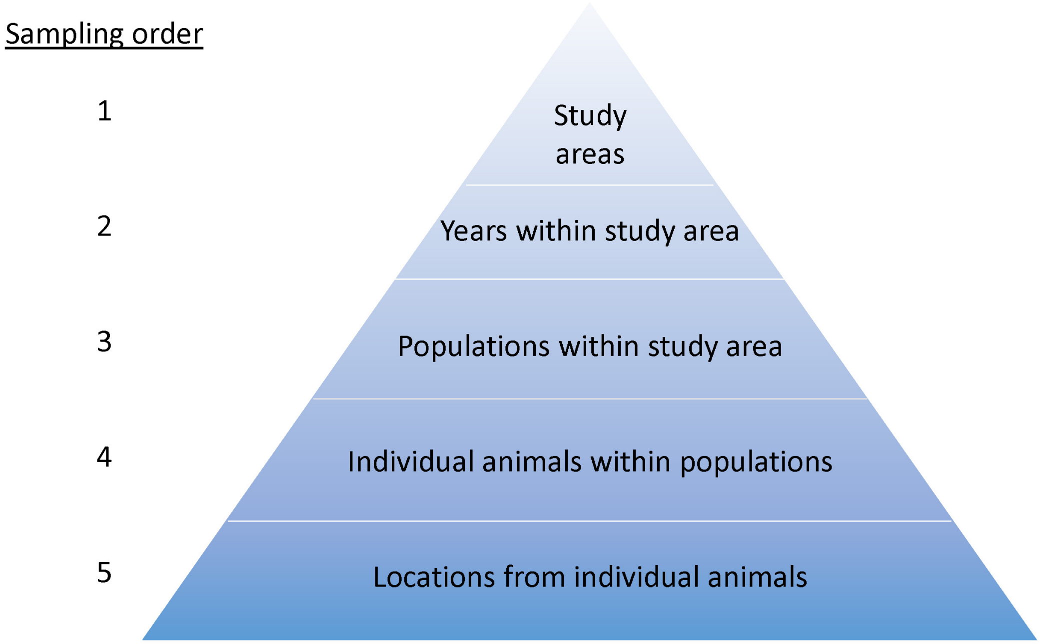

FIGURE 2 | Sampling and inference hierarchy for landscape-use modeling. Model training and testing, including estimates of precision, should replicate this order. When making inference at one level (e.g., a population), the next level in the hierarchy is the appropriate unit of replication (e.g., individual animals) for estimating precision. Estimates of precision for a single study area should consider blocking at the next available level where replication occurs. For example, if within one study area (1), multiple years are studied (2), then model evaluation should use years (2), populations (3), or individual animals (4) for blocking, depending on the available sample size at each level. Estimates for a broader landscape require a sample ($n > 1$) of study areas.

and related objectives and hypotheses to observed conditions [e.g., Rowland et al., 2018a for elk; Coe et al., 2018 and Eckrich et al., 2019 for mule deer (*Odocoileus hemionus*)]. Given the lack of a unified, consistent sampling design, this "default" inference space can be more limited than that under *a priori* allocation of replicates to match a desired target system. Despite these challenges, the emergence of large data sets on animal locations has provided new opportunities for expanding inference space. However, it is not always clear how well landscape-use models can be developed opportunistically *a posteriori*, with data from multiple replicate areas, as a form of spatially explicit meta-analysis (Gurevitch et al., 2018). Telemetry data collected across different areas and times, for example, often differ in number of animals collared, relocation frequency, fix success, and reasons for animal collaring (Rowland et al., 2018b). Moreover, few telemetry-based studies of landscape use explain how their capture protocols result in a set of collared animals that are representative of the population to which inferences will be made (Garton et al., 2001).

Differences in resource availability across time and space may also result in different patterns of landscape use, resulting in spurious conclusions (Holbrook et al., 2019), given the plethora of problems introduced by the MAUP (Bissonette, 2017). In addition, ungulate patterns of landscape use are typically density-dependent (McLoughlin et al., 2006; Godvik et al., 2009). Replication across increasingly large spatial extents and longer time periods may capture a variety of ungulate patterns of landscape use not otherwise revealed by accounting for functional responses in relation to population density (van Beest et al., 2012). At a minimum, basic knowledge of whether population density varies across replicates is needed to interpret potential variation in landscape use (McLoughlin et al., 2010). Otherwise, deriving a global model of landscape use, such as by averaging model coefficients among replicates, may result in an "average" model that represents none of the underlying areas (e.g., Russell et al., 2015). The same challenge exists for successfully building global models where management of ungulate harvest and predator complexes varies markedly across the inference space.

Despite these challenges, a combination of disparate sources of data used as replicates, both published and unpublished, has been integrated successfully in ecological meta-analysis (Gurevitch et al., 2018). Opportunistic syntheses of these data require clear ecological hypotheses to direct modeling efforts (Morrison, 2001, 2012). Opportunistic analyses further rely on integration of spatially and temporally replicated data that accounts for inherent data imprecision, and that constrains limits of inference accordingly (Johnson, 1999, 2002; Yates et al., 2018), rather than routinely rejecting the approach for lack of a unified, *a priori* design (Romesburg, 1981; Hurlbert, 1984).

We emphasize use of study areas as spatial replicates because they represent the most obvious and traditional form of replication that is geographically extensive and thus can encompass appropriate extents or targeted populations (**Figure 2**)—in contrast to more traditional use of animals as sample units and their locations as subsamples in case studies.

A noteworthy example of spatial replication was the habitat-use model for mule deer developed by Coe et al. (2018), in which nine study areas were used as replicates for inference across three million ha of the sagebrush biome (**Figure 3**). Sampling designs, however, are evolving, and different forms of spatial and temporal replication can be used to support the associated inference space (**Figure 2**). New technologies have the potential for systematic sampling over broad areas of a species range, such as with geographically extensive camera traps arrays (Ahumada et al., 2011; Menkham et al., 2019) or broad-scale aerial sampling (Nielsen et al., 2010; Bristow et al., 2019). Species distribution modeling is a specific example of landscape-use modeling designed to address broad-scale patterns of occurrence and covariates accounting for those patterns, often without classical use of replicated study areas, but instead systematically sampling across the entire inference space (e.g., Zimmermann et al., 2010; Jarnevich et al., 2015).

Consideration of an explicit inference space deserves much greater attention as part of landscape-use modeling, and is essential to robust predictions. Regardless of approach, the key steps are to identify the targeted area and conditions for desired inference, define the spatial and temporal replicates needed to support the range of conditions, and account for a variety of sources of sampling and environmental variation to enable robust predictions.

Examples

Modeling with an explicit inference space is particularly useful when evaluating future or potential conditions, such as projected effects of climate change (Salas et al., 2018), wildfire (Proffitt et al., 2019), or other disturbances on ungulate landscape use (Riggs et al., 2015). One exemplary study that defined an explicit inference space used resource selection functions (RSFs) to evaluate restoration potential for bighorn sheep in southwest Montana, United States (**Figure 4**) (Lula et al., 2020). Inference space was identified *a priori* as the historic sheep distribution across the Madison Range, with current sheep populations occupying the southwestern and northeastern portions (**Figure 4**). Model design included sampling in both populations, with the southwestern population used for model development, internal validation, and predictions and the northeastern population for external model validation. The authors carefully assessed the range of environmental variation within modeling areas, compared conditions to the targeted prediction area (i.e., the Madison Range), and limited predictions to areas with conditions similar to those used for model development and validation. Accordingly, the northern portion of the Madison Range was omitted from predictions because conditions differed from model development and validation areas, leading to potential for invalid predictions beyond the appropriate inference space.

Process Covariates and Their Ecological Scaling

Model covariates that embody ecological processes and the associated habitat requirements of a species have been referred to as process covariates (Nielsen et al., 2010). Examples in ungulate landscape-use modeling include nutrition (Rowland et al., 2018a,b, 2000; DeVoe et al., 2019); predation (Kittle et al., 2008; Ciuti et al., 2012); human disturbance (Jiang et al., 2008; Bonnot et al., 2013); land-use change (Acevedo et al., 2011; Schuette et al., 2016); climate change (Ciach and Pęksa, 2018; Salas et al., 2018); and weather (van Beest et al., 2012; Long et al., 2014). Many process covariates can also be managed to affect landscape use (Wisdom et al., 2018a,b). Because process covariates are drivers of ecological patterns, their emphasis in modeling is more likely to result in predictions of landscape use that are robust to spatiotemporal variation in the environment (Gaillard et al., 2010).

Other model covariates may provide important environmental context to enhance model predictions but may not represent explicit ecological processes, nor can they be actively managed. Examples of these contextual covariates include vegetation type, topography, soils, and geology. The specific role of contextual covariates in modeling can be unclear without empirical support. For example, ungulate selection for cool, mesic aspects during hot summers could indicate selection for areas of higher forage productivity, increased thermal relief, or both (e.g., Beck et al., 2013). Without knowledge of the specific role that aspect plays, understanding its relation to other covariates and processes is difficult.

Some covariates may also be used as surrogates for process covariates. Remotely sensed greenness metrics (Meier and Brown, 2014), for example, often are used as surrogates for ungulate nutrition (Pettorelli et al., 2007, 2011; Borowik et al., 2013). How these metrics index nutrition (e.g., forage quantity, quality) or animal productivity (e.g., pregnancy rates, first-year survival), however, is often unstated and implicitly assumed (Villamuelas et al., 2016). As with contextual covariates, the worth of a surrogate covariate relies on its documented relationship with a process covariate (Nielsen et al., 2010; Gautam et al., 2019).

Rationale for the types of covariates considered in landscape-use modeling—process, contextual, and surrogate—requires consideration of how such covariates are scaled (Wiens, 1989; McGarigal et al., 2016). Covariate scaling is the process of defining the spatial and temporal grain and extent (area or time) over which a covariate is derived, quantified, mapped, and used in model development and selection (Wheatley and Johnson, 2009; McGarigal et al., 2016). A related concept is that of the minimum mapping unit, which is the "minimum dimension of an element that can be displayed and analyzed" (Corsi et al., 2000, p. 410) and should be explicitly recognized when interpreting model results. Unfortunately, inconsistent use of scale-related terms permeates the ecological literature (Wheatley and Johnson, 2009). McGarigal et al. (2016) provide a comprehensive assessment of spatial and temporal scaling of covariates.

The scale used to derive spatial covariates can dramatically affect predicted landscape use by ungulates (e.g., Laforge et al., 2015, 2016), but often is not reported (McGarigal et al., 2016). One example of scale in this context is greenness metrics such as Normalized Difference Vegetation Index, currently delivered for 16-day periods at 250-m resolution (Meier and Brown, 2014) and often used as a surrogate to represent ungulate nutrition in modeling landscape use (e.g., see review by Villamuelas et al.,

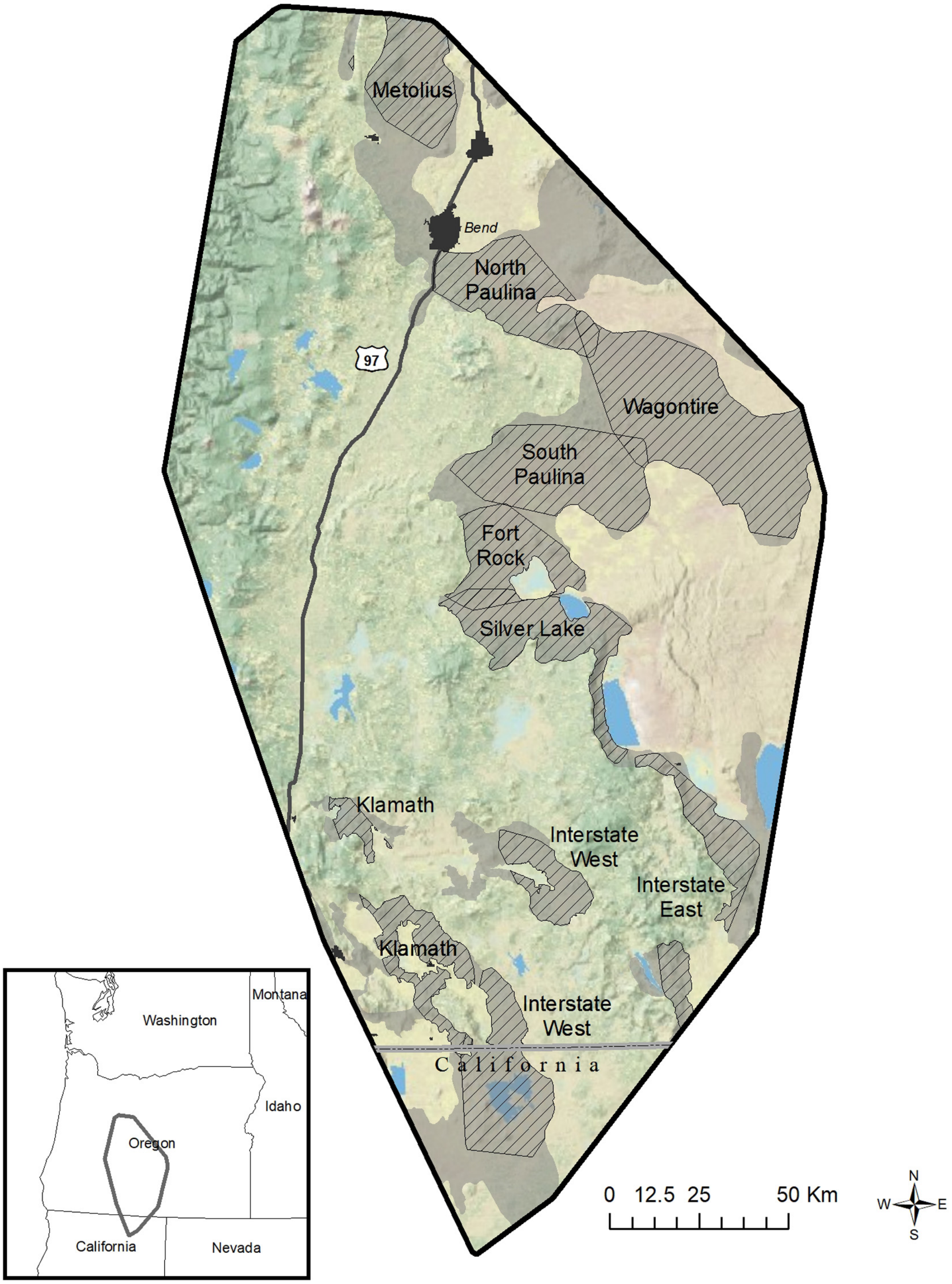

FIGURE 3 | Nine study areas (hatched areas) were used by Coe et al. (2018) as spatial replicates to model habitat use by 452 mule deer during winter over 8 years (2005–2012) in southcentral Oregon and northern California, United States. As context, study areas were embedded within a minimum convex polygon of >3-million ha that defined the year-round range of telemetered animals (black boundary). Study areas were used as units of replication in developing and validating global models of habitat use for mule deer at three spatiotemporal scales: population, home range, and foraging. Competing models of habitat use at each scale were first developed and ranked for empirical support by study area. Rankings were then summed across study areas to identify the global model with highest overall support, and model coefficients averaged among study areas to derive a global model. Validation of the global model used locations from 95 mule deer withheld from model development in eight study areas, and results were reported by study area.

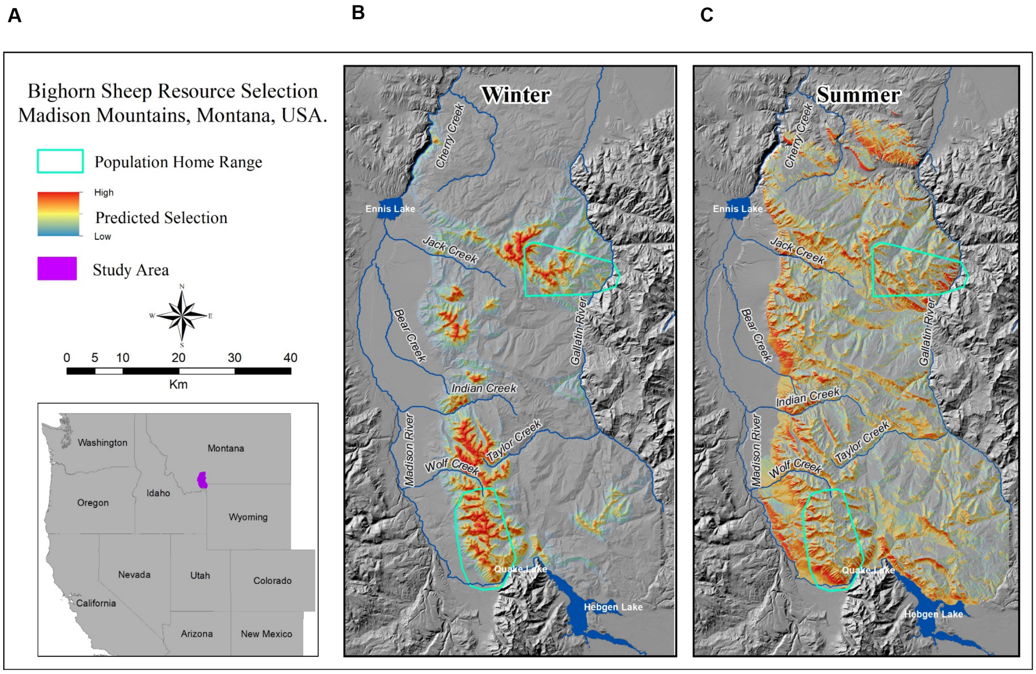

FIGURE 4 | In southwest Montana, United States **(A)**, predictions of bighorn sheep landscape use **(B,C)** from a resource selection function (RSF) were applied to an explicit inference space of historical but currently unoccupied bighorn sheep range to estimate potential winter and summer use (**B,C**, from Lula et al., 2020). Cool colors depict areas of low predicted selection, and warm colors areas of high predicted selection. The RSF was developed with telemetry data and validated with estimates of population abundance from established populations in nearby areas within the same historical range (summer and winter population home ranges, **B,C**).

2016). An implicit assumption is that this spatial (i.e., 250 m) and temporal (16 days) grain matches that of the foraging behavior and associated landscape use by the species. For ungulates that forage in very small patches, however, a much smaller grain (e.g., 10 m) may be more appropriate, owing to the fine scale at which the ungulate selects foraging sites. The challenge lies with deriving a nutrition covariate that can be mapped accurately at this grain (Morris et al., 2016) but not exceed the accuracy of associated animal location data (Garton et al., 2001).

Evaluating each covariate at multiple scales during model development and selection is essential to identify optimal patterns of landscape use which otherwise can be missed (Mateo Sánchez et al., 2014). Although ecologists have recognized the need for multi-scale habitat models for decades, implementation of such models has been uncommon (McGarigal et al., 2016). The range in scales evaluated is based on ecological rationale and *a priori* knowledge about the covariate in relation to life-history traits and species activities being modeled (Wheatley and Johnson, 2009) or determined empirically *post hoc* (McGarigal et al., 2016). Different scales are customized for each spatial covariate based on this rationale and then formally evaluated for empirical support (see the section "Model Development and Selection").

Importantly, defining and evaluating a range of scales for each covariate is different than hierarchical "levels" of landscape analysis (Mayor et al., 2009; Wheatley and Johnson, 2009), such as first, second, and third orders of selection (Johnson, 1980). Spatial orders of selection are now commonly incorporated in hierarchical modeling of landscape use (McGarigal et al., 2016) at the home range, population, study area, or species range (e.g., DeCesare et al., 2012). We do not address hierarchical modeling because of its common use, whereas covariate scaling to match ecological and management considerations of a species continues to be addressed superficially or not at all (McGarigal et al., 2016).

Examples

Rowland et al. (2018b) used a suite of process covariates to develop and validate elk nutrition and habitat-use models, each containing covariates representing sources of energy acquisition and loss that could be managed (**Figure 5**) (Wisdom et al., 2018a). The nutrition model addressed energy gain through overstory canopy cover, deemed a process covariate because it affects light penetration to the forest floor that directly influences biomass and quality of ungulate forage (e.g., Jenkins and Starkey, 1993; Peek et al., 2001, 2002; Cook et al., 2016, 2018), and because it can be managed through silvicultural prescriptions (Wisdom et al., 2018b). The response variable of the nutrition model, dietary digestible energy, was then used as a covariate in the habitat-use model that included a process covariate representing energy loss - distance to roads open to public motorized use (**Figure 5**) (Rowland et al., 2018a). Distance to roads served as an actively managed process covariate because public motorized routes are conduits for human activity that elk consistently avoid (e.g., Rowland et al., 2000; Ciuti et al., 2012; Ranglack et al., 2017). This example demonstrates the ecological underpinnings of the

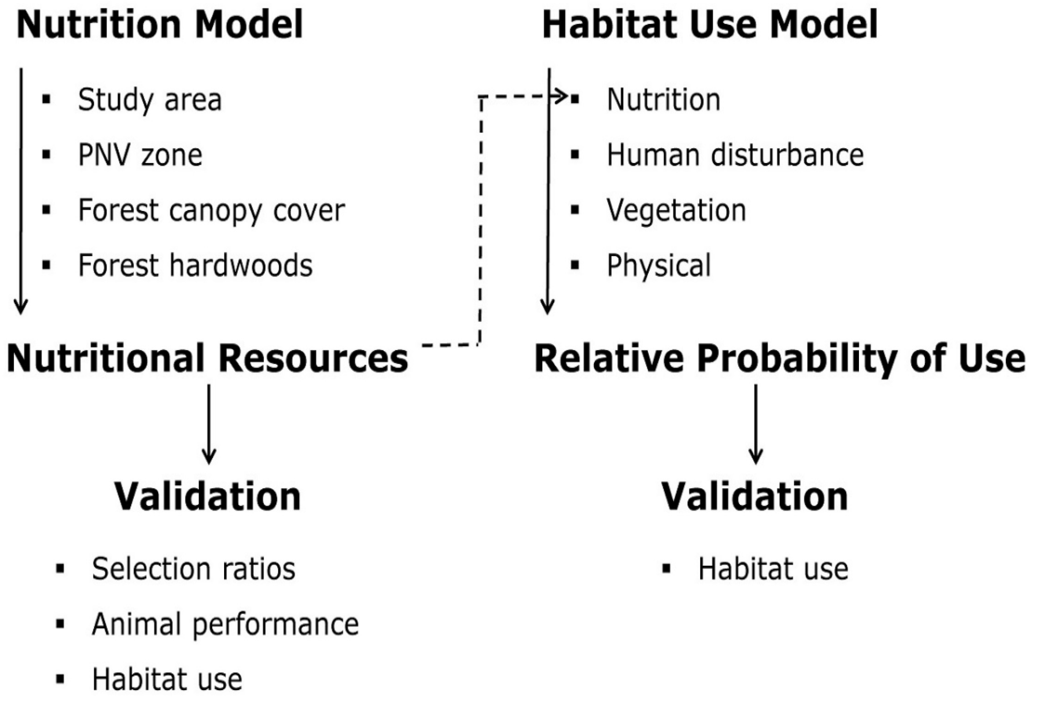

FIGURE 5 | Conceptual framework of nutrition and habitat-use models developed and validated for elk in western Oregon and western Washington, United States (from Wisdom et al., 2018a). Categories of covariates considered during model development and types of data used for validation are shown below each model or type of validation. Covariates in the nutrition model included study area and potential natural vegetation (PNV) zone as contextual covariates, and percent overhead canopy cover (forest canopy cover) and percent composition of hardwoods (forest hardwoods) as process covariates to predict dietary digestible energy (nutritional resources). Nutrition model predictions were most strongly influenced by canopy cover. Predictions of the habitat-use model were influenced by process covariates of nutrition (dietary digestible energy), human disturbance (distance to roads open to public motorized use), and vegetation (distance to cover-forage edges), and the contextual covariate percent slope (physical category). The two models were designed as complementary applications: the nutrition model identified the spatial arrangement and quality of nutritional resources, and the habitat-use model quantified the probability that areas of higher nutrition would be used by elk, given the influence of all covariates that best predicted spatial distribution.

process covariates selected for modeling, and their manipulation through active management to affect desired landscape use.

Ecological scaling of covariates was demonstrated by Laforge et al. (2015, 2016) in their landscape-use model for white-tailed deer (*Odocoileus virginianus*). They considered eight covariates in model selection, each derived at six grain sizes (Laforge et al., 2015), with grain defined as the area around used and available telemetry points. Deer responded uniquely to covariates at different grains. The slope of the functional response, measured as proportion of habitat used versus available, in relation to grain size for each covariate was strikingly different, indicating that deer response to covariates was scale-dependent. Had modeling proceeded with a single grain for all covariates, patterns of landscape use likely would have been substantially different—with the possibility that use associated with some covariates would have been undetected or substantially diluted (Laforge et al., 2015, 2016).

Ecological Model Development and Selection

Given the widespread availability of large datasets on animal locations and broad-scale spatial data, statistical models of landscape use may be complex, and in some cases their complexity may become the focus of the analysis. Contemporary models of landscape use thus often emphasize statistical methods and rote application of model selection criteria (e.g., Burnham and Anderson, 2002). A strong ecological framework for model formulation and selection will ensure that modeling is process-based and explicitly addresses the species life history, habitat relationships, and hypotheses of ecological and management interest.

Building an ecological framework for landscape-use modeling involves several steps. The first is developing ecologically plausible competing models or a list of potential covariates that align with the species' life-history traits, habitat requirements, and evolutionary behavior (see the section "Process Covariates and Their Ecological Scaling"). In contrast to considering all possible combinations of covariates, recent approaches for developing sets of plausible competing models emphasize organizing covariates into model suites, such as nutrition, predation, and human disturbance (**Figure 5**) to address specific hypotheses (Franklin et al., 2000; DeVoe et al., 2015; Lowrey et al., 2017; Rowland et al., 2018b). Suites of covariates often are organized according to their roles as sources of energy acquisition (e.g., nutrition covariates or nutrition surrogates), energy loss (e.g., human disturbance, land use, or predation covariates), or energy conservation (e.g., cover or topographic covariates) per modeling concepts of Long et al. (2014) for ungulates. Some covariates may address more than one role, such as slope to indicate areas of higher nutrition and energy conservation (i.e., flatter slopes may have deeper soils that support higher forage biomass, but also are associated with decreased movement costs).

Organizing covariates into model suites that represent specific, often competing hypotheses helps simplify otherwise large and complex competing sets of models and fosters identification of the covariates best supported by the data within a model suite. This approach also allows for important process covariates to advance to later stages of model selection based on ecological rationale for their importance rather than solely on statistical criteria (Lula et al., 2020). Additionally, this approach allows different spatial grains or functional forms of covariates to be evaluated, such that only the most supported form of each is advanced in model selection (Franklin et al., 2000; Laforge et al., 2015; Eckrich et al., 2019; Lowrey et al., 2020). We suggest a tiered or similar approach (e.g., see Franklin et al., 2000; Lowrey et al., 2020) of organizing model suites that represent ecological processes or hypotheses to prioritize inclusion of ecologically meaningful and/or manageable covariates in the final model.

Second, the process of ranking and identifying a final model with highest empirical support from the data has a well-developed history based on information-theoretic (IT) methods (Burnham and Anderson, 2002). Nearly all models of landscape use, as cited here, have used Akaike's Information Criterion (AIC), its variants (Burnham and Anderson, 2002), or other Bayesian IT statistics (Hooten and Hobbs, 2015) to guide model selection. When applied to all possible combinations of covariates or a model built solely on IT-based metrics (e.g., stepwise model building), the final landscape-use model may not be ecologically relevant or useful for management because a comparative ranking of models may overshadow ecological rationale and need for interpretable results (Arnold, 2010). However, when applied to a carefully developed process for modeling that represents ecological hypotheses of interest, statistical criteria such as AIC can help identify a plausible model with high management utility.

Examples

Lowrey et al. (2017) used an ecological framework and tiered model approach to develop and select models for mountain goat resource selection in the southwestern Greater Yellowstone Area, United States. The authors considered 12 covariates representing potential habitat attributes influencing mountain goat resource selection based on published research. To address specific hypotheses and simplify an otherwise potentially complex model list, covariates were grouped into four model suites representing terrain, vegetation, heat load, and snow. A tiered modeling and IT approach to model selection guided the progression from relatively simple univariate models focused on identifying the most explanatory functional form and grain of each covariate, to multivariate models that compared covariates within model suites. The final model suite contained supported covariates from each of the four model selection suites, from which the authors selected a final model of mountain goat resource selection. The authors' approach placed covariates into categories representing specific ecological hypotheses, which strengthens interpretation of model outcomes and provides a more robust modeling foundation.

Rowland et al. (2018b) also used a strong ecological framework to develop and select models for elk habitat use in western Oregon and Washington, United States. To create a regional landscape-use model across sites differing in resource availability, the authors placed covariates to predict elk habitat use in one of four categories to represent specific hypotheses about their relative influence and associated ecological processes (**Figure 5**). As in the prior example, covariates were chosen from each suite for advancement and combined to create a set of candidate models for evaluation and identify a final global model that addressed specific ecological hypotheses and their use in management.

Model Evaluation to Address Objectives

Model evaluation can be defined as an examination of how a model performs in relation to *a priori* expectations (Rykiel, 1996; Johnson, 2001). The word "validation" is often used in the ecological modeling literature, but this term is misleading in that no model can be truly validated but only invalidated through repeated testing in space and time under various conditions (Holling, 1978; Walters, 1986). Moreover, the term validation implies a more absolute outcome than does exploring the value of a model; model evaluation thus has been recommended as a more appropriate term (Johnson, 2001).

Conceptually and in practice, model evaluation can occur in many ways (Rykiel, 1996; Morrison et al., 2006). Identifying the most appropriate method depends on objectives, targeted inference space (see the section "Explicit Inference Space with Supporting Replication"), study design and analysis methods, and available data. Assessing the accuracy and precision of model predictions to new areas is the most common objective for evaluating ungulate models of landscape use (Boyce et al., 2002; Morrison et al., 2006).

Evaluation often is narrowly focused on assessing model predictions, such as relative probability of use, versus a set of observed data to determine their correlation. Evaluation generally relies on some form of cross-validation (Hijmans, 2012; Hjorth, 2017), which separates the original dataset into estimation (aka training) versus test data (**Figure 6**) (Hjorth, 2017). Estimation data are used to develop predictions for the test data and evaluate the strength of their relationship. From a formal statistical view, "validation data" are used to evaluate the model multiple times throughout model training and help refine model hyperparameters, whereas "testing data" are the gold standard and used only after model "training" (**Figure 6**) (Hobbs and Hooten, 2015).

Models of landscape use have traditionally evaluated model predictions versus observed data in two ways. The first establishes training and test data from a common dataset (Fielding and Bell, 1997). The second evaluates model predictions with data independent of those used to develop the model. The first type, typically based on cross-validation, is commonly used to evaluate predictions of RSFs and habitat-use models (e.g., Beck et al., 2006; Laforge et al., 2015; Lowrey et al., 2017; Plante et al.,

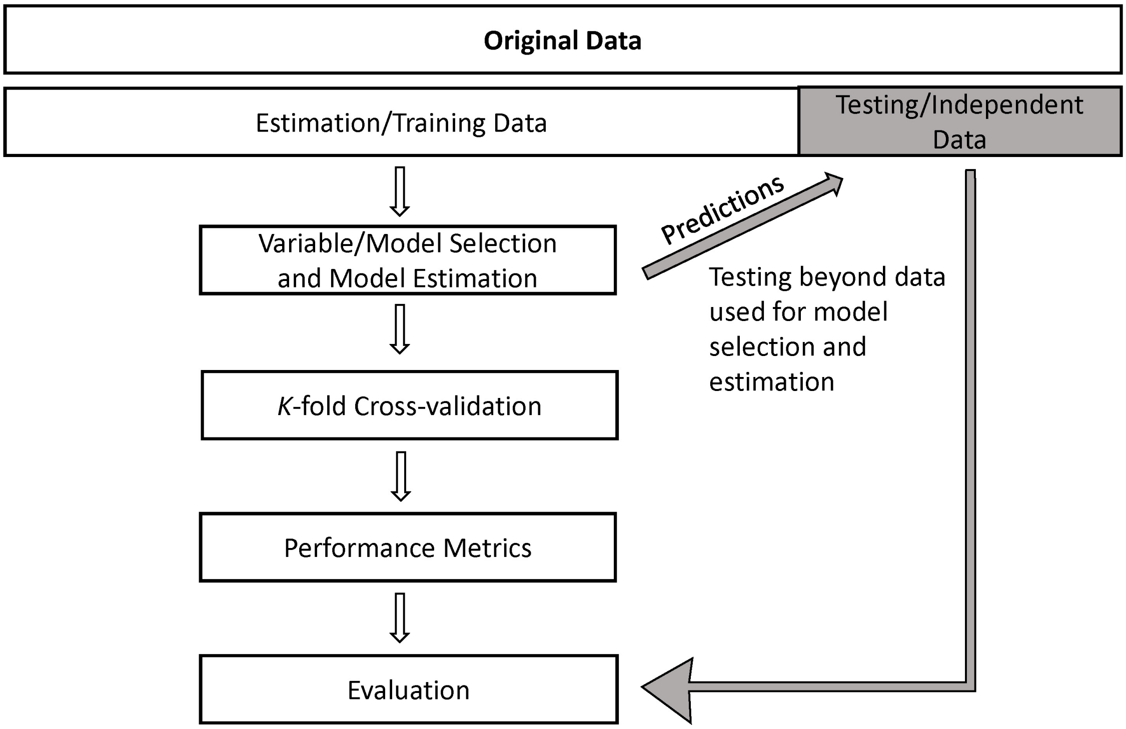

FIGURE 6 | The original (full) data set is split into training (estimation) and testing sets, prior to variable and model selection and parameter estimation. Predictions from the model fit to the training data are then made for the testing data. Evaluation of the correspondence between predictions and testing data is combined with internal evaluation of the training data using *k*-fold cross-validation. In computer science and engineering disciplines like machine learning, *k*-fold cross-validation can lead to model refinements (Broms et al., 2016), which can then be re-tested using cross-validation. However, predictions should be made to the holdout testing data only after a final model has been reached, and not during the model selection or refinement process.

2017). Original data are typically split into *k* subsets after variable and model selection, and how the specific *k* subsets or holdout data are chosen can substantially affect results (Roberts et al., 2017). Random assignment of data to the *k* subsets in cross-validation will always overestimate model performance because evaluation is based on variability at the level of *k* used to assign the subsets (**Figures 2**, **6**; e.g., study areas, animals; Gude et al., 2009). Whenever possible, assignment of data to the *k* subsets should be based on the primary sampling unit for inference (e.g., study area, **Figure 2**) to mimic the original data collection process and reduce bias in predictions (Roberts et al., 2017). This "blocking" (Roberts et al., 2017) to choose subsets is optimal because observations within blocks are not independent.

The second, preferred type of model evaluation uses holdout data that are spatially and temporally independent of those used for estimation (Roberts et al., 2017), and is especially valuable when making predictions to different environmental conditions. However, if data are only available from one study area or sample sizes are small (e.g., number of animals), all available data may be needed for model estimation and evaluation, resulting in optimistic performance (Roberts et al., 2017).

Use of training data to evaluate model predictions, be it from *k*-fold cross-validation or other methods, may be unreliable because the "model prediction parameters were selected with the estimation and test data sets, and thus might be biased" (Roberts et al., 2017). Thus, the holdout method is recommended for more insightful and realistic model evaluation. If the objective is to evaluate predictions for other areas and management scenarios, variable and model selection uncertainty must also be recognized (Hjorth, 2017). Differences in distributions of covariates between model estimation and evaluation data may point to model deficiencies or restrictions as to where or when the model can be applied with confidence.

Regardless of approach, the model evaluation process, including how to split the estimation and test datasets, should be developed before model selection and estimation (**Figure 6**) (Hjorth, 2017; Roberts et al., 2017). Evaluation can then proceed with a variety of metrics like r^2, receiver operating characteristic (ROC) curves, area under the curve (AUC), classification tables, kappa, or Bayesian hierarchical approaches (Chatfield, 1995; Rykiel, 1996; Fielding and Bell, 1997; Allouche et al., 2006; Morrison et al., 2006; Peterson et al., 2008; Matthiopoulos et al., 2015; Broms et al., 2016). Other evaluation metrics may be based on the types of knowledge gained in relation to ecological hypotheses or expectations (Bunnell, 1989), or based on simulating future conditions under changing disturbance or climate regimes (e.g., Riggs et al., 2015; White et al., 2018).

For any evaluation that examines agreement between predicted and observed landscape use, the essential consideration is the degree of independence between data used for model development versus evaluation. Optimistic results generated by nearly all forms of *k*-fold cross-validation reflect their limitations for broad inference. Modeling approaches that hold out multiple datasets that are spatially and temporally independent of those used to develop a model lead to more robust evaluation and are increasingly common (see the section "Explicit Inference Space with Supporting Replication").

Examples

Guan et al. (2015) developed landscape-use models for takin (*Budorcas taxicolor*) in the northern MinShan Mountains of Sichuan Province, China. The models were based on GPS coordinates of takin and sign of takin presence within sampled plots within a 38,000 km^2 study region, and final predictions of takin presence were based on model averaging using AIC weights. The authors evaluated their model by comparing predictions to an independent data set of takin locations collected 2005–2010 across a network of 21 nature reserves in Sichuan Province. This example illustrates the most desirable form of model evaluation, i.e., using data independent and beyond the range of those used to develop the model, rather than subsetting model development data for evaluation with *k*-fold cross-validation or ROC-based classification matrices. Coe et al. (2018) likewise demonstrated a robust form of model evaluation, using data from 95 mule deer withheld from model development in eight study areas, with results reported in relation to varying environmental conditions across study areas (**Figure 3**).

Relationships With Animal and Population Performance

Predicting spatial and temporal distributions or probability of use is the primary objective of most ungulate landscape-use models; however, linking these predictions to measures of animal performance can identify the biological consequences of landscape use and extend model utility for conservation and management (Aldridge and Boyce, 2008; Gaillard et al., 2010). Here, we define performance as measures of survival and reproduction that reflect fitness, the expected contribution of individuals to future generations (Franklin and Morrissey, 2017) and often quantified as lifetime reproductive success (LRS). Indeed, the underlying motivation behind many habitat models is that "organisms have a reason for being where we find them" (Matthiopoulos et al., 2015, p. 414). Quantifying and understanding these connections, referred to as Habitat–Performance Relationships (HPR; Gaillard et al., 2010), can inform ungulate conservation in multiple ways.

If HPR have been quantified in an area, management can target specific habitat attributes and potentially improve performance, such as higher juvenile survival. Moreover, if a model covariate correlates well with some performance index and is a key driver of landscape-use model predictions (e.g., large standardized coefficient), we can assume that areas of highest predicted use are associated with greater fitness, and target management to influence ungulate distributions and benefit the population. However, HPR can change over time, for example with shifting densities of predators or alternate prey, and thus should be considered dynamic. These measures will be increasingly important in the future by enhancing our understanding of how populations respond to environmental change (Losier et al., 2015; Matthiopoulos et al., 2019).

Performance components linked to ungulate habitat can be either direct measures of reproduction and survival (e.g., fecundity, pregnancy status; Proffitt et al., 2016; Allen et al., 2017; Cook et al., 2018) or indirect metrics such as body fat (Proffitt et al., 2016; Cook et al., 2018; Merems et al., 2020). Outputs from ungulate landscape-use models have been related to performance measures in multiple ways (**Table 2**). A seminal study is the work of McLoughlin et al. (2006), in which LRS of red deer on the Isle of Rum, Scotland was associated with selection of vegetation communities (see "Examples" section below). A similar analysis by McLoughlin et al. (2007) for female roe deer in France demonstrated that LRS was greater for individuals that incorporated specific habitat components such as meadows and thickets in their home ranges.

Because landscape-use models are niche-based and multivariate, and generally predict distributions or habitat use, we cannot directly use their outputs (e.g., probability of use) to predict fitness (Gaillard et al., 2010). We can, however, explore how specific habitat features, whether as model covariates or independent of a formal modeling framework, relate to performance. For example, Nilsen et al. (2004) documented preference for woodland habitat by roe deer on winter ranges in Norway, and then evaluated covariation of the area in woodlands with litter size. Similarly, Schrempp et al. (2019) found that quantity of "forage shrubs" was correlated with population trends of moose in northern Idaho, United States.

One category of habitat-performance relationships especially relevant to ungulates is that between quantity and juxtaposition of "security" habitat to survival or other fitness indices during hunting seasons, both for hunted and non-hunted population segments. In Norway, Lone et al. (2015) found increased survival of male European red deer that moved into dense cover at the start of the hunting season. Caribou vulnerability to harvest in Canada was greater when animals were closer to infrastructure such as roads or hunting camps, and when in open or flat terrain (Plante et al., 2017). Spitz et al. (2019) documented lower body fat of adult female elk entering winter for individuals that markedly avoided roads during hunting seasons.

Considerations in relating performance to landscape use by ungulates and its interpretation include scale, density dependence, and predator-prey dynamics. The scale of model development is especially important in choosing appropriate performance metrics. At smaller geographic and temporal scales, individual energy gain or performance may be suitable measures, whereas at larger scales, population demography or persistence of local populations are more appropriate (Gaillard et al., 2010). Habitat-performance relationships that appear robust in one system may not be translatable to another if ungulate densities or resources vary widely between systems (Gaillard et al., 2000, 2010; McLoughlin et al., 2006, 2010; Matthiopoulos et al., 2015). Similarly, predator densities and distributions can strongly affect ungulate landscape use (e.g., Frair et al., 2005; Oates et al., 2019). Thus understanding these dynamics and quantifying their

TABLE 2 | Examples of ungulate landscape-use models or habitat components that demonstrated relationships between landscape use and animal or population performance.

Landscape use model type	Habitat component	Fitness/performance metric(s)	Species	Location	References
RSF*	Proportion time spent by habitat type	Fecundity, calf survival	Moose (*Alces alces*)	Sweden	Allen et al. (2017)
RSF	Local road density, abundance of mature/mixed deciduous stands	Calf survival	Caribou (*Rangifer tarandus*)	Québec, Canada	Dussault et al. (2012)
RSF	Land cover types, e.g., mixed/deciduous stands	Adult female survival	Woodland caribou (*Rangifer tarandus*)	Québec, Canada	Losier et al. (2015)
RSF	Vegetation type (e.g., *Agrostis/Festuca*)	Lifetime reproductive success	Red deer (*Cervus elaphus*)	Scotland	McLoughlin et al. (2006)
Resource selection indices (negative binomial regression)	Home range composition	Lifetime reproductive success	Roe deer (*Capreolus capreolus*)	France	McLoughlin et al. (2007)
Integrated spatial model	Digestible forage biomass	Pregnancy rates, body fat	Elk (*Cervus canadensis*)	Western Montana, United States	Proffitt et al. (2016)
Compositional analysis	Area of preferred habitat within home range	Fecundity, winter fawn weight	Roe deer (*Capreolus capreolus*)	Norway	Nilsen et al. (2004)
	Dietary digestible energy	Pregnancy rates, body fat	Elk (*Cervus canadensis*)	Western Oregon and Washington, United States	Cook et al. (2018)
	Quantity of forage shrubs	Population trend index	Moose (*Alces alces*)	Idaho, United States	Schrempp et al. (2019)
	% herbaceous habitat in home range	Adult female survival	Black-tailed deer (*Odocoileus hemionus columbianus)*	California, United States	Forrester et al. (2015)

Resource selection function.

relative impact on ungulate habitat use and performance is requisite to reliably link habitat to performance.

Despite the potential value of establishing HPR in landscape-use models, acquiring sufficient data to do so is a daunting challenge (Garshelis, 2000; Gaillard et al., 2010). And not all landscape-use studies, depending on their objectives and applications, necessarily benefit from these linkages. The primary barrier is the long timespans required to comprehensively document HPR (Clutton-Brock, 1988; McLoughlin et al., 2006, 2007; Gaillard et al., 2010) and the costs of measuring performance – especially capture and handling of many animals. The ultimate measure of fitness, lifetime reproductive output, is seldom quantified for ungulates given their longevity and the difficulty in long-term monitoring of fecundity in individuals (Clutton-Brock, 1988) (but see McLoughlin et al., 2006 below).

Examples

Despite the difficulties in demonstrating habitat-performance linkages, some studies have produced ungulate landscape-use models that clearly establish HPR in a variety of settings. McLoughlin et al. (2006) used a dataset spanning >30 years on the Isle of Rum, Scotland for 270 free-ranging adult female red deer. They developed individual lifetime RSFs, as well as a pooled RSF, and quantified selection of primary vegetation types on the island. They measured LRS as the number of female calves surviving to 1 year for each adult female. Coefficients from the RSFs were used to predict LRS. The authors found that LRS was significantly related to use of *Agrostis/Festuca* grasslands, but that benefits of these grasslands decreased with increasing density of red deer.

In Canada, Losier et al. (2015) developed RSFs to model probability of occurrence of adult female woodland caribou (*Rangifer tarandus caribou*), and then used the top-ranked model to estimate probability of winter survival. They demonstrated that the functional responses of caribou in selecting risky habitats, i.e., clear-cuts preferred by moose, resulted in decreased survival due to increased mortality by wolves (*Canis lupus*) attracted to these habitats. This example highlights the complexities of HPR and the potential role of predators in affecting them.

Proffitt et al. (2016) developed an integrated spatial model to predict nutritional resources and evaluate their effects on elk in two study areas of different nutritional quality in Montana, United States. They found that elk exposed to lower digestible forage biomass, their index of nutritional resources, had lower body fat and pregnancy rates. The authors posited that nutritional limitations may predispose elk to predation, or limit population productivity and growth rate.

Reliable Interpretations and Uses

The final, critical steps in landscape-use modeling are to interpret results for ecological understanding and management uses, address unforeseen shortfalls in meeting objectives, and adjust inferences in relation to unmet objectives. Reliable interpretations and uses depend on successful completion of all three modeling phases: design, development, and utility (**Figure 1**).

Model design provides the baseline against which results can be interpreted in relation to collaboratively set *a priori* objectives and hypotheses. Unmet objectives or unsupported hypotheses may require adapting how and where the model is used, and inference space adjusted accordingly. New research may be initiated to augment the original spatial and temporal replication of data collection needed to support the desired inference space, or alternatively, to confirm the appropriateness of local models, each relevant to a smaller inference space. Results from model evaluation can also be used to design new modeling approaches and reformulate objectives (e.g., Walters, 1986; Hooten and Hobbs, 2015).

Model development provides further context for reliable interpretation and uses. For example, modeling ungulate nutrition and landscape use in response to climate change for an alpine ungulate (e.g., White et al., 2018) requires critical assumptions about how nutrition and other covariates are derived and mapped under climate change projections. These assumptions must be clearly articulated as covariates are developed, combined, and selected as plausible models that address climate change factors relevant to the species' ecology and management. Further, ecological scaling of covariates, such as forage biomass and quality, with sufficient precision is needed to match the spatiotemporal scales of climate-change projections and habitat use. Low precision of model outcomes can muddy interpretation, emphasizing the need for improved empirical estimates of forage covariates and possibly their scaling as prerequisites to meet modeling objectives.

Model utility builds on these two prior phases with careful interpretation of model evaluation results to assess the ecological and management value of a model. How well model predictions are supported by independently observed data, withheld as spatial or temporal replicates for evaluation, often becomes critical to the interpretation of whether the desired inference space is justified or must be adjusted. Similarly, model covariates or predictions may be hypothesized to relate to pregnancy rates, survival, or other measures of animal performance. HPR linkages resulting from modeling can then be reliably interpreted in terms of value of the model as it relates to performance.

Models can ultimately be designed, developed, and applied as part of adaptive management (Walters, 1986; Varley and Boyce, 2006; Apollonio et al., 2017), which continues to provide a useful template that embodies the coproduction process (**Figure 1**) among scientists, managers, and stakeholders (Voinov et al., 2016), despite mixed application successes (Allen and Gunderson, 2011). Learning and improvement occurs throughout the process via studies and applications codeveloped and implemented incrementally and iteratively over time (Walters, 1986).

Modeling landscape use will continue to grow in scope and practice to benefit ungulate ecology and management with approaches that foster a continual learning process. No single model can ever serve the changing demands of knowledge gain and management applications, but the reliability of model interpretations and uses can be substantially improved with consideration of ecological and management criteria throughout the modeling process (**Figure 1**).

CONCLUSION

Models of landscape use have tremendous potential to advance ecological understanding and management of ungulates and other species worldwide. The growing volume of animal location data, accessibility of spatial data at broad scales, and advances in statistical modeling and software allow for the continued refinement and expanded application of landscape-use models. Without a sound ecological and management framework, however, contemporary modeling of landscape use may continue to rely on "convenience sampling," statistical methods, and case studies lacking the spatial and temporal replication needed for broad inference. Although many of these concepts have been previously described in a variety of publications, we synthesized trends and ideas from the disparate literature to develop a coherent ecological framework that included seven criteria for designing, developing, and applying landscape-use models to advance ecological understanding and effective management of ungulates (**Table 1** and **Figure 1**). We highlighted recent examples that represent successes in this advancement and described future avenues for research to fill gaps in current understanding of ungulate modeling, such as linking landscape use to animal performance.

We view the criteria as aspirational standards, not strict rules to uniformly follow without careful consideration of modeling objectives. Not all landscape-use models will include all criteria, owing to a wide spectrum of modeling objectives and available resources. In that light, we offer our criteria as a complement to the traditional focus on statistically based methods, to help ensure a modeling process that advances ecological understanding and management utility.

AUTHOR CONTRIBUTIONS

MW developed the initial concepts and criteria for the manuscript and wrote early rough drafts. MW, RN, MR, and KP contributed equally to detailed refinement of the criteria and the intellectual thinking behind the concepts and criteria. All authors helped to write the manuscript, contributed to the article, and approved the submitted version.

FUNDING

This review was supported by Eagle Environmental, Inc.; Montana Fish, Wildlife, and Parks; and USDA Forest Service Pacific Northwest Research Station.

ACKNOWLEDGMENTS

We thank Topic Editors V. Bleich, R. Bowyer, J. Gaillard, and P. Krausman for their guidance on this work, particularly

P. Krausman for directing the peer review and revision process. We are indebted to J. Gude, B. Lowrey, D. Vales, S. Boutin, and J. Bissonette, whose comments substantially improved the intellectual rigor of concepts presented here. We thank E. Lula for preparing **Figure 4**, and L. Dick for establishing and managing the automated entry of References.

REFERENCES

Acevedo, P., Farfán, M. A., Márquez, A. L., Delibes-Mateos, M., Real, R., and Vargas, J. M. (2011). Past, present and future of wild ungulates in relation to changes in land use. *Landsc. Ecol.* 26, 19–31. doi: 10.1007/s10980-010-9538-2

Addison, P. F., Rumpff, L., Bau, S. S., Carey, J. M., Chee, Y. E., Jarrad, F. C., et al. (2013). Practical solutions for making models indispensable in conservation decision-making. *Divers. Distrib.* 19, 490–502. doi: 10.1111/ddi.12054

Ahumada, J. A., Silva, C. E., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., et al. (2011). Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philos. Trans. R. Soc. B Biol. Sci.* 366, 2703–2711. doi: 10.1098/rstb.2011.0115

Aldridge, C. L., and Boyce, M. S. (2008). Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. *Israel J. Ecol. Evol.* 54, 389–419. doi: 10.1560/ijee.54.3-4.389

Allen, A. M., Dorey, A., Malmsten, J., Edenius, L., Ericsson, G., and Singh, N. J. (2017). Habitat–performance relationships of a large mammal on a predator-free island dominated by humans. *Ecol. Evol.* 7, 305–319. doi: 10.1002/ece3.2594

Allen, C. R., and Gunderson, L. H. (2011). Pathology and failure in the design and implementation of adaptive management. *J. Environ. Manag.* 92, 1379–1384. doi: 10.1016/j.jenvman.2010.10.063

Allouche, O., Tsoar, A., and Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x

Anderson, D. R. (2001). The need to get the basics right in wildlife field studies. *Wildl. Soc. Bull.* 29, 1294–1297.

Apollonio, M., Belkin, V. V., Borkowski, J., Borodin, O. I., Borowik, T., Cagnacci, F., et al. (2017). Challenges and science-based implications for modern management and conservation of European ungulate populations. *Mamm. Res.* 62, 209–217. doi: 10.1007/s13364-017-0321-5

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manag.* 74, 1175–1178. doi: 10.1111/j.1937-2817.2010.tb01236.x

Barker, K. J., Mitchell, M. S., and Proffitt, K. M. (2019). Native forage mediates influence of irrigated agriculture on migratory behavior of Elk. *J. Anim. Ecol.* 88, 1100–1110. doi: 10.1111/1365-2656.12991

Beck, J. L., Peek, J. M., and Strand, E. K. (2006). Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. *J. Wildl. Manag.* 70, 283–294. doi: 10.2193/0022-541x(2006)70[283:eoesrn]2.0.co;2

Beck, J. L., Smith, K. T., Flinders, J. T., and Clyde, C. L. (2013). Seasonal habitat selection by elk in north central Utah. *Western North Am. Nat.* 73, 442–456. doi: 10.3398/064.073.0414

Bissonette, J. A. (2017). Avoiding the scale sampling problem: a consilient solution. *J. Wildl. Manag.* 81, 192–205. doi: 10.1002/jwmg.21187

Bolger, D. T., Newmark, W. D., Morrison, T. A., and Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* 11, 63–77.

Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., et al. (2013). Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *Eur. J. Wildl. Res.* 59, 185–193. doi: 10.1007/s10344-012-0665-8

Borowik, T., Pettorelli, N., Sönnichsen, L., and Jędrzejewska, B. (2013). Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *Eur. J. Wildl. Res.* 59, 675–682. doi: 10.1007/s10344-013-0720-0

Boyce, M. S., Johnson, C. J., Merrill, E. H., Nielsen, S. E., Solberg, E. J., and Van Moorter, B. (2016). Can habitat selection predict abundance? *J. Anim. Ecol.* 85, 11–20. doi: 10.1111/1365-2656.12359

Boyce, M. S., and McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends Ecol. Evol.* 14, 268–272. doi: 10.1016/s0169-5347(99)01593-1

Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecol. Model.* 157, 281–300. doi: 10.1016/s0304-3800(02)00200-4

Briscoe, N. J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J. J., Camac, J. S., Giljohann, K. M., et al. (2019). Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecol. Lett.* 22, 1940–1956. doi: 10.1111/ele.13348

Bristow, K. D., Clement, M. J., Crabb, M. L., Harding, L. E., and Rubin, E. S. (2019). Comparison of aerial survey methods for elk in Arizona. *Wildl. Soc. Bull.* 43, 77–92. doi: 10.1002/wsb.940

Broms, K. M., Hooten, M. B., and Fitzpatrick, R. M. (2016). Model selection and assessment for multi-species occupancy models. *Ecol.* 97, 1759–1770. doi: 10.1890/15-1471.1

Bunnell, F. L. (1989). *Alchemy and Uncertainty: What Good are Models?*. Portland, OR: USDA Forest Service.

Burnham, K. P., and Anderson, D. R. (2002). *A Practical Information-Theoretic Approach. Model Selection and Multimodel Inference*, 2nd Edn. New York: Springer.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., et al. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* 52, 675–685. doi: 10.1111/1365-2664.12432

Canfield, J. E., Grove, A., Tomasik, E., Pengeroth, D., and Kujala, Q. (2013). *U.S Forest Service and Montana Department of Fish Wildlife and Parks collaborative overview and recommendations for elk habitat management on the Custer, Gallatin, Helena, and Lewis and Clark National Forests*. Bozeman, MT: Gallatin National Forest Supervisor's Office.

Chatfield, C. (1995). Model uncertainty, data mining and statistical inference. *J. R. Stat. Soc. Ser. A* 158, 419–444.

Chen, J., Chen, J., Liao, A., Cao, X., Chen, L., Chen, X., et al. (2015). Global land cover mapping at 30 m resolution: a POK-based operational approach. *ISPRS J. Photogram. Remote Sens.* 103, 7–27. doi: 10.1016/j.isprsjprs.2014.09.002

Ciach, M., and Pęksa, Ł (2018). Human-induced environmental changes influence habitat use by an ungulate over the long term. *Curr. Zool.* 65, 129–137. doi: 10.1093/cz/zoy035

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., et al. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS One* 7:e50611. doi: 10.1371/journal.pone.0050611

Clutton-Brock, T. H. (1988). *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago, IL: University of Chicago Press.

Coe, P. K., Clark, D. A., Nielson, R. M., Gregory, S. C., Cupples, J. B., Hedrick, M. J., et al. (2018). Multiscale models of habitat use by mule deer in winter. *J. Wildl. Manag.* 82, 1285–1299. doi: 10.1002/jwmg.21484

Cook, J. G., Cook, R. C., Davis, R. W., and Irwin, L. L. (2016). Nutritional ecology of elk during summer and autumn in the Pacific Northwest. *Wildl. Monogr.* 195, 1–81. doi: 10.1002/wmon.1020

Cook, J. G., Cook, R. C., Davis, R. W., Rowland, M. M., Nielson, R. M., Wisdom, M. J., et al. (2018). Development and evaluation of a landscape nutrition model for elk in western Oregon and Washington. *Wildl. Monogr.* 199, 13–30.

Corsi, F., De Leeuw, J., and Skidmore, A. (2000). "Modeling species distribution with GIS," in *Research Techniques in Animal Ecology: Controversies and Consequences*, eds L. Boitani and T. K. Fuller (New York: Columbia University Press), 389–434.

Davies, A. L., and White, R. M. (2012). Collaboration in natural resource governance: reconciling stakeholder expectations in deer management in Scotland. *J. Environ. Manag.* 112, 160–169. doi: 10.1016/j.jenvman.2012.07.032

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., et al. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecol. Appl.* 22, 1068–1083. doi: 10.1890/11-1610.1

DeVoe, J. D., Garrott, R. A., Rotella, J. J., Challender, S., White, P. J., O'Reilly, M., et al. (2015). Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. *Ecosphere* 6, 1–20.

DeVoe, J. D., Proffitt, K. M., Mitchell, M. S., Jourdonnais, C. S., and Barker, K. J. (2019). Elk forage and risk tradeoffs during the fall archery season. *J. Wildl. Manag.* 83, 801–816. doi: 10.1002/jwmg.21638

Dussault, C., Pinard, V., Ouellet, J.-P., Courtois, R., and Fortin, D. (2012). Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Proc. R. Soc. B Biol. Sci.* 279, 4481–4488. doi: 10.1098/rspb.2012.1700

Dwinnell, S. P., Sawyer, H., Randall, J. E., Beck, J. L., Forbey, J. S., Fralick, G. L., et al. (2019). Where to forage when afraid: does perceived risk impair use of the foodscape? *Ecol. Appl.* 29:e01972.

Eckrich, C. A., Coe, P. K., Clark, D. A., Nielson, R. M., Lombardi, J., Gregory, S. C., et al. (2019). Summer habitat use of female mule deer in oregon. *J. Wildl. Manag.* 83, 576–587. doi: 10.1002/jwmg.21806

Fielding, A. H., and Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49. doi: 10.1017/s0376892997000088

Forrester, T. D., Casady, D. S., and Wittmer, H. U. (2015). Home sweet home: fitness consequences of site familiarity in female black-tailed deer. *Behav. Ecol. Sociobiol.* 69, 603–612. doi: 10.1007/s00265-014-1871-z

Frair, J. L., Merrill, E. H., Visscher, D. R., Fortin, D., Beyer, H. L., and Morales, J. M. (2005). Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc. Ecol.* 20, 273–287. doi: 10.1007/s10980-005-2075-8

Franklin, A. B., Anderson, D. R., Gutiérrez, R. J., and Burnham, K. P. (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecol. Monogr.* 70, 539–590. doi: 10.1890/0012-9615(2000)070[0539:chqafi]2.0.co;2

Franklin, O. D., and Morrissey, M. B. (2017). Inference of selection gradients using performance measures as fitness proxies. *Methods Ecol. Evol.* 8, 663–677. doi: 10.1111/2041-210x.12737

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N., Loison, A., and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., et al. (2010). Habitat-performance relationships: finding the right metric at a given spatial scale. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2255–2265. doi: 10.1098/rstb.2010.0085

Garshelis, D. L. (2000). "Delusions in habitat evaluation: measuring use, selection, and importance," in *Research Techniques in Animal Ecology: Controversies and Consequences*, eds L. Boitani, and T. K. Fuller (New York, NY: Columbia University Press), 111–164.

Garton, E. O., Wisdom, M. J., Leban, F. A., and Johnson, B. K. (2001). "Experimental design for radiotelemetry studies," in *Radio Tracking and Animal Populations*, eds J. Millspaugh and J. Marzluff (Amsterdam: Elsevier), 15–42. doi: 10.1016/b978-012497781-5/50003-7

Gautam, H., Arulmalar, E., Kulkarni, M. R., and Vidya, T. (2019). NDVI is not reliable as a surrogate of forage abundance for a large herbivore in tropical forest habitat. *Biotropica* 51, 443–456. doi: 10.1111/btp.12651

Gill, R. (1992). A review of damage by mammals in north temperate forests: 1. *Deer For. Int. J. For. Res.* 65, 145–169. doi: 10.1093/forestry/65.2.145

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898. doi: 10.1111/j.1365-2656.2006.01106.x

Godvik, I. M. R., Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R., and Mysterud, A. (2009). Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90, 699–710. doi: 10.1890/08-0576.1

Guan, T., Wang, F., Li, S., and McShea, W. J. (2015). Nature reserve requirements for landscape-dependent ungulates: the case of endangered takin (*Budorcas taxicolor*) in Southwestern China. *Biol. Conserv.* 182, 63–71. doi: 10.1016/j.biocon.2014.11.041

Gude, J. A., Mitchell, M. S., Ausband, D. E., Sime, C. A., and Bangs, E. E. (2009). Internal validation of predictive logistic regression models for decision-making in wildlife management. *Wildl. Biol.* 15, 352–369. doi: 10.2981/08-057

Gurevitch, J., Koricheva, J., Nakagawa, S., and Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature* 555:175.

Hebblewhite, M. (2008). A literature review of the effects of energy development on ungulates: implications for central and eastern Montana. *Wildl. Biol. Faculty Publ.* 48, 1–125.

Hebblewhite, M., and Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2303–2312. doi: 10.1098/rstb.2010.0087

Heffelfinger, J. R., Geist, V., and Wishart, W. (2013). The role of hunting in North American wildlife conservation. *Int. J. Environ. Stud.* 70, 399–413. doi: 10.1080/00207233.2013.800383

Hijmans, R. J. (2012). Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology* 93, 679–688. doi: 10.1890/11-0826.1

Hjorth, J. U. (2017). *Computer Intensive Statistical Methods: Validation, Model Selection, and Bootstrap*. Abingdon: Routledge.

Hobbs, N. T. (2003). Challenges and opportunities in integrating ecological knowledge across scales. *For. Ecol. Manag.* 181, 223–238. doi: 10.1016/S0378-1127(03)00135-X

Hobbs, N. T., and Hooten, M. B. (2015). *Bayesian Models: A Statistical Primer for Ecologists*. Princeton, NJ: Princeton University Press.

Holbrook, J. D., Olson, L. E., DeCesare, N. J., Hebblewhite, M., Squires, J. R., and Steenweg, R. (2019). Functional responses in habitat selection: clarifying hypotheses and interpretations. *Ecol. Appl.* 29:e01852.

Holling, C. S. (1978). *Adaptive Environmental Assessment and Management*. Hoboken, NJ: John Wiley & Sons.

Hooten, M. B., and Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecol. Monogr.* 85, 3–28. doi: 10.1890/14-0661.1

Horne, J. S., Garton, E. O., Krone, S. M., and Lewis, J. S. (2007). Analyzing animal movements using Brownian bridges. *Ecology* 88, 2354–2363. doi: 10.1890/06-0957.1

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211. doi: 10.2307/1942661

Irvine, R., Fiorini, S., Yearley, S., McLeod, J., Turner, A., Armstrong, H., et al. (2009). Can managers inform models? Integrating local knowledge into models of red deer habitat use. *J. Appl. Ecol.* 46, 344–352. doi: 10.1111/j.1365-2664.2009.01626.x

Jarnevich, C. S., Stohlgren, T. J., Kumar, S., Morisette, J. T., and Holcombe, T. R. (2015). Caveats for correlative species distribution modeling. *Ecol. Inform.* 29, 6–15. doi: 10.1016/j.ecoinf.2015.06.007

Jelinski, D. E., and Wu, J. (1996). The modifiable areal unit problem and implications for landscape ecology. *Landsc. Ecol.* 11, 129–140. doi: 10.1007/BF02447512

Jenkins, K. J., and Starkey, E. E. (1993). Winter forages and diets of elk in old-growth and regenerating coniferous forests in western Washington. *Am. Midland Nat.* 130, 299–313.

Jiang, G., Zhang, M., and Ma, J. (2008). Habitat use and separation between red deer and roe deer in relation to human disturbance in the Wandashan mountains, northeastern China. *Wildl. Biol.* 14, 92–100. doi: 10.2981/0909-6396(2008)14[92:huasbr]2.0.co;2

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. doi: 10.2307/1937156

Johnson, D. H. (1999). The insignificance of statistical significance testing. *J. Wildl. Manag.* 225, 763–772.

Johnson, D. H. (2001). *Validating and Evaluating Models. Modeling in Natural Resource Management*. Covelo: Island Press, 105–119.

Johnson, D. H. (2002). The importance of replication in wildlife research. *J. Wildl. Manag.* 66, 919–932.

Kanagaraj, R., Araujo, M. B., Barman, R., Davidar, P., De, R., Digal, D. K., et al. (2019). Predicting range shifts of Asian elephants under global change. *Divers. Distrib.* 25, 822–838.

Kittle, A. M., Fryxell, J. M., Desy, G. E., and Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* 157, 163–175. doi: 10.1007/s00442-008-1051-9

Krausman, P. R., and Bleich, V. C. (2013). Conservation and management of ungulates in North America. *Int. J. Environ. Stud.* 70, 372–382. doi: 10.1080/00207233.2013.804748

Krebs, C. J. (1989). *Ecological Methodology*. New York, NY: Harper & Row.

Laforge, M. P., Brook, R. K., van Beest, F. M., Bayne, E. M., and McLoughlin, P. D. (2016). Grain-dependent functional responses in habitat selection. *Landsc. Ecol.* 31, 855–863. doi: 10.1007/s10980-015-0298-x

Laforge, M. P., Vander Wal, E., Brook, R. K., Bayne, E. M., and McLoughlin, P. D. (2015). Process-focussed, multi-grain resource selection functions. *Ecol. Model.* 305, 10–21. doi: 10.1016/j.ecolmodel.2015.03.003

Lele, S. R., Merrill, E. H., Keim, J., and Boyce, M. S. (2013). Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *J. Anim. Ecol.* 82, 1183–1191. doi: 10.1111/1365-2656.12141

Lone, K., Loe, L. E., Meisingset, E. L., Stamnes, I., and Mysterud, A. (2015). An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Anim. Behav.* 102, 127–138. doi: 10.1016/j.anbehav.2015.01.012

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., and Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol. Monogr.* 84, 513–532. doi: 10.1890/13-1273.1

Losier, C. L., Couturier, S., St-Laurent, M. H., Drapeau, P., Dussault, C., Rudolph, T., et al. (2015). Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *J. Appl. Ecol.* 52, 496–504. doi: 10.1111/1365-2664.12400

Lowrey, B., Devoe, J., Proffitt, K. M., and Garrott, R. A. (2020). Hiding without cover? Defining elk security in a beetle-killed forest. *J. Wildl. Manag.* 84, 138–149. doi: 10.1002/jwmg.21781

Lowrey, B., Garrott, R. A., Miyasaki, H. M., Fralick, G., and Dewey, S. R. (2017). Seasonal resource selection by introduced mountain goats in the southwest greater yellowstone area. *Ecosphere* 8:e01769. doi: 10.1002/ecs2.1769

Lula, E. S., Lowrey, B., Proffitt, K. M., Litt, A. R., Cunningham, J. A., Butler, C. J., et al. (2020). Is habitat constraining bighorn sheep restoration? A case study. *J. Wildl. Manag.* 84, 588–600. doi: 10.1002/jwmg.21823

Mateo Sánchez, M. C., Cushman, S. A., and Saura, S. (2014). Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). *Int. J. Geogr. Inform. Sci.* 28, 1531–1546. doi: 10.1080/13658816.2013.776684

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H. L., Morales, J. M., and Haydon, D. T. (2015). Establishing the link between habitat selection and animal population dynamics. *Ecol. Monogr.* 85, 413–436. doi: 10.1890/14-2244.1

Matthiopoulos, J., Field, C., and MacLeod, R. (2019). Predicting population change from models based on habitat availability and utilization. *Proc. R. Soc. B* 286:20182911. doi: 10.1098/rspb.2018.2911

Mayor, S. J., Schneider, D. C., Schaefer, J. A., and Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience* 16, 238–247.

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., and Cushman, S. A. (2016). Multi-scale habitat selection modeling: a review and outlook. *Landsc. Ecol.* 31, 1161–1175. doi: 10.1007/s10980-016-0374-x

McLoughlin, P., Gaillard, J.-M., Boyce, M., Bonenfant, C., Messier, F., Duncan, P., et al. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* 88, 3192–3201. doi: 10.1890/06-1974.1

McLoughlin, P. D., Boyce, M. S., Coulson, T., and Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proc. R. Soc. B Biol. Sci.* 273, 1449–1454. doi: 10.1098/rspb.2006.3486

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., and Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *J. Anim. Ecol.* 79, 4–12. doi: 10.1111/j.1365-2656.2009.01613.x

Meadow, A. M., Ferguson, D. B., Guido, Z., Horangic, A., Owen, G., and Wall, T. (2015). Moving toward the deliberate coproduction of climate science knowledge. *Weather Clim. Soc.* 7, 179–191. doi: 10.1175/WCAS-D-14-00050.1

Meier, G., and Brown, J. F. (2014). *Remote Sensing of Land Surface Phenology*. Reston: US Geol. Surv.

Menkham, K., Sukmasuang, R., Pla-Ard, M., Charaspet, K., Panganta, T., Trisurat, Y., et al. (2019). Population and habitat use of Asian elephants (*Elephas maximus*) and five ungulate species in Khao Ang Rue Nai Wildlife Sanctuary, Chachoengsao Province, Thailand. *Biodivers. J. Biol. Divers.* 20, 2213–2221.

Merems, J. L., Shipley, L. A., Levi, T., Ruprecht, J., Clark, D. A., Wisdom, M. J., et al. (2020). Nutritional-landscape models link habitat use to condition of mule deer (*Odocoileus hemionus*). *Front. Ecol. Evol.* 8:98. doi: 10.3389/fevo.2020.00098

Merkle, J. A., Anderson, N. J., Baxley, D. L., Chopp, M., Gigliotti, L. C., Gude, J. A., et al. (2019). A collaborative approach to bridging the gap between wildlife managers and researchers. *J. Wildl. Manag.* 83, 1644–1651. doi: 10.1002/jwmg.21759

Middleton, A. D., Sawyer, H., Merkle, J. A., Kauffman, M. J., Cole, E. K., Dewey, S. R., et al. (2019). Conserving transboundary wildlife migrations: recent insights from the greater yellowstone ecosystem. *Front. Ecol. Environ.* 18, 83–91. doi: 10.1002/fee.2145

Morris, D. W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136, 1–13. doi: 10.1007/s00442-003-1241-4

Morris, L. R., Proffitt, K. M., and Blackburn, J. K. (2016). Mapping resource selection functions in wildlife studies: concerns and recommendations. *Appl. Geogr.* 76, 173–183. doi: 10.1016/j.apgeog.2016.09.025

Morrison, M. L. (2001). A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *J. Wildl. Manag.* 65, 613–623.

Morrison, M. L. (2012). The habitat sampling and analysis paradigm has limited value in animal conservation: a prequel. *J. Wildl. Manag.* 76, 438–450. doi: 10.1002/jwmg.333

Morrison, M. L., Marcot, B. G., and Mannan, R. W. (2006). *Wildlife-Habitat Relationships: Concepts and Applications*. Washington, DC: Island Press.

Muff, S., Signer, J., and Fieberg, J. (2019). Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. *J. Anim. Ecol.* 89, 80–92. doi: 10.1111/1365-2656.13087

Nel, J. L., Roux, D. J., Driver, A., Hill, L., Maherry, A. C., Snaddon, K., et al. (2016). Knowledge co-production and boundary work to promote implementation of conservation plans. *Conserv. Biol.* 30, 176–188. doi: 10.1111/cobi.12560

Nielsen, S. E., McDermid, G., Stenhouse, G. B., and Boyce, M. S. (2010). Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biol. Conserv.* 143, 1623–1634. doi: 10.1016/j.biocon.2010.04.007

Nielson, R. M., and Sawyer, H. (2013). Estimating resource selection with count data. *Ecol. Evol.* 3, 2233–2240. doi: 10.1002/ece3.617

Nilsen, E. B., Linnell, J. D., and Andersen, R. (2004). Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. *J. Anim. Ecol.* 73, 44–50. doi: 10.1111/j.1365-2656.2004.00790.x

Oates, B. A., Merkle, J. A., Kauffman, M. J., Dewey, S. R., Jimenez, M. D., Vartanian, J. M., et al. (2019). Antipredator response diminishes during periods of resource deficit for a large herbivore. *Ecology* 100:e02618. doi: 10.1002/ecy.2618

Openshaw, S. (1984). *The Modifiable Areal Unit Problem Concepts and Techniques in Modern Geography*. Norwich: Geobooks.

Peek, J. M., Dennis, B., and Hershey, T. (2002). Predicting population trends of mule deer. *J. Wildl. Manag.* 66, 729–736. doi: 10.2307/3803138

Peek, J. M., Korol, J. J., Gay, D., and Hershey, T. (2001). Overstory–understory biomass changes over a 35-year period in southcentral Oregon. *For. Ecol. Manag.* 150, 267–277. doi: 10.1016/S0378-1127(00)00585-5

Peterson, A. T., Papeş, M., and Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* 213, 63–72. doi: 10.1016/j.ecolmodel.2007.11.008

Pettorelli, N., Pelletier, F., Hardenberg, A. V., Festa-Bianchet, M., and Côté, S. D. (2007). Early onset of vegetation growth vs. rapid green-up: impacs on juvenile mountain ungulates. *Ecology* 88, 381–390. doi: 10.1890/06-0875

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M., et al. (2011). The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Clim. Res.* 46, 15–27. doi: 10.3354/cr00936

Plante, S., Dussault, C., and Côté, S. D. (2017). Landscape attributes explain migratory caribou vulnerability to sport hunting. *J. Wildl. Manag.* 81, 238–247. doi: 10.1002/jwmg.21203

Proffitt, K. M., DeVoe, J., Barker, K., Durham, R., Hayes, T., Hebblewhite, M., et al. (2019). A century of changing fire management alters ungulate forage in a wildfire-dominated landscape. *For. Int. J. For. Res.* 92, 523–537. doi: 10.1093/forestry/cpz017

Proffitt, K. M., Graigg, J. L., Garrott, R. A., Hamlin, K. L., Cunningham, J., Gude, J. A., et al. (2010). Changes in Elk resource selection and distributions associated with a late-season elk hunt. *J. Wildl. Manag.* 74, 210–218. doi: 10.2193/2008-593

Proffitt, K. M., Hebblewhite, M., Peters, W., Hupp, N., and Shamhart, J. (2016). Linking landscape-scale differences in forage to ungulate nutritional ecology. *Ecol. Appl.* 26, 2156–2174. doi: 10.1002/eap.1370

Ranglack, D. H., Proffitt, K. M., Canfield, J. E., Gude, J. A., Rotella, J., and Garrott, R. A. (2017). Security areas for elk during archery and rifle hunting seasons. *J. Wildl. Manag.* 81, 778–791. doi: 10.1002/jwmg.21258

Reinking, A. K., Smith, K. T., Mong, T. W., Read, M. J., and Beck, J. L. (2019). Across scales, pronghorn select sagebrush, avoid fences, and show negative responses to anthropogenic features in winter. *Ecosphere* 10:e02722. doi: 10.1002/ecs2.2722

Reyers, B., Nel, J. L., O'Farrell, P. J., Sitas, N., and Nel, D. C. (2015). Navigating complexity through knowledge coproduction: mainstreaming ecosystem services into disaster risk reduction. *Proc. Natl. Acad. Sci. U.S.A.* 112, 7362–7368. doi: 10.1073/pnas.1414374112

Riggs, R. A., Keane, R. E., Cimon, N., Cook, R., Holsinger, L., Cook, J., et al. (2015). Biomass and fire dynamics in a temperate forest-grassland mosaic: integrating multi-species herbivory, climate, and fire with the FireBGCv2/GrazeBGC system. *Ecol. Model.* 296, 57–78. doi: 10.1016/j.ecolmodel.2014.10.013

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., et al. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* 40, 913–929. doi: 10.1111/ecog.02881

Romesburg, H. C. (1981). Wildlife science: gaining reliable knowledge. *J. Wildl. Manag.* 45, 293–313.

Rowland, M. M., Nielson, R. M., Wisdom, M. J., Coe, P. K., Cook, J. G., Hafer, J. M., et al. (2018a). Linking nutrition with landscape features in a regional habitat-use model for elk in Western Oregon and Washington. *Wildl. Monogr.* 199, 31–49.

Rowland, M. M., Wisdom, M. J., Johnson, B. K., and Kie, J. G. (2000). Elk distribution and modeling in relation to roads. *J. Wildl. Manag.* 64, 672–684.

Rowland, M. M., Wisdom, M. J., Nielson, R. M., Cook, J. G., Cook, R. C., Johnson, B. K., et al. (2018b). Modeling elk nutrition and habitat use in Western Oregon and Washington. *Wildl. Monogr.* 199, 1–102.

Royle, J. A., Chandler, R. B., Yackulic, C., and Nichols, J. D. (2012). Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods Ecol. Evol.* 3, 545–554. doi: 10.1111/j.2041-210X.2011.00182.x

Russell, R. E., Gude, J. A., Anderson, N. J., and Ramsey, J. M. (2015). Identifying priority chronic wasting disease surveillance areas for mule deer in Montana. *J. Wildl. Manag.* 79, 989–997. doi: 10.1002/jwmg.914

Rykiel, E. J. (1996). Testing ecological models: the meaning of validation. *Ecol. Model.* 90, 229–244. doi: 10.1016/0304-3800(95)00152-2

Salas, E. A. L., Valdez, R., Michel, S., and Boykin, K. G. (2018). Habitat assessment of Marco Polo sheep (*Ovis ammon* polii) in Eastern Tajikistan: modeling the effects of climate change. *Ecol. Evol.* 8, 5124–5138. doi: 10.1002/ece3.4103

Sawyer, H., Kauffman, M. J., Nielson, R. M., and Horne, J. S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecol. Appl.* 19, 2016–2025. doi: 10.1890/08-2034.1

Sawyer, H., LeBeau, C. W., McDonald, T. L., Xu, W., and Middleton, A. D. (2019). All routes are not created equal: an ungulate's choice of migration route can influence its survival. *J. Appl. Ecol.* 56, 1860–1869.

Sawyer, H., Nielson, R. M., Lindzey, F., and McDonald, L. L. (2006). Winter habitat selection of mule deer before and during development of a natural gas field. *J. Wildl. Manag.* 70, 396–403. doi: 10.2193/0022-541x(2006)70[396:whsomd]2.0.co;2

Schrempp, T. V., Rachlow, J. L., Johnson, T. R., Shipley, L. A., Long, R. A., Aycrigg, J. L., et al. (2019). Linking forest management to moose population trends: the role of the nutritional landscape. *PLoS One* 14:e0219128. doi: 10.1371/journal.pone.0219128

Schuette, P., Creel, S., and Christianson, D. (2016). Ungulate distributions in a rangeland with competitors, predators and pastoralists. *J. Appl. Ecol.* 53, 1066–1077. doi: 10.1111/1365-2664.12610

Sekhar, N. U. (1998). Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India. *Environ. Conserv.* 25, 160–171. doi: 10.1017/s0376892998000204

Shean, D. E., Alexandrov, O., Moratto, Z. M., Smith, B. E., Joughin, I. R., Porter, C., et al. (2016). An automated, open-source pipeline for mass production of digital elevation models (DEMs) from very-high-resolution commercial stereo satellite imagery. *ISPRS J. Photogram. Remote Sens.* 116, 101–117. doi: 10.1016/j.isprsjprs.2016.03.012

Spitz, D. B., Rowland, M. M., Clark, D. A., Wisdom, M. J., Smith, J. B., Brown, C. L., et al. (2019). Behavioral changes and nutritional consequences to elk (*Cervus canadensis*) avoiding perceived risk from human hunters. *Ecosphere* 10:e02864. doi: 10.1002/ecs2.2864

Turner, W., Rondinini, C., Pettorelli, N., Mora, B., Leidner, A. K., Szantoi, Z., et al. (2015). Free and open-access satellite data are key to biodiversity conservation. *Biol. Conserv.* 182, 173–176. doi: 10.1016/j.biocon.2014.11.048

van Beest, F. M., Van Moorter, B., and Milner, J. M. (2012). Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim. Behav.* 84, 723–735. doi: 10.1016/j.anbehav.2012.06.032

Varley, N., and Boyce, M. S. (2006). Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecol. Model.* 193, 315–339. doi: 10.1016/j.ecolmodel.2005.09.001

Villamuelas, M., Fernández, N., Albanell, E., Gálvez-Cerón, A., Bartolomé, J., Mentaberre, G., et al. (2016). The Enhanced Vegetation Index (EVI) as a proxy for diet quality and composition in a mountain ungulate. *Ecol. Indic.* 61, 658–666. doi: 10.1016/j.ecolind.2015.10.017

Voinov, A., Kolagani, N., McCall, M. K., Glynn, P. D., Kragt, M. E., Ostermann, F. O., et al. (2016). Modelling with stakeholders – Next generation. *Environ. Model. Softw.* 77, 196–220. doi: 10.1016/j.envsoft.2015.11.016

Walters, C. J. (1986). *Adaptive Management of Renewable Resources*. New York, NY: Macmillan Publishers Ltd.

Ward, A. I., White, P. C., Smith, A., and Critchley, C. H. (2004). Modelling the cost of roe deer browsing damage to forestry. *For. Ecol. Manag.* 191, 301–310. doi: 10.1016/j.foreco.2003.12.018

Wheatley, M., and Johnson, C. (2009). Factors limiting our understanding of ecological scale. *Ecol. Complex.* 6, 150–159. doi: 10.1016/j.ecocom.2008.10.011

White, K. S., Gregovich, D. P., and Levi, T. (2018). Projecting the future of an alpine ungulate under climate change scenarios. *Glob. Chang. Biol.* 24, 1136–1149. doi: 10.1111/gcb.13919

Wiens, J. A. (1989). Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397.

Wisdom, M. J., Rowland, M. M., Nielson, R. M., Cook, J. G., Johnson, B. K., Coe, P. K., et al. (2018a). Modeling to evaluate elk habitat: contemporary approaches for Western Oregon and Washington. *Wildl. Monogr.* 199, 8–12.

Wisdom, M. J., Rowland, M. M., Nielson, R. M., Cook, J. G., Johnson, B. K., Hafer, J. M., et al. (2018b). Nutrition and habitat-use models for elk management in western Oregon and Washington. *Wildl. Monogr.* 199, 50–69.

Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., et al. (2018). Outstanding challenges in the transferability of ecological models. *Trends Ecol. Evol.* 33, 790–802. doi: 10.1016/j.tree.2018.08.001

Zimmermann, N. E., Edwards, T. C. Jr., Graham, C. H., Pearman, P. B., and Svenning, J. C. (2010). New trends in species distribution modelling. *Ecography* 33, 985–989. doi: 10.1111/j.1600-0587.2010.06953.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 03 July 2020
doi: 10.3389/fevo.2020.00204

Frequency and Density Associated Grouping Patterns of Male Roosevelt Elk

*Floyd W. Weckerly**

Department of Biology, Texas State University, San Marcos, TX, United States

Group-size variation has been examined within a framework of costs and benefits to ecological factors such as food limitations and risks from predators. Social interactions between males from male–male competition might also influence group size particularly in polygynous males. To explore the role of social and ecological factors on group size outside the mating season I examined the influence of abundance on male grouping patterns in a population of Roosevelt elk (*Cervus elaphus roosevelti*) in northwestern California, USA. Male grouping patterns were complex, males often group with other males, but they also can be transient members of female groups. Because male–male competition is pervasive even outside of the mating season, sizes of groups comprised of males only should be positive and linearly related to abundance of the male population or frequency associated. Whereas the number of males in female groups should be inversely related to female abundance or density associated. Males associating with females is more likely at low female abundance because females might still be reproductively active and per capita forage should be abundant. Across a 23-year study I examined whether male or female abundance was related to male only group sizes and the number of males in female groups. Size of male-only groups displayed a positive, linear relationship with male abundance and the number of males in female groups exhibited an inverse, linear relationship with female abundance. Uncovering forces influencing male grouping patterns required using the appropriate metric of abundance. Social factors likely influenced sizes of male-only groups and ecological factors probably influenced male prevalence in female groups.

Keywords: density dependence, gregariousness, forage acquisition, frequency dependence, polygyny, predation risk, redwood forest, ungulate

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Kelley M. Stewart,
University of Nevada, Reno,
United States
Matthew Jason Kauffman,
University of Wyoming, United States

****Correspondence:***
Floyd W. Weckerly
fw11@txstate.edu

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *03 December 2019*
Accepted: *03 June 2020*
Published: *03 July 2020*

Citation:
Weckerly FW (2020) Frequency and Density Associated Grouping Patterns of Male Roosevelt Elk.
Front. Ecol. Evol. 8:204.
doi: 10.3389/fevo.2020.00204

INTRODUCTION

Variation in group size usually is examined within a framework of costs and benefits to forage acquisition and detecting and diluting predation risks in groups comprised of females or without regard to group composition (Bell, 1971; Alexander, 1974; Jarman, 1974; Underwood, 1982; Pulliam and Caraco, 1984; Wrangham and Rubenstein, 1986; Heard, 1992; Peterson et al., 2005; Proffitt et al., 2012). Dynamics of male groups size, however, differ from those of females in many ungulate populations (Clutton-Brock et al., 1982; Weckerly, 2001; Childress and Lung, 2003; Jedrzejewski et al., 2006; Richardson and Weckerly, 2007; Winnie and Creel, 2007; Vander Wal et al., 2013;

Marino and Baldi, 2014). As such, factors that dictate grouping patterns in males might differ from those of females.

Male grouping patterns outside of the mating season are complex. Adult males aggregate with other adult males or with females. Groups comprised of adult males or male-only groups are prevalent but mixed-sex groups also exist. The frequency of mixed-sex groups and the number of males in those groups appears to be dynamic (Ortega and Franklin, 1995; Thirgood, 1996; Weckerly et al., 2001; Chiyo et al., 2014; Galezo et al., 2018; Wang et al., 2018; Meldrum and Ruckstuhl, 2019). But the processes influencing male-only groups and the number of males in mixed-sex groups have rarely been examined.

Male-only group sizes might be influenced by male–male competition for access to females even outside of the mating season (Weckerly, 2001; Childress and Lung, 2003; Winnie and Creel, 2007; Vander Wal et al., 2012; Peterson and Weckerly, 2018). As a result of male–male competition, aggressive interactions between males can be frequent (McCullough, 1969; Weckerly et al., 2001). Male-only groups, therefore, are probably not a cohesive collection of individuals. Rather, male-only groups might display fusion-fission dynamics where individuals mix with differing sets of males (Ortega and Franklin, 1995; Thirgood, 1996; Weckerly, 2001).

As the number of males in a population dictate the number of potential interactors, sizes of male-only groups should be associated with male abundance. A positive, linear relationship or frequency associated relationship would be anticipated when there are no dramatic changes in ecological factors such as forage distribution and predation risks across a range of abundances (Vander Wal et al., 2013). Two linear relationships are plausible. There could be a 1:1 or isometric relationship between male abundance and male-only group size. For each one animal increase in abundance, there is also a one animal increase in group size. All males are coalesced into one group which is also the size of the male population. One large group might improve forage detection and acquisition and mitigate individual predation risks. An isometric relationship has been proposed and observed when females inhabit an area where forage patches such as meadows are embedded in forests that have little forage (Street et al., 2013; Weckerly, 2017; McGuire, 2018; Lesmerises et al., 2018).

The alternative frequency associated relationship is a small group relationship, a possibility not previously considered. This scenario should occur when male-only group sizes are fueled by male–male competition and fusion–fission group dynamics is prevalent at all male abundances. As a result, an isometric relationship would not be possible and group sizes would be smaller than male abundance. The regression of male abundance on male-only group size would have a small slope (<1.0) and an intercept of 0.0.

After the mating season mixed-sex groups are often ephemeral and occur when individuals of one sex enter groups comprised of the opposite sex (Galezo et al., 2018; Meldrum and Ruckstuhl, 2019). Polygynous males might enter and leave female groups to forage or assess mating opportunities (Weckerly et al., 2001; Galezo et al., 2018). But male entry should be conditional on the environmental setting. One environmental setting would be negative feedbacks between food supplies and female abundances or an abundance associated relationship (McCullough, 1979; Weckerly, 2017). Males should associate with females for fitness returns perhaps when forage is less limited. At high female abundance the more limited forage and the remote likelihood that some females are in estrus limits fitness payoffs from visits to female groups (Morrison, 1960; Guinness et al., 1971, 1978; Asher et al., 2011; Keller et al., 2015; Johnson et al., 2019). Furthermore, when males are aggregated with females, time in the group will be transient because of foraging costs associated with aggregating with females (Turner et al., 2005; Peterson and Weckerly, 2018. Males might spend their time assessing and seeking mating opportunities at the expense of feeding or female proximity, not forage *per se*, limits or interferes with male foraging (Prins, 1989; Turner et al., 2005; Peterson and Weckerly, 2018).

Herein I had two objectives. One, I determine whether the male abundance–male-only group size relationship was isometric or small group. Two, I examined if female abundance was inversely related to the number of males in mixed-sex groups. The study population was an unhunted and nonmigratory population of Roosevelt elk that inhabited a landscape with a stable composition of discrete forage habitats in an ecosystem dominated by forest that had little forage. The mild climate precluded climatic extremes from differentially affecting size dimorphic females and males, which can prompt differential habitat selection and affect group size (Aublet et al., 2009). Across the 23-year study, female abundance changed by more than a factor of three and male abundance changed by more than a factor of four. These attributes made this study system appealing for clarifying abundance associations with male grouping patterns. To my knowledge, no one has examined forces driving both male-only group size and number of males in mixed-sex groups. Specifically, showing how male-male competition can constrain male-only group sizes and a density-dependent mechanism to maintain sex-specific groups. This research offers new insights into the evolution of gregariousness in male groups.

MATERIALS AND METHODS

Study Area

The study population inhabited the lower part of the Prairie Creek drainage in Redwood National and State Parks, Humboldt County, California USA (41.2132°N, 124.0046°W). The prime habitat for foraging by elk was the Boyes and Davison meadow complexes, which had flat topography and were about 3 km apart (Peterson and Weckerly, 2017). Boyes meadow was 51 ha and the Davison meadows were 50–60 ha in total area. For the first 19 years of the study from 1997 to 2015, Davison meadows were 50 ha. In late 2015 an adjacent 10 ha meadow to the south of Davison meadows that was privately owned was purchased by a non-profit organization and deeded to Redwood National and State Parks. Under private ownership elk were hazed when they ventured onto the parcel. Hazing ceased in late 2015 and elk began using the meadow in early 2016, which continued into 2019 (McGuire, 2018; Koetke, 2019). Summers were generally cool and dry, and winters were mild and wet. Precipitation mostly fell from

October to April, usually 120–180 cm. Snow was rare; respective mean minimum and maximum winter temperatures were 2 and 10°C. In summer, the respective mean minimum and maximum temperatures were about 10 and 20°C (Starns et al., 2015). Forage in meadows was mostly annual and perennial grasses with some forbs. Green-up of meadow vegetation began with autumn rains; plants grew slowly into late winter and more rapid growth began in early spring. Vegetation biomass peaked in May or June (Starns et al., 2015). Discrete meadows were surrounded by second- and old-growth redwood (*Sequoia sempervirens*)-conifer forests that dominated the area. Elk were non-migratory and not legally hunted in Redwood National and State Parks. Mountain lions (*Puma concolor*) and black bears (*Ursus americanus*) inhabit the parks. Mountain lions can prey on elk of all ages whereas black bears mostly prey on neonatal elk (Weckerly, 2017).

Surveys and Groups

Systematic surveys were conducted in January to collect data on group sizes and estimate abundances. January is roughly 3 months after the mating season when most conceptions occur (Weckerly, 2017). Although rare, copulations and conceptions do occur 3 months after the mating season (Guinness et al., 1978; Johnson et al., 2019). Furthermore, males still had developed antlers in January (Weckerly, 2017). Beginning at dawn, surveys were conducted for 1.75 h. The route was driven in a vehicle and all elk that were detected (solitary or in groups) were counted and classified as adult females (≥1 year old), juveniles, subadult, or yearling males (1–2 years), and adult males (≥2 years). Age classifications were delineated based on body size of females and juveniles and antler dimensions of subadult and adult males. Subadult males had unbranched antlers and adult males had branched antlers. Elk were grouped when two or more individuals displayed coordinated movement which meant they were often within 50 m of one another. When necessary to obtain an accurate count, I exited the vehicle and approached elk to within 10–200 m. Elk in the Prairie Creek drainage were accustomed to people and thus did not flee at my approach. In 1997 and 2000–2019, 10 surveys were conducted in each year. In 1998 and 1999, 5 surveys were conducted in each year. Field procedures were approved under animal care and use protocols approved through Texas State University (KSMJK6_02, 0735_1106_07, 1035_1112_31, 1019_1031_23, IACUC20168174611, A4147-01).

Up to 1 month before surveys began in January, I searched both Boyes and Davison meadow complexes for elk that I could uniquely identify from morphological distinctions (scars, ear slits, antler and pelage anomalies, and sometimes ear tags). These "naturally" marked elk also were noted during systematic surveys. The frequency of naturally marked elk and count data were used to estimate male abundances with Bowden's mark-resight estimator when the count data in a year indicated that individual males were missed during surveys (Bowden and Kufeld, 1995; Weckerly, 2017). I was likely to miss known individual males if there were unmarked males counted during surveys. Later in the time series when males were less abundant, I usually was able to uniquely identify all males based on antler and pelage anomalies and thus the tally of marked males was my index of male abundance. Adult females, juveniles, and subadult males were socially bonded and formed a cohesive group, hereafter referred to as the Davison herd. Individuals in the Davison herd had high sighting probabilities (>0.80) so I used the highest count as the index of female abundance (Peterson and Weckerly, 2017; Weckerly, 2017).

Group Metrics and Analyses

I used an animal focused metric of male-only group size, typical group size (Jarman, 1974). Typical group size is calculated as $\sum G_i^2 / \sum G_i$ where G is the number of individuals in the ith group. Solitary elk were included in typical group size calculations. Another reason why I selected typical group size is that this metric will be the same as the arithmetic mean of group sizes when all groups are the same size (Heard, 1992). When there is variability, typical group size is smaller than mean group size and the deviation between typical and mean group sizes increases with greater variation in group sizes. These features between mean and typical group sizes were convenient for assisting in distinguishing the two kinds of frequency associated group sizes, isometric and small-group relationships.

One tacit assumption about typical group size is that all animals in the population are detected (Jarman, 1974). This assumption was not met in every survey of my male-only groups so group-size estimates might be biased. To circumvent the detection issue, I only used survey data where the sum of all male-only group sizes and number of males in mixed-sex groups equaled the estimated male abundances. In years when Bowden's estimates of male abundance were necessary, I used surveys where the sum was at least the lower bound of the 95 percent confidence interval of estimated abundances.

To assess whether fusion-fission grouping occurred I calculated the proportion of groups observed during surveys that were comprised of unique compositions (Sueur et al., 2011). In a year when two or more surveys occurred where all males were detected, unique compositions were either when there were different-sized groups or when group sizes were the same, but groups had unique combinations of known individuals. In 20 of the 23 years there were a total of 98 surveys that met these criteria. The range in number of surveys in a year with unique combinations was 2–10 (median = 3.5). My metric of fusion-fission grouping was the proportion of the 98 surveys with unique compositions.

I estimated the number of males in mixed-sex groups (Davison herd) in two ways. I calculated the median of the number of males in the Davison herd in each year. I chose the median over the mean because the distribution of group sizes tend to be skewed right (Reiczigel et al., 2008). I also reported the high count of males in the Davison herd across the surveys conducted in each year. If the number of males in the Davison herd is ephemeral, then I expected the high count of males to be more strongly related to herd abundance than median number of males. I assumed that when males were in the Davison herd they were readily detected because I observed the herd repeatedly at close distances.

Least-squares regressions were estimated between abundances (Davison herd, male population) and response variables (median

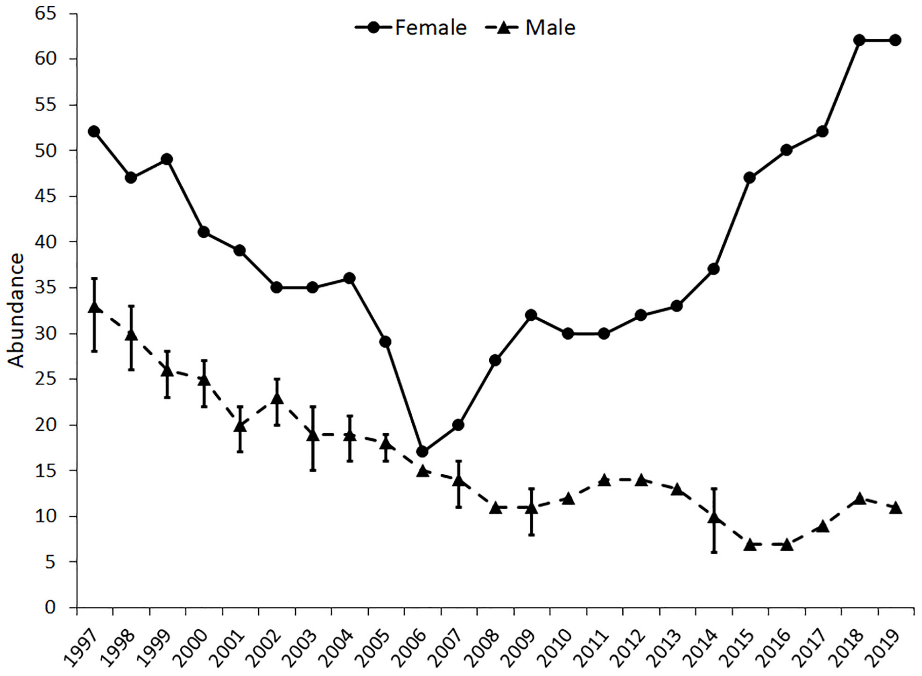

FIGURE 1 | Time series of abundances of the Davison herd (female) and male population. Error bars are 95 percent confidence intervals for years when male abundances were estimated using Bowden's mark-resight estimator.

number and high count of males in Davison herd). Because there were unequal number of male-only groups across years (**Supplementary Material**), I estimated a regression weighted by number of male-only groups in each year (Ryan, 1997). Weights were positively related to number of male-only groups.

I considered likely changes in *K* (environmental carrying capacity) that occurred across the 23 years of the study (Weckerly, 2017; Koetke, 2019). Because of a population irruption that began in 1991 a correction in density-dependent herd growth associated with a population decline likely occurred in the first 9 years of the study from 1997 to 2005. From 2006 to 2016 density-dependent growth was emerging, and from 2017 to 2019 when a new 10-ha forage patch became available to the herd (McGuire, 2018). Beginning in 2017 a new, higher *K* likely was emerging. I used a nested models analysis (Sokal and Rohlf, 2012) to assess if relationships between abundance and number of males differed between 1997–2005 and 2006–2016 or if one relationship across the 20 years would suffice. Data in 2017–2019 were excluded from regression analysis because of few data points. Regressions were estimated from 10,000 bootstrapped samples of data and I reported 95 percent confidence intervals of regression coefficients.

RESULTS

Abundance of the Davison herd declined from 1997 to 2006 (**Figure 1**). The abundance in 2006 was also the year of lowest abundance (17 elk) for the herd across the 23-year time series. After 2006 the herd steadily increased but there was a noticeable increase in herd abundance between 2017 and 2018. The abundances in 2018 and 2019 were the largest (62) documented in the time series. The temporal pattern in male abundance was strikingly different. The highest abundance of 33 was early in the time series (1997) and then progressively declined to a low of 7 in 2015 and 2016.

Males in male-only groups displayed fusion-fission dynamics as there were unique compositions in 78 of the 98 surveys (80%). Among the 220 surveys conducted in 23 years there were 154 surveys (70%) with males in the Davison herd (i.e., mixed-sex groups). Across these 154 surveys, the proportion of males from the male population that were in the Davison herd ranged from 0.03 to 0.89. The respective 25th, 50th, and 75th percentiles were 0.08, 0.10, and 0.22. In roughly 25% of surveys, a substantial part of the male population was in the Davison herd on the Davison meadow complex.

Male abundance, but not Davison herd abundance, displayed a relationship with male-only group sizes (**Table 1**). Abundance of the Davison herd was weakly related to median number of males in the Davison herd but more strongly related to high count of males in the Davison herd. Male abundance, however, had little influence on either of the two measures of number of males in the Davison herd.

Male abundance displayed a frequency associated, small-group relationship with male-only group size (**Figure 2**). The estimated intercept of the regression passed through the origin and the estimated slope (0.42) was < 1.0. There was an abundance associated response, however, between Davison herd abundance and high count of males in that herd between 1997 and 2016 (**Figure 3**). Considering likely changes in *K* between 1997

TABLE 1 | Coefficients of determination (r^2) from bootstrapped regressions.

Abundance	Group metric		
	Male-only	**Median number of males**	**High count in number of males**
Female	0.02	0.14	0.37
Male	0.63	0.001	0.05

Regressions weighted by number of male-only groups were estimated between female or male abundances and typical size of male-only groups. Simple linear regressions were estimated between female or male abundances and median number of males in the female (Davison) herd and high count of number of males in female herd.

and 2005, and from 2006 to 2016 did not affect the inverse relationship between herd abundance and high count of males [$F_{(2,16)} = 1.9$, $P = 0.175$].

DISCUSSION

There were three novel aspects to my study. One, I examined abundance relationships in the two possible male grouping patterns, male-only groups and males in mixed-sex groups (Davison herd). Two, I uncovered the metric of abundance that was related to each of the group types. Three, I described frequency and density associated relationships that were used to identify when social and ecological factors were likely affecting male grouping patterns. These outcomes are important to understanding the evolution of male gregariousness, which is complex.

As expected, male abundance was related to male-only group size, which displayed a small-group relationship. Thus, social factors likely played a role in influencing male group sizes after the mating season. Males presumably interact with other males to learn social skills or to maintain a high social status once that is attained (Weckerly, 2001). As male abundance determines the number of possible interactors, it was more strongly related to male-only group size than was female abundance. The constant fusion-fission group dynamics means that group size is less than the largest possible group size, precluding the manifestation of an isometric relationship. An isometric relationship was displayed by the Davison herd (Weckerly, 2017). These females and juveniles are in one cohesive group presumably because it improves forage acquisition and lessens risks from predators when discrete forage patches are embedded in forests that have little forage (Street et al., 2013). The small-group relationship is consistent with social and not ecological factors influencing male-only group sizes because an isometric relationship was not found and the fusion-fission group size dynamics. Male–male competition, a driver of fusion-fission dynamics, is constant across male abundances and constrains their group sizes.

Small male-only group sizes in polygynous and group-living herbivores is common outside of the mating season (Hirth, 1977; Owen-Smith, 1993; Winnie and Creel, 2007; Li et al., 2012; Vander Wal et al., 2013; Weckerly and Ricca, 2014). Small male-only group size can ostensibly be attributable to fewer adult males relative to adult females in populations. Males typically have shorter longevity than females probably because of sexual selection and large body size (Owen-Smith, 1993; Toïgo and Gaillard, 2003; Tidiere et al., 2015). Nonetheless, when considering abundance of males and the number of males that potentially could be grouped, I observed that male-only group sizes were still small. Small male-only group size is likely because of fusion-fission dynamics brought about by male–male competition and because males occurred with females at times. The implication is that male-only group sizes should be small because male–male interactions to improve reproductive success should be constantly occurring across a variety of environmental settings.

Ecological factors probably have a role in male-only group sizes outside of the mating season (Winnie and Creel, 2007; Chiyo et al., 2014). Boyes and Davison meadow complexes are rather small forage patches (51–60 ha) situated in expanses of forests that presumably provide much less forage for elk. Consequently, females and males frequent the same meadows and are often in proximity (Weckerly, 2017). Consequently, the patchiness of forage habitat might have influenced the high frequency (70%) across all years that one or more males were in the Davison herd (mixed-sex groups). When the landscape is comprised of more open forage habitat, frequency of mixed-sex groups appears to be lower (Conradt, 1999; Peterson and Weckerly, 2017). Males associating with female groups is probably filtered through local environmental settings (Bleich et al., 1997).

An inverse relationship between female abundance and number of males in mixed-sex groups provides a mechanism for females, which are subordinate to males, to reduce male entry into female groups (Weckerly et al., 2001). At low female abundance, relative to K, food limitations should be lessened and, consequently, males might seek females to assess mating possibilities. Males entering female groups probably receive little interference to group entry from individual females. Although my study was conducted 3 or so months after the mating season, estrous females might exist at that time (Guinness et al., 1978; Weckerly, 2017; Johnson et al., 2019), generating the motivation for males to enter female groups. At high female abundance, relative to carrying capacity, males are reluctant to seek out and associate with females because per capita food resources are low. Additionally, there is the cost of reduced foraging time when males aggregate with females because males have low tolerance for foraging animals in close proximity or because males are assessing and possibly courting females which I did observe (Prins, 1989; Turner et al., 2005; Peterson and Weckerly, 2018).

Because I did not detect an influence of a likely change in K on the relationship between Davison herd size and number of males in that herd it calls into question whether food limitations have a pronounced impact on male entry into the Davison herd (Koetke, 2019). The Davison herd presumably went through a four-stage irruption between 1991 and 2016 (Weckerly, 2017). The first two stages, rapid growth and peak of the irruption, occurred from 1991 to 1997, the third stage, herd decline occurred from 1998 to 2006, and the fourth stage, emergence of a new K, occurred between 2006 and 2016. Between 1997 and 2005 there might not have

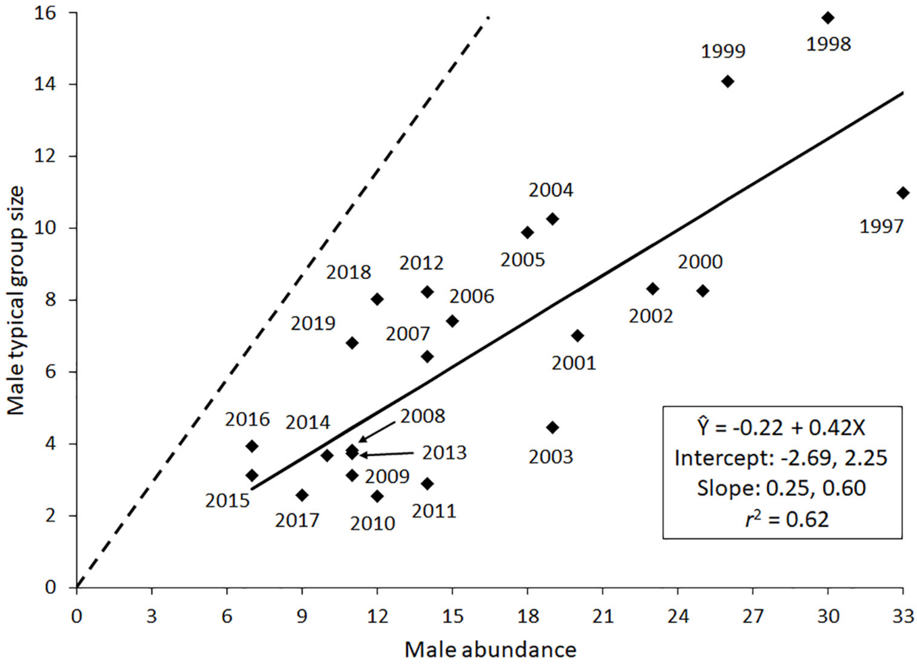

FIGURE 2 | Scatterplot of data and weighted regression estimating relationship between male abundance and male-only group size. The regression coefficients, r^2, and lower and upper 95% confidence intervals for each regression coefficient are also reported. The dashed line represents an isometric relationship.

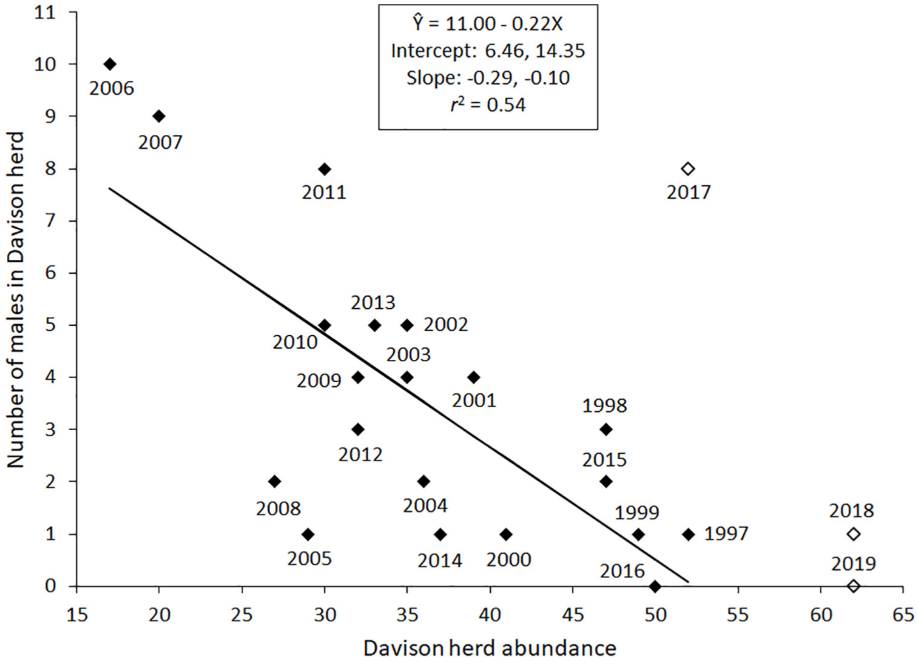

FIGURE 3 | Scatterplot of data and regression estimating high count of males in the Davison herd from Davison herd abundance for 1997–2016 (solid diamonds). The years 2017–2019 have open diamonds. Data in those years were not included in analysis because the herd expanded use into a new forage habitat and the result is likely to be an increase in *K* carrying capacity.

been a large enough range in herd sizes to detect a change in the relationship between herd abundance and number of males in the herd.

Perhaps males are more strongly cued to females that possibly are in or going to be in estrus. The "female in estrus" possibility seems more likely at low herd abundance when females are likely to be in a higher nutritional plane which should improve the chances that females are reproductive. This possibility might also be playing out after 2015. In late 2015 a new forage patch became available. In a matter of months after the patch became accessible, the Davison herd was using the new patch (McGuire, 2018). Inclusion of this forage patch presumably alleviated forage limitations among females in the Davison herd as recruitment increased for the next 2 years (McGuire, 2018; Koetke, 2019). A new and elevated K seemed likely from 2017 to 2019. In 2017 there might have been more females in better physiological condition than in 2018 and 2019. In turn, more males entered the Davison herd in 2017 than in the other 2 years. K and influences on males associating with females, outside the mating season, might be less than the influence of K on prevalence of reproductively active females.

The inverse relationship between Davison herd abundance and number of males in that herd is not likely because of increased vulnerability to predators at small group sizes when population abundance is also low (Thirgood, 1996; Meldrum and Ruckstuhl, 2019). In my study population, group size is a weaker correlate of vigilance in females and males than proximity of individuals across a range of abundances (Peterson and Weckerly, 2018). When individuals lift their heads when grazing it is more likely to be in response to conspecific interactions than to risks from predators. Moreover, in the open, flat meadows of the study area individual vulnerability to attack and capture by mountain lions or black bears is probably less than in nearby forests (Weckerly, 2017).

An abundance-associated mechanism for reducing male entry into female groups is useful to explaining intersexual habitat use, population level phenomenon like sexual segregation, and reducing the prospect of male harassment (Parker, 1979; McCullough, 1999; Wearmouth et al., 2012). Ultimately, females should aggregate in habitat with abundant and nutritious forage for fitness returns as should males. Although resource use and selection by size-dimorphic females and males differs, there remains considerable niche overlap, particularly at low abundances, which means that females and males can be in proximity (Kie and Bowyer, 1999; Long et al., 2009). The abundance-associated relationship uncovered herein offers a proximate mechanism to preclude males from aggregating with females as well as reduce male harassment.

The inverse relationship between Davison herd (female) abundance and number of males in the herd was weaker than the male abundance–male-only group size relationship. Perhaps the inverse relationship was spurious. A spurious correlation might manifest if only young sexually mature but socially immature males associated with females more than older males (Owen-Smith, 1993; Bleich et al., 1997; Wang et al., 2018). I did not know the age structure of the male population or the age of males that frequented the Davison herd. But, about 25 percent of the time, a substantial part of the male population was aggregated with females. On those occasions it seemed unlikely that most of the male population was comprised of young and socially immature males. It was plausible that more than just young and socially immature males aggregated with females.

The relationship between Davison herd abundance and median number of males in the Davison herd was weak. Because males are transient members of female groups, my measure of central tendency, the median, failed to capture the dynamic of males entering the Davison herd and the length of time males remained in the herd. As such, measures of central tendency probably cannot capture that dynamic across weekly or monthly time scales.

Male grouping patterns from small to large total abundance are complex because male-only groups and males in mixed-sex groups associate with different measures of abundances. Furthermore, female and male abundances do not have to be strongly connected. Male abundance was highest early in the time series, which might have been associated with dispersing males seeking forage and assessing mating opportunities (Loe et al., 2009). Davison meadow became available to elk in 1991 and there was rapid growth of both female and male abundances until 1997 when the Davison herd peaked in abundance (Weckerly, 2017). After 1997 male abundance steadily declined as did the Davison herd abundance. Herd abundance began to rebound in 2007 but male abundance did not. After 2006, male survival might have declined. Alternatively, males typically disperse from natal herds as yearlings. Therefore, the rate that males dispersed into Boyes and Davison meadow complexes from the Davison and other herds in the region might have declined because of forage limitations in the Davison meadows (Peterson and Weckerly, 2017). Perhaps there were few males to disperse to the Boyes and Davison meadow complexes. Whatever the possible mechanism(s), lower male abundance when female abundances were high also has been documented in two other populations of *C. elaphus* that were not hunted (Coulson et al., 2004; Cobb, 2010).

Male grouping patterns 3 months after the mating season were influenced by both ecological and social factors. Ecological factors influenced prevalence of males in female groups and social factors had a large influence on size of groups comprised of adult males. Uncovering the roles of ecological and social factors required the appropriate metric of abundance. In the past, abundance–group size relationships used total abundance (females and male), but in this study the male abundance–male-only group size and Davison herd abundance–number of males in the herd relationships were more informative. Uncovering the appropriate metric of abundance was needed to directly examine why male and female group sizes display such different dynamics. Information that was needed to provide additional insights into the evolution of male gregariousness.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Texas State University, Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

FW was responsible for all aspects of the study: developing the questions, designing the study, collecting, analyzing and interpreting the data, and writing the manuscript.

FUNDING

Funding was provided by the Alamo Safari Club, California Fish and Wildlife, Granite Bay Safari Club, Rocky Mountain Elk Foundation, Houston Safari Club, and Save the Redwoods League.

ACKNOWLEDGMENTS

I am grateful to the students that assisted in field work: A. Duarte, J. Hunt, R. Keheler, L. Koetke, N. Kolbe, M. Longoria, R. Luna, K. McFarland, A. McGuire, M. O'Day, L. Peterson, K. Richardson, M. Ricca, S. Shelton, S. Robinson, H. Starns, G. Street, L. Williamson, and D. Wolcott. I thank L. Koetke, Z. Espinoza, and two reviewers for comments on a previous draft.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00204/full#supplementary-material

REFERENCES

Alexander, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5, 325–383.

Asher, G. W., Scott, I. C., Archer, J. A., Ward, J. F., and Littlejohn, R. P. (2011). Seasonal luteal cyclicity of pubertal and adult red deer (*Cervus elaphus*). *Anim. Reprod. Sci.* 125, 138–147. doi: 10.1016/j.anireprosci.2011.03.009

Aublet, J. F., Festa-Bianchet, M., Bergero, D., and Bassano, B. (2009). Temperature constraints on foraging behaviour of male Alpine ibex (Capra ibex) in summer. *Oecologia* 159, 237–247. doi: 10.1007/s00442-008-1198-4

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Sci. Am.* 225, 86–93. doi: 10.1038/scientificamerican0771-86

Bleich, V. C., Bowyer, R. T., and Wehausen, J. D. (1997). Sexual segregation in mountain sheep: resources or predation? *Wildlife Monogr.* 134, 3–50.

Bowden, D. C., and Kufeld, R. C. (1995). Generalized mark-resight population size estimation applied to Colorado moose. *J. Wildlife Manag.* 59, 840–851.

Childress, M. J., and Lung, M. A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim. Behav.* 66, 389–398. doi: 10.1006/anbe.2003.2217

Chiyo, P. I., Wilson, J. W., Archie, E. A., Lee, P. C., Moss, C. J., and Alberts, S. C. (2014). The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants. *Behav. Ecol.* 25, 1494–1504. doi: 10.1093/beheco/aru152

Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red deer: Behavior and Ecology of two Sexes*. Chicago, IL: University of Chicago.

Cobb, M. A. (2010). *Spatial Ecology and Population Dynamics of Tule elk (Cervus elaphus nannodes) at Point Reyes National Seashore, California*. Dissertation, University of California, Berkeley, Berkeley, CA.

Conradt, L. (1999). Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Anim. Behav.* 57, 1151–1157. doi: 10.1006/anbe.1999.1067

Coulson, T., Guinness, F., Pemberton, J., and Clutton-Brock, T. (2004). The demographic consequences of releasing a population of red deer from culling. *Ecology* 85, 411–422. doi: 10.1890/03-0009

Galezo, A. A., Krzyszczyk, E., and Mann, J. (2018). Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behav. Ecol.* 29, 377–386. doi: 10.1093/beheco/arx177

Guinness, F., Lincoln, G. A., and Short, R. V. (1971). The reproductive cycle of the female red deer, *Cervus elaphus* L. *J. Reprod. Fertil.* 27, 427–438. doi: 10.1530/jrf.0.0270427

Guinness, F. E., Gibson, R. M., and Clutton-Brock, T. H. (1978). Calving times of red deer (*Cervus elaphus*) on Rhum. *J. Zool.* 185, 105–114. doi: 10.1111/j.1469-7998.1978.tb03316.x

Heard, D. C. (1992). The effect of wolf predation and snow cover on musk-ox group size. *Am. Natural.* 139, 190–204. doi: 10.1086/285320

Hirth, D. H. (1977). Social behavior of white-tailed deer in relation to habitat. *Wildlife Monogr.* 53, 1–55.

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* 48, 215–267. doi: 10.1163/156853974x00345

Jedrzejewski, W., Saedtke, H., Kamler, J. F., Jedrzejewska, B., and Stenkewitz, U. (2006). Group size dynamics of red deer in Bialowieza Primeval Forest. Poland. *J. Wildlife Manag.* 70, 1054–1059. doi: 10.2193/0022-541x(2006)70[1054:gsdord]2.0.co;2

Johnson, B. K., Jackson, D. H., Cook, R. C., Clark, D. A., Coe, P. K., Cook, J. G., et al. (2019). Roles of maternal condition and predation in survival of juvenile elk in Oregon. *Wildlife Monogr.* 201, 3–60. doi: 10.1002/wmon.1039

Keller, B. J., Bleisch, A. D., Millspaugh, J. J., Lehman, C. P., Kragel, J. J., Hansen, L. P., et al. (2015). Extended duration of parturution season in North American elk (*Cervus elaphus*). *Am. Midland Natural.* 173, 162–167. doi: 10.1674/0003-0031-173.1.162

Kie, J. G., and Bowyer, R. T. (1999). Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *J. Mammal.* 80, 1004–1020. doi: 10.2307/1383271

Koetke, L. J. (2019). *Elk Population Dynamics When Carrying Capacities Vary Across and Within Herds*. Thesis, Texas State University, San Marcos, TX.

Lesmerises, F., Johnson, C. J., and St-Laurent, M.-H. (2018). Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. *Anim. Behav.* 140, 39–47. doi: 10.1016/j.anbehav.2018.03.014

Li, C., Jiang, Z., Li, L., Li, Z., Fang, H., Li, C., et al. (2012). Effects of reproductive status, social rank, sex and group size on vigilance patterns in przewalski's gazelle. *PLoS One* 7:e32607. doi: 10.1371/journal.pone.0032607

Loe, L. E., Mysterud, A., Veiberg, V., and Langvatn, R. (2009). Negative density-dependent emigration of males in an increasing red deer population. *Proc. R. Soc. Lon. B* 2763, 2581–2587. doi: 10.1098/rspb.2009.0224

Long, R. A., Rachlow, J. L., and Kie, J. G. (2009). Sex-specific responses of North American elk to habitat manipulation. *J. Mammal.* 90, 423–432. doi: 10.1644/08-mamm-a-181.1

Marino, A., and Baldi, R. (2014). Ecological correlates of group-size variation in a resource-defense ungulate, the sedentary Guanaco. *PLoS One* 9:e89060. doi: 10.1371/journal.pone.0089060

McCullough, D. R. (1969). The tule elk: its history, behavior, and ecology. *Univ. Calif. Publ. Zool.* 88, 1–191.

McCullough, D. R. (1979). *The George Reserve Deer Herd: Population Ecology of a k Selected Species*. Ann Arbor, MI: University of Michigan Press.

McCullough, D. R. (1999). Density dependence and life-history strategies of ungulates. *J. Mammal.* 80, 1130–1146. doi: 10.2307/1383164

McGuire, A. G. (2018). *Roosevelt elk Response to a Newly Available Forage Patch*. Thesis, Texas State University, San Marcos, TX.

Meldrum, G. E., and Ruckstuhl, K. E. (2019). Mixed-sex group formation in bighorn sheep in winter: trading costs of synchrony for benefits of group living. *Anim. Behav.* 77, 919–929. doi: 10.1016/j.anbehav.2008.12.023

Morrison, J. A. (1960). Characteristics of estrus in captive elk. *Behaviour* 16, 84–92. doi: 10.1163/156853960x00052

Ortega, I. M., and Franklin, W. L. (1995). Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. *Rev. Chil. Histor. Nat.* 68, 489–500.

Owen-Smith, N. (1993). Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *J. Anim. Ecol.* 62, 428–440.

Parker, G. A. (1979). "Sexual selection and sexual conflict," in *Reproductive Competition in Insects*, eds M. S. Blum and N. A. Blum (London: Academic Press), 123–166. doi: 10.1016/b978-0-12-108750-0.50010-0

Peterson, L. M., and Weckerly, F. W. (2017). Male group size, female distribution and changes in sexual segregation by Roosevelt elk. *PLoS One* 12:e0187829. doi: 10.1371/journal.pone.0187829

Peterson, L. M., and Weckerly, F. W. (2018). Social behavior and changes in foraging behavior in a gregarious ungulate. *J. Mammal.* 99, 1422–1429.

Peterson, M. N., Lopez, R. R., Laurent, E. J., Frank, P. A., Silvy, N. J., and Liu, J. (2005). Wildlife loss through domestication: the case of endangered Key deer. *Conserv. Biol.* 19, 939–944. doi: 10.1111/j.1523-1739.2005.00069.x

Prins, H. H. T. (1989). Condition changes and choice of social environment in African buffalo bulls. *Behaviour* 108, 297–324.

Proffitt, K. M., Gude, J. A., Shamhart, J., and King, F. (2012). Variations in elk aggregation patterns across a range of elk population sizes at Wall Creek. Montana. *J. Wildlife Manag.* 76, 847–856. doi: 10.1002/jwmg.310

Pulliam, H. R., and Caraco, T. (1984). "Living in groups: is there an optimum group size?," in *Behavioral Ecology: AN Evolutionary approach*, 2nd Edn, eds J. R. Krebs and N. B. Dvies (Oxford: Blackwell), 122–147.

Reiczigel, J., Lang, Z., Rozsa, L., and Tothmersz, B. (2008). Measures of sociality: two different views of group size. *Anim. Behav.* 75, 715–721. doi: 10.1016/j.anbehav.2007.05.020

Richardson, K. E., and Weckerly, F. W. (2007). Intersexual social behavior of urban white-tailed deer and its evolutionary implications. *Can. J. Zool.* 85, 759–766. doi: 10.1139/z07-057

Ryan, T. P. (1997). *Modern Regression Methods*. New York, NY: Wiley.

Sokal, R. R., and Rohlf, F. J. (2012). *Biometry: The principles and Practice of Statistics in Biological Research*. New York, NY: W. H. Freeman and Company.

Starns, H. D., Weckerly, F. W., Ricca, M. A., and Duarte, A. (2015). Vegetation changes associated with a population irruption by Roosevelt elk. *Ecol. Evol.* 5, 109–120. doi: 10.1002/ece3.1327

Street, G. M., Weckerly, F. W., and Schwinning, S. (2013). Modeling forage mediated aggregation in a gregarious ruminant. *Oikos* 122, 929–937. doi: 10.1111/j.1600-0706.2012.20974.x

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., et al. (2011). Collective decision-making and fission-fussion dynamics: a conceptual framework. *Oikos* 120, 1608–1617. doi: 10.1111/j.1600-0706.2011.19685.x

Thirgood, S. J. (1996). Ecological factors influencing sexual segregation and group size in fallow deer (Dama dama). *J. Zool.* 239, 783–797. doi: 10.1111/j.1469-7998.1996.tb05478.x

Tidiere, M., Gaillard, J.-M., Muller, D. W. H., Lackey, L. B., Gimenez, O., Clauss, M., et al. (2015). Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants. *Evolution* 69, 3123–3140. doi: 10.1111/evo.12801

Toïgo, C., and Gaillard, J.-M. (2003). Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environmental harshness? *Oikos* 101, 376–384. doi: 10.1034/j.1600-0706.2003.12073.x

Turner, W. C., Jolles, A. E., and Owen-Smith, N. (2005). Alternating sexual segregation during the mating season by male African buffalo (Syncerus caffer). *J. Zool.* 267, 291–299.

Underwood, R. (1982). Vigilance behaviour in grazing African antelopes. *Behaviour* 79, 81–106.

Vander Wal, E., van Beest, F. M., and Brook, R. K. (2013). Density-dependent effects on group size are sex-specific in a gregarious ungulate. *PLoS One* 8:e53777. doi: 10.1371/journal.pone.0053777

Vander Wal, E., Yip, H., and McLoughlin, P. D. (2012). Sex-based differences in density-dependent sociality: an experiment with a gregarious ungulate. *Ecology* 93, 206–212. doi: 10.1890/11-0020.1

Wang, M., Alves, J., da Silva, A. A., Yang, W., and Ruckstuhl, K. E. (2018). The effect of male age on patterns of sexual segregation in Siberian ibex. *Sci. Rep.* 8:13095.

Wearmouth, V. J., Southall, E. J., Morritt, D., Thompson, R. C., Cuthill, I. C., Partridge, J. C., et al. (2012). Year-round sexual harassment as a behavioral mediator of vertebrate population dynamics. *Ecol. Monogr.* 82, 351–366. doi: 10.1890/11-2052.1

Weckerly, B. (2017). *Population Ecology of Roosevelt elk: Conservation and Management in Redwood National and State Parks*. Reno, NV: University of Nevada Press.

Weckerly, F. W. (2001). Are large male roosevelt elk less social because of aggression? *J. Mammal.* 82, 414–421. doi: 10.1093/jmammal/82.2.414

Weckerly, F. W., and Ricca, M. A. (2014). Aggression and coexistence in female caribou. *Arctic* 67, 189–195.

Weckerly, F. W., Ricca, M. A., and Meyer, K. P. (2001). Sexual segregation in Roosevelt elk: cropping rates and aggression in mixed-sex groups. *J. Mammal.* 82, 825–835. doi: 10.1093/jmammal/82.3.825

Winnie, J. J., and Creel, S. (2007). Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim. Behav.* 73, 215–225. doi: 10.1016/j.anbehav.2006.07.007

Wrangham, R. W., and Rubenstein, D. I. (1986). "Social evolution in birds and mammals," in *Ecological Aspects of Social Evolution*, eds D. I. Rubenstein and R. W. Wrangham (Princeton, NJ: Princeton University Press), 452–470. doi: 10.2307/j.ctt7zvwgq.24

Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 18 August 2020
doi: 10.3389/fevo.2020.00274

One in the Hand Worth Two in the Bush? Reproductive Effort of Young Males Is Not Affected by the Presence of Adult Males

Kevin L. Monteith[1,2]*, Kyle B. Monteith[2], Jonathan A. Jenks[2] and Rhiannon P. Jakopak[1]

[1] Haub School of Environment and Natural Resources, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, United States, [2] Department of Natural Resource Management, South Dakota State University, Brookings, SD, United States

Reproduction is a costly endeavor, and most large, long-lived, and iteroparous mammals exhibit conservative life-history tactics wherein an individual may forego or abandon a reproduction event for the sake of survival. Nevertheless, risks and benefits associated with reproduction are not equal across males and females, nor across their life. Whereas expenditure for females is associated with rearing young (e.g., lactation), expenditure for males occurs with securing mating opportunities. Young males may be more successful when dominant males are lacking, but it is less clear whether—and at what cost—young males will expend effort when those opportunities arise. We designed an experiment to quantify reproductive effort (e.g., food intake, somatic loss [body mass and fat]) of male white-tailed deer (*Odocoileus virginianus*) to better understand the reproductive ecology of male ungulates, with an emphasis on determining how adult males (≥4.5-years old) affect timing and extent of reproductive effort expended by yearling males (1.5-years old). Food intake, hormone levels, body mass, and somatic loss during rut were similar between yearling males that interacted with adult males and those that did not. Somatic loss by all males was greatest during peak estrus of females, but forage intake relative to metabolic body mass for yearling males was nearly twice that of adult males. Testosterone levels were lower for yearling than adult males early in rut and were related negatively to forage intake. Whereas adult males lost 20% (23.5 kg) of body mass and 31% (5.3 percentage points [ppt]) of body fat during the rut, yearling males lost 12% (9.3 kg) of body mass and 22% (4.7 ppt) of body fat. Reproductive effort by young males was not influenced by the presence of adult males, though young males expended less reproductive effort than adults. Instead, reproductive allocation occurred in a state-dependent manner, where pre-season levels of somatic reserves dictated reproductive effort, regardless of age. Like female ungulates, male deer displayed risk-sensitive reproductive allocation wherein current reproductive allocation occurred as a function of resources garnered during the prior season and were expended in a way that should have avoided over-investing and creating a tradeoff between reproduction and survival.

Keywords: life-history theory, nutritional condition, *Odocoileus virginianus*, risk-sensitive reproductive allocation, state dependent, trade-offs, ungulates

Edited by:
Paul Richard Krausman,
University of Arizona, United States

Reviewed by:
Marco Festa-Bianchet,
Université de Sherbrooke, Canada
Francisco Garcia-Gonzalez,
Estación Biológica de Doñana (EBD),
Spain

****Correspondence:***
Kevin L. Monteith
kevin.monteith@uwyo.edu

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *18 February 2020*
Accepted: *31 July 2020*
Published: *18 August 2020*

Citation:
Monteith KL, Monteith KB,
Jenks JA and Jakopak RP (2020) One
in the Hand Worth Two in the Bush?
Reproductive Effort of Young Males Is
Not Affected by the Presence of Adult
Males. Front. Ecol. Evol. 8:274.
doi: 10.3389/fevo.2020.00274

INTRODUCTION

Reproduction is a costly endeavor, and animals must balance the potential fitness benefits of investing energy into reproduction with other functions critical to life, such as avoiding predators, somatic growth, and maintenance (Kozłowski, 1992). The amount of energy and resources invested into reproduction is a reoccurring decision that iteroparous animals make throughout much of their life, with implications for lifetime reproductive output, individual condition, and survival (Stearns, 1992). Most large, long-lived, and iteroparous mammals exhibit conservative life-history tactics wherein an individual will either forego or withhold some degree of resources from reproduction for the sake of survival. Individuals who do not have sufficient resources to devote to reproduction are unsuccessful competitors or, in extreme cases, risk mortality (Andersson, 1994). Throughout their lives, individuals are balancing the risk of investing resources into reproduction in the near term with the potential reward of increasing fitness over the long term.

For female ungulates, reproduction is resource-intensive, and females balance risks and potential fitness benefits of reproduction in a risk-sensitive manner (Monteith et al., 2013b, 2014b; Bårdsen et al., 2014). Female ungulates exhibit a pronounced period of extensive maternal care wherein the majority of resources necessary to sustain growth and development of offspring comes from the mother (Clutton-Brock et al., 1989; Monteith et al., 2014a). This resource demand is met by drawing on somatic reserves or increasing forage intake, or some combination thereof (Jönsson, 1997; Panzacchi et al., 2010; Tollefson et al., 2010; Monteith et al., 2014b). Nevertheless, if resources are inadequate to sustain offspring growth and survival, female ungulates will withhold resources necessary to preserve their survival at the cost of their offspring (Martin and Festa-Bianchet, 2010; Shallow et al., 2015)—a concept known as risk-sensitive reproductive allocation (Bårdsen et al., 2008).

The risks and benefits associated with reproduction are not equal across males and females. Male ungulates similarly exhibit a period of extensive resource allocation; however, this expenditure typically occurs during a truncated window of time associated with the mating season (i.e., rut), except for territorial species where expenditures may occur over a longer period through territory maintenance (Mysterud et al., 2004; Corlatti et al., 2014). Nevertheless, reproductive effort among male ungulates often has been thought of in more of a risk-prone manner influenced by sexual selection (Andersson, 1994). During the rut, male ungulates may expend energy to obtain or maintain status within a dominance hierarchy, retain a territory, or search for and tend receptive females, all with the underlying goal of securing mating opportunities (Mysterud et al., 2004). Reproductively active males spend more time resting and breeding and little time foraging (Willisch and Ingold, 2007). Expenditures associated with the rut can result in males losing ≥ 25% of their body mass (McElligott et al., 2003). Though mass loss associated with rut has been proposed to be largely caused by increased reproductive activity, there also is pronounced hypophagia in some males (Miquelle, 1990; Willisch and Ingold, 2007; Mysterud et al., 2008a), which is consistent with the inability of activity alone to explain patterns of mass loss (McElligott et al., 2003; Foley et al., 2018). Regardless, the substantial reproductive effort (e.g., reductions in forage intake, loss in somatic reserves) results in males exhibiting reductions in nutritional condition following the mating season (Yoccoz et al., 2002; Mysterud et al., 2003) and potentially negative effects to survival during the ensuing winter (Clutton-Brock, 1982; Stevenson and Bancroft, 1995; Ditchkoff et al., 2001). Indeed, physiological consequences of the rut have been proposed to contribute to a risky lifestyle; consequently, skewed sex ratios emerge through disproportionate mortality among males (Berger and Gompper, 1999). Nevertheless, evaluations of reproductive effort among males is underrepresented in the literature when compared with females (Bleu et al., 2016), likely because of methodological issues associated with measuring reproductive effort in males (Mysterud et al., 2004).

Reproductive costs—and the associated risks and benefits—are not static across life. Using too many resources in any single reproduction event, especially at a young age, may compromise growth and survival thereafter, which is fundamentally counter to the conservative life-history tactic possessed by most large, long-lived, iteroparous mammals (Stearns, 1992). Yet, social status might mediate the extent to which individuals expend resources in a single reproduction event. Mating success often is determined by social status, which is associated with traits such as body mass, age, size of antlers or horns, and demeanor (Townsend and Bailey, 1981; Miller et al., 1987; Kruuk et al., 2002; DeYoung et al., 2006). The presence of competitors who are larger, older, and dominant reduces the utility of younger and smaller males attempting to compete because adult males tend to dominate aggressive interactions (Mysterud et al., 2003; DeYoung et al., 2006; Willisch and Neuhaus, 2010). In other words, the domineering presence of adult males may suppress reproductive effort of young males (Miller and Marchinton, 1995). In the presence of mature males, young males are expected to reduce resources allocated to reproduction, because though they may increase current reproductive success, they may jeopardize lifetime reproductive success and overall fitness by risking injury and compromising growth and survival thereafter (Geist, 1971; Hogg and Forbes, 1997). If adult males are absent, however, it could be advantageous for young males to expend reproductive effort and participate in mating. Without having to compete with an adult male, a young male could reduce age at first reproduction, leading to increased fitness (Cole, 1954). For example, though it comes at the cost of survival, young male Soay sheep (*Ovis aries*) were more likely to participate in reproduction following population crashes that led to a sex ratio skewed toward females (i.e., reduced number of older males), whereas young males rarely participated in mating before the crash (Stevenson and Bancroft, 1995). Though it may be reproductively advantageous in the short term, it is unclear the level of somatic costs a young male might incur from participating in breeding at a young age and whether the social environment would alter the level of reproductive effort.

To better understand how young males navigate the relative risks and benefits of breeding at a young age, we quantified extent and timing of reproductive effort (i.e., weekly forage intake, change in body mass and body fat, and hormone levels; Charnov, 2002) for young and adult male white-tailed deer using a manipulative experiment. In particular, we determined the extent to which yearling males (1.5 years old) expended reproductive effort in the presence (i.e., yearlings subordinate) and absence (i.e., yearlings dominant) of adult males (≥ 4.5 years old) in an experimental framework, along with assessing hormones that may mediate such processes. We evaluated hypotheses and associated predictions examining whether yearling males altered their reproductive effort based on their social environment.

We hypothesized that yearlings would vary forage intake and subsequent somatic (i.e., body mass and fat) loss based on the presence of adult males. If young males reduce participation in the rut in the presence of adult males or increase reproductive effort in their absence, we predicted higher levels of forage intake and less somatic loss of young males when adult males were present than when they were absent (**Figure 1**).

Second, we hypothesized that yearling males would vary in the degree to which they track timing of estrus in females according to their social status. We predicted that expenditures of young male deer would be less synchronous with estrus in females when in the presence of adult males (**Figure 1**). Conversely, in the absence of adult males, young male deer would better synchronize their efforts with estrus in females.

We also hypothesized that hormone levels of yearlings would vary based on whether adult males were present, providing a possible mechanism to mediate flexibility in reproductive effort in yearling males. Hormone levels of males typically increase as rut progresses and then decline post-rut (Miller et al., 1987; Newman et al., 1998; Pelletier et al., 2003; Corlatti et al., 2012). Moreover, hormone levels may be correlated with dominance rank (Pelletier et al., 2003) and forage intake (Ryg, 1982; Newman et al., 1998) and thus, suppression of yearling males by adult males should result in lower levels of serum testosterone and cortisol in young, subordinate males during the rut (**Figure 1**).

In contrast to the aforementioned hypotheses, reproductive allocation by males may occur in a risk-sensitive manner, much like that of females. If so, and in accordance with an hypothesis of risk-sensitive reproductive allocation, forage intake and somatic loss should be a function of the reserves a male possesses pre-rut and how the animal is currently allocating energy (i.e., growth vs. maintenance). Therefore, yearling males should exhibit higher forage intake and experience less somatic loss than adult males because they are smaller and still allocating resources to growth (Monteith et al., 2009); and consequently, the presence of adult males should not affect reproductive effort by young males. Moreover, across age classes, somatic reserves expended during the rut should be a function of reserves present at the beginning of the rut. Although this hypothesis has previously been termed the individual quality hypothesis (Pelletier et al., 2006), the term individual quality also has been used to explain a different theoretical idea (Bergeron et al., 2011). Therefore, we chose to reference the idea of state-dependent allocation to reproduction as being risk-sensitive reproductive allocation, which also is in keeping with this body of work for females (Bårdsen et al., 2008; Monteith et al., 2013b; Bårdsen et al., 2014).

STUDY AREA AND METHODS

We conducted our research at the Wildlife and Fisheries Sciences Research Facilities at South Dakota State University, Brookings, South Dakota, United States (44°20′N, 96°47′W), where we managed a herd of hand-raised white-tailed deer that were accustomed to small enclosures (Delger et al., 2011; Monteith et al., 2014a, 2019). Elevation was 490 m above sea level and temperature in the region varied from −29°C in the winter to >38°C in the summer, with mean annual temperatures of 7–9°C (Spuhler et al., 1971). Annual precipitation generally varied from 33.0 to 63.5 cm with snowfall ranging from 63.5 cm to 114.0 cm (Spuhler et al., 1971).

Research animals were adult (≥4-years old; range = 4–10 years old) and yearling (1.5-years old) male white-tailed deer that represented three treatment groups: adult males, dominant yearlings (adult males absent), and subordinate yearlings (adult males present). We used all yearling males available within any particular year for the study and we randomly assigned them to treatment groups. Based on assigned status, subordinate

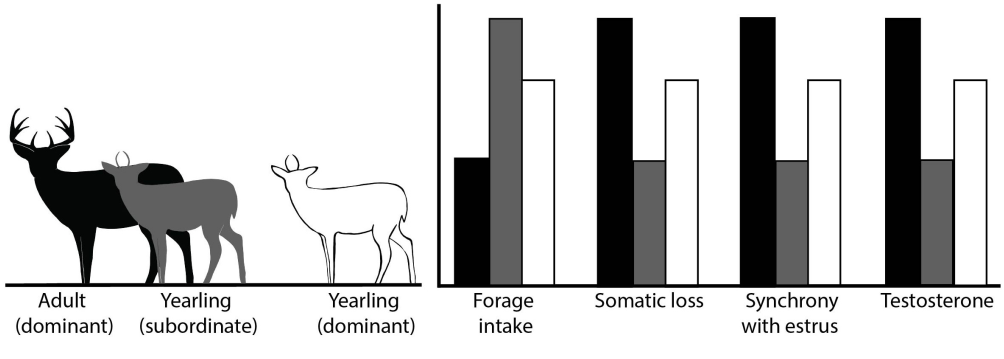

FIGURE 1 | Conceptual illustration of the associated predicted outcomes of variables of interest, which included forage intake, somatic loss (e.g., body mass and body fat), degree of synchrony of reproductive effort with estrus in females, and hormone levels for our study evaluating reproductive effort in male white-tailed deer. Treatment groups included subordinate yearlings (1.5-years old) which were maintained in the presence of adult males (≥4.5-years old), and dominant yearlings maintained without adult males, Brookings, SD, United States.

yearlings were housed and allowed to interact with adult males and females, whereas dominant yearlings were housed only with 1 other yearling male and females. Although we did not quantify dominance hierarchy among groups directly, based on daily observations of interactions between males, yearlings in the presence of adult males were clearly subordinate to those adult males. In contrast, the demeanor and level of aggression displayed by dominant yearling males in the absence of adult males was different than subordinate yearlings. Dominant yearling males frequently engaged in aggressive interactions and pursued females in their enclosure in contrast to subordinate yearlings.

Although sample size within each year varied depending upon the availability of yearling males, 1–2 dominant yearling males were housed with 1 female, and 2–3 subordinate yearlings were housed with 2–3 adult males and 2 females. Different males were used in the study each year, with the exception of 2 adult males that were used 2 years, and 3 adult males were used previously as yearling males in the study (2 were dominant yearlings and 1 was a subordinate). Through the remainder of the year, unless animals were used in other trials (Monteith et al., 2014a), all deer that were part of the captive herd, which ranged between 24 and 67 adult animals, were housed together in a 4-ha enclosure.

During weekly trials, males were confined to a 3.0-m^2 enclosure (1.22 m by 2.44 m) with access to feed and water *ad libitum* without confounding competitive interactions of other individuals for forage (Monteith et al., 2014a). Designated groups were allowed to interact freely during the weekends, whereas during trials (Monday–Friday), we released males into an adjacent enclosure (>280 m^2) for a minimum of 1 h each morning to allow adult and subordinate yearling males and females, or dominant yearlings and females to interact to maintain dominance hierarchies.

We conducted trials during 5 years, 2006–2008 and 2010–2011. We fed deer rations of shelled corn and pelleted soy hulls during 2006–2008, and switched rations in 2010–2011 to a mixed feed of shelled corn, oats, distillers grain, and pelleted soy hulls (Monteith et al., 2014a, 2019). Feed types were offered in separate containers to allow monitoring of intake rates. Shelled corn was 88% digestible with 8% crude protein content while the shelled corn, oats, and distillers grain mixture was 87% digestible with 15% protein, both of which were considered high-quality forage, whereas pelleted soy hulls were 62% digestible with 12% crude protein and were considered lower quality forage (Monteith et al., 2009, 2014a, 2019). We offered feed and water *ad libitum*; diets were the normal composition of feeds that animals were maintained on outside of the study similar to other captive studies involving white-tailed deer (Mautz et al., 1976).

We monitored food intake and body mass weekly beginning in mid-October for 9 weeks until mid-December to encompass the entire mating season, which typically peaks in early November for deer in the Northern Great Plains (Miller and Marchinton, 1995). We monitored feed intake for 5 days during each weekly trial. We measured daily intake rates of feed by weighing orts daily with a hanging scale accurate to 45.4 g (Hanson Scale Company, model 600, Shutuba, MS, United States). We collected and dried a sample of each feed to a constant weight at 50°C to calculate dry matter intake (Monteith et al., 2014a). We weighed deer weekly using a walk-on scale accurate to 454 g (Adrian J. Paul Company, Duncan, OK, United States). We then calculated daily forage intake of dry matter as a function of metabolic body mass (g/kg $BM^{0.75}$) per day (Robbins, 1983).

During 2006–2008 and 2010–2011, we chemically immobilized each male in mid-October to determine nutritional condition and hormone concentrations at the beginning of the rut. Nevertheless, in 2010–2011, we also immobilized males in mid-December to quantify change in nutritional condition during the rut and determine post-rut hormone levels. We chemically immobilized males by remote delivery of a combination of telazol, ketamine, and xylazine and antagonized with tolazoline (Monteith et al., 2012). While immobilized, we determined nutritional condition of each male using ultrasonography. We measured maximum depth (± 0.1 cm) of rump fat cranial to the cranial process of the tuber ischium and parallel to the spine using electronic calipers with a portable ultrasound device (Aloka 210; Aloka, Inc., Wallinford, CT, United States) and a 5-MHz linear transducer following protocols developed for mule deer (Stephenson et al., 2002; Cook et al., 2010). Because rump fat thickness was >0.3 cm, body condition scores were not necessary to estimate ingesta-free body fat (Cook et al., 2007). Given their similarities in morphology and fat deposition, we assumed that equations developed to estimate ingesta-free body fat (IFBFat) for mule deer (*Odocoileus hemionus*) would be sufficient for white-tailed deer (Monteith et al., 2012). Therefore, we used a combination of body mass and rump fat thickness to estimate scaled IFBFat (Cook et al., 2010). We evaluated change in IFBFat proportionally, but also by the decline in percentage points (ppt), which is a representation of the amount of fat lost scaled to body size (Monteith et al., 2013b). We collected blood from immobilized deer via venipuncture of the cephalic vein, and kept samples cool until centrifugation within 6 h of collection and stored serum at 20°C until assayed. Blood serum was subsequently analyzed by chemiluminescent immunoassay for testosterone and cortisol concentration (University of Michigan MLabs, Detroit, MI, United States).

To obtain the temporal pattern of estrus cycles of female deer, we back-calculated date of estrus from date of parturition based on the average gestation length for six adult females where we observed copulation and parturition. Average date of copulation for those six females was 10 November ($SE = 2.5$ days), and average gestation length was 197 days (± 2.4 days). For all females used during the study ($n = 22$), mean date of parturition was 27 May (± 1.6 days) resulting in an average date of standing estrus of 12 November (± 1.7 days, median = 14 November), which indicated that 86% of mating occurred during weeks 45–47.

During the remainder of each year, animals were confined to various pens within the 4-ha enclosure and had access to shelled corn or the shelled corn, oats, distillers grain mix, pelleted soyhulls, alfalfa, and water *ad libitum* (Monteith et al., 2009, 2014a, 2019; Delger et al., 2011). All animals also had limited access to natural forage within the facilities. Facilities and procedures for research on captive deer followed guidelines outlined by the American Society of Mammalogists (Sikes, 2016) and were approved by the Institutional Animal Care

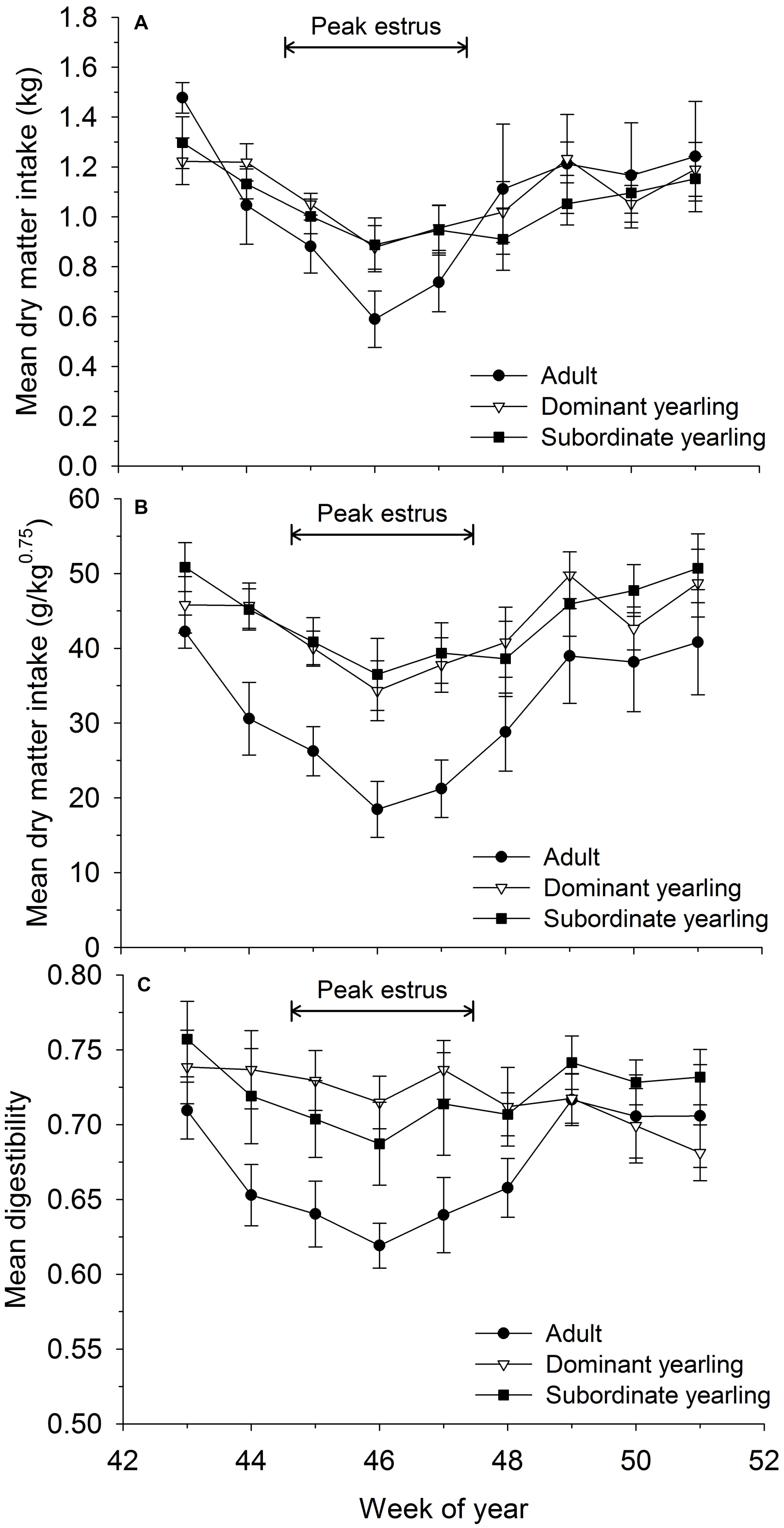

FIGURE 2 | Voluntary feed intake measured weekly as **(A)** absolute dry matter intake (kg/day ± SE), **(B)** dry matter intake relative to metabolic body mass (g/kg$^{0.75}$/day ± SE), and **(C)** apparent digestibility (% ± SE) for adult (≥4.5-years old; *n* = 12), dominant yearling (1.5-years old in absence of and adult male; *n* = 11), and subordinate yearling (1.5-years old with adult male present; *n* = 9) male white-tailed deer during 2006–2008 and 2010–2011, Brookings, SD, United States. Weeks correspond to mid-October through mid-December. Weeks of peak estrus represent dates when 86% of estimated conception events occurred.

and Use Committee (Approval No. 09-020A) at South Dakota State University.

Statistical Analyses

We pooled data for corresponding weeks during the 5 years of the study to provide adequate sample size for statistical analyses. We used mean daily values of feed intake per week to represent a datum for each individual deer. We evaluated weekly trends in body mass and food intake by assessing differences in temporal patterns with their associated error among treatments (Johnson, 1999). Because we repeatedly monitored the same individuals through time within each year, we used repeated-measures analysis of variance with a heterogeneous autoregressive error structure and a lag of one to evaluate differences across weeks, treatment groups, and their interaction for feed intake, digestibility, and body mass. If the interaction term for treatment and week was not significant, we removed it from the model before examining effects of treatment and week on the response variable to avoid spurious results with a non-significant interaction term (Zar, 1999). To evaluate differences among treatment groups in measures of nutritional condition or serum parameters at specific instances in time (e.g., single sample events before rut), we used analysis of variance. We used Bonferroni corrections to maintain experiment-wise error rates to examine pair-wise comparisons when main effects were significant ($\alpha = 0.05$; Zar, 1999). We also used simple least-squares regression to evaluate relationships between serum testosterone and food intake, and initial body mass with change in body mass over rut (Neter et al., 1996).

RESULTS

We monitored weekly patterns of forage intake and body mass of male white-tailed deer for 9 weeks during each autumn (i.e., mid-October to mid-December). We conducted our study during 5 years (2006–2008 and 2010–2011) and monitored 12 adult males, 11 dominant yearling males, and 9 subordinate yearlings.

Mean dry matter intake varied as a function of week ($F_{8,225} = 7.86$, $P < 0.001$), with a ~33% reduction in intake rates coinciding with peak estrus of females (**Figure 2A**). Although dry matter intake was generally higher for yearling than adult males (**Figure 2A**) and the treatment by week interaction approached significance ($F_{16,225} = 1.58$, $P = 0.075$), all groups followed a similar pattern and were statistically similar ($F_{2,29} = 0.05$, $P = 0.95$). In contrast, mean dry matter intake relative to metabolic body mass differed among weeks ($F_{8,240} = 7.52$, $P < 0.001$) and treatment groups ($F_{2,29} = 5.65$, $P = 0.008$). The difference among treatment groups, however, was largely the result of adult males, which consumed markedly less food relative to metabolic body mass than yearling males (both $P < 0.03$). Subordinate and dominant yearlings followed similar patterns ($P = 0.34$). Mean (±SE) dry matter intake relative to metabolic body mass of adult males during peak rut (week 46) was 52% that of yearling males (**Figure 2B**) and decreased from 42.2 g/kg$^{0.75}$/day (± 2.2) in mid-October to 18.5 g/kg$^{0.75}$/day (±3.7) during the peak of the rut in mid-November (**Figure 2B**; week 46). Coincident with depressed intake rates, digestibility of consumed forage (as a measure of forage quality) varied by week ($F_{8,241} = 5.06$, $P < 0.001$) and followed similar patterns to intake rates with reductions in digestibility during weeks with low food intake (**Figure 2**). Digestibility of diet consumed by adult males was consistently lower than yearling males throughout most of the autumn (**Figure 2C**), but not significantly so ($F_{2,29} = 1.88$, $P = 0.17$).

Body mass of males through autumn differed by treatment ($F_{2,29} = 27.03$, $P < 0.001$), week ($F_{8,224} = 37.44$, $P < 0.001$), and their interaction ($F_{16,224} = 5.14$, $P < 0.001$). Adult males were consistently larger (~33%) than dominant and subordinate yearling males (both $P < 0.001$), whereas dominant and subordinate yearlings were similar in size ($P = 0.26$). Weekly patterns of body mass were indicative of a general decline over autumn, which was most striking for adult males (**Figure 3A**). Weekly change in body mass varied as a function of treatment ($F_{2,29} = 21.53$, $P < 0.001$) and week ($F_{7,21} = 6.28$, $P < 0.001$). Adult males lost more body mass on a weekly basis than yearling males (both $P < 0.001$), whereas change in body mass was similar between dominant and subordinate yearlings ($P = 0.57$). Adult

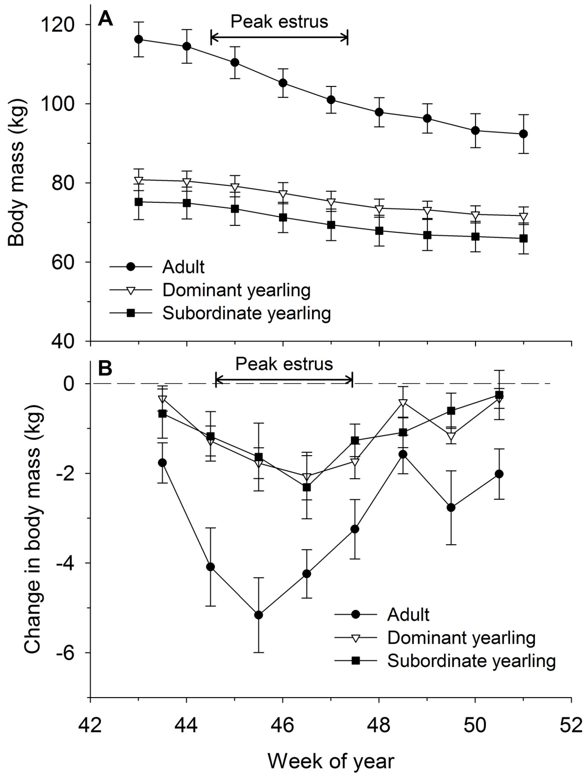

FIGURE 3 | Weekly **(A)** body mass (kg ± SE) and absolute change in body mass **(B)** between weeks (kg ± SE) for adult (≥4.5-years old; *n* = 12), dominant yearling (1.5-years old and adult male absent; *n* = 11), and subordinate yearling (1.5-years old and adult male present; *n* = 9) white-tailed deer during 2006–2008 and 2010–2011, Brookings, SD, United States. Weeks correspond to mid-October through mid-December. Weeks of peak estrus represent dates when 86% of estimated conception events occurred.

males consistently lost more body mass each week than yearling males, which was greatest during peak of the rut when adult males lost > 4 kg of body mass per week (∼4% decline per week). Loss of body mass during autumn differed among treatment groups ($F_{2,29} = 30.09$, $P < 0.001$). Adult males lost 20% of body mass and yearlings lost 12% during autumn (both $P < 0.001$), whereas mass loss by dominant and yearling males was nearly identical ($P = 1.0$; **Table 1**). With all treatment groups combined, there was a strong linear relationship between initial body mass (mid-October) and change in body mass ($r^2 = 0.68$, $\beta = -0.31$, $P < 0.001$; through mid-December), with larger males losing more body mass over the autumn rut than smaller males (**Figure 4**, **5**). At the onset of rut, adult males had slightly less IFBFat than yearling males ($F_{2,21} = 3.00$, $P = 0.071$; **Table 1**). Although treatment groups expended similar amounts of IFBFat during the rut ($F_{2,21} = 2.52$, $P = 0.14$; **Table 1**), IFBFat decreased 31% (5.3 ppt) among adult males compared with a 22% (4.7 ppt) decline in yearling males.

Serum testosterone levels in mid-October differed between treatment groups ($F_{2,30} = 19.86$, $P < 0.001$), which was mostly a function of elevated testosterone in adult males (both $P < 0.001$) compared with both groups of yearling males, which were not different ($P = 1.0$). Mean (±SE) serum testosterone levels were 18.6 ng/ml (±2.75, $n = 10$) for adult males, 5.65 ng/ml (±1.56, $n = 11$) for dominant yearlings, and 6.4 ng/ml (±1.11, $n = 8$) for subordinate yearlings. Differences among treatment groups in serum testosterone were diminished post-rut when all males exhibited low levels of testosterone (**Figure 6**). Although patterns seemed less consistent for yearling males (**Figure 7**), dry matter intake relative to metabolic body mass measured during the same week of serum collection in mid-October was related negatively to testosterone levels ($r^2 = 0.31$, $\beta = -0.75$, $P = 0.001$). Sample size was limited, but in contrast to testosterone, no patterns were apparent for serum cortisol concentrations either pre- or post-rut (all $P > 0.10$; **Figure 6**), or among treatment groups (all $P > 0.10$).

DISCUSSION

Reproductive expenditures by male ungulates can be substantial and may lead to future consequences for fitness (Stevenson and Bancroft, 1995; Mysterud et al., 2003, 2004, 2008a; Pelletier et al., 2006). The strong hierarchical social structure of male ungulates in autumn that is dominated largely by the presence of prime-aged males may confer benefits to young males throughout their life if the social dominance suppresses their rutting activity and forces them to conserve their somatic reserves. These ideas have appealing implications for management (Miller and Marchinton, 1995) and seem to have some empirical support (Mysterud et al., 2003), but had yet to be thoroughly tested. In contrast to the hypothesis that adult males suppress reproductive effort in young males during rut, food intake (**Figure 2**), hormone levels (**Figure 6**), and loss in somatic reserves (**Figure 3**) of yearling males was not affected by the presence of large, dominant males. Subordinate and dominant yearlings, and adult males exhibited pronounced hypophagia and mass loss in synchrony with the estrus cycle of females (**Figure 2**), but degree of hypophagia and mass loss was heightened in adult males. Indeed, reproductive effort as measured by reduction in food intake and associated mass loss occurred in a risk-sensitive manner, with larger males losing more mass during the rut compared with small males (i.e., yearling; **Figure 4**). Therefore, like females, male deer invested in reproduction in a way that capitalized on a reproductive opportunity, but presumably without over-investing and compromising survival at a young age, and the opportunity to reproduce thereafter. In accordance with the old proverbial saying that cautions against risk taking and being satisfied with what one has now—one in the hand is worth two in the bush—males capitalized on a reproductive opportunity in hand while young. But, by doing so in a risk-sensitive manner, they still protected growth and survival that are necessary to secure future reproductive opportunities.

Young males expended reproductive effort (**Figure 3**), which is consistent with them taking advantage of a reproductive opportunity (Hogg and Forbes, 1997; Yoccoz et al., 2002; DeYoung et al., 2006; Foley et al., 2018). Despite the absence of an effect of adult males on reproductive expenditures of yearling males (**Figure 3**), lower reproductive effort by young males is likely a function of past selective pressures acting on post-rut survival and the continued need to grow to bolster reproductive success as adults. Such strategies suggest a natural regulating factor that inhibited overexertion in reproduction for a long-lived mammal that typically peaks in reproductive success after asymptotic body mass has been attained (DeYoung et al., 2006), especially considering that the bulk of reproductive expenditures in males must be associated with hypophagia as opposed to activity (Foley et al., 2018). Male white-tailed

TABLE 1 | Initial body mass and ingesta-free body fat (IFBFat) measured in mid-October, and the corresponding change in those variables over the autumn until mid-December for adult (≥4.5-years old; $n = 12$), dominant yearling (1.5-years old in absence of and adult male; $n = 11$), and subordinate yearling (1.5-years old with adult male present; $n = 9$) white-tailed deer during 2006–2008 and 2010–2011, Brookings, South Dakota, United States.

	Adult			**Dominant yearling**			**Subordinate yearling**		
Treatment	$\bar{x}$	***SE***		$\bar{x}$	***SE***		$\bar{x}$	***SE***	
Initial body mass (kg)	116.24	4.40	A	80.78	2.72	B	75.20	4.50	B
Change body mass (kg)	−23.50	1.96	A	−9.07	0.85	B	−9.42	1.45	B
Initial IFBFat (%)	17.28	0.69	A	20.20	1.25	A	22.23	1.77	A
Change IFBFat (pp)	−5.29	0.36	A	−5.60	0.69	A	−3.70	0.66	A

Different letters correspond to statistically significant differences between groups.

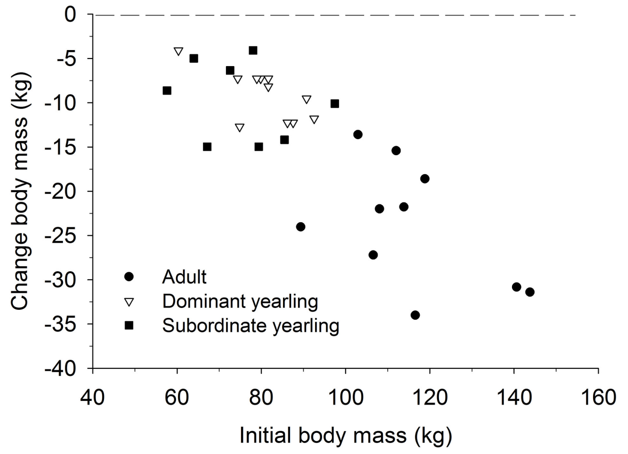

FIGURE 4 | Relationship between the cumulative change in body mass over the rut (mid-Oct to mid-Dec) and initial body mass (kg) in mid-Oct for adult (≥4.5-years old; *n* = 10), dominant yearling (1.5-years old and adult male absent; *n* = 11), and subordinate yearling (1.5-years old and adult male present; *n* = 9) white-tailed deer during 2006–2008 and 2010–2011, Brookings, SD, United States.

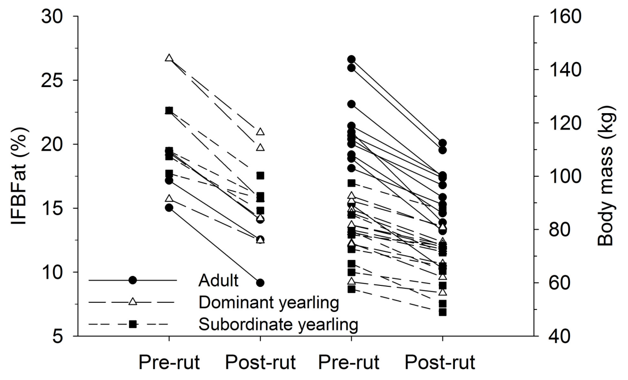

FIGURE 5 | Pair-wise comparisons of percent ingesta-free body fat (IFBFat) and body mass (kg) measured immediately before the rut in mid-Oct and after the rut in mid-Dec for adult (≥4.5-years old), dominant yearling (1.5-years old and adult male absent), and subordinate yearling (1.5-years old and adult male present) white-tailed deer during 2006–2008 and 2010–2011 (IFBFat only during 2010–2011), Brookings, SD, United States.

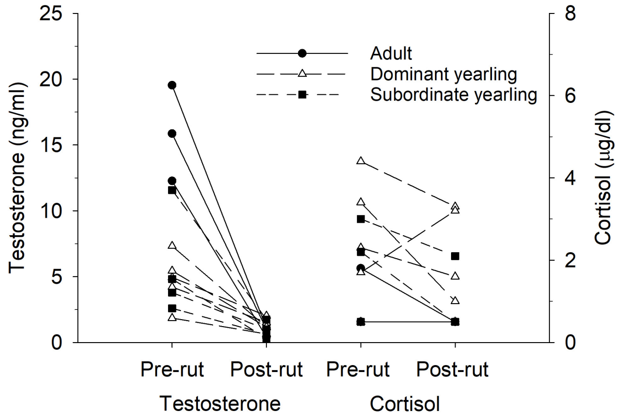

FIGURE 6 | Pair-wise comparisons of serum concentrations of testosterone (ng/ml) and cortisol (µg/dl) measured immediately before the rut in mid-Oct and after the rut in mid-Dec for adult (≥4.5-years old; *n* = 3), dominant yearling (1.5-years old and adult male absent; *n* = 5), and subordinate yearling (1.5-years old and adult male present; *n* = 4) white-tailed deer during 2010–2011, Brookings, SD, United States.

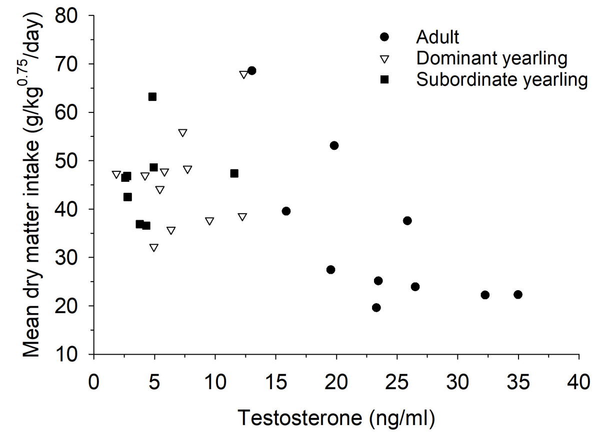

FIGURE 7 | Relationship between mean dry matter intake relative to metabolic body mass (g/kg$^{0.75}$/day) and serum testosterone (ng/ml) during week 43 for adult (≥4.5-years old; *n* = 10), dominant yearling (1.5-years old and adult male absent; *n* = 11), and subordinate yearling (1.5-years old and adult male present; *n* = 8) white-tailed deer during 2006–2008 and 2010–2011, Brookings, SD, United States.

deer typically reach mature body size at 4.5 years-of-age and therefore, are rapidly growing at 1.5 years-of-age (Monteith et al., 2009). If resources are diverted from growth to reproduction, future competitive ability may be adversely affected if growth is attenuated. In most situations, reproductive success of young males is lower than all other age groups (Hogg, 1984; DeYoung et al., 2006; Jones et al., 2011). Consequently, expending substantial resources toward reproduction at an age when the fitness return is typically low, at the expense of future survival and reproduction is a poor choice for yearling males. Therefore, young males have apparently adopted a risk-sensitive reproductive strategy much like that displayed by many female ungulates (Bårdsen et al., 2010; Monteith et al., 2013b), wherein allocation of resources to reproduction is sensitive to current nutritional state and the future risk to survival associated with depleting those reserves.

Male mammals can detect estrus in females by olfactory cues, and male behavior is commonly used by researchers as a tool to identify estrus in females (Komers et al., 1994a; Bowyer et al., 2007). It is important for males to time their reproductive effort to maximize the number of females that they can inseminate during the rut and make the most efficient use of effort expended toward reproduction. Prime-aged, dominant males often better match their reproductive effort with timing of estrus in females than do young, subordinate males (Preston et al., 2003;

Mason et al., 2012). Adult male white-tailed deer closely timed their reproductive effort with estrus in females, with extreme hypophagia exhibited during the 3 weeks when 86% of the females used in the study ovulated (**Figure 2**). During those same 3 weeks, loss of body mass was greatest at ∼4% lost per week (**Figure 3**). Although yearling males exhibited comparable patterns in appetite suppression and mass loss, hypophagia was not as striking as adult males, and peak loss in body mass was delayed by 1 week (between weeks 46 and 47, compared with 45 and 46 in adult males). Similarly, young red deer (*Cervus elaphus*) delayed reproductive effort relative to adults (Mysterud et al., 2008b) and young male bison (*Bison bison*) tended females after estrus had already occurred (Komers et al., 1994b). Although adult males may have affected timing of reproductive effort in the subordinate yearling group, the presence of a similar pattern among dominant yearlings suggests that young males may be less experienced and less effective at timing reproductive effort with female estrus, or their behavior represents an adaptive advantage to wait until most adult males have expended their reserves during the rut.

In accordance with other work that measured reproductive effort of male ungulates by behavior or change in body mass (Yoccoz et al., 2002; Forsyth et al., 2005; Mainguy and Cote, 2008; Foley et al., 2018), reproductive expenditure by adult and yearling males differed markedly. Age-specific patterns of reproductive effort among males have indicated lower reproductive effort of young and old compared with prime-age males (Yoccoz et al., 2002; Mysterud et al., 2004; Forsyth et al., 2005; Pelletier et al., 2006). Greater reproductive effort by prime-aged males has been explained by the mating strategy-effort hypothesis, suggesting that effort should be highest in prime-aged males because they are better able to sustain the costs (Yoccoz et al., 2002; Mainguy and Cote, 2008). Nevertheless, such a pattern may similarly emerge as a result of risk-sensitive allocation of effort, wherein prime-age males that are finished growing should have greater reserves to allocate toward reproduction than young males that are actively growing or old males that are accumulating progressively less reserves as they age (McElligott et al., 2003). Accordingly, with rising population density, male red deer expended less reserves to reproduction because of reduced body mass going into the rut (Yoccoz et al., 2002). Likewise, old males commonly allocate less to reproduction (Yoccoz et al., 2002), which has been thought to be associated with senescence in reproduction, but we suspect is simply another example of allocation of effort to reproduction occurring in a risk-sensitive manner.

Regardless of the differences in timing and magnitude of feed intake between adult and yearling males, reproductive effort of male white-tailed deer was associated with a rapid and marked decline in voluntary feed intake (**Figure 2**), which was independent of the availability of food or their activity. Seasonal cycles of antler chronology, reproductive activity, and dominance are closely associated with fluctuations in reproductive hormones of male ungulates (Miller et al., 1987). Though our statistical power was limited given small sample size, testosterone levels of males at the initiation of the rut were markedly higher for adult than yearling males (**Figure 6**). As predicted, the mechanisms behind hypophagia during the rut seem to be closely tied to serum testosterone levels. Although we were unable to sample testosterone on a weekly basis, circulating testosterone had a negative influence on food intake relative to metabolic body mass for males during the same week (**Figure 7**). Exogenous administration of testosterone to male fallow deer (*Dama dama*) outside of the typical rut resulted in similar suppression in voluntary food intake to that observed during the natural rut (Newman et al., 1998). Therefore, lower levels of circulating testosterone by young males is the likely pathway by which a higher level of appetite is sustained during rut (**Figure 2**). Such a link between animal state and appetite or resource allocation may highlight exciting opportunities to help reveal the mechanistic pathways between animal state and resource allocation (Monteith et al., 2013b).

Although our results may not be entirely representative of a free-ranging situation where energy expenditures in locomotion may further magnify reproductive effort (Parker et al., 1984) and social interactions likely are more frequent (Mainguy and Cote, 2008), our study does indicate that energetic costs of reproduction for males likely are born out more through depression in appetite as opposed to just locomotive activity. Indeed, locomotive activity itself was insufficient to explain loss in body mass of white-tailed deer (Foley et al., 2018), and degree of rutting behavior was not associated with mass loss in fallow deer (McElligott et al., 2003). The voluntary hypophagia displayed by males during rut may serve to alleviate a demanding activity budget to allow more time to engage in activities that could promote reproductive success or energy savings and rest (Willisch and Ingold, 2007; Mainguy and Cote, 2008; Mysterud et al., 2008a). Consequently, if somatic costs of reproduction in male ungulates are largely a function of reduction in food intake, it could make interpretation of reproductive effort and associated costs more difficult via indirect measures of reproductive effort such as activity or movement. Because forage intake during rut appears to be under strong hormonal control (**Figure 7**), hypophagia and subsequent somatic costs may link strongly to nutritional state. This link may be a physiological pathway to maintain risk-sensitive allocation to reproduction among male ungulates.

The relative abundance and composition of males can have important effects on large ungulate populations, including effects on birth synchrony, timing, fecundity, and energy expenditures of females during the rut (Mysterud et al., 2002). Humans can influence the social landscape of male ungulates through hunting pressure (Jenks et al., 2002; LaSharr et al., 2019) and, in so doing, may alter the extent to which young animals invest or participate in reproduction. Because of a desire to harvest males with sizeable antlers or horns, certain hunting regimes may remove disproportionately more older than young individuals from the population (Monteith et al., 2013a; LaSharr et al., 2019). Harvest regimes that remove these older, likely dominant animals may allow more breeding opportunities for younger males. Increased opportunities to mate for young males has prompted concerns associated with greater expenditures during rut (Ditchkoff et al., 2001), which is consistent with observed increases in reproductive effort of young males in populations with a young male age structure or female biased sex ratio

(Komers et al., 1994b; Mysterud et al., 2003). Nevertheless, tradeoffs associated with reproduction and survival in male ungulates is not a ubiquitous phenomenon (Mysterud et al., 2004; Festa-Bianchet, 2012), and our work indicates that even when presented with the opportunity to engage in reproduction at a young age without adult males, young males invest conservatively in reproduction.

Given expenditures of males during the rut, particularly those of adult males (**Figure 4**), management efforts focused at maintaining adequate habitat and moderating density dependence to improve pre-rut condition would help to maximize the resources available for growth and reproduction (Monteith et al., 2018). All males in our study were in good nutritional condition leading into rut. Although males in our study displayed risk-sensitive allocation, it is not known if adult males in poor nutritional condition at the onset of rut will compensate by increasing appetite to reduce somatic losses. Therefore, subsequent work should focus on understanding whether risk-sensitive reproductive tactics are displayed in free-ranging males where energetic expenditures are likely greater and social interactions potentially more frequent.

Differential evolutionary trajectories of the sexes are rooted in evolutionary theory (Darwin, 1871) and are profound for polygynous ungulates (Clutton-Brock, 1982; Bowyer, 2004). Rare, longitudinal data of direct measures of reproductive effort for a sexually dimorphic ungulate reveals more similarity in patterns of reproductive effort between males and females than previously appreciated. Unlike females, reproductive effort of males may be expended during a truncated window and manifest largely through a suppression in appetite rather than provisioning offspring. But like females, males displayed reproductive effort in a risk-sensitive manner wherein they invested in reproduction as a function of the resources available to them at the onset of rut. In accordance with life-history theory, young males conservatively invested in reproduction and prime-aged males invested heavily, but in a manner that should not have prompted a tradeoff in survival for reproductive effort. Indeed, under a risk-sensitive framework, reproductive costs should be masked or absent with respect to age or social rank. And instead, direct investment in reproduction for males may emanate largely from success in resource acquisition during the previous season and thus, the somatic reserves at hand.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Institutional Animal Care and Use Committee (Approval No. 09-020A) at South Dakota State University.

AUTHOR CONTRIBUTIONS

KLM conceived of the idea. KLM, JJ, and KBM wrote the proposals to acquire financial support for the project. KLM and KBM conducted the study and analyzed the data. KLM and RJ led the writing of the manuscript, and all authors contributed to its completion.

FUNDING

Funding for this project was provided by National Fish and Wildlife Foundation through Quality Deer Management Association, Federal Aid to Wildlife Restoration Funds administered through South Dakota Department of Game, Fish and Parks (Study No. 7538, W-75-R), Berryman Institute, South Dakota Agricultural Experiment Station, and Joseph F. Nelson undergraduate research grant. We acknowledge support from Haub School of Environment and Natural Resources at University of Wyoming, and Department of Natural Resources at South Dakota State University.

ACKNOWLEDGMENTS

We thank L. Schmitz, J. Delger, J. Howell, E. Kjellsen, R. DeVore, A. Peterson, B. Borah, and J. Lindgren for help with captive deer studies. We also thank K. Adams for support and facilitating funding for the project. We thank M. Festa-Bianchet, F. Garcia-Gonzalez, and P. Krausman for critical feedback that helped improve our manuscript.

REFERENCES

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University.

Bårdsen, B.-J., Fauchald, P., Tveraa, T., Langeland, K., Yoccoz, N. G., and Ims, R. A. (2008). Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology* 89, 829–837. doi: 10.1890/07-0414.1

Bårdsen, B.-J., Næss, M. W., Tveraa, T., Langeland, K., and Fauchald, P. (2014). Risk-sensitive reproductive allocation: fitness consequences of body mass losses in two contrasting environments. *Ecol. Evol.* 4, 1030–1038. doi: 10.1002/ece3.1010

Bårdsen, B.-J., Tveraa, T., Fauchald, P., and Langeland, K. (2010). Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia* 162, 627–639. doi: 10.1007/s00442-009-1537-0

Berger, J., and Gompper, M. E. (1999). Sex ratios in extant ungulates: products of contemporary predation or past life histories? *J. Mammal.* 80, 1084–1113. doi: 10.2307/1383162

Bergeron, P., Baeta, R., Pelletier, F., Reale, D., and Garant, D. (2011). Individual quality: tautology or biological reality? *J. Anim. Ecol.* 80, 361–364. doi: 10.1111/j.1365-2656.2010.01770.x

Bleu, J., Gamelon, M., and Saether, B. E. (2016). Reproductive costs in terrestrial male vertebrates: insights from bird studies. *Proc. R. Soc. B Biol. Sci.* 283:20152600. doi: 10.1098/rspb.2015.2600

Bowyer, R. T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *J. Mammal.* 85, 1039–1052. doi: 10.1644/bbl-002.1

Bowyer, R. T., Bleich, V. C., Manteca, X., Whiting, J. C., and Stewart, K. M. (2007). Sociality, mate choice, and timing of mating in American bison (*bison bison*):

effects of large males. *Ethology* 113, 1048–1060. doi: 10.1111/j.1439-0310.2007.01411.x

Charnov, E. L. (2002). Reproductive effort, offspring size and benefit-cost ratios in the classification of life histories. *Evol. Ecol. Res.* 4, 749–758.

Clutton-Brock, T. H. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. Chicago, IL: The University of Chicago Press.

Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature* 337, 260–262. doi: 10.1038/337260a0

Cole, L. C. (1954). The population consequences of life history phenomena. *Q. Rev. Biol.* 29, 103–137. doi: 10.1086/400074

Cook, R. C., Cook, J. G., Stephenson, T. R., Myers, W. L., Mccorquodale, S. M., Vales, D. J., et al. (2010). Revisions of rump fat and body scoring indices for deer, elk, and moose. *J. Wildlife Manag.* 74, 880–896. doi: 10.2193/2009-031

Cook, R. C., Stephenson, T. R., Myers, W. L., Cook, J. G., and Shipley, L. A. (2007). Validating predictive models of nutritional condition for mule deer. *J. Wildlife Manag.* 71, 1934–1943. doi: 10.2193/2006-262

Corlatti, L., Bassano, B., and Wright, J. (2014). Contrasting alternative hypotheses to explain rut-induced hypophagia in territorial male chamois. *Ethology* 120, 32–41. doi: 10.1111/eth.12177

Corlatti, L., Béthaz, S., Von Hardenberg, A., Bassano, B., Palme, R., and Lovari, S. (2012). Hormones, parasites and male mating tactics in alpine chamois: identifying the mechanisms of life history trade-offs. *Anim. Behav.* 84, 1061–1070. doi: 10.1016/j.anbehav.2012.08.005

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. London: Murray.

Delger, J. A., Monteith, K. L., Schmitz, L. E., and Jenks, J. A. (2011). Preference of white-tailed deer for corn hybrids and agricultural husbandry practices during the growing season. *Hum. Wildlife Interact.* 5, 32–46.

DeYoung, R. W., Demarais, S., Honeycutt, R. L., Gee, K. L., and Gonzales, R. A. (2006). Social dominance and male breeding success in captive white-tailed deer. *Wildlife Soc. Bull.* 34, 131–136. doi: 10.2193/0091-7648(2006)34[131:sdambs]2.0.co;2

Ditchkoff, S. S., Welch, E. R., Lochmiller, R. L., Masters, R. E., and Starry, W. R. (2001). Age-specific causes of mortality among male white-tailed deer support mate-competition theory. *J. Wildlife Manag.* 65, 552–559.

Festa-Bianchet, M. (2012). The cost of trying: weak interspecific correlations among life-history components in male ungulates. *Can. J. Zool.* 90, 1072–1085. doi: 10.1139/z2012-080

Foley, A. M., Hewitt, D. G., Deyoung, R. W., Schnupp, M. J., Hellickson, M. W., and Lockwood, M. A. (2018). Reproductive effort and success of males in scramble-competition polygyny: evidence for trade-offs between foraging and mate search. *J. Anim. Ecol.* 87, 1600–1614. doi: 10.1111/1365-2656.12893

Forsyth, D. M., Duncan, R. P., Tustin, K. G., and Gaillard, J.-M. (2005). A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. *Ecology* 86, 2154–2163. doi: 10.1890/03-0738

Geist, V. (1971). *Mountain Sheep*. Chicago, IL: University of Chicago Press.

Hogg, J. T. (1984). Mating in bighorn sheep: multiple creative male strategies. *Science* 225, 526–529. doi: 10.1126/science.6539948

Hogg, J. T., and Forbes, S. H. (1997). Mating in bighorn sheep: frequent male reproduction via a high-risk "unconventional" tactic. *Behav. Ecol. Sociobiol.* 41, 33–48. doi: 10.1007/s002650050361

Jenks, J. A., Smith, W. P., and Deperno, C. S. (2002). Maximum sustained yield harvest versus trophy management. *J. Wildlife Manag.* 66, 528–535.

Johnson, D. H. (1999). The insignificance of statistical significance testing. *J. Wildlife Manag.* 63, 763–772.

Jones, P. D., Strickland, B. K., Demarais, S., and Deyoung, R. W. (2011). Inconsistent association of male body mass with breeding success in captive white-tailed deer. *J. Mammal.* 92, 527–533. doi: 10.1644/10-mamm-a-294.1

Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78, 57–66.

Komers, P. E., Messier, F., Flood, P. F., and Gates, C. C. (1994a). Reproductive-behavior of male wood bison in relation to progesterone level in females. *J. Mammal.* 75, 757–765. doi: 10.2307/1382527

Komers, P. E., Messier, F., and Gates, C. C. (1994b). Plasticity of reproductive-behavior in wood bison bulls - when subadults are given a chance. *Ethol. Ecol. Evol.* 6, 313–330. doi: 10.1080/08927014.1994.9522984

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends Ecolo. Evol.* 7, 15–19. doi: 10.1016/0169-5347(92)90192-e

Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F., and Clutton-Brock, T. (2002). Antler size in red deer: heritability and selection but no evolution. *Evolution* 56, 1683–1695. doi: 10.1111/j.0014-3820.2002.tb01480.x

LaSharr, T. N., Long, R. A., Heffelfinger, J. R., Bleich, V. C., Krausman, P. R., Bowyer, R. T., et al. (2019). Hunting and mountain sheep: do current harvest practices affect horn growth? *Evol. Appl.* 12, 1823–1836. doi: 10.1111/eva.12841

Mainguy, J., and Cote, S. D. (2008). Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. *Behav. Ecol. Sociobiol.* 62, 935–943. doi: 10.1007/s00265-007-0517-9

Martin, J. G. A., and Festa-Bianchet, M. (2010). Bighorn ewes transfer the costs of reproduction to their lambs. *Am. Nat.* 176, 414–423. doi: 10.1086/656267

Mason, T. H., Stephens, P. A., Willis, S. G., Chirichella, R., Apollonio, M., and Richards, S. A. (2012). Intraseasonal variation in reproductive effort: young males finish last. *Am. Nat.* 180, 823–830. doi: 10.1086/668082

Mautz, W. W., Silver, H., Holter, J. B., Hayes, H. H., and Urban, W. E. (1976). Digestibility and related nutritional data for 7 northern deer browse species. *J. Wildlife Manag.* 40, 630–638.

McElligott, A. G., Naulty, F., Clarke, W. V., and Hayden, T. J. (2003). The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* 5, 1239–1250.

Miller, K. V., and Marchinton, R. L. (1995). *Quality Whitetails: The Why and How of Quality Deer Management*. Mechanicsburg, PA: Stackpole Books.

Miller, K. V., Marchinton, R. L., Forand, K. J., and Johansen, K. L. (1987). Dominance, testosterone levels, and scraping activity in a captive herd of white-tailed deer. *J. Mammal.* 68, 812–817. doi: 10.2307/1381558

Miquelle, D. (1990). Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27, 145–151. doi: 10.1007/bf00168458

Monteith, K. B., Monteith, K. L., Bowyer, R. T., Leslie, D. M., and Jenks, J. A. (2014a). Reproductive effects on fecal nitrogen as an index of diet quality: an experimental assessment. *J. Mammal.* 95, 301–310. doi: 10.1644/12-mamm-a-306.1

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2014b). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monogr.* 186, 1–62. doi: 10.1002/wmon.1011

Monteith, K. B., Monteith, K. L., and Jenks, J. A. (2019). Condensed tannins as a deterrent to crop depredation by white-tailed deer: effects of concentration and learning. *Wildlife Soc. Bull.* 43, 693–700. doi: 10.1002/wsb.1028

Monteith, K. L., Long, R. A., Bleich, V. C., Heffelfinger, J. R., Krausman, P. R., and Bowyer, R. T. (2013a). Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. *Wildlife Monogr.* 183, 1–28. doi: 10.1002/wmon.1007

Monteith, K. L., Stephenson, T. R., Bleich, V. C., Conner, M. M., Pierce, B. M., and Bowyer, R. T. (2013b). Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *J. Anim. Ecol.* 82, 377–388. doi: 10.1111/1365-2656.12016

Monteith, K. L., Long, R. A., Stephenson, T. R., Bleich, V. C., Bowyer, R. T., and Lasharr, T. N. (2018). Horn size and nutrition in mountain sheep: can ewe handle the truth? *J. Wildlife Manag.* 82, 67–84. doi: 10.1002/jwmg.21338

Monteith, K. L., Monteith, K. B., Delger, J. A., Schmitz, L. E., Brinkman, T. J., Deperno, C. S., et al. (2012). Immobilization of white-tailed deer with telazol, ketamine, and xylazine, and evaluation of antagonists. *J. Wildlife Manag.* 76, 1412–1419. doi: 10.1002/jwmg.383

Monteith, K. L., Schmitz, L. E., Jenks, J. A., Delger, J. A., and Bowyer, R. T. (2009). Growth of male white-tailed deer: consequences of maternal effects. *J. Mammal.* 90, 651–660. doi: 10.1644/08-mamm-a-191r1.1

Mysterud, A., Bonenfant, C., Loe, L. E., Langvatn, R., Yoccoz, N. G., and Stenseth, N. C. (2008a). Age-specific feeding cessation in male red deer during rut. *J. Zool.* 275, 407–412. doi: 10.1111/j.1469-7998.2008.00453.x

Mysterud, A., Bonenfant, C., Loe, L. E., Langvatn, R., Yoccoz, N. G., and Stenseth, N. C. (2008b). The timing of male reproductive effort relative to female ovulation in a capital breeder. *J. Anim. Ecol.* 77, 469–477. doi: 10.1111/j.1365-2656.2008.01365.x

Mysterud, A., Coulson, T., and Stenseth, N. C. (2002). The role of males in the dynamics of ungulate populations. *J. Anim. Ecol.* 71, 907–915. doi: 10.1046/j.1365-2656.2002.00655.x

Mysterud, A., Holand, O., Roed, K. H., Gjostein, H., Kumpula, J., and Nieminen, M. (2003). Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *J. Zool.* 261, 341–344. doi: 10.1017/s0952836903004114

Mysterud, A., Langvatn, R., and Stenseth, N. C. (2004). Patterns of reproductive effort in male ungulates. *J. Zool.* 264, 209–215. doi: 10.1017/s0952836904005618

Neter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. (1996). *Applied Linear Statistical Models*. Boston, MA: WCB McGraw-Hill.

Newman, R. E., Mcconnell, S. J., Weston, R. H., Reeves, M., Bernasconi, C., Baker, P. J., et al. (1998). The relationship between plasma testosterone concentrations and the seasonal variation in voluntary feed intake in fallow bucks (dama dama). *J. Agric. Sci.* 130, 357–366. doi: 10.1017/s0021859698005279

Panzacchi, M., Herfindal, I., Linnell, J. D. C., Odden, M., Odden, J., and Andersen, R. (2010). Trade-offs between maternal foraging and fawn predation risk in an income breeder. *Behav. Ecol. Sociobiol.* 64, 1267–1278. doi: 10.1007/s00265-010-0941-0

Parker, K. L., Robbins, C. T., and Hanley, T. A. (1984). Energy expenditures for locomotion by mule deer and elk. *J. Wildlife Manag.* 48, 474–488.

Pelletier, F., Bauman, J., and Festa-Bianchet, M. (2003). Fecal testosterone in bighorn sheep (*Ovis canadensis*): behavioural and endocrine correlates. *Can. J. Zool.* 81, 1678–1684. doi: 10.1139/z03-156

Pelletier, F., Hogg, J. T., and Festa-Bianchet, M. (2006). Male mating effort in a polygynous ungulate. *Behav. Ecol. Sociobiol.* 60, 645–654. doi: 10.1007/s00265-006-0208-y

Preston, B. T., Stevenson, I. R., and Wilson, K. (2003). Soay rams target reproductive activity towards promiscuous females' optimal insemination period. *Proc. R. Soc. B* 270, 2073–2078. doi: 10.1098/rspb.2003.2465

Robbins, C. T. (1983). *Wildlife Feeding and Nutrition*. Orlando, FL: Academic Press.

Ryg, M. (1982). Seasonal changes in weight gain, growth hormone, and thyroid hormones in intact and castrated male moose (*Alces alces* alces). *Can. J. Zool.* 60, 2941–2946. doi: 10.1139/z82-371

Shallow, J. R. T., Hurley, M. A., Monteith, K. L., and Bowyer, R. T. (2015). Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer. *J. Mammal.* 96, 194–205. doi: 10.1093/jmammal/gyu024

Sikes, R. S. (2016). 2016 guidelines of the American society of mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688. doi: 10.1093/jmammal/gyw078

Spuhler, W., Lytle, W. F., and Moe, D. (1971). Climate of South Dakota. *South Dakota State Univer. Agric. Exper. Sta. Bull.* 582:30.

Stearns, S. C. (1992). *The Evolution of Life-Histories*. Oxford: Oxford University Press.

Stephenson, T. R., Bleich, V. C., Pierce, B. M., and Mulcahy, G. P. (2002). Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. *Wildlife Soc. Bull.* 30, 557–564.

Stevenson, I. R., and Bancroft, D. R. (1995). Fluctuating trade-offs favour precocial maturity in male soay sheep. *Proc. R. Soc. B Biol. Sci.* 262, 267–275. doi: 10.1098/rspb.1995.0205

Tollefson, T. N., Shipley, L. A., Myers, W. L., Keisler, D. H., and Dasgupta, N. (2010). Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *J. Wildlife Manag.* 74, 974–986. doi: 10.2193/2008-529

Townsend, T. W., and Bailey, E. D. (1981). Effects of age, sex and weight on social rank in penned white-tailed deer. *Am. Midland Nat.* 106, 92–101.

Willisch, C. S., and Ingold, P. (2007). Feeding or resting? The strategy of rutting male alpine chamois. *Ethology* 113, 97–104.

Willisch, C. S., and Neuhaus, P. (2010). Social dominance and conflict reduction in rutting male alpine ibex, capra ibex. *Behav. Ecol.* 21, 372–380. doi: 10.1093/beheco/arp200

Yoccoz, N. G., Mysterud, A., Langvatn, R., and Stenseth, N. C. (2002). Age- and density-dependent reproductive effort in male red deer. *Proc. R. Soc. B Biol. Sci.* 269, 1523–1528. doi: 10.1098/rspb.2002.2047

Zar, J. H. (1999). *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice Hall.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 21 August 2020
doi: 10.3389/fevo.2020.00269

Density-Dependent Foraging Behaviors on Sympatric Winter Ranges in a Partially Migratory Elk Population

Evelyn Merrill[1]*, Joshua Killeen[1], Jed Pettit[1], Madeline Trottier[1], Hans Martin[2], Jodi Berg[3,4], Holger Bohm[1], Scott Eggeman[2] and Mark Hebblewhite[2]

[1] Department of Biological Sciences, Faculty of Science, University of Alberta, Edmonton, AB, Canada, [2] Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry & Conservation, University of Montana, Missoula, MT, United States, [3] Idaho Department of Fish and Game, Lewiston, ID, United States, [4] Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, United States

OPEN ACCESS

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Kevin Lee Monteith,
University of Wyoming, United States
Nicolas Morellet,
Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement (INRAE), France
Douglas William Smith,
Yellowstone National Park,
United States

****Correspondence:***
Evelyn Merrill
emerrill@ualberta.ca

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *27 February 2020*
Accepted: *29 July 2020*
Published: *21 August 2020*

Citation:
Merrill E, Killeen J, Pettit J, Trottier M, Martin H, Berg J, Bohm H, Eggeman S and Hebblewhite M (2020) Density-Dependent Foraging Behaviors on Sympatric Winter Ranges in a Partially Migratory Elk Population. Front. Ecol. Evol. 8:269. doi: 10.3389/fevo.2020.00269

Many large herbivore populations are partially migratory, in which the population is comprised of both non-migratory (resident) and migratory individuals. Density-dependence contributes to regulating the dynamics of partially migratory populations by altering habitat selection, vital rates, or rates of behavioral switching between migratory tactics. Studies of mechanisms leading to these shifts have focused mainly on their behavior on summer range, overlooking the potential for density-dependent effects during winter that may influence decisions to migrate. We hypothesized that competition for food and safety from wolf predation risk on winter ranges would differentially affect habitat selection, movements, and grouping behavior of migrant and resident female North American elk (*Cervus canadensis*) on their sympatric winter range. We used GPS locations from 92 adult female elk in 155 elk-winters at Ya Ha Tinda, Alberta, Canada, over a 14-year period when the elk population declined by ~70% to test our hypotheses. Elk showed consistently strong selection for areas of high forage biomass that corresponded to longer residence times and shorter return times to areas of high forage biomass. The strength of the selection diminished at high elk population size as did the extent to which elk traded off forage for safety from wolf predation risk. Elk increased movement rates and extended return times only to the riskiest areas. Median group size and mean sociality among elk increased at low population size, with resident elk groups being larger and more cohesive than migrant groups. Similar density-dependent responses by migrant and resident female elk on sympatric winter range indicate resident elk do not alter foraging behaviors to compensate for exposure to low nutritional resources in summer, implicating seasonal differences in nutrition are not mediated by winter densities in this system. We discuss the implications of competition on winter ranges for the maintenance of partial migration in ungulates in montane systems.

Keywords: *Cervus canadensis*, density-dependent habitat selection, foraging movements, partial migration, predation risk

INTRODUCTION

Density dependence plays a central role in understanding a variety of ecological processes including population dynamics and community organization. Density influences habitat selection and movements by animals to determine species distributions at both small and large scales (Owen-Smith et al., 2010; Almeida et al., 2015). Partial migration, where individuals follow resident or migratory tactics of movement (Dingle and Drake, 2007), is hypothesized to result from density-dependent trade-offs between costs and benefits influenced by phenotype, individual state, or the behavior of conspecifics in the population (Berg et al., 2019). Migratory and resident tactics therefore may be maintained by differential density-dependent regulation of vital rates that must demographically balance each other over the long term (Kaitala et al., 1993; Hebblewhite and Merrill, 2011). Further, there is limited evidence that migratory tactics are genetically fixed, and recent data show that at least in some populations ungulates switch between migratory tactics (Berg et al., 2019), and that switching may be density dependent (Eggeman et al., 2016). How density-dependent changes in behaviors of large herbivores might contribute to switching and more broadly the maintenance of partial migration has not been well-studied.

In temperate montane systems, migratory ungulates typically move to areas of high-quality resources in summer (Mysterud et al., 2011; Middleton et al., 2013; Monteith et al., 2018), where they meet reproductive demands and gain body reserves to improve survival and reproduction during the resource-limited winter (Cook et al., 2004, 2013; Monteith et al., 2014). In such systems, most studies focus on exposure to forage resources and predation risk when ungulates are on separate ranges to explain density-dependent maintenance of partial migration, and assume individuals derive equal costs and benefits when together on their sympatric range (e.g., Kaitala et al., 1993; Ball et al., 2001; Hebblewhite and Merrill, 2009). However, foraging behaviors of migrant and resident ungulates may differ when on sympatric ranges, which may offset fitness advantages of migration (Robinson and Merrill, 2013; Found and St. Clair, 2016). Such differences may result from differential exposure to external conditions or social grouping, and the demographic consequence may be exacerbated by conspecific density, which in most montane systems typically is higher in winter than in summer because of snow constraints (Cagnacci et al., 2011). Further, if migration is flexible with individual variation attributed to year-to-year condition-dependence in a facultative manner (Nelson, 1995; Fieberg et al., 2008; Grovenburg et al., 2011; Monteith et al., 2011, but see Sawyer et al., 2019), then a better understanding of the forage-predation trade-offs migrants and residents make as population densities change may contribute to our understanding of the maintenance of partial migration.

Under density-dependent habitat selection, non-territorial animals are expected to distribute themselves in a manner that achieves equal fitness within habitats, which is altered by the density of conspecifics present (Fretwell and Lucas, 1970; Rosenzweig, 1981; Morris, 2003). Studies have shown that ungulates change their habitat selection across densities (McLoughlin et al., 2006; Perez-Barberia et al., 2013; Mansson et al., 2017), but habitat-selection analyses alone may not reveal the behavioral mechanisms behind trade-offs in the selection process (Bastille-Rousseau et al., 2010). Strong selection of resource-rich patches is expected to emerge because foragers exhibit area-restricted search whereby they decrease the speed and increase the tortuosity of movements that results in high patch-residence times, as compared with moving directly through resource-poor patches (Benhamou, 1992; Anderson et al., 2008; Avgar et al., 2011). If resource depletion increases with conspecific abundance, herbivores may be forced to explore the same areas more intensively to obtain the necessary resources, which would result in higher concentration and predictability of individuals in high-quality areas (Almeida et al., 2015). Alternatively, individuals may move more to explore larger areas, leaving a patch after a shorter time (Jiang and Hudson, 1993; Shipley and Spalinger, 1995; Searle et al., 2005), making them less predictable but more likely to encounter predators (Daly et al., 1990; McKenzie et al., 2012). Individuals are expected to return when patch resources recover or depletion in other patches increases the value of the patch (Barraquand and Benhamou, 2008; Van Moorter et al., 2009; Seidel and Boyce, 2015). Concomitantly, in gregarious species, high rates of interaction and conflicts of direction in movement of individuals may limit group speeds (Fortin et al., 2009; Pays et al., 2012; Sigaud et al., 2017), which in turn may put constraints on exploring the environment, reducing foraging intake, or result in group fission (Lardy et al., 2016). Herbivores make compromises between foraging and safety (Lima and Dill, 1990; Verdolin, 2006; Visscher et al., 2017), leading to the generality that risky foraging decreases (Abrams, 1993; Brown, 1999). To escape predation, prey alter movement strategies to reduce predator encounters in time and space (Kie and Bowyer, 1999). Van Moorter et al. (2016) reported the strength of selection of resources by female moose (*Alces alces*) was associated with high variation in both residence and return times reflecting resource heterogeneity, but their study took place under low risk from natural predators. In contrast, residence times of North American elk (*Cervus canadensis*) in Wisconsin were unrelated to selection but reflected frequent, unpredictable returns to preferred areas on the landscape, which was hypothesized to be a strategy that reduced predation (Anderson et al., 2008).

Group size and cohesion reflect how foragers balance limiting factors (Visscher et al., 2017). Indeed, by associating with large groups, individuals can dilute the per capita probability of mortality (Hamilton, 1971), provide "many eyes" for predator detection (Dehn, 1990; Brown and Kotlar, 2004), or reduce foraging costs from vigilance, at least under encounter-limited foraging (Fortin et al., 2004; Robinson and Merrill, 2013). But foraging in large groups can have other consequences, such as increasing conspecific interference or rates of depletion resulting in increased movement rates (Molvar and Bowyer, 1994; Kausrud et al., 2006; Mobaek et al., 2012). These trade-offs may depend on the social relationships that exist among animals within a group (Weckerly, 1999; Millspaugh et al., 2004; Vander Wal et al., 2013, 2014). Therefore, changes in abundance that alter grouping patterns are likely to alter the outcomes of trade-offs between reducing predation risk and accessing forage (Fortin et al., 2009; Pays et al., 2012).

In this paper, we evaluated the assumption that migrant and resident elk make similar trade-offs between foraging opportunities and safety from wolves on the sympatric winter range of the Ya Ha Tinda adjacent to Banff National Park (BNP) (**Figure 1**) in response to ∼70% population decline over a 14-year period (Hebblewhite et al., 2018). Previously, we have reported migrant elk are exposed to higher forage quality on summer ranges consistent with the forage maturation hypothesis (Hebblewhite and Merrill, 2008), and indicating migrants may enter winter in better condition. This assumption is supported by migrants having higher fecal nitrogen, pregnancy rates, and calf weights (Hebblewhite and Merrill, 2011). At the same time, on winter ranges we observed differences in foraging behaviors of migrant and resident that constrained synchronizing food processing with vigilance, which we hypothesized could alter foraging benefits between migratory tactics particularly under encounter-limited foraging (Robinson and Merrill, 2013). If changes in winter density differentially influences forage-predation trade-offs of migrant and resident elk, differences in winter foraging could contribute to demographic balancing among migratory tactics (Hebblewhite and Merrill, 2011; Eggeman et al., 2016).

To test hypotheses concerning density-dependent foraging, we focused on diurnal trade-offs in selection for abundant forage areas under predation risk, and on changes in social cohesion and group sizes because elk are most active during the day in winter (**Supplementary Figure S2**). We assumed diurnal periods corresponded to time spent foraging. We predicted elk would exhibit density-dependent habitat selection, but we expected the extent of response to be less for residents because they needed to compensate for low forage quality in summer (Hebblewhite and Merrill, 2009). Because residents maintained larger, more cohesive groups than migrants (Robinson et al., 2010; Hebblewhite et al., 2018), we also expected the strength of selection for high-forage areas by residents would be associated with longer residence times and high return times. In contrast, because migrant elk maintained less coherent groups that were less familiar with risk from predators including humans (Robinson and Merrill, 2013), we predicted greater trade-offs between high-forage areas and safety and increased movements in risky areas. Elucidating behavioral mechanisms associated with changes in density on populations of partially migratory ungulates in winter is key to broadening our understanding of how forage trade-offs on seasonal ranges interact and contribute to condition-dependent switching and the maintenance of partial migration (Berg et al., 2019).

FIGURE 1 | North American elk (*Cervus canadensis*) on the Ya Ha Tinda winter range adjacent to Banff National Park, Alberta, Canada, with permission from Camille Roberge.

MATERIALS AND METHODS

Study Area

Elk winter range is located on the eastern slopes of the Canadian Rocky Mountains adjacent to BNP, and overlaps with Parks Canada's 4,000-ha Ya Ha Tinda horse ranch (Hebblewhite et al., 2006 for details). The study area is montane temperate, with temperatures in the area averaging 9°C during May–September, and −4.1°C during winter. Precipitation averages 319 mm during summer (May–September) with an average of 157 cm of snowfall. During the study, resident elk remained on the grassland year-round, whereas migrants moved either west into Banff National Park or east to multiple-use forests (Eggeman et al., 2016). During this study, the partially migratory elk population declined from ∼1,400 animals in 2002–2003 to ∼450 in 2015–2016. The leading cause of the decline was high predation by gray wolves (*Canis lupus*) on adult females (Hebblewhite et al., 2006, 2018), combined with high predation by grizzly (*Ursus arctos*) and black bears (*Ursus americanus*) on neonatal elk (Berg, 2019). Switching among migratory tactics occurs but is relatively low (15%/yr; Eggeman et al., 2016). Elk were the most abundant ungulate during our study, but other ungulates included moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and bighorn sheep (*Ovis canadensis*). The main predators of elk in winter when our observations occurred were wolves (5.7–8.9 wolves/1,000 km^2; Hebblewhite, 2006) and First Nations peoples in winter. Cougars (*Puma concolor*) also were active during winter and thought to be increasing in this region (Knopff et al., 2014).

Elk Population Size

Elk population size was surveyed every winter as trend counts within the same area when migrant and resident elk were on their sympatric winter range (Eggeman et al., 2016). Aerial surveys were conducted by Alberta Fish and Wildlife (2002–2010) or Parks Canada (2011–2016) using rotary-wing or fixed-wing aircraft every winter (January–February after heavy snowfall to maximize sightability) except for the winter of 2012–2013 and 2015–2016 when we used maximum counts of elk on winter grounds (**Supplementary Table S1**). Aerial counts were adjusted for sightability by a 15% increase based on previous research (Hebblewhite, 2000). In most years, these numbers were repeatedly verified from the ground.

Elk Capture and Monitoring

Adult female elk were captured and fitted with Global Positioning System (GPS) collars (Lotek GPS 3300, 4400, 7000; LOTEK Inc., Aurora, ON, Canada; n = 92) or very high frequency (VHF) collars (LMRT-4, LOTEK Inc., Aurora, ON, Canada; n = 147) between February 2002 (winter 2001–2002) and March 2015 (winter 2014–2015) on the winter range using either corral trapping, helicopter net gunning or darting from horseback (Animal Care Protocols: University of Alberta 353212, 611812, 000624, University of Montana AUP 004-16, Parks Canada BAN-2014-16756). We collected GPS fixes at a variety of intervals, but rarefied data to a consistent 2-h schedule. Location error (∼34 m) and fix-rate bias (<10%) were low enough to avoid bias in the selection models (Hebblewhite and Merrill, 2007; Hebblewhite and Merrill, 2008). Although all collared elk migrated back to the Ya Ha Tinda to winter, not all elk arrived by 1 November (**Supplementary Figure S1**). We included only those locations of migrant elk that arrived on Ya Ha Tinda by 1 November and only female elk that had at least 100 locations during the winter (155 elk winters from 92 adult female elk). We omitted potentially erroneous GPS fixes (<1%, including unreasonably long-steps) and GPS fixes that were not preceded by two consecutive GPS fixes were removed in the selection and movement analyses because three consecutive fixes were required to calculate turn angles. We classified individuals as migrant or resident each year using all locations from the previous spring and summer based on the net squared displacement (NSD) method (Bunnefeld et al., 2011; Borger and Fryxell, 2012) in the R package MigrateR (Spitz et al., 2017), combined with *post-hoc* spatial rules and visual confirmation by plotting movements of individual animals (Eggeman et al., 2016 for details). Data are available on Movebank (Eggeman et al., 2016).

We defined winter as 1 November to 31 March because 95% of migrants completed their fall migrations and were on the winter range by 1 November, and 100% of the elk were still on the winter range on 31 March (Eggeman et al., 2016). The diurnal period was defined as 0600–1900 h when elk most actively foraged based on their movements (**Supplementary Figure S2**). Selection and movement analyses were based on 155 elk winters of data from 92 unique GPS-collared individuals (**Supplementary Table S2**). The average number of days tracked for each elk-winter was 58.4 (*SD* = 42.9; range 9–151) days with a mean of 608.0 (*SD* = 450.5; range 107–1,806) locations.

Movement-Independent Resource Selection

We used integrated Step Selection Analysis (iSSA) to estimate selection for areas varying in forage and predation risk for individual elk while controlling for movement rates based on fixed-time step lengths and directional persistence based on turn angles. The iSSA method is an extension of the step selection function approach (Fortin et al., 2005; Thurfjell et al., 2014) that accounts for animal movement; failure to adequately control for the movement process may lead to biased resource-selection estimates (Forester et al., 2009). The iSSA simultaneously estimates movement and resource-selection parameters allowing for effects of environmental variables on selection processes to be distinguished from movement (Avgar et al., 2016). We used the R package amt (Avgar et al., 2016) to conduct the iSSA using a binomial link. We fit a gamma distribution to observed step lengths and a Von Mises distribution to observed turn angles using Maximum Likelihood methods. We randomly drew 10 available steps per observed step using these distributions. Covariate values for forage biomass and wolf predation risk were then extracted for the endpoints of all observed and available steps.

Wolf predation risk (hereafter, predation risk) was quantified using a diurnal, resource-selection function (RSF) for winter developed from GPS and VHF telemetry data from five wolf packs (n = 30 wolves) in the Ya Ha Tinda from 2002 to 2004 and weighted by the kill rate/pack/day (see Hebblewhite, 2006 for details). The wolf RSF was modeled as a function of landcover, elevation (m), slope (%), aspect class (north, south, flat), distance to forest edges (km), and distance to human activity (km). We extended the predation risk to 2005–2016 by incorporating changes over time in annual wolf pack size, land cover, and distance to edge but used the same RSF model to predict selection (Berg, 2019). We determined that predation risk using this approach was correlated to wolf-scat surveys conducted later in the study in summer (i.e., 2013–2016; Spilker, 2018), and assumed similar correspondence in winter.

Herbaceous (graminoids and forbs) biomass (g/m^2) was predicted across Ya Ha Tinda during 2002–2004 from empirical GLM models based on landcover type, MODIS greenness, and elevation that varied annually (Hebblewhite, 2006; Hebblewhite and Merrill, 2008). For 2005–2015, we used the predicted forage biomass layer from 2002 to 2004 that corresponded most closely in terms of summer precipitation, but updated estimates of forage biomass in burns (prescribed and wildfires: Banff Fire Database 2015, Parks Canada) and clearcuts (Sundre Forest Products, 2015) using a forage biomass-successional model (Berg, 2019 for details). We assumed late summer spatial patterns in forage biomass corresponded to forage spatial patterns in winter (Hebblewhite, 2006).

We fit conditional logistic regression models for each elk in each winter (individual elk-winters) using the function amt:fit_issf in the R package amt and summarized selection by migratory tactic. We included movement variables (ln steplength and cosine turn angle), forage biomass, predation risk, and their interaction in all models because we were explicitly testing for differences in the same variables between migrants and residents rather than finding the best model for each individual. Both forage biomass and predation risk variables were standardized by subtracting the mean and dividing by the standard deviation to allow for comparisons of effect size among individuals. To test our hypotheses that elk selection changed with elk population size, we modeled the iSSA-derived coefficients of individual elk for forage biomass, predation risk, and their interaction separately using migratory tactic (migrant as reference) and annual elk abundance (counts) of elk on the Ya Ha Tinda winter range. We used Generalized Linear Mixed-effect Models (GLMMs) with elk identity as a random intercept assuming a Gaussian distribution, and weighted the model coefficients for each elk-winter by 1/variance of the coefficient (Gillies et al., 2006).

Daily Movement, Resident and Return Times

We used elk diurnal locations (0600–1900; **Supplementary Figure S2**) to calculate daily step lengths (m), residence times (hrs), and return times (hrs) for all GPS-collared elk used in the resource selection analyses. We based step lengths on the straight-line distance between 2-h relocations of GPS-collared elk. Residence time was the duration of time spent within the vicinity (800-m radius) of any diurnal location and was estimated using the package adehabitatLT (Barraquand and Benhamou, 2008). We used a circle of 800-m radius as the spatial threshold because that distance approximated the median distance (m) moved during the active period, and outputs based on radii from 400 to 1,600 m were correlated ($r > 0.30$, $p < 0.005$). We calculated return times as the amount of time (hrs) it took to revisit an area within a 200-m radius of a previous GPS location after 48 h using the R package recurse (Bracis et al., 2018). We determined these threshold values for return times produced qualitatively similar relationships with elk population size (**Supplementary Figure S3**). The mean residence and return times were calculated for all the locations within the movement path of each individual during winter, except elk that never returned to a previously used area; these elk were not included in the return-time analysis. This procedure reduced the number of elk used in the analysis by one migrant and three resident-elk winters.

To associate step length, residence time, and return time to environmental conditions, we related each metric to forage biomass or wolf predation risk at the start-point location, migration status (migrant = reference), and their interaction using a GLMM with elk identity and year as random effects assuming a Gaussian distribution. We used Akaike Information Criterion (AIC) to compare the fit of linear and non-linear (quadratic) fit of the models. To assess our hypotheses that overall movement characteristics differentially changed with elk population size between migratory tactics, we used GLMMs, assuming a Gaussian distribution, to model each movement metric including elk population size, migratory tactic, and their interaction as covariates, elk identity as a random intercept.

Elk Associations and Group Sizes

Because data for elk group size were not associated with the GPS locations of elk, group size could not be explicitly integrated into selection and movement analyses (*sensu* Berger et al., 2015). Instead, we determined group sizes visually from the ground at an interval of approximately 7–10 days during most winters using VHF-telemetry to locate both VHF- and GPS-collared elk (Hebblewhite and Merrill, 2011). We defined a group associated with a collared individual as one to n individuals that interacted with each other, headed in the same direction, or used a confined area at the time of observation. We determined elk group size by scanning with binoculars or telescope and using a clicker-counter to count individuals. We assessed the change in the distribution of group sizes with elk population size with quartile regression (Proffitt et al., 2012; Brennan et al., 2015), and differences in the median of group sizes between periods of high (>600 elk) and low (<600) elk population size within migratory status using a median test. We used a break point of 600 because the population had declined by approximately one-half its size at the beginning of the study (**Supplementary Table S1**).

We assessed association among classes of dyads of GPS-collared migrant and resident elk using the coefficient of sociality (C_s, Kenward et al., 1993) within the R package wildlifeDI (Long et al., 2014). C_s varies between −1 and 1 and is calculated for dyads of GPS-collared elk as:

$$C_S = \frac{\mathrm{d}_E - \mathrm{d}_O}{\mathrm{d}_E + \mathrm{d}_O}, \tag{1}$$

where d_O is the mean Euclidean distance between simultaneous locations of an elk dyad, and d_E is the mean Euclidean distance of n^2 permutations of the simultaneous fixes of a dyad (Kenward et al., 1993). For this analysis, we considered locations that were within 1 h as "simultaneous" because collars took fixes every 2-h and some collars did not fix on the same hour. To assess our hypothesis that migrant elk were more associated with resident elk at low elk abundance, we used GLMs to relate C_S to elk population size and dyad type (resident-migrant, migrant-migrant, and resident-migrant; migrant-migrant as reference) and their interaction.

RESULTS

Movement-Independent Resource Selection

Selection for high-forage areas was consistent across nearly all (99%) elk, whereas most (76%) elk selected for rather than against areas of high predation risk (**Table 1**), likely because forage biomass and predation risk were positively correlated ($r = 0.44$, $p < 0.001$, $n = 1{,}000$). Nevertheless, 75% of the elk showed a trade-off in forage to avoid wolf predation by reducing their selection for high-forage areas under high risk (i.e., negative $F \times W$ interaction; **Table 1**). There were no main or interactive effects of migratory tactic in how elk selected for areas ($p > 0.52$).

As elk population size increased, the strength of elk selection for areas of high forage biomass decreased ($\beta = -0.00020$, $SE = 0.000040$, $p < 0.001$; **Figure 2A**). In contrast, elk increased their selection for risky areas ($\beta = 0.00016$, $SE = 0.000032$, $p < 0.001$; **Figure 2B**) as elk population size increased, but they also exhibited a weaker trade-off (**Figure 2C**) for high-forage areas as predation risk increased ($\beta = -0.00057$, $SE = 0.000027$, $p < 0.036$; **Supplementary Figure S4**). Migrant and resident elk showed similar changes in selection with elk population size ($p > 0.34$).

TABLE 1 | Population-level standardized selection coefficients and frequency of their +/− direction for individual female elk for forage biomass (F), wolf resource selection (W), Forage by Predation interaction (F × W), turn angle and natural log of step length for migrant (M) and resident (R) elk derived using integrated Step Selection Approach at the Ya Ha Tinda winter range adjacent to Banff National Park, Alberta, Canada, during winters from 2002–2003 to 2015–2016.

Covariate	Migration status	β	95% CI		Elk-winters	
			Lower	Upper	+	−
Forage biomass (F)	M	0.371	0.359	0.382	63	0
	R	0.388	0.375	0.400	92	2
Wolf predation risk (W)	M	0.101	0.090	0.112	50	13
	R	0.050	0.039	0.060	70	24
Interaction F × W	M	−0.050	−0.068	−0.032	12	51
	R	−0.050	−0.057	−0.044	28	66
Cosine of turning angle	M	0.041	0.019	0.064	49	14
	R	0.073	0.061	0.084	70	24
Natural log step length	M	0.222	0.213	0.230	61	2
	R	0.207	0.198	0.216	90	4

Overlap of 95% confidence limits (95% CI) indicates significant overlap between selection coefficients of migrants and resident and with zero (no selection). Elk winters indicate the sample size of individuals used in the analysis with some individuals used in more than 1 year.

Diurnal Movement Rates, Residence, and Return Times

Consistent with strong selection for forage biomass, elk reduced step lengths (β = −44.66, SE = 5.61, $p = 0.001$; **Figure 3A**), increased residence time (β = 0.94, SE = 0.24, $p = 0.001$; **Figure 3C**), and had shorter return times (β = −38.05, SE = 3.57, $p = 0.001$; **Figure 3E**) to areas of high forage biomass during the foraging period. Residents altered step lengths less, residence time less, and return time more in response to forage biomass than migrants (**Figure 3A**, **Supplementary Table S3**, $F \times M$ interaction). In contrast, elk exhibited more complicated and nonlinear responses to increasing predation risk (**Supplementary Table S3**). At low predation risk, elk had long step lengths (**Figure 3B**), low residence time (**Figure 3D**), and long return times (**Figure 3F**) that initially declined (step length and return times) or increased (residence time) as predation risk increased, which is similar to responses to increasing forage biomass. Nonetheless, at very high predation risk, the slopes of the relationships changed or tended to level off (**Figure 3** and **Supplementary Table S3**). Overall, migrant and residents responded similarly in step lengths with predation risk, whereas residence time and return times were higher for residents than migrant (**Figure 3** and **Supplementary Table S3**).

Mean step lengths of elk increased (β = 0.121, SE = 0.042, $p = 0.004$; **Figure 4A**) and residence time of elk decreased (β = −0.11, SE = 0.001, $p = 0.001$; **Figure 4B**) with elk population size, with no interaction with migratory tactic ($p > 0.26$). As elk population size changed, there was no consistent change in return times for elk following either movement tactic (**Figure 4C** and **Supplementary Table S4**).

Elk Group Sizes and Associations

We counted the number of individuals associated with each marked elk from 1 November to 30 March in 59 to 717 groups/yr across the 14-year period. Only the upper 75th quartile of group sizes decreased with decreasing elk population size (β = 0.134, SE = 0.005, $p < 0.001$), with group sizes of resident elk decreasing more than migrants (β = 32.0, SE = 4.15, $p < 0.001$). Median group size with which marked elk were associated was smaller

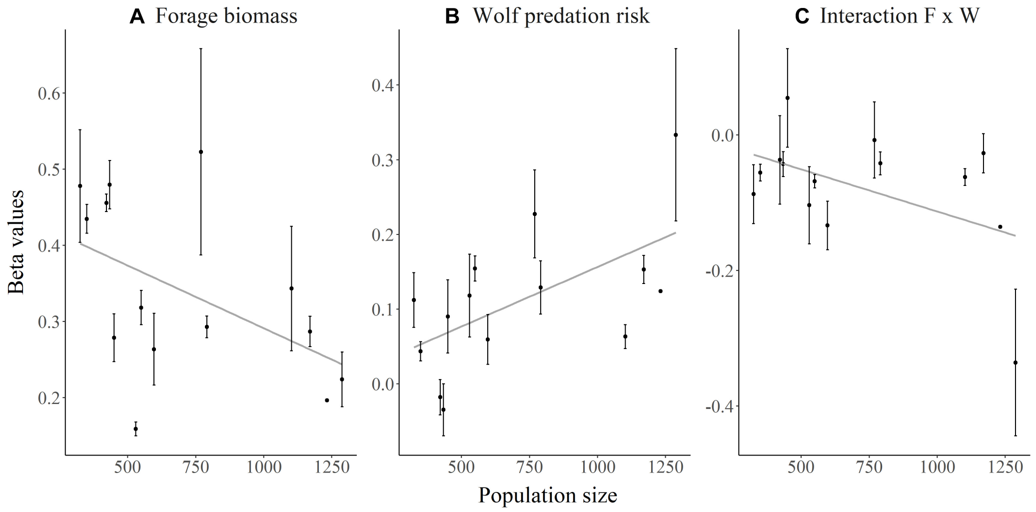

FIGURE 2 | Relationships between elk population size on the Ya Ha Tinda winter range adjacent to Banff National Park in Alberta, Canada, during winters from 2002–2003 to 2015–2016 and the mean selection coefficients (β) extracted from each individual elk's winter selection model for **(A)** forage biomass, **(B)** wolf predation risk, and **(C)** the interaction of forage biomass (F) and wolf predation risk (W). Selection coefficients were derived from diurnal locations of GPS-collared female elk using integrated step selection analysis (details in text). Error bars show ±1 standard error. No differences ($p > 0.52$) occurred in the relationship between selection and elk population size between migrant and resident elk for any coefficient.

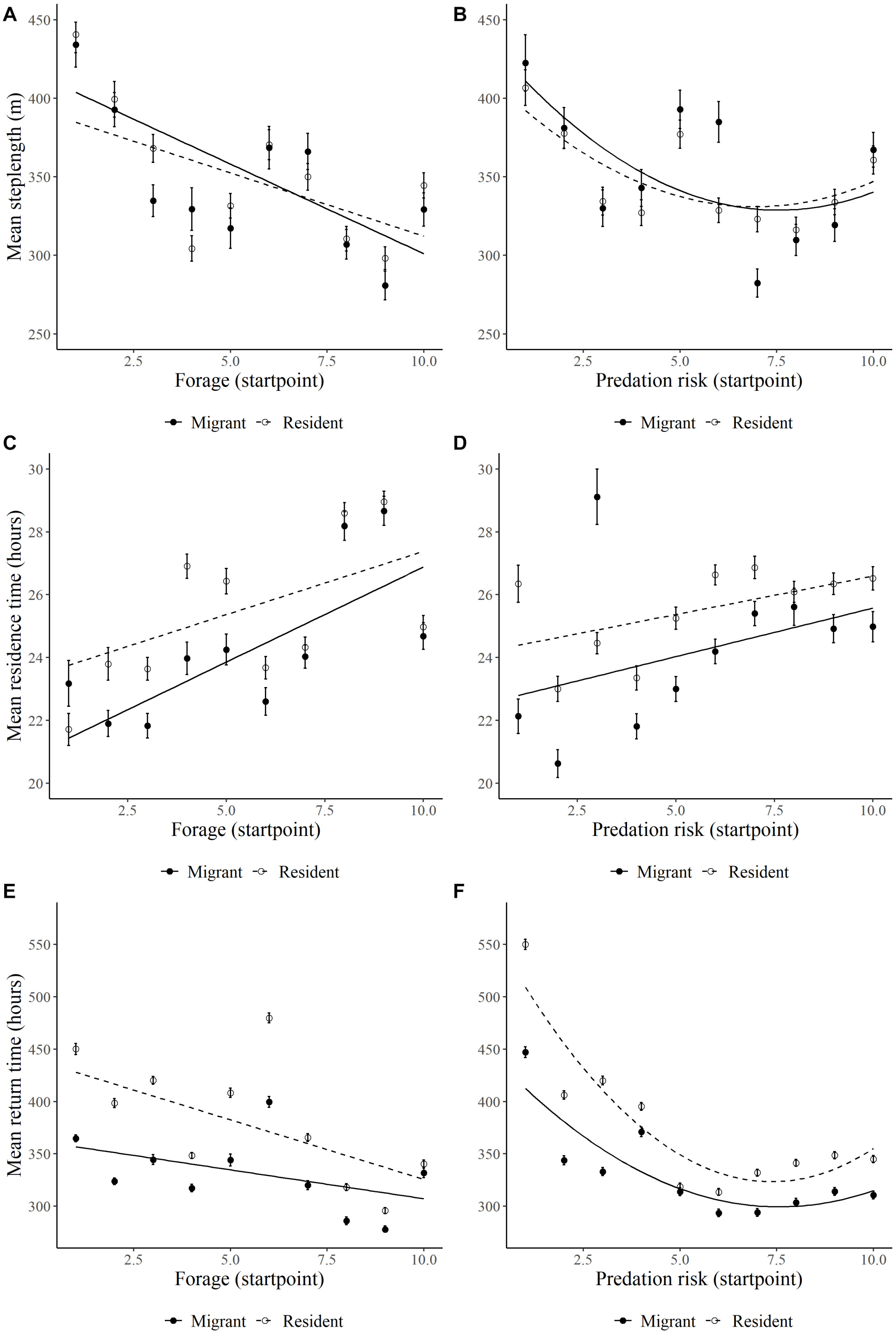

FIGURE 3 | Relationships between forage biomass and wolf predation risk and **(A,B)** mean diurnal step length (m), **(C,D)** residence time (hrs, 800-m radius), **(E,F)** and return time (hrs, 200-m radius, 48-h) of GPS-collared on Ya Ha Tinda winter range adjacent to Banff National Park, Alberta, Canada, during winters from 2002/2003 to 2015/2016. Forage biomass and wolf predation risk were measured at the initiation of a step (start point) and the relationship is graphed as to the means of 10 bins of the *x*-axis. Error bars show ±1 standard error. Lines are best-fit models for migrant (solid circle/line) and resident (open circle/dotted line) elk. **Supplementary Table S3** provides for model results.

at high (>600 elk) than at low elk population size (<600) in both residents (201 vs 275, median test: $X^2 = 49.9$, $p < 0.001$) and migrants (171 vs 253, $X^2 = 51.91$, $p < 0.001$). A difference in median group size existed between migrant and resident elk only when elk population size was low (253, $X^2 = 7.35$, $p = 0.007$; **Figure 5**).

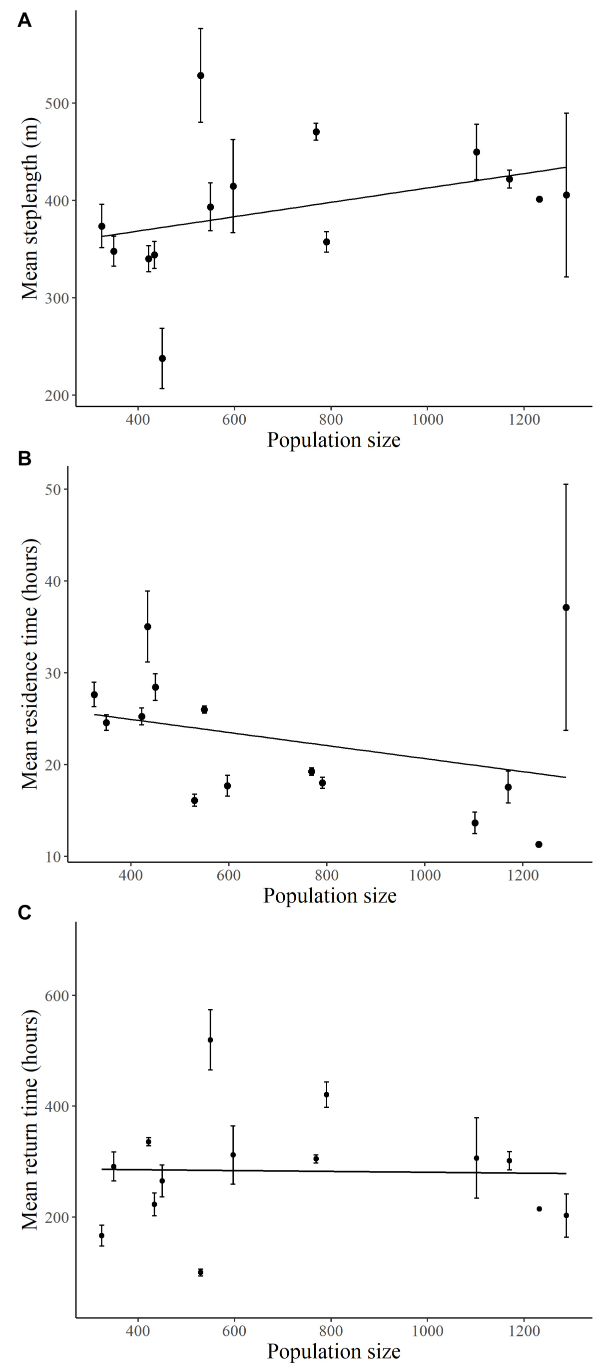

FIGURE 4 | Relationships between elk population size on the Ya Ha Tinda winter range adjacent to Banff National Park, Alberta, Canada, during winters from 2002–2003 to 2015–2016 and **(A)** diurnal step lengths (2-h), **(B)** residence times (within 800 m), and **(C)** return times (200 m, 48 h) of GPS-collared elk. Error bars show +1 standard error. Lines are best-fit models for migrant (solid circle/line) and resident (open circle/dotted line) elk. **Supplementary Table S4** provides model results.

Estimates of the C_S were derived for 14 ± 22 (mean ± SD) resident-resident, 14 ± 22 migrant-migrant, and 38 ± 64 migrant-resident GPS-collared elk dyads/year across the 14-year period. Overall, migrant-migrant and migrant-resident dyads had similar coefficients of sociality (C_S, p = 0.26), which were mostly higher than resident-resident dyads (p = 0.04, **Supplementary Table S5**). As density decreased, coefficients of sociality of migrant-migrant and migrant-resident dyads increased more than for resident-resident dyads (**Figure 6**).

DISCUSSION

Contrary to our predictions, we documented only minor differences in the selection and movement responses of migrant and resident elk to forage biomass and predation risk on sympatric winter ranges. Both migrant and resident elk consistently showed selection for areas of high forage biomass during the daytime when elk spend most of their foraging time (Ensing et al., 2014; Kohl et al., 2018; **Supplementary Figure S2**). The strong selection for areas of high forage biomass emerged from longer residence times and shorter return times (Almeida et al., 2015). Shorter return times to areas of high forage biomass compared with low biomass areas have been reported previously during the growing season in other elk populations (Wolf et al., 2009; Seidel and Boyce, 2015), but not during winter. In contrast, elk showed a weaker and less consistent response to spatially avoiding predation risk. Indeed, we noted positive selection for areas of high predation risk overall, which we attribute to the correlation between forage biomass and predation risk in our and other ecosystems (e.g., Yellowstone; Kohl et al., 2018). Only at the very highest levels of predation risk did we observe elk moving more quickly through risky areas and not returning to them as soon, which was reflected in reduced selection for areas of high forage biomass as predation risk increased. The same trade-off in resource selection was reported for resident elk in summer (Hebblewhite and Merrill, 2009).

We expected stronger selection responses by elk to predation risk because wolves are the leading cause of mortality for adult females in this system (Hebblewhite et al., 2018). Several factors may contribute to the moderate response. First, the extent of response may reflect the frequency of reactive vs proactive responses to the risk of predation (Creel et al., 2014; Moll et al., 2017; Cusack et al., 2020). Because we used a RSF-based predation risk, that variable reflected primarily habitat conditions associated with wolves (i.e., risky places), where elk are expected to proactively make trade-offs in selection or alter their movements because of perceived vulnerability (Kauffman et al., 2007; Creel, 2018; Kohl et al., 2018). Based on the strong spatial pattern of vigilance of elk at Ya Ha Tinda (Robinson and Merrill, 2013), we conclude that elk at the Ya Ha Tinda perceived predation risk, but they avoided only the riskiest places during the day by moving through them quickly. Cusack et al. (2020) reported that elk in Yellowstone National Park did not exhibit proactive avoidance of predation risk, which they attributed to wolves moving frequently throughout the winter range of elk such that elk had imprecise knowledge of their locations. In contrast, Creel et al. (2005) showed that where elk are directly confronted by wolves, elk shifted out of preferred grazing sites in open meadows into the cover of coniferous woodland. We did

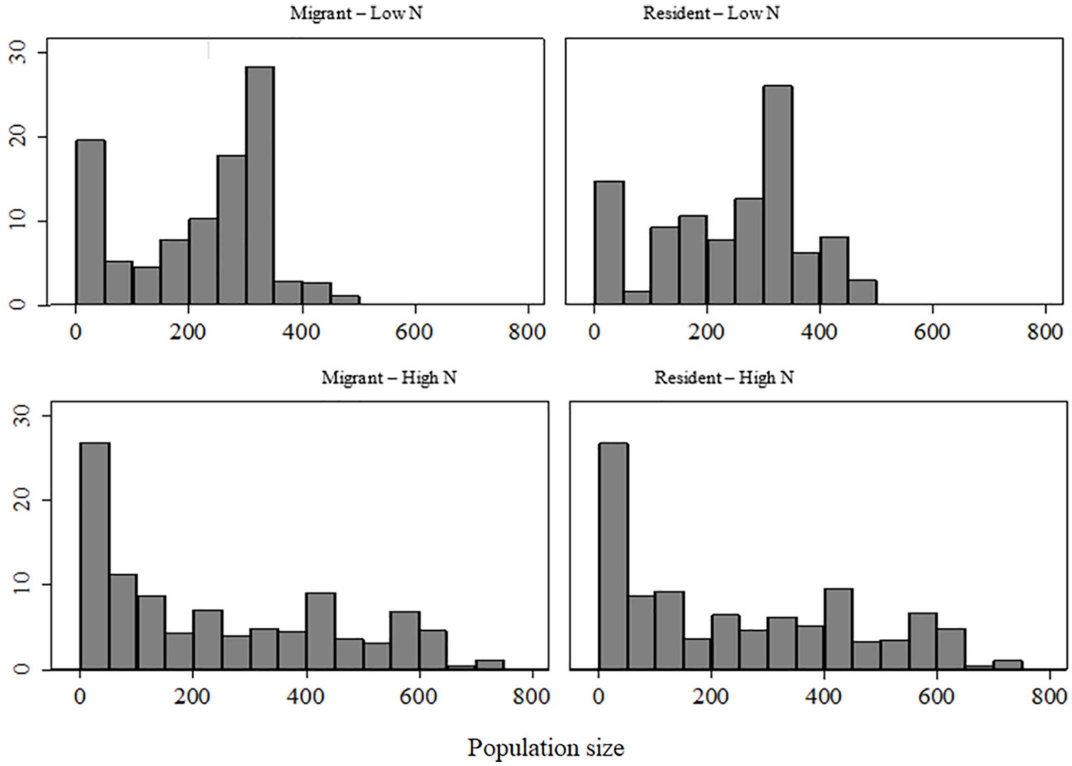

FIGURE 5 | Percent frequency of observed group sizes associated with migrant and resident elk recorded during winters of high (>600) and low (<600) elk population size on the Ya Ha Tinda winter range adjacent to Banff National Park, Alberta, Canada. Population size (N) was determined from aerial surveys. **Supplementary Table S1** provides population sizes.

not have simultaneous locations of wolves and elk to address fine-scale temporal responses, but Robinson and Merrill (2013) also reported elk vigilance was not as closely related to wolf presence or sign in the area as to where elk were located, specifically relative to distance to timber and human infrastructure. We also did not have comparable data to assess predation risk from cougars, but cougars were detected only four times as compared with wolves 98 times on 44 remote cameras on the winter range in 2017–2018 (Flowers, 2019).

If elk were frequently subject to direct threats of predation by the wolves during diurnal foraging at Ya Ha Tinda, we might have observed stronger trade-offs for safe areas. Fewer encounters may result from reduced movement of wolves during the day, but our analysis included crepuscular periods, when wolf activity has been reported to be highest (Krawchuk, 2014). Nevertheless, wolves generally remained on the periphery of the open grasslands during the daytime in winter, which we have attributed to wolves' avoidance of human activity (Hebblewhite and Merrill, 2009; Robinson et al., 2010). These so-called "human-shield" areas that seem capable of allowing herbivores to exploit resources in safe areas are widespread across ungulate systems (Ogutu et al., 2005; Berger, 2007; Rogala et al., 2011; Whittington et al., 2019). Thus, elk exhibited less reactively to risk, but avoided "risky places" by moving through them quickly. In either instance, Ya Ha Tinda elk could more fully exploit forage resources across the productive grassland during the daytime. In contrast, by shifting their distribution to use areas near human infrastructure at night when wolves move into the grassland (Hebblewhite and Merrill, 2009; Robinson et al.,

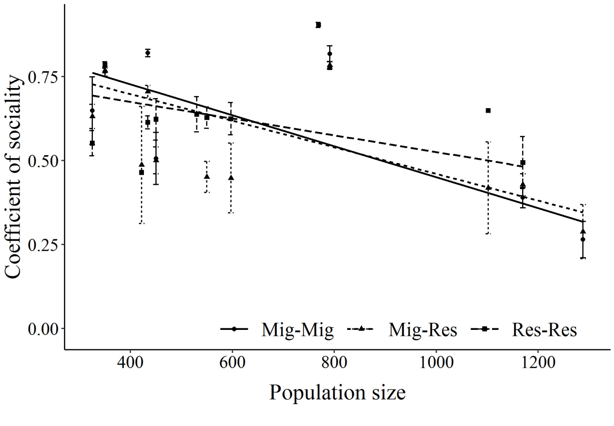

FIGURE 6 | Relationship between the coefficient of sociality of GPS-collared elk dyads by migrant-migrant (Mig_Mig, circle, solid line), migrant and resident (Mig_Res, triangle, dotted line) and resident and resident (Res_Res, square, dashed line) dyad type on Ya Ha Tinda winter range adjacent to Banff National Park, Alberta, Canada, during winters from 2002–2003 to 2015–2016. Error bars show ±1 standard error. **Supplementary Table S5** provides model results.

2010), night-time responses are more consistent with the "risky times" hypothesis; similar responses of elk have been documented in Yellowstone to temporal variation in both wolf and cougar predation risk (Kohl et al., 2019).

Second, elk at Ya Ha Tinda maintained large aggregations (median $>$ 200 elk across all years), which allowed them to avoid predation even if directly confronted by wolves. Creel et al. (2008) argued that aggregation is a type of proactive response to predation. Large prey aggregations are common in open habitats (Clutton-Brock et al., 1987; Pays et al., 2007; Gower et al., 2009), which are expected to reduce the per capita risk to an individual as well as the number of overall encounters (Huggard, 1993; Hebblewhite and Pletscher, 2002; McLellan et al., 2010). Because homogeneously distributed resources are thought to facilitate decisions in movement directions and speed, Sueur et al. (2011) hypothesized that groups should be more cohesive in such landscapes. We argue that the maintenance of large group sizes and the availability of a human-mediated refuge from wolves has allowed an increasing number of resident elk to remain on the Ya Ha Tinda year-round while the population has declined (Hebblewhite and Merrill, 2011).

At the same time, we documented few differences in selection and movement responses of migrant and resident elk as density changed. Our prediction that resident elk would exhibit weaker density-dependent habitat selection to compensate for lower forage quality in summer was not supported. Instead, migrant and resident elk similarly diminished their selection for areas of high forage biomass as elk abundance increased (Morris, 2003; Fortin et al., 2008). Thus, our results add to the growing empirical evidence for density-dependent selection in large herbivores (Clutton-Brock et al., 1987; McLoughlin et al., 2006; Perez-Barberia et al., 2013; van Beest et al., 2014). The inverse relationship between residence times and elk population size indicated elk did not intensify search efforts within the same area as population size increased, but rather that interference or exploitive competition forced them to leave patches sooner and explore other areas to meet their requirements (Almeida et al., 2015). Fortin et al. (2009) argued that exploitative competition among foraging bison was insufficient to explain reduced time spent in grassland patches of even large groups of bison because vegetation removed during a foraging bout was $<$6%. We suggest short residence times during winters at high elk population size reflected cumulative forage depletion because over-winter forage use was as high as 94% during the period of highest elk abundance (McInenly, 2003). Patterns of snowfall may complicate this interpretation, because low snowfall years coincided mostly with years of high elk population size. With reduction in snow, when access to forage is greater, we would expect longer residence time (rather than travel), but this is not the case. We suggest that short residence time is because of forage depletion.

If forage depletion were the major driver of increased foraging movements at high elk population size, we also would have expected the weakest forage-predation risk trade-offs because individuals would become increasingly food stressed (Peacor, 2003). Instead, the trade-off of high-forage areas for safety intensified as elk population size increased (**Figure 1C** and **Supplementary Figure S4**). One explanation is that individual elk were associated with a broader range of group sizes at high elk population size (**Figure 5**). At high population size, large groups may be associated with increasing probability of group fission (Body et al., 2015) because of intra-group competition and reduced coordination in travel (Pépin and Gerard, 2008; Fortin et al., 2009; Pays et al., 2012). This may account for relatively more small groups at high elk population size. We cannot rule out a relatively higher detection bias in counting small groups vs large groups in the field, but because groups were tracked by finding collared animals, we still would have located small groups even if we missed some individuals within the group. Instead, shifts in the portions of large and small group sizes with elk population size likely reflects the nonlinear relationship between density and group sizes described for gregarious ungulates across a number of systems (Mansson et al., 2017).

As the population of elk declined, we were surprized that the median group size increased rather than decreased (McLellan et al., 2010). Because wolf predation on elk is not density dependent in this system and wolf abundance did not decline (Hebblewhite et al., 2018), per capita predation risk from wolves may have increased as elk abundance declined leading to stronger gregariousness. Maintaining relatively large groups under high predation risk reflects an optimal group size in terms of trade-offs in group foraging constraints, reducing predator encounters, and maximizing dilution effects (Focardi and Pecchioli, 2005). Associated with the increase in group size, we observed an increase in spatial cohesion among elk, particularly between migrants and between migrants and residents. In contrast, cohesion remained more constant in resident animals across populations sizes. This outcome might be expected because residents maintain large groups year-round whereas migrant groups are smaller and more dispersed in summer (Hebblewhite et al., 2006; Hebblewhite and Merrill, 2011). More empirical studies linking sociality, habitat selection, and population density are needed to understand the generality of what we observed in this study (Webber and Vander Wal, 2018).

Implications for Maintaining Partial Migration

In the face of widespread decline of migratory behavior in ungulates, there is growing emphasis in understanding the behavioral mechanisms that maintain partial migration to facilitate conservation efforts (Nicholson et al., 1997; White et al., 2007; Rickbeil et al., 2019; Sawyer et al., 2019). Partial migration is thought to be maintained by density-dependent fitness balancing between strategies at the population-level or by switching at the individual level (Lundberg, 1988; Kaitala et al., 1993). Previously, we concluded that maintenance of partial migration of elk at the Ya Ha Tinda was a result of demographic balancing of vital rates despite very different resource selection strategies in summer to escape predation and find forage. At the time, it was unknown whether year-round residents would have the foraging advantages once on their sympatric winter ranges. Subsequently, we have garnered little support for differences in space use or foraging behaviors by elk in winter (Robinson et al., 2010, this study) that might offset the nutritional carry-over effects that migrant elk accrue in summer. Thus, we expected that as density declined, residents should exhibit the most improvement in reproduction, which did not occur (Hebblewhite et al., 2018). Instead, we observed density-independent predation by wolves, which we have argued has kept elk well below ecological carrying capacity (*K*) such that little improvement in recruitment would be expected as density has declined (Hebblewhite et al., 2018). More distinct differences in density-dependent responses between migrant and resident large herbivores may be evident when populations are closer to *K* under low predation (e.g., Mysterud et al., 2011).

Nevertheless, our study provides some unique insight into how seasonal foraging and grouping patterns may contribute to the directional patterns we report in switching migratory tactics with changes in density (Eggeman et al., 2016). During the recent decline of the Ya Ha Tinda elk population, we documented an overall switching rate of 15%/yr, with resident elk being more likely to switch to being a migrant when the elk population was high, whereas migrant elk were more likely to switch to being a resident when the population was low. We hypothesize that the propensity of a resident elk to switch its migratory tactic at a high population reflects the effect of a lower quality summer range (Hebblewhite and Merrill, 2009) combined with density-dependent constraints on winter foraging, which is consistent with condition-dependent switching due to lower body reserves in spring when the decision to migrate occurs. An increase in the propensity for resident elk to migrate when the previous summer's precipitation was low (Eggeman et al., 2016) supports this hypothesis. In contrast, the increased propensity of a migrant to remain as a resident at low density may stem not only from relaxed density-dependent competition (Mysterud et al., 2011, this study), but may be socially facilitated especially in open areas where herbivores tend to aggregate under high predation (Couzin et al., 2011; Lesmerises et al., 2018). Individuals in large groups would increase their conspecific interactions and social bonding without the same scramble competition for resources. In particular, if a migrant loses a calf to predation during the previous summer, the security of the human refuge and social ties on the winter range may foster the shift in migratory tactic (Switzer, 1997; Hoover, 2003; Gehr et al., 2020).

Our study fills a gap in the partial migration literature by pointing to key behaviors that may help explain the dynamics of different migratory tactics leading to the maintenance or loss of partial migration (Berg et al., 2019). Nevertheless, it falls short of linking these behaviors to reproductive outcomes. Previous reproduction within the context of spatial patterns of seasonal predation in conjunction with weather conditions may be key factors if the propensity to migrate is condition-dependent. Even where conservation efforts can prevent major habitat loss and barriers to migration, we expect migration patterns of ungulates to be dynamic in the face of large carnivore recovery and environmental change, and a focus on animal behavior may serve as a first indicator of what is to come (Sih, 2013; Greggor et al., 2016).

DATA AVAILABILITY STATEMENT

The datasets generated for this study will not be made publicly available. Global Positioning System (GPS) and VHF telemetry data are available on the Movebank Data Repository: Hebblewhite et al. (2020).

ETHICS STATEMENT

The animal study was reviewed and approved by Animal Care Protocols: University of Alberta 353212, 611812, 000624, University of Montana AUP 004-16, Parks Canada BAN-2014-16756.

AUTHOR CONTRIBUTIONS

JK, JP, MT, HM, and EM analyzed data and wrote sections of manuscript drafts. JB, HB, SE, and MH collected data and provided input to data analysis and manuscript writing. All authors approved this publication.

FUNDING

This work was supported by funding from Banff National Park, Alberta Fish and Wildlife, National Science Foundation LTREB grant 1556248, The Natural Sciences and Engineering Research Council of Canada (NSERC Discovery to EM), Montana Institute of Ecosystems (supported by National Science Foundation EPSCoRR RII Track 1 award), Universities of Alberta, and Montana, Alberta Conservation Association, Shikar Safari Club, International, Safari Club International, Safari Club International-Northern Alberta Chapter, Rocky Mountain Elk Foundation, Alberta Fish and Game and Hunting for Tomorrow for Ministers Special License funds.

ACKNOWLEDGMENTS

We thank to M. J. Nyland, R. J. Smith, C. White, J. Whittington, B. Fyten, D. Gummer, B. Hunt, T. Shury, K. Heuer, T. Hurd, many other Parks Canada and Ya Ha Tinda ranch staff, and E. Bruns, J. Allen, and A. Hubbs from Alberta Fish and Wildlife, and for supporting this long-term project. We acknowledge the field help of C. Suthmeier, T. Weeks, M. Hessami, S. Hazenberg, S. Wales, C. Intering, C. Roberge, A. Bohm, S. L. Glines, P. Smolko, A. Deedy, and many volunteers.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00269/full#supplementary-material

REFERENCES

Abrams, P. A. (1993). Does increased mortality favor the evolution of more rapid senescence? *Evolution* 47, 877–887. doi: 10.1111/j.1558-5646.1993.tb01241.x

Almeida, P. J. A. L., Vieira, M. V., Prevedello, J. A., Kajin, M., Forero-Medina, G., and Cerqueira, R. (2015). What if it gets crowded? Density-dependent tortuosity in individual movements of a Neotropical mammal. *Aust. Ecol.* 40, 758–764. doi: 10.1111/aec.12250

Anderson, D. P., Forester, J. D., and Turner, M. G. (2008). When to slow down: Elk residency rates on a heterogeneous landscape. *J. Mammal* 89, 105–114. doi: 10.1644/07-MAMM-A-035.1

Avgar, T., Kuefler, D., and Fryxell, J. M. (2011). Linking rates of diffusion and consumption in relation to resources. *Am. Nat.* 178, 182–190. doi: 10.1086/660825

Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods Ecol. Evol.* 7, 619–630. doi: 10.1111/2041-210X.12528

Long, J. A., Nelson, T. A., Webb, S. L., and Gee, K. L. (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *J. Anim. Ecol.* 83, 1216–1233. doi: 10.1111/1365-2656.12198

Ball, J. P., Nordengren, C., and Wallin, K. (2001). Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildl. Biol.* 7, 39–47. doi: 10.2981/wlb.2001.007

Barraquand, F., and Benhamou, S. (2008). Animal movements in heterogeneous landscapes: identifying profitable places and homogenous movement bouts. *Ecology* 89, 3336–3348. doi: 10.1890/08-0162.1

Bastille-Rousseau, G., Fortin, D., and Dussault, C. (2010). Inference from habitat-selection analysis depends on foraging strategies. *J. Anim. Ecol.* 79, 1157–1163. doi: 10.1111/j.1365-2656.2010.01737.x

Benhamou, S. (1992). Efficiency of area-concentrated searching behavior in a continuous patchy environment. *J. Theor. Biol.* 159, 67–81. doi: 10.1016/S0022-5193(05)80768-4

Berg, J. E. (2019). *Shifts in Strategy: Calving and Calf Survival in a Partially Migratory elk Population*. Dissertation thesis. Edmonton, AB: University of Alberta.

Berg, J. E., Hebblewhite, M., St. Clair, C. C., and Merrill, E. H. (2019). Prevalence and mechanisms of partial migration in ungulates. *Front. Ecol. Evol.* 7:325. doi: 10.3389/fevo.2019.00325

Berger, J. (2007). Fear, human shields, and the re-distribution of prey and predators in protected areas. *Biol. Lett.* 3, 620–623. doi: 10.1098/rsbl.2007.0415

Berger, J., Schaller, G. B., Cheng, E., Kang, A., Krebs, M., Li, L., et al. (2015). Legacies of past exploitation and climate affect mammalian sexes differently on the roof of the world - the case of wild yaks. *Sci. Rep.* 5:8676. doi: 10.1038/srep08676

Body, G., Weladji, R. B., Holand, O., and Nieminen, M. (2015). Measuring variation in the frequency of group fission and fusion from continuous monitoring of group sizes J. *Mammal* 96, 791–799. doi: 10.1093/jmammal/gyv084

Borger, L., and Fryxell, J. M. (2012). "Quantifying individual differences in dispersal using net squared displacement," in *Dispersal Ecology and Evolution*, eds J. Clobert, M. Baguette, T. Benton, and J. Bullock (Oxford, UK: Oxford University Press), 222–230. doi: 10.1093/acprof:oso/9780199608898.003.0017

Bracis, C., Bildstein, K. L., and Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography* 41, 1801–1811. doi: 10.1111/ecog.03618

Brennan, A., Cross, P. C., and Creel, S. (2015). Managing more than the mean: using quantile regression to identify factors related to large elk groups. *J. Appl. Ecol.* 52, 1656–1664. doi: 10.1111/1365-2664.12514

Brown, J. S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* 1, 49–71.

Brown, J. S., and Kotlar, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7, 999–1014. doi: 10.1111/j.1461-0248.2004.00661.x

Bunnefeld, N., Borger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., et al. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J. Anim. Ecol.* 80, 466–476. doi: 10.1111/j.1365-2656.2010.01776.x

Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A. J. M., Morellet, N., et al. (2011). Partial migration in roe deer: migratory and resident tactics are end points of a behavioral gradient determined by ecological factors. *Oikos* 120, 1790–1802. doi: 10.1111/j.1600-0706.2011.19441.x

Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1987). Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in Red Deer. *J. Anim. Ecol.* 56, 857–871. doi: 10.2307/4953

Cook, R. C., Cook, J. G., and Mech, L. D. (2004). Nutritional condition of northern Yellowstone elk. *J. Mammal* 85, 714–722. doi: 10.1644/BRG-131

Cook, R. C., Cook, J. G., Vales, D. J., Johnson, B. K., Mccorquodale, S. M., Shipley, L. A., et al. (2013). Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildl. Monogr.* 184, 1–45. doi: 10.1002/wmon.1008

Couzin, I. D., Ioannou, C. C., Demirel, G., Gross, T., Torney, C. J., Hartnett, A., et al. (2011). Uninformed individuals remote democratic consensus in animal groups. *Science* 334, 1578–1580. doi: 10.1126/science.1210280

Creel, S. (2018). The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecology* 21, 947–956. doi: 10.1111/ele.12975

Creel, S., Schuette, P., and Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.* 25, 73–784. doi: 10.1093/beheco/aru050

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., and Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397. doi: 10.1890/05-0032

Creel, S., Winnie, J. A., Christianson, D., and Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Anim. Behav.* 76, 1139–1146. doi: 10.1016/j.anbehav.2008.07.006

Cusack, J. J., Kohl, M. T., Metz, M. C., Coulson, T., Stahler, D. R., Smith, D. W., et al. (2020). Weak spatiotemporal response of prey to predation risk in a freely interacting system. *J. Anim. Ecol.* 89, 120–131. doi: 10.1111/1365-2656.12968

Daly, M., Wilson, M., Behrends, P. R., and Jacobs, L. F. (1990). Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. *Anim. Behav.* 40, 380–389. doi: 10.1016/S0003-3472(05)80934-0

Dehn, M. M. (1990). Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* 26, 337–242. doi: 10.1007/BF00171099

Dingle, H., and Drake, V. A. (2007). What is migration? *Bioscience* 57, 113–121. doi: 10.1641/B570206

Eggeman, S. L., Hebblewhite, M., Bohm, H., Whittington, J., and Merrill, E. H. (2016). Behavioral flexibility in migratory behavior in a long-lived large herbivore. *J. Anim. Ecol.* 85, 785–797. doi: 10.1111/1365-2656.12495

Ensing, E. P., Ciuti, S., de Wijs, F. A. L. M., Lentferink, D. H., ten Hoedt, A., Boyce, M. S., et al. (2014). GPS based daily activity patterns in European red deer and North American elk (*Cervus elaphus*): indication for a weak circadian clock in Ungulates. *PLoS One* 9:e106997. doi: 10.1371/journal.pone.0106997

Fieberg, J., Kuehn, D. W., and DelGiudice, G. D. (2008). Understanding variation in autumn migration of northern white-tailed deer by long-term study. *J. Mammal* 89, 1529–1539. doi: 10.1644/07-MAMM-A-277.1

Flowers, J. A. (2019). *The Waiting Game: elk Avoid Predator Encounters at Fine Spatial Scales*. Dissertation/Master's thesis. Edmonton, AB: University of Alberta.

Focardi, S., and Pecchioli, E. (2005). Social cohesion and foraging decrease with group size in fallow deer (Dama dama). *Behav. Ecol. Sociobiol.* 59, 84–91. doi: 10.1007/s00265-005-0012-0

Forester, J. D., Im, H. K., and Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* 90, 3554–3565. doi: 10.1890/08-0874.1

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330. doi: 10.1890/04-0953

Fortin, D., Boyce, M. S., Merrill, E. H., and Fryxell, J. M. (2004). Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107, 172–180. doi: 10.1111/j.0030-1299.2004.12976.x

Fortin, D., Fortin, M. E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology* 90, 2480–2490. doi: 10.1890/08-0345.1

Fortin, D., Morris, D. W., and McLoughlin, P. D. (2008). Habitat selection and the evolution of specialists in heterogeneous environments. *Isr. J. Ecol. Evol.* 54, 311–328. doi: 10.1560/IJEE.54.3-4.311

Found, R., and St. Clair, C. C. (2016). Behavioral syndromes predict loss of migration in wild elk. *Anim. Behav.* 115, 35–46. doi: 10.1016/j.anbehav.2016.02.007

Fretwell, S. D., and Lucas, H. L. J. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19, 16–36. doi: 10.1007/BF01601955

Gehr, B., Bonnot, N. C., Heurich, M., Cagnacci, F., Ciuti, S., Hewison, A. J. M., et al. (2020). Stay home, stay safe-site familiarity reduces predation risk in a large herbivore in two contrasting study sites. *J. Anim. Ecol.* 89, 1329–1339. doi: 10.1111/1365-2656.13202

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898. doi: 10.1111/j.1365-2656.2006.01106.x

Gower, C. N., Garrott, R. A., White, P. J., Cherry, S., and Yoccoz, N. G. (2009). “Elk group size and wolf predation: a flexible strategy when faced with variable risk,” in *Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Book Series: Terrestrial Ecology Series*, Vol. 3, eds R. A. Garrott, P. J. White, and F. G. R. Watson (San Diego, CA: Academic Press), 401–422.

Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., et al. (2016). Research priorities from animal behaviour for maximising conservation progress. *Trends Ecol. Evol.* 31, 953–964. doi: 10.1016/j.tree.2016.09.001

Grovenburg, T. W., Jacques, C. N., Klaver, R. W., DePerno, C. S., Brinkman, T. J., Swanson, C. C., et al. (2011). Influence of landscape characteristics on migration strategies of white-tailed deer. *J. Mammal* 92, 534–543. doi: 10.1644/09-MAMM-A-407.1

Hamilton, W. D. (1971). Geometry for the selfish herd. *J. Theoret. Biol.* 31, 295–311. doi: 10.1016/0022-5193

Hebblewhite, M. (2000). *Wolf and Elk Predator-Prey Dynamics in Banff National Park*. Dissertation/Master’s thesis. Missoula, MT: University of Montana.

Hebblewhite, M. (2006). *Linking Predation Risk and Forage Dynamics to Landscape-Scale Ungulate Population Dynamics*. Dissertation/Master’s thesis. Edmonton, AB: University of Alberta.

Hebblewhite, M., Eacker, D. R., Eggeman, S., Bohm, H., and Merrill, E. H. (2018). Density-independent predation affects migrants and residents equally in a declining partially migratory elk population. *Oikos* 127, 1304–1318. doi: 10.1111/oik.05304

Hebblewhite, M., Merrill, E., and McDermid, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* 78, 141–166. doi: 10.1890/06-1708.1

Hebblewhite, M., and Merrill, E. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90, 3445–3454. doi: 10.1890/08-2090.1

Hebblewhite, M., and Merrill, E. (2011). Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. *Oikos* 120, 1860–1870. doi: 10.1111/j.1600-0706.2011.19436.x

Hebblewhite, M., and Merrill, E. H. (2007). Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152, 377–387. doi: 10.1007/s00442-007-0661-y

Hebblewhite, M., and Merrill, E. H. (2008). Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *J. Appl. Ecol.* 45, 834–844. doi: 10.1111/j.1365-2664.2008.01466.x

Hebblewhite, M., Merrill, E. H., Martin, H., Berg, J. E., Bohm, H., and Eggeman, S. L. (2020). Data from: Study “Ya Ha Tinda elk project, Banff National Park, 2001-2020 (females)”. *Movebank Data Repos.* doi: 10.5441/001/1.5g4h5t6c

Hebblewhite, M., Merrill, E. H., Morgantini, L. E., White, C., Allen, R., Bruns, E., et al. (2006). Is the migratory behavior of montane elk populations in peril? The case of Alberta’s Ya Ha Tinda elk herd. *Wildlife. Soc. B* 34, 1280–1294. doi: 10.2193/0091-7648(2006)34[1280:itmbom]2.0.co;2

Hebblewhite, M., and Pletscher, D. (2002). Effects of elk group size on predation by wolves. *Can. J. Zool.* 80, 800–809. doi: 10.1139/z02-059

Hoover, J. P. (2003). Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84, 416–430. doi: 10.1890/0012-9658(2003)084[0416:drfsfi]2.0.co;2

Huggard, D. J. (1993). Prey selectivity of wolves in Banff National Park. I. Prey species. *Can. J. Zool.* 71, 130–139. doi: 10.1139/z93-019

Jiang, Z., and Hudson, R. J. (1993). Optimum grazing of wapiti (*Cervus elaphus*) on grassland: patch and feeding station departure rules. *Evol. Ecol. Sci.* 7, 488–498. doi: 10.1007/BF01237643

Kaitala, A., Kaitala, V., and Lundberg, P. (1993). A theory of partial migration. *Am. Nat.* 142, 59–81. doi: 10.1086/285529

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., and Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecol. Lett.* 10, 690–700. doi: 10.1111/j.1461-0248.2007.01059.x

Kausrud, K., Mysterud, A., Rekdal, Y., Holand, O., and Austrheim, G. (2006). Density-dependent foraging behavior of sheep on alpine pastures: effects of scale. *J. Zool.* 270, 63–71. doi: 10.1111/j.1469-7998.2006.00118.x

Kenward, R. E., Marcstrom, V., and Karlbom, M. (1993). Post-nestling behavior in goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. *Anim. Behav.* 46, 371–378. doi: 10.1006/anbe.1993.1199

Kie, J. G., and Bowyer, R. T. (1999). Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *J. Mammal* 80, 1004–1020. doi: 10.2307/1383271

Knopff, K. H., Webb, N. F., and Boyce, M. S. (2014). Cougar population status and range expansion in Alberta during 1991-2010. *Wild. Soc. Bull.* 38, 116–121. doi: 10.1002/wsb.369

Kohl, M. T., Ruth, T. K., Metz, M. C., Stahler, D. R., Smith, D. W., White, P. J., et al. (2019). Do prey select for vacant hunting domains to minimize a multi-predator threat? *Ecol. Lett.* 22, 1724–1733. doi: 10.1111/ele.13319

Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., et al. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* 88, 638–652. doi: 10.1002/ecm.1313

Krawchuk, K. E. (2014). *Is Niche Separation Between Wolves and Cougars Realized in the Rocky Mountains?* Dissertation/Master’s thesis. Edmonton, AB: University of Alberta.

Lardy, S., Fortin, D., and Pays, O. (2016). Increased exploration capacity promotes group fission in gregarious foraging herbivores. *PLoS One* 11:e0167516. doi: 10.1371/journal.pone.0167516

Lesmerises, F., Johnson, C., and St-Laurent, M.-H. (2018). Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. *Anim. Behav.* 140, 39–47. doi: 10.1016/j.anbehav.2018.03.014

Lima, S. L., and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640. doi: 10.1139/z90-092

Lundberg, P. (1988). The evolution of partial migration in birds. *Trends Ecol. Evol.* 3, 172–175. doi: 10.1016/0169

Mansson, J., Prima, M. C., Nicholson, K. L., Wikenros, C., and Sand, H. (2017). Group or ungroup - moose behavioral response to recolonization of wolves. *Front. Zool.* 14:10. doi: 10.1186/s12983-017-0195-z

McInenly, L. E. (2003). *Seasonal Effects of Defoliation on Montane Rough Fescue (Festuca campestris, Rydb.)*. Dissertation/Master’s thesis. Edmonton, AB: University of Alberta.

McKenzie, H. W., Merrill, E. H., Spiteri, R. J., and Lewis, M. A. (2012). How linear features alter predator movement and the functional response. *Interf. Foc.* 2, 205–216. doi: 10.1098/rsfs.2011.0086

McLellan, B. N., Serrouya, R., Wittmer, H. U., and Boutin, S. (2010). Predator-mediated Allee effects in multi-prey systems. *Ecology* 91, 286–292. doi: 10.1890/09-0286.1

McLoughlin, P. D., Boyce, M. S., Coulson, T., and Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependant, multi-variable resource selection. *Proc. R. Soc. B* 273, 1449–1454. doi: 10.1098/rspb.2006.3486

Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., et al. (2013). Linking anti-predator behavior to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecol. Lett.* 16, 1023–1030. doi: 10.1111/ele.12133

Millspaugh, J. J., Brundige, G. C., Gitzen, R. A., and Raedeke, K. J. (2004). Herd organization of cow elk in Custer State Park, South Dakota. *Wildl. Soc. Bull.* 32, 506–514. doi: 10.2193/0091-7648(2004)32[506:hoocei]2.0.co;2

Mobaek, R., Mysterud, A., Loe, L. E., Holand, O., and Austrheim, G. (2012). Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem. *Oikos* 121, 1364–1369. doi: 10.1111/j.1600-0706.2012.20286.x

Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., et al. (2017). The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J. Anim. Ecol.* 86, 749–765. doi: 10.1111/1365-2656.12680

Molvar, E. M., and Bowyer, R. T. (1994). Costs and benefits of group living in a recently social ungulate - the Alaskan moose. *J. Mammal* 75, 621–630. doi: 10.2307/1382509

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wild. Monogr.* 186, 1–62. doi: 10.1002/wmon.1011

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Klaver, R. W., et al. (2011). Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2, 1–34. doi: 10.1890/ES10-00096.1

Monteith, K. L., Hayes, M. M., Kauffman, M. J., Copeland, H. E., and Sawyer, H. (2018). Functional attributes of ungulate migration: landscape features facilitate movement and access to forage. *Ecol. Appl.* 28, 2153–2164. doi: 10.1002/eap.1803

Morris, D. W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136, 1–13. doi: 10.1007/s00442-003-1241-4

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? *Oikos* 120, 1817–1825. doi: 10.1111/j.1600-0706.2011.19439.x

Nelson, M. E. (1995). Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Can. J. Zool.* 73, 1069–1076. doi: 10.1139/z95-127

Nicholson, M. C., Bowyer, R. T., and Kie, J. G. (1997). Habitat selection and survival of mule deer: tradeoffs associated with migration. *J. Mammal* 78, 483–504. doi: 10.2307/1382900

Ogutu, J. O., Bhola, N., and Reid, R. (2005). The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *J. Zool.* 265, 281–293. doi: 10.1017/S0952836904006302

Owen-Smith, N., Fryxell, J., and Merrill, E. H. (2010). Foraging theory upscaled: the behavioral ecology of herbivore movement. *Phil. Trans. R. Soc. B* 365, 2267–2278. doi: 10.1098/rstb.2010.0095

Pays, O., Benhamou, S., Helder, R., and Gerard, J. F. (2007). The dynamics of group formation in large mammalian herbivores: an analysis in the European roe deer. *Anim. Behav.* 74, 1429–1441. doi: 10.1016/j.anbehav.2007.02.012

Pays, O., Fortin, D., Gassani, J., and Duchesne, J. (2012). Group dynamics and landscape features constrain the exploration of herds in fusion-fission societies: the case of European roe deer. *PLoS One* 7:e34678. doi: 10.1371/journal.pone.0034678

Peacor, S. D. (2003). Phenotypic modifications to conspecific density arising from predation risk assessment. *Oikos* 100, 409–415. doi: 10.1034/j.1600-0706.2003.12043.x

Pépin, D., and Gerard, J. F. (2008). Group dynamics and local population density dependence of group size in the *Pyrenean chamois*, *Rupicapra pyrenaica*. *Anim. Behav.* 75, 361–369. doi: 10.1016/j.anbehav.2006.09.030

Perez-Barberia, F. J., Hooper, R. J., and Gordon, I. J. (2013). Long-term density-dependent changes in habitat selection in red deer (*Cervus elaphus*). *Oecologia* 173, 837–847. doi: 10.1007/s00442-013-2686-8

Proffitt, K. M., Gude, J. A., Shamhart, J., and King, F. (2012). Variations in elk aggregation patterns across a range of elk population sizes at Wall Creek, Montana. *J. Wildl. Manag.* 76, 847–856. doi: 10.1002/jwmg.310

Rickbeil, G. J. M., Merkle, J. A., Anderson, G., Atwood, M. P., Beckmann, J. P., Cole, E. K., et al. (2019). Plasticity in elk migration timing is a response to changing environmental conditions. *Glob. Chang. Biol.* 25, 2368–2381. doi: 10.1111/gcb.14629

Robinson, B. G., Hebblewhite, M., and Merrill, E. H. (2010). Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* 164, 265–275. doi: 10.1007/s00442-010-1620-6

Robinson, B. G., and Merrill, E. H. (2013). Foraging–vigilance trade-offs in a partially migratory population: comparing migrants and residents on a sympatric range. *Anim. Behav.* 85, 849–856. doi: 10.1016/j.anbehav.2013.02.004

Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., and Musiani, M. (2011). Human activity differentially redistributes large mammals in the Canadian Rockies. *Ecol. Soc.* 16:16. doi: 10.5751/ES-04251-160316

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology* 62, 327–335. doi: 10.2307/1936707

Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinnell, S. P. H., and Monteith, K. L. (2019). Migratory plasticity is not ubiquitous among large herbivores. *J. Anim. Ecol.* 88, 450–460. doi: 10.1111/1365-2656.12926

Searle, K. R., Hobbs, N. T., and Shipley, L. A. (2005). Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. *Oikos* 111, 417–424. doi: 10.1111/j.0030-1299.2005.13918.x

Seidel, D. P., and Boyce, M. S. (2015). Patch-use dynamics by a large herbivore. *Mov. Ecol.* 3:7. doi: 10.1186/s40462-015-0035-8

Shipley, L., and Spalinger, D. (1995). Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. *Oecologia* 104, 112–121. doi: 10.1007/BF00365569

Sigaud, M., Merkle, J. A., Cherry, S. G., Fryxell, J. M., Berdahl, A., and Fortin, D. (2017). Collective decision-making promotes fitness loss in a fusion-fission society. *Ecol. Lett.* 20, 33–40. doi: 10.1111/ele.12698

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* 85, 1077–1088. doi: 10.1016/j.anbehav.2013.02.017

Spilker, E. (2018). *Spatial Predation Risk and Interactions Within a Predator Community on the Rocky Mountains East Slopes, Alberta*. Dissertation/Master's thesis. Edmonton, AB: University of Alberta.

Spitz, D., Hebblewhite, M., and Stephenson, T. R. (2017). 'MigrateR': extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography* 40, 788–799. doi: 10.1111/ecog.02587

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., et al. (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* 120, 1608–1617. doi: 10.1111/j.1600-0706.2011.19685.x

Switzer, P. V. (1997). Past reproductive success affects future habitat selection. *Behav. Ecol. Sociobiol.* 40, 307–312. doi: 10.1007/s002650050346

Thurfjell, H., Ciuti, S., and Boyce, M. (2014). Applications of step-selection functions in ecology and conservation. *Mov. Ecol.* 2:4. doi: 10.1186/2051-3933-2-4

van Beest, F. M., McLoughlin, P. D., Vander Wal, E., and Brook, R. K. (2014). Density-dependent habitat selection and partitioning between two sympatric ungulates. *Oecologia* 175, 1155–1165. doi: 10.1007/s00442-014-2978-7

Van Moorter, B., Rolandsen, C. M., Basille, M., and Gaillard, J. M. (2016). Movement is the glue connecting home ranges and habitat selection. *J. Anim. Ecol.* 85, 21–31. doi: 10.1111/1365-2656.12394

Van Moorter, B., Visscher, D., Benhamou, S., Borger, L., Boyce, M. S., and Gaillard, J. M. (2009). Memory keeps you at home: a mechanistic model for home range emergence. *Oikos* 118, 641–652. doi: 10.1111/j.1600-0706.2008.17003.x

Vander Wal, E., Laforge, M., and McLoughlin, P. (2014). Density dependence in social behavior: home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. *Behav. Ecol. Sociobiol.* 68, 383–390. doi: 10.1007/s00265-013-1652-0

Vander Wal, E., Van Beest, F. M., and Brook, R. K. (2013). Density-dependent effects on group size are sex-specific in a gregarious ungulate. *PLoS One* 8:e53777. doi: 10.1371/journal.pone.0053777

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems Behav. *Ecol. Sociobiol.* 60, 457–464. doi: 10.1007/s00265-006-0172-6

Visscher, D. R., Merrill, E. H., and Martin, P. K. (2017). Hierarchical trade-offs between risk and reward mediated by behavior. *Mamm. Res.* 62, 129–140. doi: 10.1007/s13364-016-0290-0

Webber, Q. M. R., and Vander Wal, E. (2018). An evolutionary framework outlining the integration of individual social and spatial. *J. Anim. Ecol.* 87, 113–127. doi: 10.1111/1365-2656.12773

Weckerly, F. W. (1999). Social bonding and aggression in female Roosevelt elk. *Can. J. Zool.* 77, 1379–1384. doi: 10.1139/z99-101

White, P. J., Davis, T. L., Barnowe-Meyer, K. K., Crabtree, R. L., and Garrott, R. A. (2007). Partial migration and philopatry of Yellowstone pronghorn. *Biol. Conserv.* 135, 502–510. doi: 10.1016/j.biocon.2006.10.041

Whittington, J., Petah, L., and Hunt, B. (2019). Temporal road closures improve habitat quality for wildlife. *Scient. Rep.* 9:3772. doi: 10.1038/s41598-019-40581-y

Wolf, M., Frair, J., Merrill, E., and Turchin, P. (2009). The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* 32, 401–410. doi: 10.1111/j.1600-0587.2008.05626.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 26 August 2020
doi: 10.3389/fevo.2020.00279

Genetic and Environmental Indicators of Climate Change Vulnerability for Desert Bighorn Sheep

Tyler G. Creech[1]*†, Clinton W. Epps[1], John D. Wehausen[2], Rachel S. Crowhurst[1], Jef R. Jaeger[3], Kathleen Longshore[4], Brandon Holton[5], William B. Sloan[6] and Ryan J. Monello[7]

[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, United States, [2] White Mountain Research Center, University of California, Bishop, CA, United States, [3] School of Life Sciences, University of Nevada, Las Vegas, Las Vegas, NV, United States, [4] Western Ecological Research Center, U.S. Geological Survey, Henderson, NV, United States, [5] Grand Canyon National Park, National Park Service, Grand Canyon, AZ, United States, [6] Southeast Utah Group, National Park Service, Moab, UT, United States, [7] Pacific Island Network, Inventory and Monitoring Program, National Park Service, Hawaii National Park, Hawaii, HI, United States

Edited by:
Vernon Bleich,
University of Nevada, Reno,
United States

Reviewed by:
Francesc Mestres,
University of Barcelona, Spain
Inger Suzanne Prange,
Appalachian Wildlife Research
Institute (United States), United States

***Correspondence:**
Tyler G. Creech
tyler@largelandscapes.org

†Present address:
Tyler G. Creech,
Center for Large Landscape
Conservation, Bozeman, MT,
United States

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 12 December 2019
Accepted: 06 August 2020
Published: 26 August 2020

Citation:
Creech TG, Epps CW,
Wehausen JD, Crowhurst RS,
Jaeger JR, Longshore K, Holton B,
Sloan WB and Monello RJ (2020)
Genetic and Environmental Indicators
of Climate Change Vulnerability
for Desert Bighorn Sheep.
Front. Ecol. Evol. 8:279.
doi: 10.3389/fevo.2020.00279

Assessments of organisms' vulnerability to potential climatic shifts are increasingly common. Such assessments are often conducted at the species level and focused primarily on the magnitude of anticipated climate change (i.e., climate exposure). However, wildlife management would benefit from population-level assessments that also incorporate measures of local or regional potential for organismal adaptation to change. Estimates of genetic diversity, gene flow, and landscape connectivity can address this need and complement climate exposure estimates to establish management priorities at broad to local scales. We provide an example of this holistic approach for desert bighorn sheep (*Ovis canadensis nelsoni*) within and surrounding lands administered by the U.S. National Park Service. We used genetic and environmental data from 62 populations across the southwestern U.S. to delineate genetic structure, evaluate relationships between genetic diversity and isolation, and estimate relative climate vulnerability for populations as a function of five variables associated with species' responses to climate change: genetic diversity, genetic isolation, geographic isolation, forward climate velocity within a population's habitat patch (a measure of geographic movement rate required for an organism to maintain constant climate conditions), and maximum elevation within the habitat patch (a measure of current climate stress, as lower maximum elevation is associated with higher temperature, lower precipitation, and lower population persistence). Genetic structure analyses revealed a high-level division between populations in southeastern Utah and populations in the remainder of the study area, which were further differentiated into four lower-level genetic clusters. Genetic diversity decreased with population isolation, whereas genetic differentiation increased, but these patterns were stronger for native populations than for translocated populations. Populations exhibited large variation in predicted vulnerability across the study area with respect to all variables, but native populations occupying relatively intact landscapes, such as Death Valley and Grand Canyon national parks, had the lowest overall vulnerability. These results provide local and regional context for conservation and management decisions regarding bighorn populations in a changing climate. Our study further demonstrates how assessments combining multiple factors could allow a more integrated response, such as increasing efforts to maintain connectivity and thus potential for adaptation in areas experiencing rapid climate change.

Keywords: connectivity, genetic diversity, genetic structure, *Ovis canadensis*, vulnerability

INTRODUCTION

As evidence for the effects of climate change on biodiversity accumulates (Parmesan and Yohe, 2003; Bellard et al., 2012; Wiens, 2016), assessments of species' vulnerability to predicted climatic shifts have become increasingly common (Chapman et al., 2014). By providing information on species' exposure (the magnitude of climate change experienced), sensitivity (the degree to which fitness is affected by a given change in climate), and adaptive capacity (the potential to persist *in situ* or shift ranges), such assessments can improve our understanding of responses and inform high-level decisions about conserving biodiversity (Dawson et al., 2011). Natural resource agencies are increasingly considering climate vulnerability in management plans (Johnson, 2014; Halofsky et al., 2015; Staudinger et al., 2015), but there are two common characteristics of climate vulnerability assessments that may limit their utility for informing management strategies.

First, climate vulnerability assessments are typically conducted at the species level (Pearson et al., 2014; Pacifici et al., 2015; Urban, 2015), but many of the management decisions that most directly influence species are made at the population level. Natural resource managers must consider how to allocate agency resources among populations within their jurisdiction, and population-level assessments are especially relevant for broadly distributed species of conservation concern because populations are extirpated before species go extinct (Razgour et al., 2018). There is increasing evidence that climate vulnerability can vary considerably among populations (Bay et al., 2018; Razgour et al., 2019) and that failure to consider intraspecific variation can lead to misleading predictions regarding the overall climate vulnerability of a species (D'Amen et al., 2013; Schwalm et al., 2016; Razgour et al., 2019).

Second, vulnerability assessments tend to focus on climate exposure while overlooking other components of vulnerability, such as adaptive capacity (Butt et al., 2016). Assessments often rely on correlative modeling approaches (e.g., ecological niche, bioclimatic envelope, or species distribution models) that use associations between known species occurrences and climatic or other environmental variables to predict the distributions of species across geographic space (Wiens et al., 2009; Anderson, 2013; Porfirio et al., 2014; Foden et al., 2019). These models can be coupled with climate projections to infer climate exposure based on predicted changes in geographic distribution or habitat suitability (Araújo and Peterson, 2012; Foden et al., 2019). However, such assessments typically do not account for the ability of species to adjust to novel climatic conditions via evolutionary adaptation and phenotypic plasticity (Merilä and Hendry, 2014), which can be difficult to measure but potentially critical for understanding how climate change affects species (but see Bush et al., 2016; Razgour et al., 2019). Correlative approaches also rarely consider how effects of climate change on species distribution or persistence may depend on habitat connectivity or changes in landscape configuration (Brooker et al., 2007). These limitations suggest that a more multi-faceted approach to vulnerability assessment may be needed to establish population-level management priorities that better reflect the range of factors influencing vulnerability (Hoban, 2018; Razgour et al., 2018).

Genetic information can inform vulnerability assessments by characterizing the potential for evolutionary adaptation to climate change (Carroll et al., 2014), although whether specific populations can evolve climate-sensitive traits is rarely known (Urban et al., 2016). In the absence of that knowledge, other relevant questions may be addressed with genetic data. *(1) How genetically diverse are populations?* Genetic diversity is positively correlated with population fitness and persistence for many species (Reed and Frankham, 2003; Frankham, 2005), albeit not universally (Linløkken, 2018), and the amount of standing genetic variation in populations is thought to be the best indicator of their potential for contemporary evolution in response to climate change (Hendry et al., 2011; Sgro et al., 2011). *(2) How is genetic variation distributed among populations?* Genetically unique populations may be particularly valuable for maintaining species-level evolutionary potential (Petit et al., 2008), and identifying unique populations allows them to be managed as distinct taxa potentially adapted to different local environments (Buchalski et al., 2016). Neutral genetic variation also has been used to distinguish phylogenetic lineages and analyze potential climate-mediated range shifts under the assumption that different lineages likely contain different adaptive diversity (Ikeda et al., 2017), although that approach has been challenged (Smith et al., 2019). *(3) How connected are populations via gene flow?* Genetic isolation (or conversely, connectivity) of populations may be especially influential for evolutionary adaptation to climate change. Gene flow with neighboring populations can help maintain genetic variation upon which selection acts and can introduce adaptive alleles or gene combinations that confer fitness benefits in novel environments (Sexton et al., 2011). For small, fragmented populations in which effects of genetic drift are strong, gene flow facilitated by connectivity with neighboring populations is likely to be particularly important for both maintaining genetic diversity and allowing spread of alleles conveying fitness advantage (Epps et al., 2005; Creech et al., 2017).

Genetic measures of isolation provide estimates of connectivity and genetic structure, as well as variation in genetic diversity (Hedgecock et al., 2007; Lowe and Allendorf, 2010; Meirmans and Hedrick, 2011). However, genetic measures of isolation may become decoupled from landscape-based measures of isolation as a result of wildlife translocations (Malaney et al., 2015; Jahner et al., 2019) or rapid landscape change (Epps and Keyghobadi, 2015). Consequently, genetic-based isolation measures may poorly reflect the degree to which populations are linked via natural dispersal and subsequent gene flow with neighboring populations in the contemporary landscape. In such cases, spatial measures of population isolation may be more useful, such as landscape resistance modeling (Epps et al., 2007; Chetkiewicz and Boyce, 2009) or even Euclidean distance among habitat patches (Prugh, 2009).

As a case study, we illustrate how genetic and environmental data can be combined to assess population-level vulnerability and inform management priorities for desert bighorn sheep (*Ovis canadensis nelsoni*) within and surrounding lands administered by the U.S. National Park Service (NPS). Desert bighorn sheep, one of three subspecies of North American bighorn sheep (Wehausen and Ramey, 2000), range across the southwestern U.S. and northern Mexico. Bighorn are habitat specialists that rely on steeply sloped, rugged terrain with sparse vegetation and good visibility to detect and evade predators (Gionfriddo and Krausman, 1986; Sappington et al., 2007). Much of the best remaining habitat and many of the largest populations of desert bighorn are located on federal lands, including lands managed by NPS (**Figure 1**), and these federal lands have greater exposure to climate change than the U.S. as a whole (Gonzalez et al., 2018). Bighorn population dynamics are closely tied to temperature and precipitation patterns (Wehausen et al., 1987; Douglas, 2001; Epps et al., 2004; Bender and Weisenberger, 2005). Projected changes to the climate of the southwestern U.S. during this century include higher annual average temperatures, longer and hotter summer heat waves, reduced winter and spring precipitation, less reliable surface water supply, and more frequent and severe droughts (Garfin et al., 2014). If manifested, such climatic changes could negatively affect bighorn sheep populations by increasing physiological stress or by reducing availability of forage or water. Yet, evaluating the effect of these changes using a correlative approach would be challenging because of the definitive influence of landscape configuration and isolation on genetic diversity and gene flow of bighorn populations (Epps et al., 2005, 2006; Creech et al., 2017). Moreover, potential climate-related adaptive variation among desert bighorn sheep populations has been identified (Buchalski et al., unpublished) that suggests responses may differ in different habitats.

We developed an extensive genetic dataset for desert bighorn sheep across 10 NPS units and surrounding lands, and we used population-level measures of genetic diversity and region-wide analyses of genetic structure and gene flow to estimate relative capacity of populations to cope with climate change via evolutionary adaptation. We complemented genetic analyses with estimates of population isolation based on empirically derived landscape resistance models, which may better characterize isolation of desert bighorn populations with a history of translocation. We estimated climate exposure of populations using a species-neutral climate change metric (forward climate velocity; Loarie et al., 2009) and an environmental variable associated with persistence probability of desert bighorn populations (maximum elevation of habitat patch; Epps et al., 2004).

We took advantage of the history of population augmentation and reintroduction efforts for desert bighorn sheep in portions of our study area to explore the influence of translocations on genetic diversity and genetic structure. We expected that translocated populations would not be in genetic equilibrium with nearby populations because their genetic makeup would reflect influences of the artificial movements of individuals from potentially distant populations, rather than (or in addition to) influences of natural gene flow with neighboring populations constrained by landscape characteristics and time. Because of this expected decoupling of geographic influences from gene flow and resulting genetic diversity in translocated populations, we predicted that: (1) populations that were more geographically isolated (i.e., further from neighboring populations) would have lower genetic diversity, but this negative relationship would be stronger for native than for translocated populations; (2) populations that were more genetically isolated (i.e., more genetically differentiated from nearby populations) would have lower genetic diversity, but this negative relationship would be stronger for native than for translocated populations; and (3) populations that were more geographically isolated would be more genetically isolated, but this positive relationship would be stronger for native than for translocated populations.

Finally, we considered the implications of our results for management of desert bighorn sheep, including how the information from this study could contribute to assessments of the relative vulnerability of desert bighorn populations to climate change effects.

MATERIALS AND METHODS

Study Area

The study area encompassed 10 NPS units and adjacent lands (e.g., state lands, Bureau of Land Management lands, U.S. Forest Service lands, or Indian reservations) that contained bighorn populations likely to interact with those on NPS lands (**Figure 1**). This study area included the majority of desert bighorn sheep on NPS lands and was heterogeneous with respect to many landscape characteristics that influence bighorn sheep. In all areas, bighorn habitat was defined by steep terrain and proximity to reliable surface water. However, the configuration of such habitat varied considerably, including areas where habitat was very discretely distributed (e.g., the Mojave Desert) and areas where habitat was relatively continuous (e.g., the Grand Canyon area). Three arid regions with different climate regimes and biota were represented: the Mojave and Sonoran deserts and the

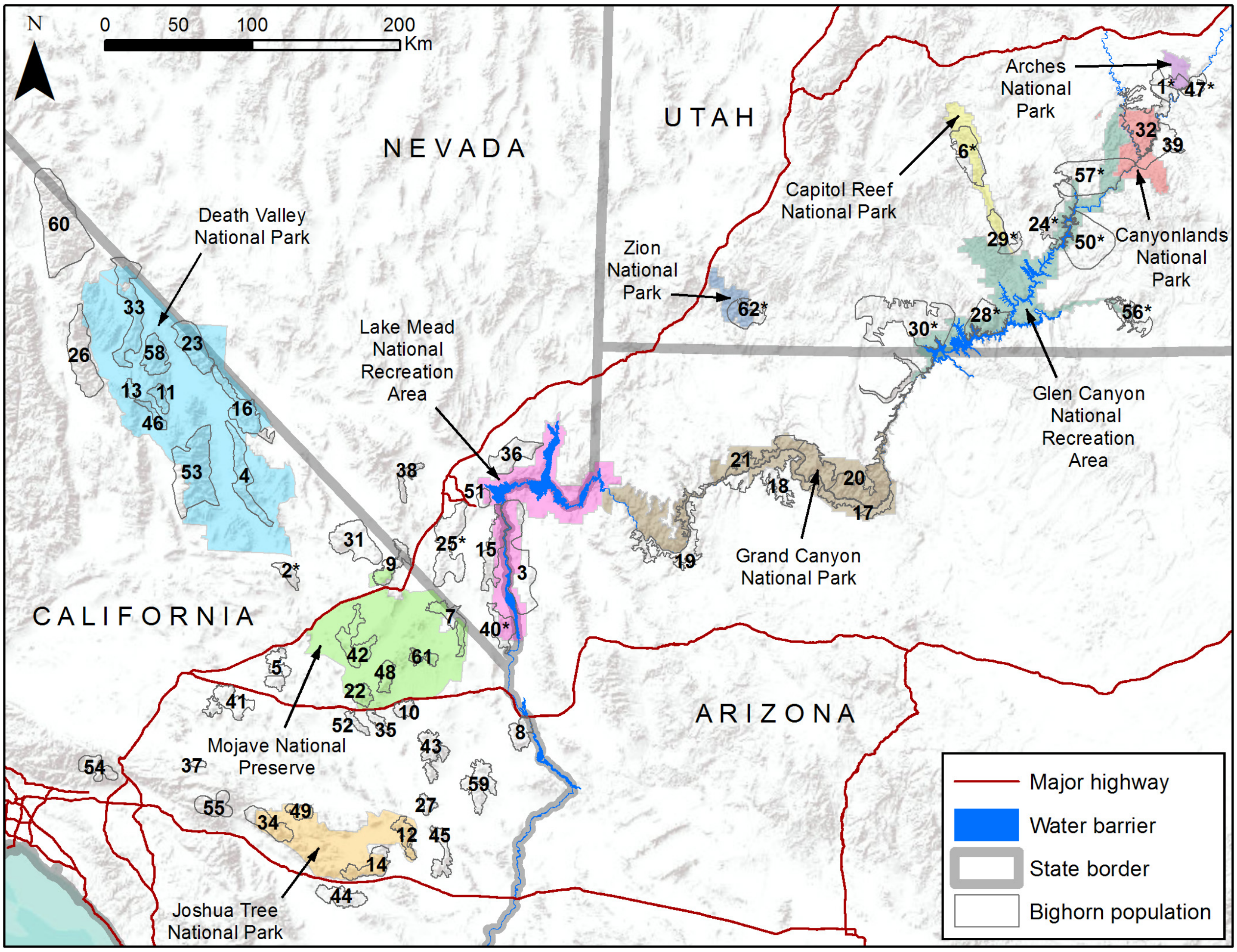

FIGURE 1 | Map of study area including 10 National Park Service units (colored polygons) and 62 desert bighorn sheep populations (numbered hollow gray polygons). See **Table 1** for names of populations associated with numbered polygons.

Colorado Plateau (Bender, 1982). In most areas the landscape was minimally altered by anthropogenic development (urbanization, highways, mining, water impoundments, etc.), but the extent of developments was greatest in southern California and Nevada. The degree to which population history of bighorn sheep had been directly influenced by management actions also varied. Populations in California, Arizona, and southern Nevada were predominately native, while Utah contained many populations that were reintroduced during the past half century using individuals sourced from distant areas in some cases (Epps et al., 2003; Utah Division of Wildlife Resources, 2013; Wild Sheep Working Group, 2015; Jahner et al., 2019).

Genetic Sampling and Genotyping Methods

We primarily used non-invasive sampling of fecal pellets to obtain DNA from individuals (Wehausen et al., 2004) and combined genetic datasets from multiple projects covering different portions of the study area. Populations were sampled during 2000–2003 in the southern Mojave Desert (Epps et al., 2006), 2003–2007 in southern Nevada and near Lake Mead (Jaeger and Wehausen, 2012), and 2003–2013 in Death Valley National Park and surrounding habitat. These sampling efforts generally targeted waterholes where bighorn sheep congregated during the summer months. Populations in northern Arizona and southern Utah were sampled during 2011–2014 with survey, radiotelemetry, and sightings data from state wildlife agencies and NPS used to identify areas in which to focus efforts. DNA sources also included a small number of blood and tissue samples (<5% of all samples) collected from carcasses discovered in the field or contributed by managing agencies, including California Department of Fish and Wildlife, Nevada Department of Wildlife, Arizona Game and Fish Department, U.S. Geological Survey, and NPS. Differences in sampling periods among populations were unlikely to significantly influence our findings because (1) dynamics of genetic structure and diversity operate on a generational basis, and the 14-year period between the earliest and latest sampling efforts represented only approximately two bighorn generations, (2) no major changes to the landscape (e.g., highway or dam construction) occurred during this period that would strongly impact gene flow, and (3) follow-up research on a subset of Mojave Desert populations showed no significant changes in genetic diversity over the course of a ∼12-year period (Epps et al., 2018).

Samples were processed and genotyped in three different laboratories (corresponding to the different projects) using similar techniques. Each lab genotyped samples at a slightly different set of neutral or neutral-acting microsatellite loci (14–17 loci per sample, depending on the laboratory, with 10 loci common to all laboratories). Nickerson (2014) tested both linked and putatively neutral loci for evidence of selection in bighorn populations within the Mojave Desert region using outlier tests, and only locus BL4 (linked to interferon gamma gene) showed potential evidence of positive selection. Evaluation of later BL4 data in the Mojave region (Epps et al., 2018) showed that the signal of positive selection for BL4 was transitory (i.e., no longer present two bighorn sheep generations later). Due to the high strength of genetic drift in these small populations (Creech et al., 2017), even loci linked to known genes largely reflect patterns at putatively neutral loci (Nickerson, 2014). To realign allele sizes for consistency across laboratories, we genotyped a small subset of samples at each locus used by multiple laboratories and translated all allele sizes to match those used in the most recent project. A full description of genetic laboratory protocols for the most recent project (samples from 2011 to 2014) can be found in **Supplementary Material**, and protocols for earlier projects can be found in Epps et al. (2006) and Jaeger and Wehausen (2012).

Defining Populations and Habitat Polygons

We grouped individuals into populations based on the location where they were sampled, then created an associated habitat polygon representing the geographic area inhabited by each population for use in spatially explicit analyses. In the Mojave and Sonoran deserts (southern California, southern Nevada, and southwestern Arizona) habitat was generally distributed in discrete patches of steeply sloped terrain separated by broad valleys, which made assigning individuals to populations and mapping associated habitat polygons relatively straightforward. We used a 10% slope cutoff to establish the boundaries of habitat polygons in these regions (Epps et al., 2007) and relied on expert opinion to modify polygon boundaries in areas where this cutoff did not accurately represent the extent of habitat known to be used by a population.

In the Colorado Plateau region (northern Arizona, southern and southeastern Utah) habitat was more continuously distributed and establishing populations and habitat polygon boundaries was less straightforward. We defined populations based on the spatial clustering of individuals (i.e., groups of samples whose locations were clearly separated from other groups) and used the spatially explicit genetic clustering program GENELAND (Guillot et al., 2005) to assign individuals to populations when we were unsure of population boundaries. After establishing populations, we created habitat polygons by generating a minimum convex polygon (MCP) from sample locations, adding a 10 km buffer to reflect the likely use of areas beyond the MCP, and removing areas inside the buffered MCP that were not suitable habitat (e.g., flat terrain, water bodies).

We used bighorn sheep translocation records from the Western Association of Fish and Wildlife Agencies (Wild Sheep Working Group, 2015) to determine whether populations were native or had a history of translocation (reintroduction or augmentation with individuals from other populations) to aid in interpretation of genetic structure results.

Genetic Structure

Individuals were distributed relatively continuously rather than in discrete populations in portions of our study area, and preliminary analyses suggested a pattern of genetic isolation by distance (**Supplementary Figure S1**) that could produce misleading patterns of genetic structure (Kalinowski, 2011; Janes et al., 2017; Perez et al., 2018) when analyzed using common Bayesian clustering algorithms such as STRUCTURE (Pritchard et al., 2000). We therefore relied on two analytical methods expected to perform more reliably when applied to genetic datasets that deviate from the classic island model of population structure. First, we used discriminant analysis of principal components (DAPC), a multivariate method that summarizes between-group genetic differentiation while ignoring within-group variation and making no assumptions about the underlying population genetic model (Jombart et al., 2010). We conducted DAPC using the *adegenet* package (Jombart, 2008) for R (R Development Core Team, 2017) and determined the most likely number of genetic clusters using 20 replicate runs of K-means clustering. We used alpha-score optimization to determine the number of retained principal components that represented the best trade-off between discrimination power and overfitting. We used a scatterplot of the first two discriminant functions to assess relatedness between clusters and estimated population-level cluster assignment probabilities by averaging individual assignment probabilities for the most likely number of clusters. Initial results suggested a major genetic split between one cluster and all remaining clusters, and we repeated the analysis after excluding the divergent cluster to identify any additional hierarchical structure.

We used the clustering program TESS3 (Caye et al., 2018) as an alternative approach to determine genetic structure. This program requires no assumptions about linkage or Hardy-Weinberg equilibrium and can incorporate information on sample locations using a spatial regularization parameter λ that adjusts the strength of spatial dependence (i.e., the degree to which geographically proximate individuals are more likely than distant individuals to share ancestral genotypes). We considered λ values spanning a range of spatial dependence strengths, allowing the number of clusters (K) to vary from 1 to 20, with 50 replicates for each K-value. We retained the run with the lowest root mean squared error for each K-value and examined cross-validation plots based on a cross-entropy criterion (Frichot and François, 2015) to determine the optimal number of clusters for each λ value tested. All genetic structure analyses were run using a subset of our genetic data that included 10 loci used by all labs and for all geographic regions, thus avoiding potential bias in these analyses caused by missing data.

To confirm the pattern of isolation by distance among populations in our study area, we calculated geographic distances (Euclidean distances between centroids of populations' habitat polygons) and genetic distances (Weir and Cockerham (1984) F_{ST}) for all pairs of populations. We then performed a Mantel test of the relationship between log-transformed geographic distance and linearized genetic distance (F_{ST}/[1-F_{ST}]; Rousset, 1997).

Genetic Diversity

We assessed genetic diversity using genotypes at neutral microsatellite loci. For each population we calculated allelic richness (A_r), the average number of alleles per locus after correcting for variation in sample sizes among populations, using rarefaction (Leberg, 2002) with a minimum sample size of six individuals. To facilitate comparisons with populations from other studies, we also calculated expected heterozygosity (H_e), a common genetic diversity metric that is insensitive to sample size. We used the *gstudio* package (Dyer, 2014) for R to calculate both metrics.

Isolation

We quantified the isolation of each population using both geographic (i.e., landscape) and genetic measures. We used both approaches because genetic differentiation metrics based on direct measures of gene flow among populations such as F_{ST} are strongly influenced by time lags, translocations, and other non-equilibrium situations. In particular, the extensive history of translocations in parts of the study area made F_{ST} a questionable indicator of natural gene flow among some populations, and thus of limited value for predicting how landscape structure will influence future population connectivity. We assessed geographic isolation using a landscape resistance-based approach rather than Euclidean distance to account for the fact that populations geographically close to each other but separated by terrain that is highly resistant to dispersal (e.g., broad valleys or highways) may be less connected than geographically distant populations separated by terrain that is favorable for dispersal. We used a resistance model previously developed for desert bighorn sheep in our study area that included a Gaussian effect of slope (where moderate slopes were less resistant than shallow or steep slopes) and strong barrier effects of major water bodies and interstate highways (Creech et al., 2017; **Supplementary Material**). Terrain ruggedness is also known to influence bighorn habitat use (Sappington et al., 2007) and potentially dispersal but was not included in the resistance model because it was very highly correlated with slope at the spatial resolution (∼100 m) at which the resistance model was developed. We used the model to calculate effective distance (a measure that combines geographic distance and relative habitat resistance) along the least-cost path between the borders of each pair of habitat polygons using Linkage Mapper version 1.1.1 (McRae and Kavanagh, 2011). We quantified geographic isolation of each population as the harmonic mean of effective distances to the nearest three neighboring populations (Epps et al., 2005). We then quantified genetic isolation of each population as the mean pairwise F_{ST} (Weir and Cockerham, 1984) with these three nearest neighboring populations determined by effective distances.

Relationships Among Genetic Diversity and Isolation Measures

We used simple linear regression to test our predictions that (1) native populations would show stronger negative relationships between genetic diversity and geographic isolation than translocated populations, and (2) native populations would show stronger negative relationships between genetic diversity and genetic isolation than translocated populations. For each combination of genetic diversity (allelic richness) and isolation measure (mean pairwise F_{ST} or mean effective distance to three nearest neighboring populations), we fit separate regression models for native ($n = 48$) and translocated ($n = 14$) populations. We also fit separate regression models of the relationship between genetic isolation and geographic isolation for native and translocated populations to determine whether the degree of concordance between these isolation measures was affected by translocations. We compared model r^2 and P-values to determine the relative strength of relationships for the two types of populations.

Climate Change Exposure

We used forward climate velocity as an index of the relative exposure of bighorn populations to climate change (Carroll et al., 2015). Forward climate velocity is a measure of the local direction and speed of climate change that indicates how species would need to shift distributions to remain within climatic envelopes (Dobrowski et al., 2013; Hamann et al., 2015). It is a species-neutral measure of exposure that may serve as a useful alternative to more complex correlative models when climate variables influencing the geographic distribution of a species are poorly understood or are believed to vary across the range (Brito-Morales et al., 2018). We obtained gridded spatial data on forward climate velocity based on mean projections for the 2050s from an ensemble of 15 CMIP5 global climate models (AdaptWest Project, 2015). We considered two emissions scenarios: (1) RCP4.5, a moderate emissions scenario that assumes climate policies are able to stabilize climate change by 2100, and (2) RCP8.5, a high emissions scenario that assumes that greenhouse gas emissions continue to rise throughout the twenty-first century (van Vuuren et al., 2011). Climate velocities were derived from a principal component analysis of 11 biologically relevant climate variables, and thus represent predicted potential shifts in overall climate rather than shifts in any single climate variable. We believe this approach was suitable for assessing relative exposure of desert bighorn populations across a large geographic range because although temperature and precipitation are known to influence fitness of desert bighorn sheep, the specific climatic conditions to which bighorn are most sensitive are not fully understood and may vary geographically. For each emissions scenario, we calculated the mean forward climate velocity for grid cells within each population habitat polygon as an estimate of predicted exposure to climate change.

Additionally, we calculated the maximum elevation within each habitat polygon from a 10 m resolution digital elevation model as an indicator of the relative climate stress currently experienced by desert bighorn populations. Previous research in the Mojave Desert region of California found higher extinction risk and lower genetic diversity in populations occupying mountain ranges with lower maximum elevation, which is typically associated with higher temperature and less precipitation (Epps et al., 2004, 2006). We used simple linear regression to explore whether any relationship existed between patch-level estimates of the two measures of climate change exposure (forward climate velocity and maximum elevation).

Overall Vulnerability

To aid in interpretation of results across multiple variables related to climate vulnerability, we created an index of overall vulnerability. We converted population values for genetic diversity (using A_r values only), genetic isolation, geographic isolation, forward climate velocity (using RCP4.5 values only), and maximum elevation to percentiles, reversing the order of values as necessary to ensure that higher percentiles represented greater vulnerability for all variables. We then calculated the mean percentile across the five variables for each population as an index of that population's overall vulnerability with respect to the components of vulnerability included in our analysis. We recognize that these components likely vary in their relative influence on overall vulnerability, but we assigned them equal weight as a potentially useful starting point for making comparisons among populations.

RESULTS

We genotyped 1,652 individuals from 62 populations (**Figure 1**). DAPC results indicated that the most likely number of clusters varied from four to 28, with a modal value of 11 across replicate runs (**Supplementary Figure S2**), suggesting that the program had difficulty reliably determining the number of genetic clusters. We generated individual- and population-level assignment probabilities assuming $K = 11$, and results revealed a single cluster corresponding to populations in southeastern Utah that was differentiated from all other clusters further west (**Figure 2**, upper panel). Nine populations had highest assignment to this distinct cluster, including seven of the 14 translocated populations within our study area. When these nine populations comprising the distinct cluster were excluded from the dataset, reanalysis suggested that remaining populations comprised 10 clusters that were not highly distinct, with most populations showing strongly mixed assignment (**Figure 2**, lower panel).

TESS3 results suggested that the most likely number of clusters was five, regardless of the strength of spatial dependence assumed by the model (**Figure 3** and **Supplementary Figure S3**). Clusters roughly corresponded to the following geographic groupings: (1) southeastern Utah populations within and around Arches National Park (ARCH), Canyonlands National Park (CANY), Capitol Reef National Park (CARE), and Glen Canyon National Recreation Area (GLCA); (2) southern Nevada/western Arizona populations within and around Lake Mead National Recreation Area (LAKE), along with Zion National Park (ZION); (3) northern Arizona populations within and around Grand Canyon National Park (GRCA); (4) southern California populations north of Interstate 15, within and around Death Valley National Park (DEVA); and (5) southern California populations south of I-15, within and around Mojave National Preserve (MOJA)

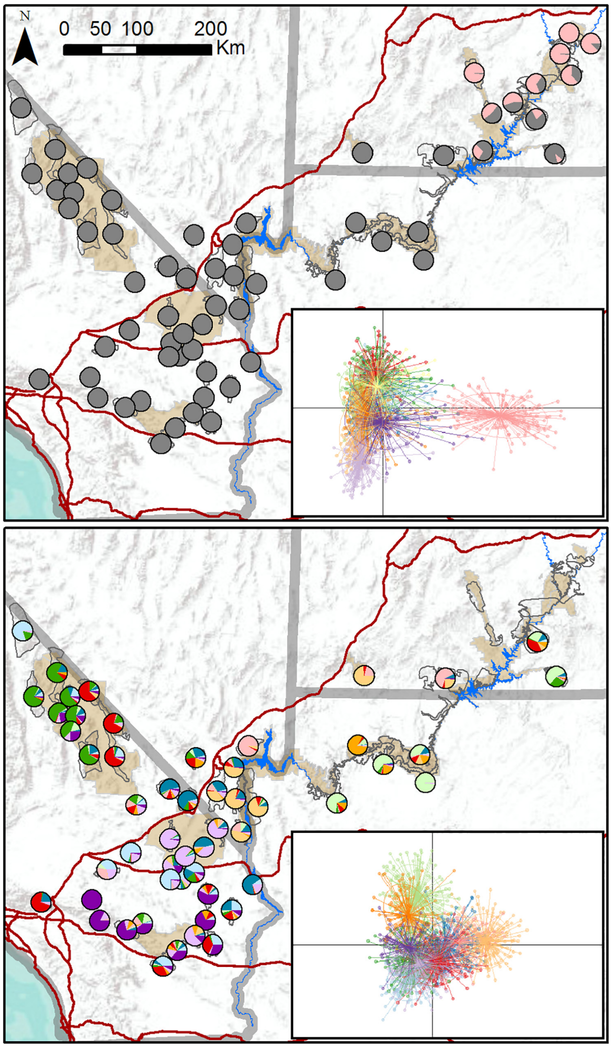

FIGURE 2 | Maps of population assignments to genetic clusters from initial DAPC analysis of all 62 desert bighorn sheep populations in study area (upper panel), and from secondary DAPC analysis of further hierarchical structure after removing populations in southeastern Utah assigned to distinct cluster in initial analysis (lower panel). In pie charts in upper panel map, all clusters other than distinct southeastern Utah cluster are shown in gray to highlight key genetic division. Inset figures in each panel are scatterplots of first two principal component axes from DAPC analyses, with dots representing individuals, colors representing inferred clusters, and ellipses represent 67 percent confidence regions for clusters. Clusters with less overlap in scatterplot are more genetically distinct. Major water barriers and interstate highways are shown in dark blue and red, respectively, tan shaded areas show National Park Service units; and hollow gray polygons show habitat polygons associated with populations.

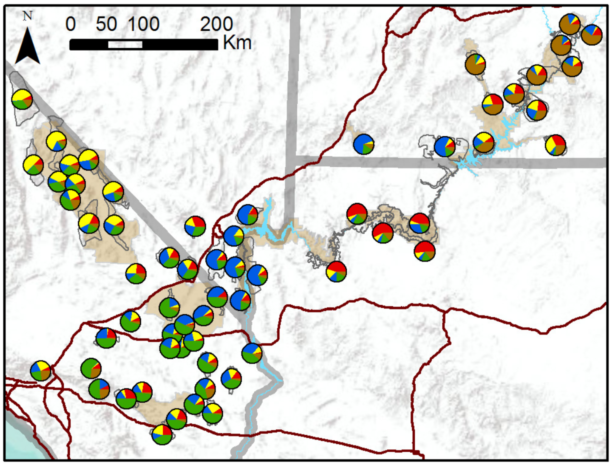

FIGURE 3 | Map of population assignments to five genetic clusters from TESS3 analysis of all 62 desert bighorn sheep populations in study area. Major water barriers and interstate highways are shown in light blue and dark red, respectively, tan shaded areas show National Park Service units; and hollow gray polygons show habitat polygons associated with populations.

and Joshua Tree National Park (JOTR). Ancestry was mixed for most populations, with assignment probabilities of > 10 percent to two or more clusters (**Figure 3**), and the vast majority of individuals within populations also exhibited assignment probabilities of > 10% to multiple clusters (**Supplementary Figure S4**). Most populations with highest assignment to the southeastern Utah cluster, and nearly half of populations with highest assignment to the southern Nevada/western Arizona cluster, were translocated. Populations with highest assignment to the remaining clusters were almost exclusively native. A Mantel test confirmed that populations exhibited genetic isolation by distance across the study area ($r = 0.21$, $p < 0.001$).

Allelic richness across the 62 populations ranged from 2.32 to 3.90 with a mean of 3.24, while expected heterozygosity ranged from 0.44 to 0.70 with a mean of 0.60 (**Table 1**). A_r and H_e of populations were highly correlated ($r = 0.95$). We focus henceforth on A_r results because A_r is sensitive to population bottlenecks and is considered a better indicator of evolutionary potential than other genetic diversity metrics (Leberg, 2002; Allendorf and Luikart, 2009). We observed the highest genetic diversity in populations located within or near eastern DEVA, LAKE, and GRCA (**Figure 4A**). Populations in southeastern Utah exhibited the lowest genetic diversity (especially the Arches-Gemini Bridges and Island in the Sky populations), as did many populations in the southern Mojave Desert (e.g., N. San Bernardino Mts./Cushenbury Mts., Newberry Mts./Ord Mts./Rodman Mts., and Iron Mts. populations).

Mean pairwise F_{ST} with neighboring populations varied from 0.03 to 0.30 (**Table 1**). The most genetically isolated populations (i.e., those with highest pairwise F_{ST} with neighboring populations) occupied island ranges in the Mojave Desert, including the Newberry Mts./Ord Mts./Rodman Mts., N. San Bernardino Mts./Cushenbury Mts., San Gabriel Mts., and Turtle Mts. populations (**Figure 4B**). Populations near the California-Nevada border in the area between MOJA, DEVA, and LAKE (e.g., Eldorado Mts., N. Spring Range, Clark Mts./S. Spring Range populations) were the least genetically isolated from their neighbors.

The most geographically isolated populations (i.e., those with highest effective distances to neighboring populations) were located in the southern Mojave Desert, primarily outside of MOJA and JOTR (e.g., Chemehuevi Mts., Orocopia Mts., Cady Mts. populations), as well as the Zion population in southern Utah (**Figure 4C**). These populations tended to occupy island ranges surrounded by desert flats that were unfavorable to dispersal. In contrast, populations within and around DEVA, GRCA, and southeastern Utah, where steeply sloped terrain was more continuous, were relatively well connected geographically to their neighbors.

Genetic diversity of populations was negatively associated with degree of genetic isolation (**Figure 5**), and this relationship was stronger for native ($r^2 = 0.53$, $p < 0.001$) than for translocated ($r^2 = 0.29$, $p = 0.047$) populations. Genetic diversity was also negatively associated with geographic isolation (**Figure 6**) for native populations ($r^2 = 0.27$, $p < 0.001$), however, there was no relationship between genetic diversity and geographic isolation for translocated populations ($r^2 = 0.007$, $p = 0.769$). Geographic and genetic measures of isolation were positively associated (**Figure 7**) for native populations ($r^2 = 0.44$, $p < 0.001$), but this association was weak for translocated populations ($r^2 = 0.12$, $p = 0.220$).

Mean forward climate velocities of populations were on average 50% higher for the RCP8.5 emissions scenario than for the RCP4.5 scenario, but velocities for the two scenarios were highly correlated ($r = 0.95$; **Supplementary Figure S5**). Because we were primarily interested in the relative differences in velocity among populations, we henceforth focus on results for the RCP4.5 scenario (but see **Supplementary Figure S6**). The highest forward climate velocities were observed for the southernmost populations in the study area within and around JOTR, particularly the Eagle Mts. and Orocopia Mts. populations, and for the White Mts. and Inyo Mts. populations in the northern Mojave Desert (**Figure 4D**). The lowest forward climate velocities were observed for populations within and around GRCA and LAKE, with low-to-moderate values for populations in the northeastern portion of GLCA, ZION, portions of DEVA, and the San Gabriel Mts. population in the western Mojave Desert.

Maximum elevation of habitat polygons ranged from 987 to 3,498 m (**Table 1**). Populations in the southern Mojave Desert from JOTR and MOJA east to the Colorado River (e.g., Iron Mts., S. Bristol Mts., Chemehuevi Mts. populations) had the lowest maximum elevations, while populations in the northern Mojave Desert (e.g., White Mts. and Inyo Mts. populations) and western Mojave Desert (e.g., San Gabriel Mts. and San Gorgonio Mts. populations) had the highest maximum elevations (**Figure 4E**). Maximum elevation and mean forward climate velocity were not related to each other ($r^2 = 0.003$, $p = 0.64$), although a weak negative relationship was observed if one extreme outlier population (White Mts.) was removed from the analysis ($r^2 = 0.12$, $p = 0.006$; **Figure 8**).

TABLE 1 | Characteristics of 62 desert bighorn sheep populations in the study area, including translocation history, genetic diversity, geographic and genetic isolation, forward climate velocity, and maximum elevation.

Population name	Pop. number[a]	Pop. abbrev.[b]	Sample size[c]	Trans-located[d]	H_e[e]	A_r[f]	Genetic isolation[g]	Geographic isolation[h]	Forward climate velocity[i] (km/year) [RCP4.5/RCP8.5]	Maximum elevation[j] (m)
Arches/Gemini Bridges	1	ARGE	7	Yes	0.44	2.32	0.142	1251	1.18/1.58	1791
Avawatz Mts	2	AVA	12	Yes[k]	0.67	3.41	0.090	1,078,945	0.99/1.51	1864
Black (AZ) Mts	3	BLAZ	38	No	0.65	3.46	0.122	778,288	0.36/0.50	1647
Black (CA) Mts	4	BLCA	41	No	0.61	3.53	0.098	188,089	1.02/1.87	1933
Cady Mts	5	CADY	12	No	0.59	3.15	0.155	1,230,484	1.78/3.07	1393
Capitol Reef	6	CARE	25	Yes	0.50	2.80	0.091	365,733	0.96/2.70	2408
Castle Peaks/Castle Mts/Piute Range	7	PCC	32	No	0.64	3.49	0.058	475,135	1.32/1.90	1763
Chemehuevi Mts	8	CHE	7	No	0.49	2.66	0.173	1,349,437	0.81/0.96	1093
Clark Mts/S. Spring Range	9	CSS	47	No	0.59	3.39	0.040	113,662	1.51/2.02	2388
Clipper Mts	10	CLIP	16	No	0.65	3.21	0.090	462,227	1.07/1.48	1392
Cottonwood Canyon	11	COT	15	No	0.64	3.42	0.075	58,209	0.52/0.87	1992
Coxcomb Mts	12	COX	7	No	0.58	3.05	0.115	434,060	3.05/3.55	1314
Dodd Spring	13	DODD	8	No	0.63	3.12	0.063	37,183	0.65/1.12	2253
Eagle Mts	14	EMO	31	No	0.65	3.65	0.053	541,602	4.08/5.28	1612
Eldorado Mts	15	ELD	60	No	0.68	3.77	0.030	216,777	0.98/1.27	1519
Funeral Mts	16	FUN	69	No	0.69	3.87	0.054	56,860	0.91/1.40	2020
Grand Canyon-River Left, East	17	GCRLE	46	No	0.60	3.33	0.115	876	0.30/0.54	2286
Grand Canyon-River Left, Mid	18	GCRLM	47	No	0.69	3.90	0.079	875	0.30/0.51	2224
Grand Canyon-River Left, West	19	GCRLW	27	No	0.64	3.69	0.115	297,420	0.86/1.04	1971
Grand Canyon-River Right, East	20	GCRRE	54	No	0.65	3.80	0.099	880	0.39/0.71	2692
Grand Canyon-River Right, West	21	GCRRW	85	No	0.62	3.68	0.109	882	0.46/0.69	2473
Granite Mts	22	GRAN	21	No	0.63	3.48	0.061	299,660	1.26/1.99	2043
Grapevine Mts	23	GRAP	25	No	0.70	3.79	0.055	67,675	0.84/1.34	2649
Henry Mts	24	HEN	13	Yes	0.64	3.27	0.071	927	0.59/1.09	2497
Highland Range/McCullough Range	25	HMC	64	Yes[l]	0.67	3.63	0.050	357,282	1.02/1.39	2129
Inyo Mts	26	INYO	31	No	0.60	3.21	0.102	247,364	2.08/4.03	3387
Iron Mts	27	IRON	11	No	0.46	2.53	0.124	335,734	3.91/4.63	987
Kaiparowits-East	28	KEAST	22	Yes	0.68	3.65	0.091	347,341	0.69/1.44	2317
Kaiparowits-Escalante	29	KESC	15	Yes	0.63	3.23	0.074	257,861	0.97/1.39	2206
Kaiparowits-West	30	KWEST	55	Yes	0.68	3.90	0.112	190,170	0.76/1.28	2181
Kingston Mts/Mesquite Mts	31	KME	26	No	0.62	3.40	0.048	116,907	1.41/1.92	2205
Island in the Sky	32	ISKY	80	No	0.47	2.65	0.100	1251	1.19/1.63	1936
Last Chance Range/Corridor Canyon	33	LACH	22	No	0.65	3.55	0.065	103,593	1.05/1.58	2633

(Continued)

TABLE 1 | Continued

Population name	Pop. number[a]	Pop. abbrev.[b]	Sample size[c]	Trans-located[d]	H_e[e]	A_r[f]	Genetic isolation[g]	Geographic isolation[h]	Forward climate velocity[i] (km/year) [RCP4.5/RCP8.5]	Maximum elevation[j] (m)
Little San Bernardino Mts	34	LSB	12	No	0.63	3.37	0.130	209,655	1.00/1.54	1764
Marble Mts	35	MAR	47	No	0.68	3.76	0.054	300,351	1.63/2.09	1159
Muddy Mts	36	MUD	34	No	0.58	3.18	0.117	801,802	0.66/0.79	1644
N. San Bernardino Mts/Cushenbury Mts	37	NSB	15	No	0.45	2.43	0.212	538,010	2.95/3.29	2516
N. Spring Range	38	NSP	17	No	0.64	3.38	0.046	687,305	0.65/0.733	2459
Needles/Lockhart Basin	39	NEED	7	No	0.57	2.84	0.161	369,862	1.26/1.81	1965
Newberry (NV) Mts	40	NNV	15	Yes[m]	0.68	3.67	0.053	542,568	0.65/0.92	1699
Newberry (CA) Mts/Ord Mts/Rodman Mts	41	NOR	15	No	0.46	2.43	0.300	1,216,827	1.86/2.79	1908
Old Dad Peak/Kelso Mts/Marl Mts/Indian Spring/Club Peak	42	OKM	37	No	0.52	3.01	0.109	495,915	1.87/2.51	1496
Old Woman Mts	43	OWO	26	No	0.51	2.95	0.124	483,531	1.82/2.29	1597
Orocopia Mts	44	ORO	18	No	0.57	2.91	0.149	1,346,372	4.28/5.32	1146
Palen Mts/Riverside Granite Mts	45	PRG	10	No	0.61	2.92	0.129	418,909	2.64/2.82	1309
Panamint Buttes	46	PANB	12	No	0.55	3.00	0.101	37,219	0.80/1.28	2215
Professor Valley	47	PROF	13	Yes	0.57	2.76	0.158	401,479	0.88/1.38	2062
Providence Mts	48	PROV	20	No	0.63	3.38	0.075	223,783	1.28/2.08	2159
Queen Mt	49	QUE	11	No	0.59	3.18	0.081	399,414	1.57/2.47	1717
Red Canyon/White Canyon/Scorup Canyon	50	SCOR	14	Yes	0.64	3.26	0.142	451,652	0.90/1.36	2138
River Mts	51	RVNV	46	No	0.64	3.48	0.072	218,130	0.98/1.10	1132
S. Bristol Mts	52	SBR	14	No	0.60	3.18	0.088	3,96,889	2.16/2.59	1052
S. Panamint Range	53	SPAN	29	No	0.60	3.31	0.123	327,301	0.84/1.15	3352
San Gabriel Mts	54	SGA	6	No	0.51	2.49	0.288	1,307,621	0.43/0.59	3055
San Gorgonio Mts	55	SGO	17	No	0.54	2.70	0.124	248,632	2.37/2.74	3498
San Juan River	56	SJRV	30	Yes	0.64	3.19	0.149	681,776	1.82/3.52	1963
San Rafael-Dirty Devil River	57	SRDD	11	Yes	0.61	3.08	0.088	928	0.74/1.19	2164
Tin Mt	58	TIN	22	No	0.65	3.58	0.045	96,013	1.19/1.83	2719
Turtle Mts	59	TUR	14	No	0.59	3.18	0.195	803,063	1.31/1.80	1289
White Mts	60	WHT	25	No	0.52	2.74	0.172	552,873	7.15/12.73	4325
Wood Mts/Hackberry Mts	61	WHA	23	No	0.61	3.34	0.047	353682	1.72/2.35	1880
Zion	62	ZION	21	Yes	0.55	2.94	0.178	1,227,605	0.19/0.29	2377

[a]*Population number used in* ***Figure 1****.* [b]*Population abbreviation used in* ***Figures 5–9****.* [c]*Number of unique genotypes (i.e., individuals) sampled in population.* [d]*Indicates whether population has received individuals translocated from outside populations; populations that received only small numbers of translocated individuals that may have had only minor genetic influence are flagged.* [e]*Allelic richness, a measure of population genetic diversity.* [f]*Expected heterozygosity, a measure of population genetic diversity.* [g]*Mean of pairwise* F_{ST} *values with three nearest neighbors, as measured by effective distances along least-cost paths between habitat polygon boundaries using a landscape resistance model derived from Creech et al. (2017).* [h]*Mean of effective distances to three nearest neighbors, as measured along least-cost paths between habitat polygon boundaries using a landscape resistance model derived from Creech et al. (2017).* [i]*Mean of forward climate velocity (km/year) values from AdaptWest Project (2015) for pixels within each habitat polygon; higher values are associated with greater exposure to climate change. Values are shown for two emissions scenarios, RCP4.5 and RCP8.5.* [j]*Maximum elevation within habitat polygon.* [k]*Minor translocation of 5 sheep from Old Dad Peak in 1992.* [l]*Minor translocation of 16 sheep from Muddy Mts. in 1994.* [m]*Single individual translocated from River Mts. in 1996.*

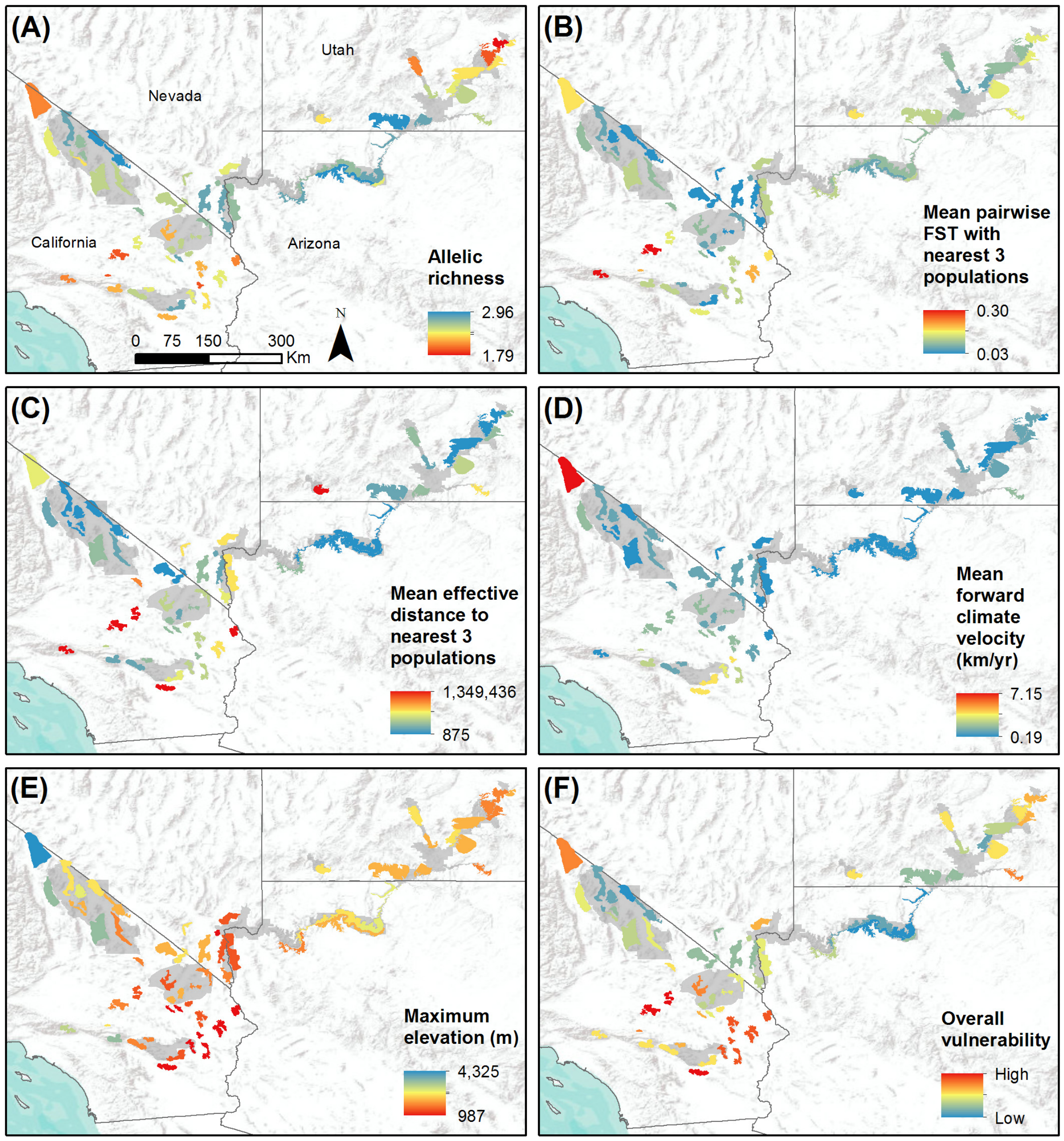

FIGURE 4 | Study-wide comparison of populations with respect to variables that may influence population vulnerability to climate change. Populations are shown with colored polygons. National Park Service units are shaded gray. **(A)** Genetic diversity, measured as allelic richness. **(B)** Genetic isolation, measured as mean pairwise F_{ST} with three nearest populations. **(C)** Geographic isolation, measured as effective distance to three nearest populations. **(D)** Mean forward climate velocity for RCP4.5 emissions scenario. **(E)** Maximum elevation in meters. **(F)** Overall vulnerability, measured as mean percentile across variables **(A–E)**. For all variables, red polygons indicate highest vulnerability and blue polygons indicate lowest vulnerability.

When vulnerability results were combined across all variables (i.e., genetic diversity, genetic isolation, geographic isolation, climate velocity, and maximum elevation), the populations with highest overall vulnerability were primarily located in the southern Mojave Desert and in southeastern Utah. Populations in and around DEVA and GRCA exhibited the lowest overall vulnerability (**Figures 4F, 9**).

DISCUSSION

Much emphasis has recently been placed on identifying and prioritizing species that are most vulnerable to climate change (Thomas et al., 2004; Williams et al., 2008; Summers et al., 2012; Foden et al., 2013). In contrast, our analysis yielded information that may be useful in prioritizing conservation

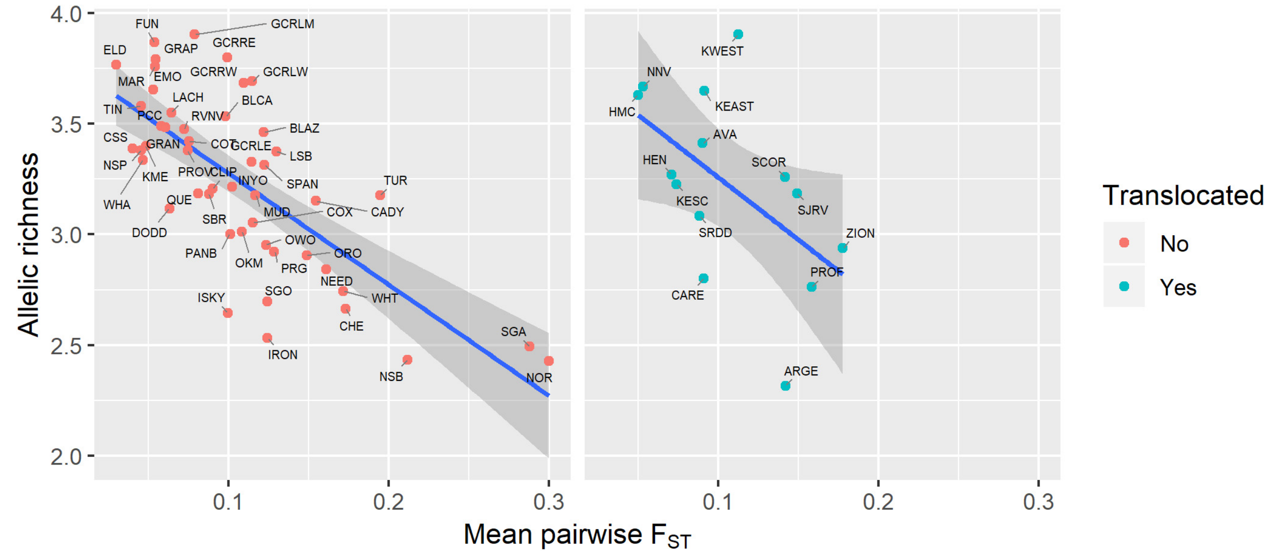

FIGURE 5 | Relationship between genetic diversity (measured as allelic richness) and genetic isolation (measured as mean pairwise F_{ST} with three nearest populations) for native and translocated desert bighorn sheep populations. Blue line and dark gray band show best fit line and 95% confidence interval, respectively, from linear regression model. See **Table 1** for full population names.

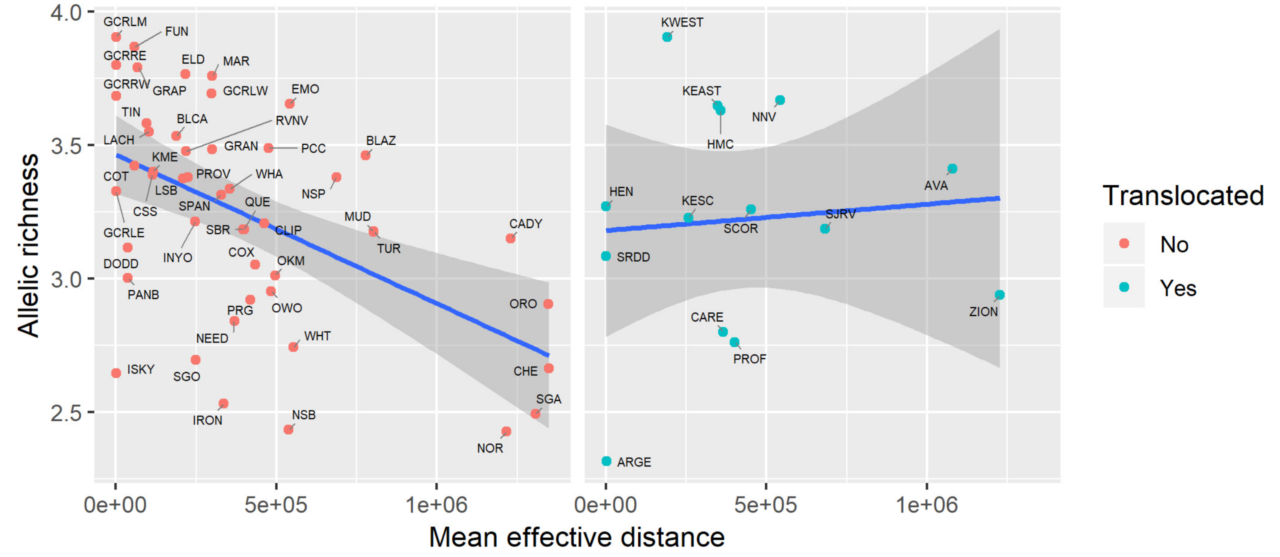

FIGURE 6 | Relationship between genetic diversity (measured as allelic richness) and geographic isolation (measured as mean effective distance to nearest three neighbors) for native and translocated desert bighorn sheep populations. Blue line and dark gray band show best fit line and 95 percent confidence interval, respectively, from linear regression model. See **Table 1** for full population names.

actions for populations of a single species, an approach that has been employed much less frequently in the context of climate change (but see Blair et al., 2012; Razgour et al., 2018). We found wide variation among desert bighorn sheep populations with respect to several key genetic and environmental characteristics expected to influence their vulnerability to climate change. Our analysis showed local and regional correspondence along several axes of vulnerability: for instance, the southernmost populations in the study area had the highest forward climate velocities; in that region, likewise, elevations were lowest and many populations had high isolation and low genetic diversity (**Figure 4**). Other areas showed low vulnerability due to low forward climate velocity, high elevation, and high genetic and geographic connectivity, such as DEVA and GRCA (**Figure 4**). These assessments provide important context for management of desert bighorn sheep across the region. By incorporating estimates of genetic structure and diversity, gene flow, and landscape connectivity, we were able to characterize evolutionary

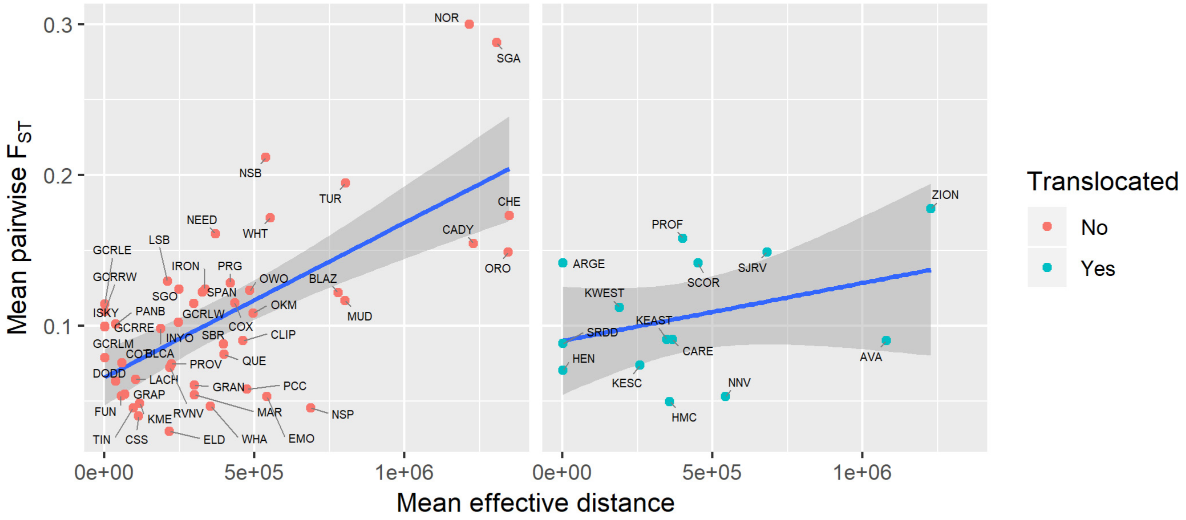

FIGURE 7 | Relationship between genetic isolation (measured as mean pairwise F_{ST} with three nearest populations) and geographic isolation (measured as mean effective distance to nearest three neighbors) for native and translocated desert bighorn sheep populations. Blue line and dark gray band show best fit line and 95 percent confidence interval, respectively, from linear regression model. See **Table 1** for full population names.

aspects of climate vulnerability that are often missing from commonly used correlative approaches.

Our assessment of genetic structure incorporated nearly all native populations of desert bighorn sheep found within the "Nelson" lineage described by Buchalski et al. (2016), which encompasses populations in the Mojave Desert and parts of the Great Basin and Colorado Plateau ecoregions. Concordant with being part of a single lineage of desert bighorn sheep, we found that populations throughout our study area exhibited mixed ancestry, with nearly all populations (and individuals within populations) assigning to multiple genetic clusters with non-negligible probabilities in both TESS3 and DAPC analyses (**Figures 2**, **3**). This is consistent with the pattern of isolation by distance observed in our data set. Previous studies have in some cases suggested clearer genetic divisions, but those studies were conducted at smaller spatial extents or used different analytical approaches aimed at distinguishing recent gene flow. For instance, Jaeger and Wehausen (2012) found almost no gene flow between populations on opposite sides of the Colorado River in the LAKE region; yet our analysis suggested that populations on opposite sides of the Colorado River within either the LAKE or GRCA region were more genetically similar than were geographically distant populations located on the same side of the river. In another case, the strong genetic separation described by Epps et al. (2018) between populations north and south of Interstate 40 in southern California was much weaker according to our analysis (**Figures 2**, **3**). These conflicting results are suggestive of hierarchical genetic structure. The previous studies conducted at smaller spatial extents revealed lower-level structure, while our analysis, which included more of the total genetic variation present within the subspecies, revealed higher-level structure. The seemingly contradictory findings may also speak to the relatively recent influence of dams on gene flow across and along the Colorado River. Prior to construction of dams in the early-to-mid twentieth century, bighorn sheep would have been able to cross the Colorado River relatively easily during periods of low streamflow. The large reservoirs and dam-regulated streamflow in recent decades appear to have largely prevented such crossings and increased genetic divergence of populations on opposite sides of the river. Thus, our current large-scale analysis reflecting longer-term patterns did not indicate a strong barrier effect of the Colorado River, while analyses using methods that characterize recent gene flow (e.g., assignment tests) suggest otherwise (Creech et al., unpublished; Wehausen et al., unpublished).

The most significant genetic division in our study area appeared to be between populations in southeastern Utah (in and around ARCH, CANY, and CARE) and all other populations (**Figure 2**). The history of the populations in this region provides a plausible explanation for this pattern. Nearly all populations in southeastern Utah went extinct between the late 1800s and the 1940s as a result of livestock-borne diseases, unregulated harvest, and mining activities (Singer and Gudorf, 1999), leaving only a small remnant population in CANY. This population bottleneck likely reduced genetic diversity and interrupted gene flow with adjacent regions, causing allele frequencies to diverge, and resulting in the genetic distinction of this remnant population. Reintroductions of bighorn sheep populations to southeastern Utah beginning in the mid-1970s using individuals sourced from the remnant CANY population (Utah Division of Wildlife Resources, 2013) likely did little to change the genetic distinction of this region. Other signatures of past translocation events were also present in the genetic structure results; for instance, the Zion population was most similar to populations in LAKE because it was reestablished using individuals translocated from the River Mountains in Nevada. Although southeastern Utah populations exhibited relatively low isolation and low forward climate velocity, the loss of genetic diversity due to demographic

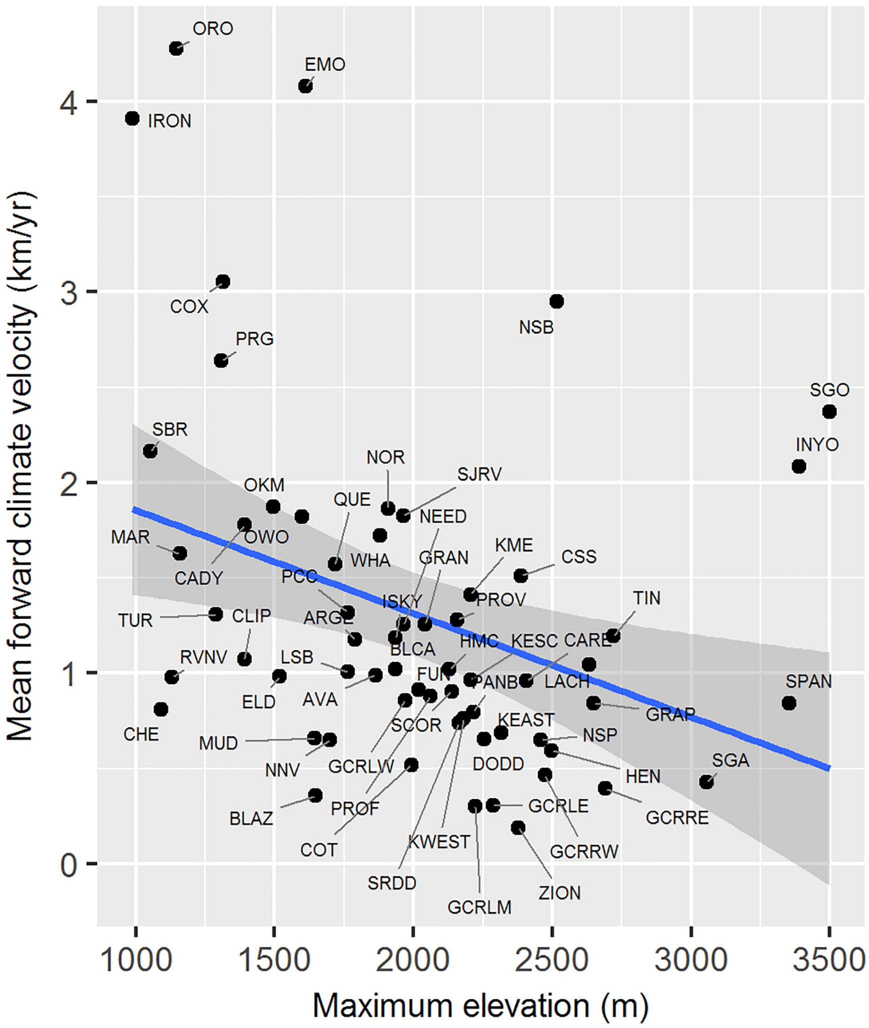

FIGURE 8 | Relationship between mean forward climate velocity and maximum elevation of habitat polygons associated with desert bighorn sheep populations. Blue line and dark gray band show best fit line and 95 percent confidence interval, respectively, from linear regression model. See **Table 1** for full population names. White Mts. population was removed as an extreme outlier (mean forward climate velocity = 12.73 km/year; maximum elevation = 4,322 m) prior to fitting regression model.

history and reintroduction significantly elevated their overall vulnerability in our assessment (**Figure 4**).

Genetic diversity varied strongly among populations, but was high throughout much of our study area in comparison to estimates from other parts of the range of bighorn sheep, suggesting that potential for evolutionary adaptation in these mostly native populations remains high despite small population sizes and rapid genetic drift (e.g., Epps et al., 2005). GRCA, DEVA, and LAKE contained some of the most genetically diverse bighorn sheep populations reported in the literature. Populations occupying these NPS units had mean expected heterozygosities of 0.64, 0.63, and 0.65, respectively. These estimates are higher than microsatellite-based H_e estimates for most desert bighorn sheep populations outside our study area: Boyce et al. (1997) reported mean H_e of 0.55 for populations in the Peninsular Ranges of southern California and 0.50 for populations in southern New Mexico; and Gutiérrez-Espeleta et al. (2000) found mean H_e of 0.57 for populations in southern Arizona. H_e of populations in our study area also compared favorably to reported mean H_e for Rocky Mountain bighorn sheep (*O. c. canadensis*) populations of 0.57 (Gutiérrez-Espeleta et al., 2000), 0.55 (Forbes et al., 1995), and 0.63 (Driscoll et al., 2015). We note, however, that these previous studies used sets of microsatellite loci that were similar but not identical to those used in our study, which could potentially influence these comparisons.

Our results also suggest that genetic diversity of some populations in our study area may be in flux because translocated populations have not yet reached equilibrium. As predicted, geographic isolation was negatively correlated with genetic diversity for native but not for translocated populations (**Figure 6**), and the negative correlation between genetic isolation and genetic diversity that we observed was stronger for native than for translocated populations (**Figure 5**). The stronger correlation between genetic isolation and geographic isolation

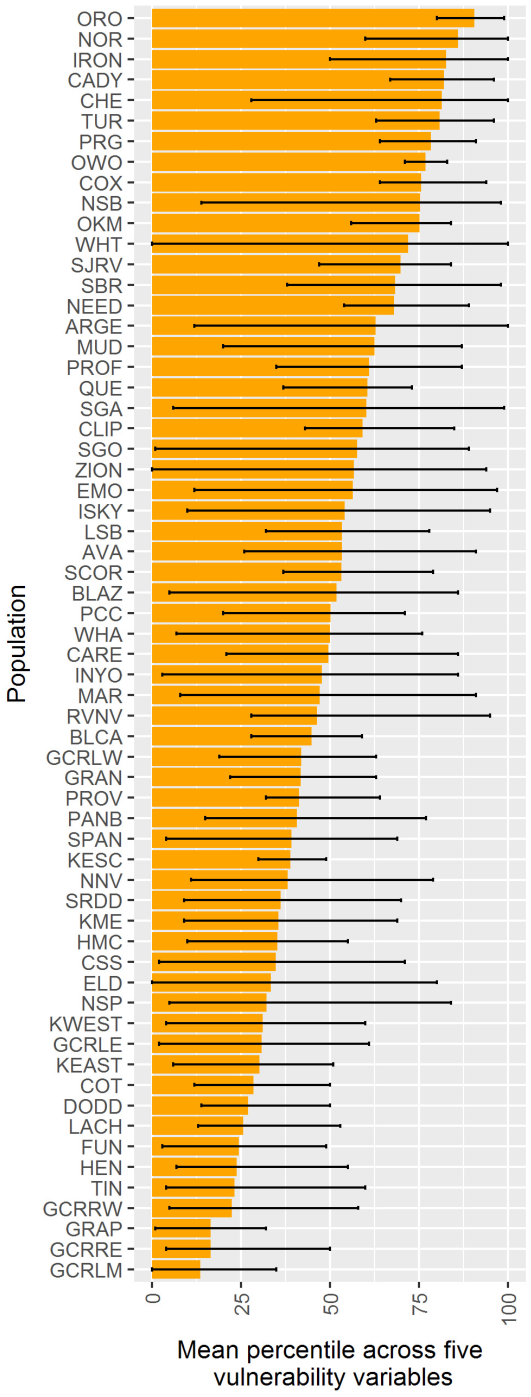

FIGURE 9 | Comparison among 62 desert bighorn populations of overall vulnerability to climate change based on five characteristics: genetic diversity (measured as allelic richness), genetic isolation, geographic isolation, mean forward climate velocity (for RCP4.5 emissions scenario), and maximum elevation. For each characteristic, we converted population values to percentiles (with higher percentiles associated with greater vulnerability). Boxes extend to the mean percentile value for each population across all size variables; whiskers show minimum and maximum percentile across the five characteristics for each population. Populations are sorted top to bottom from highest mean percentile (i.e., greatest overall vulnerability) to lowest. See **Table 1** for full population names.

for native than for translocated populations (**Figure 7**) was also consistent with our predictions. These results suggest that despite the small census sizes and rapid genetic drift typical for desert bighorn sheep populations (Epps et al., 2003, 2005), translocated populations do not appear to have achieved equilibrium with respect to influences of landscape connectivity on genetic diversity and genetic differentiation. Where translocation events have muddied the relationship between landscape characteristics and gene flow, geographic measures of isolation may provide a more accurate picture of potential for future gene flow. Geographic isolation measures may also be more useful where populations have not yet reached genetic equilibrium following major changes to the landscape (e.g., highway or dam construction). We therefore suggest that managers consider both geographic and genetic measures when assessing population isolation in regions where translocation efforts have occurred.

We assessed genetic diversity of populations using neutral microsatellite markers because a major goal of our research was to explore landscape influences on gene flow, and neutral markers provide unbiased estimates of demographic processes, such as gene flow and genetic drift (Holderegger et al., 2006). Evolutionary potential, however, depends on adaptive genetic variation – variation at genes that affect fitness – rather than neutral variation. While the correlation between neutral genetic variation and quantitative variation cannot always be assumed (Reed and Frankham, 2001), genetic diversity at neutral and adaptive-linked microsatellite loci were shown to be strongly correlated for desert bighorn sheep populations in the Mojave Desert (Nickerson, 2014). Heterozygosity estimates for bighorn sheep derived from microsatellites and SNPs were also correlated (Miller et al., 2014). Thus, we believe that our genetic diversity estimates may be useful if imperfect indicators of evolutionary potential of desert bighorn sheep populations. Genomic methods such as outlier tests and genotype-environment association analyses (e.g., Prunier et al., 2011; Razgour et al., 2018) could provide more direct estimates of adaptive genetic variation and also shed light on relative sensitivity of populations to climate change by revealing populations harboring alleles associated with higher fitness in novel climates. Yet, one such recent effort determined that the strong hierarchical spatial structure observed in bighorn sheep confounds interpretation of adaptive differences across many habitats (Buchalski et al., unpublished).

The forward climate velocity estimates in our analysis are subject to considerable uncertainty associated with climate model projections and emissions scenarios. This issue affects all vulnerability analyses that rely on climate projections. However, several aspects of our analysis give us confidence in our velocity-based conclusions regarding climate exposure. First, the velocity data we used were generated using a diverse set of climate variables and an ensemble of climate models, minimizing the effects of individual variables or models that behave as outliers. Second, we considered mid-term (2050s) climate projections, avoiding the increased uncertainty associated with longer-term projections. Third, we considered two emissions scenarios that bracket a wide range of possible climate trajectories. Fourth, our conclusions were based on relative differences in velocity among populations, which were largely consistent between emissions scenarios, rather than absolute magnitudes of climate velocity.

The weak relationship observed between our two measures of climate change exposure is not necessarily surprising because they were chosen to represent different components of exposure: maximum elevation as an index of current climate stress, and forward climate velocity as an index of the magnitude of expected climatic change. In some cases, these metrics indicated opposite conclusions regarding relative exposure of populations, as illustrated by the White Mts. population near the northwestern limit of our study area. This population had the highest maximum elevation, indicating low climate stress at present because the population presumably experiences relatively cool and wet conditions. The White Mts. population also had the highest mean forward climate velocity, indicating high exposure over the long term, because it already occupies the highest-elevation habitat in the vicinity and long-distance dispersal would be necessary to find suitable future habitat at even higher elevation or higher latitude. Interestingly, a recent analysis of adaptive genetic variation in desert bighorn sheep suggests that the White Mts. population has a high frequency of an allele associated with high-elevation habitat (Buchalski et al., unpublished); high-elevation habitat presents different life-history challenges due to altitude and cold stress, suggesting that local adaptation could be expected. The question of whether effects on populations will be greater in areas experiencing the largest climatic changes or in areas where climatic conditions are closest to tolerance limits has not been well explored (but see Beever et al., 2010), despite having important implications for management.

We urge caution in interpreting maximum elevation results at a range-wide scale. Evidence for the relationship between maximum elevation and population persistence comes from populations in the southern Mojave Desert, where elevation is strongly associated with precipitation and forage availability (Epps et al., 2004). Whether elevation is as strong a determinant of population persistence in other regions is not clear, nor is it clear whether cross-regional comparisons are appropriate given major differences in climate, vegetation type, and topography. We suspect that maximum elevation is most useful as a measure of differences in climate change exposure among populations within a region.

Refining Estimates of Population Vulnerability

Our assessment of vulnerability does not consider a component of adaptive capacity that is likely to be important for desert bighorn. The ability of individuals of a given genotype to modify their phenotype in response to environmental conditions, known as phenotypic plasticity, is an important mechanism for climate adaptation that can vary among individuals and populations, but it is not well understood and can be difficult to measure (Merilä and Hendry, 2014; Nicotra et al., 2015). Of the *in situ* mechanisms for adaptation to climate change, plastic responses may be at least as important as evolutionary responses for many species (Hoffmann and Sgro, 2011), although these two mechanisms can be difficult to distinguish (Merilä and Hendry, 2014). Experimental or observational studies of plasticity could provide useful information for prioritizing vulnerable desert bighorn populations (e.g., Renaud et al., 2019).

We avoided using correlative models in our assessment of climate vulnerability because they have several limitations with respect to desert bighorn sheep. Correlative models do not realistically reflect dispersal limitations that influence the geographic distributions of bighorn populations. They may be difficult to apply at the subspecies level because occurrence may be linked with different (and unknown) climatic variables in different parts of the highly variable historic range. Correlative models also typically have not accounted for biotic interactions or changes in vegetation type, which could be critically important for bighorn sheep given that predicted shifts from forest to shrub communities in the southwestern U.S. (Williams et al., 2010) could create new habitat for bighorn. Recent research, however, shows promise of overcoming some of these limitations. For instance, a study of forest bats by Razgour et al. (2019) incorporated information on local climate adaptations from genotype-environment association analysis directly into ecological niche models, and then combined this with a landscape genetic analysis to infer how dispersal barriers are likely to influence potential for evolutionary adaption to climate change. Innovative approaches such as that hold great promise for producing more useful and comprehensive climate vulnerability assessments. In the meantime, less complex approaches such as ours may serve wildlife managers constrained by the amount of time and resources allocated to researching climate vulnerability for any particular species or population.

Management Implications

Maintaining genetic diversity of, and gene flow among, desert bighorn populations will be critical for facilitating evolutionary adaptation to climate change, and actions to preserve or restore connectivity could be effective tools for achieving this objective. A previous simulation study of gene flow for desert bighorn sheep in parts of the study area (Creech et al., 2017) suggested that the spread of adaptive genetic variation is strongly influenced by habitat configuration, with faster spread occurring in areas less fragmented by natural and anthropogenic barriers to dispersal. Reductions in connectivity and gene flow due to anthropogenic barriers such as interstate highways can sometimes be addressed with wildlife crossing structures, although monetary costs can be very high (Corlatti et al., 2009). For example, overpasses for desert bighorn sheep constructed along Highway 93 in the Black Mountains of Arizona facilitated > 1,700 crossings in the first three years after construction (Gagnon et al., 2013). Crossing structures in other areas, such as along Interstates 10, 15, and 40 in southern California, could greatly enhance regional connectivity (Creech et al., 2014), and there may also be opportunities to improve connectivity by modifying existing infrastructure (e.g., highway fencing around underpasses). In some cases, bighorn sheep may eventually discover routes over or under such barriers on their own (Epps et al., 2018). Where connectivity challenges cannot be addressed through barrier mitigation actions, periodic translocation of individuals from nearby populations could be used to provide gene flow (Weeks et al., 2011; Hedrick and Wehausen, 2014).

Ultimately, any management action that promotes large population sizes should help to reduce vulnerability by preserving genetic diversity (Hedrick, 2011). This could include actions that target stressors, whether climatic or non-climatic, such as maintaining or adding artificial water sources (Dolan, 2006; Longshore et al., 2009), controlling predator populations (Wehausen, 1996; Ernest et al., 2002; Rominger et al., 2004), enhancing forage quality (e.g., via prescribed burning; Holl et al., 2004), reducing effects of recreation (Longshore and Thompson, 2013; Wiedmann and Bleich, 2014), or minimizing disease risk by preventing co-mingling with domestic animals (Wehausen et al., 2011). We note, however, that the feasibility of management actions may vary by jurisdiction (e.g., predator control is typically not employed on NPS lands).

Our analysis assumed that connectivity is beneficial to desert bighorn sheep populations because of its critical role in promoting gene flow and maintaining genetic diversity, but connectivity can also facilitate the spread of disease among populations (Simberloff and Cox, 1987; Hess, 1994, 1996). This threat is particularly acute for bighorn sheep, which are susceptible to diseases introduced by domestic livestock beginning with European settlement in the late 1800s (Wehausen et al., 2011). Disease has led to declines across large portions of bighorn sheep range and continues to affect bighorn populations, even within our study area; for instance, respiratory disease outbreaks have been detected in several populations in the Mojave Desert in recent years (Epps et al., 2018). Thus, the risk of disease transmission should be considered before undertaking management actions to increase dispersal among populations. This trade-off between evolutionary potential and disease risk represents one of the fundamental questions that must be clarified for management in the face of both disease and climate change.

Our results underscore the need to maintain native desert bighorn sheep populations in ecologically intact landscapes to facilitate evolutionary adaptation. Unlike other systems where restoration through translocation has dramatically influenced genetic diversity and structure (Whittaker et al., 2004; Malaney et al., 2015; e.g., Jahner et al., 2019), we found that desert bighorn in regions with few anthropogenic barriers to dispersal where populations have persisted without significant reintroduction or augmentation efforts, such as DEVA and GRCA, tended to exhibit high genetic diversity and low isolation. In contrast, populations in landscapes that are more fragmented (i.e., southern California) or heavily influenced by translocations (i.e., southeastern Utah) tended to be less genetically diverse and more isolated. This pattern is consistent with previous studies that have found low genetic diversity or fitness in reintroduced bighorn sheep populations (Whittaker et al., 2004; Wiedmann and Sargeant, 2014). Fortunately, areas that support some of the most genetically diverse and connected populations in our study area are also predicted to have relatively low climate change exposure (e.g., DEVA and GRCA).

The climate vulnerability results from our analysis should help NPS and other natural resource management agencies make more informed decisions about allocating resources among desert bighorn populations, but they do not establish an optimal management strategy. Should efforts be focused on populations with the greatest climate vulnerability in hopes of preserving populations throughout desert bighorn range? Or should managers dedicate resources primarily to bolstering populations that appear most likely to persist in the face of climate change? Current data and analysis cannot fully inform these decisions, and management priorities will also depend on a variety of factors not considered here. For instance, the contributions of genetically unique populations to the evolutionary potential of the species, the susceptibility of connected populations to disease outbreaks, and the public recreational value of populations that provide hunting and wildlife watching opportunities could all influence bighorn management strategies.

We believe the climate vulnerability assessment approach demonstrated here could be applied to the management of many wildlife species other than bighorn sheep. Species that exist in discrete populations due to naturally patchy habitat distribution or the existence of anthropogenic dispersal barriers are likely better suited to this approach than are species that are continuously distributed throughout their range. For well-studied species, previous research identifying specific environmental and climatic factors that influence exposure, sensitivity, adaptive capacity, or landscape connectivity could be used to further tailor this approach. However, vulnerability assessments for poorly studied species may need to rely more on species-neutral measures of climate vulnerability components (e.g., climate velocity or coarse-filter connectivity models based on landscape naturalness). Increasing use of genetic techniques in wildlife management and conservation (Pierson et al., 2016; Smith et al., 2016) suggests that genetic data needed to apply our approach may already exist for some species. Given the capacity for genetic data to expand our understanding of climate change vulnerability, acquiring these data for additional species and populations should be a priority.

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed for this study can be found in the FigShare respository at: https://doi.org/10.6084/m9.figshare.c.4998887.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the study used non-invasive genetic sampling methods.

AUTHOR CONTRIBUTIONS

TC, CE, and RM contributed to conception and design of the study. KL was instrumental in the development of the study that added data for 10 populations in the LAKE region. TC, CE, JW, JJ, KL, BH, WS, and RM performed the field work. RC, CE, JJ, and JW performed the lab work. TC wrote the first draft of the manuscript. TC, CE, and RC wrote sections of the manuscript. All authors contributed to manuscript revision and read and approved the submitted version.

FUNDING

Funding for this research was provided by a Provost's Distinguished Graduate Fellowship from Oregon State University and NPS's Climate Change Response Program (PMIS 162673). Sampling and data development in southern Nevada, adjacent Arizona, and southeastern California was funded by the Bureau of Land Management (Agreements FAA010017 and FAA060067) and NPS through LAKE (Coop Agreement H8R07060001, Task Agreements J8R07070011 and J8R07070012). Funding to NPS, LAKE was from the Southern Nevada Public Lands Management Act. The first sampling and data development in the DEVA region in California from the White and Inyo Mountains to Death Valley was funded by the California Department of Fish and Wildlife. Funding for sampling in GRCA was provided by NPS's Natural Resources Preservation Program (PMIS 157851) and the Grand Canyon Conservancy.

ACKNOWLEDGMENTS

We thank S. Ratchford, S. Holt, L. Manning, C. Crow, G. Lenhart, M. Miller, J. Spaak, M. Lamb, and L. Pilkington for assistance with field logistics and sample collection. C. Peterson and M. Corbin helped with genotyping samples and J. Greenwood assisted with extractions. M. Buchalski provided advice on genetic structure analyses.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00279/full#supplementary-material

REFERENCES

AdaptWest Project (2015). *Velocity of climate change grids for North America*. Available online at: https://adaptwest.databasin.org/pages/adaptwest-velocitywna (accessed January 1, 2016).

Allendorf, F. W., and Luikart, G. (2009). *Conservation and the Genetics of Populations*. Chichester: John Wiley & Sons.

Anderson, R. P. (2013). A framework for using niche models to estimate impacts of climate change on species distributions. *Ann. N. Y. Acad. Sci.* 1297, 8–28. doi: 10.1111/nyas.12264

Araújo, M. B., and Peterson, A. T. (2012). Uses and misuses of bioclimatic envelope modeling. *Ecology* 93, 1527–1539. doi: 10.1890/11-1930.1

Bay, R. A., Harrigan, R. J., Underwood, V. L., Lisle Gibbs, H., Smith, T. B., and Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science* 359, 83–86. doi: 10.1126/science.aan4380

Beever, E. A., Ray, C., Mote, P. W., and Wilkening, J. L. (2010). Testing alternative models of climate-mediated extirpations. *Ecol. Appl.* 20, 164–178. doi: 10.1890/08-1011.1

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377. doi: 10.1111/j.1461-0248.2011.01736.x

Bender, G. L. (1982). *Reference Handbook on the Deserts of North America*. Westport, CT: Greenwood Press.

Bender, L. C., and Weisenberger, M. E. (2005). Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. *Wildl. Soc. Bull.* 33, 956–964. doi: 10.2193/0091-7648(2005)33[956:pdapdo]2.0.co;2

Blair, M. E., Rose, R. A., Ersts, P. J., Sanderson, E. W., Redford, K. H., Didier, K., et al. (2012). Incorporating climate change into conservation planning: identifying priority areas across a species' range. *Front. Biogeogr.* 4, 157–167. doi: 10.21425/F5FBG12668

Boyce, W. M., Hedrick, P. W., Muggli-Cockett, N. E., Kalinowski, S., Penedo, M. C. T., and Ramey, R. R. (1997). Genetic variation of major histocompatibility complex and microsatellite loci: a comparison in bighorn sheep. *Genetics* 145, 421–433.

Brito-Morales, I., García Molinos, J., Schoeman, D. S., Burrows, M. T., Poloczanska, E. S., Brown, C. J., et al. (2018). Climate velocity can inform conservation in a warming world. *Trends Ecol. Evol.* 33, 441–457. doi: 10.1016/j.tree.2018.03.009

Brooker, R. W., Travis, J. M. J., Clark, E. J., and Dytham, C. (2007). Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *J. Theor. Biol.* 245, 59–65. doi: 10.1016/j.jtbi.2006.09.033

Buchalski, M. R., Sacks, B. N., Gille, D. A., Penedo, M. C. T., Ernest, H. B., Morrison, S. A., et al. (2016). Phylogeographic and population genetic structure of bighorn sheep (*Ovis canadensis*) in North American deserts. *J. Mammal.* 97, 823–838. doi: 10.1093/jmammal/gyw011

Bush, A., Mokany, K., Catullo, R., Hoffmann, A., Kellermann, V., Sgrò, C., et al. (2016). Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecol. Lett.* 19, 1468–1478. doi: 10.1111/ele.12696

Butt, N., Possingham, H. P., De Los Rios, C., Maggini, R., Fuller, R. A., Maxwell, S. L., et al. (2016). Challenges in assessing the vulnerability of species to climate change to inform conservation actions. *Biol. Conserv.* 199, 10–15. doi: 10.1016/j.biocon.2016.04.020

Carroll, C., Lawler, J. J., Roberts, D. R., Hamann, A., Wilson, K. A., and Ridgely, R. S. (2015). Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. *PLoS One* 10:e0140486. doi: 10.1371/journal.pone.0140486

Carroll, S. P., Jorgensen, P. S., Kinnison, M. T., Bergstrom, C. T., Denison, R. F., Gluckman, P., et al. (2014). Applying evolutionary biology to address global challenges. *Science* 346:1245993. doi: 10.1126/science.1245993

Caye, K., Jay, F., Michel, O., and François, O. (2018). Fast inference of individual admixture coefficients using geographic data. *Ann. Appl. Stat.* 12, 586–608. doi: 10.1214/17-aoas1106

Chapman, S., Mustin, K., Renwick, A. R., Segan, D. B., Hole, D. G., Pearson, R. G., et al. (2014). Publishing trends on climate change vulnerability in the conservation literature reveal a predominant focus on direct impacts and long time-scales. *Divers. Distrib.* 20, 1221–1228. doi: 10.1111/ddi.12234

Chetkiewicz, C.-L. B., and Boyce, M. S. (2009). Use of resource selection functions to identify conservation corridors. *J. Appl. Ecol.* 46, 1036–1047. doi: 10.1111/j.1365-2664.2009.01686.x

Corlatti, L., Hacklaender, K., and Frey-Roos, F. (2009). Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. *Conserv. Biol.* 23, 548–556. doi: 10.1111/j.1523-1739.2008.01162.x

Creech, T. G., Epps, C. W., Landguth, E. L., Wehausen, J. D., Crowhurst, R. S., Holton, B., et al. (2017). Simulating the spread of selection-driven genotypes using landscape resistance models for desert bighorn sheep. *PLoS One* 12:e0176960. doi: 10.1371/journal.pone.0176960

Creech, T. G., Epps, C. W., Monello, R. J., and Wehausen, J. D. (2014). Using network theory to prioritize management in a desert bighorn sheep metapopulation. *Landsc. Ecol.* 29, 605–619. doi: 10.1007/s10980-014-0016-0

D'Amen, M., Zimmermann, N. E., and Pearman, P. B. (2013). Conservation of phylogeographic lineages under climate change. *Glob. Ecol. Biogeogr.* 22, 93–104. doi: 10.1111/j.1466-8238.2012.00774.x

Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., and Mace, G. M. (2011). Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53–58. doi: 10.1126/science.1200303

Dobrowski, S. Z., Abatzoglou, J., Swanson, A. K., Greenberg, J. A., Mynsberge, A. R., Holden, Z. A., et al. (2013). The climate velocity of the contiguous United States during the 20th century. *Glob. Chang. Biol.* 19, 241–251. doi: 10.1111/gcb.12026

Dolan, B. F. (2006). Water developments and desert bighorn sheep: implications for conservation. *Wildl. Soc. Bull.* 34, 642–646. doi: 10.2193/0091-7648(2006)34[642:wdadbs]2.0.co;2

Douglas, C. L. (2001). Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. *Wildl. Soc. Bull.* 29, 297–305.

Driscoll, C. C., Driscoll, J. G., Hazekamp, C., Mitton, J. B., and Wehausen, J. D. (2015). A tale of two markers: population genetics of colorado rocky mountain bighorn sheep estimated from microsatellite and mitochondrial data. *J. Wildl. Manage.* 79, 819–831. doi: 10.1002/jwmg.895

Dyer, R. J. (2014). *gstudio: Spatial Utility Functions from the Dyer Laboratory. R package version* 1.2 (accessed January 1, 2016).

Epps, C. W., Bleich, V. C., Wehausen, J. D., and Torres, S. G. (2003). Status of bighorn sheep in California. *Desert Bighorn Counc. Trans.* 47, 20–35.

Epps, C. W., Crowhurst, R. S., and Nickerson, B. S. (2018). Assessing changes in functional connectivity in a desert bighorn sheep metapopulation after two generations. *Mol. Ecol.* 27, 2334–2346. doi: 10.1111/mec.14586

Epps, C. W., and Keyghobadi, N. (2015). Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. *Mol. Ecol.* 24, 6021–6040. doi: 10.1111/mec.13454

Epps, C. W., McCullough, D. R., Wehausen, J. D., Bleich, V. C., and Rechel, J. L. (2004). Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conserv. Biol.* 18, 102–113. doi: 10.1111/j.1523-1739.2004.00023.x

Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., and McCullough, D. R. (2006). Elevation and connectivity define genetic refugia for mountain sheep as climate warms. *Mol. Ecol.* 15, 4295–4302. doi: 10.1111/j.1365-294x.2006.03103.x

Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., Ramey, R. R., and McCullough, D. R. (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecol. Lett.* 8, 1029–1038. doi: 10.1111/j.1461-0248.2005.00804.x

Epps, C. W., Wehausen, J. D., Bleich, V. C., Torres, S. G., and Brashares, J. S. (2007). Optimizing dispersal and corridor models using landscape genetics. *J. Appl. Ecol.* 44, 714–724. doi: 10.1111/j.1365-2664.2007.01325.x

Ernest, H. B., Rubin, E. S., and Boyce, W. M. (2002). Fecal DNA analysis and risk assessment of mountain lion predation of bighorn sheep. *J. Wildl. Manage.* 66, 75–85.

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vié, J.-C., Akçakaya, H. R., Angulo, A., et al. (2013). Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS One* 8:e65427. doi: 10.1371/journal.pone.0065427

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., et al. (2019). Climate change vulnerability assessment of species. *Wiley Interdiscip. Rev. Clim. Chang.* 10:e551.

Forbes, S. H., Hogg, J. T., Buchanan, F. C., Crawford, A. M., and Allendorf, F. W. (1995). Microsatellite evolution in congeneric mammals: domestic and bighorn sheep. *Mol. Biol. Evol.* 12, 1106–1113.

Frankham, R. (2005). Genetics and extinction. *Biol. Conserv.* 126, 131–140.

Frichot, E., and François, O. (2015). LEA: an R package for landscape and ecological association studies. *Methods Ecol. Evol.* 6, 925–929. doi: 10.1111/2041-210x.12382

Gagnon, J. W., Loberger, C. D., Sprague, S. C., Priest, M., Boe, S., Ogren, K., et al. (2013). "Evaluation of desert bighorn sheep overpasses along US Highway 93 in Arizona, USA," in *Proceedings of the 2013 International Conference on Ecology and Transportation*, Scottsdale, AZ.

Garfin, G., Franco, G., Blanco, H., Comrie, A., Gonzalez, P., Piechota, R., et al. (2014). "Chapter 20: Southwest," in *Climate Change Impacts in the United States: The Third National Climate Assessment*, eds J. M. Melillo, T. C. Richmond, and G. W. Yohe (Washington, DC: U.S. Global Climate Change Research Program), 462–486.

Gionfriddo, J. P., and Krausman, P. R. (1986). Summer habitat use by mountain sheep. *J. Wildl. Manage.* 50, 331–336.

Gonzalez, P., Wang, F., Notaro, M., Vimont, D. J., and Williams, J. W. (2018). Disproportionate magnitude of climate change in United States national parks. *Environ. Res. Lett.* 13:104001. doi: 10.1088/1748-9326/aade09

Guillot, G., Mortier, F., and Estoup, A. (2005). GENELAND: a computer package for landscape genetics. *Mol. Ecol. Notes* 5, 712–715. doi: 10.1111/j.1471-8286.2005.01031.x

Gutiérrez-Espeleta, G. A., Kalinowski, S. T., Boyce, W. M., and Hedrick, P. W. (2000). Genetic variation and population structure in desert bighorn sheep: implications for conservation. *Conserv. Genet.* 1, 3–15.

Halofsky, J. E., Peterson, D. L., and Marcinkowski, K. W. (2015). *Climate Change Adaptation in United States Federal Natural Resource Science and Management Agencies: A Synthesis*. Washington, DC: U.S. Global Change Research Program.

Hamann, A., Roberts, D. R., Barber, Q. E., Carroll, C., and Nielsen, S. E. (2015). Velocity of climate change algorithms for guiding conservation and management. *Glob. Chang. Biol.* 21, 997–1004. doi: 10.1111/gcb.12736

Hedgecock, D., Barber, P., and Edmands, S. (2007). Genetic approaches to measuring connectivity. *Oceanography* 20, 70–79. doi: 10.5670/oceanog.2007.30

Hedrick, P. (2011). *Genetics of Populations*. Sudbury, MA: Jones & Bartlett Learning.

Hedrick, P. W., and Wehausen, J. D. (2014). Desert bighorn sheep: changes in genetic variation over time and the impact of merging populations. *J. Fish Wildl. Manag.* 5, 3–13. doi: 10.3996/082013-jfwm-055

Hendry, A. P., Kinnison, M. T., Heino, M., Day, T., Smith, T. B., Fitt, G., et al. (2011). Evolutionary principles and their practical application. *Evol. Appl.* 4, 159–183. doi: 10.1111/j.1752-4571.2010.00165.x

Hess, G. (1996). Disease in metapopulation models: implications for conservation. *Ecology* 77, 1617–1632. doi: 10.2307/2265556

Hess, G. R. (1994). Conservation corridors and contagious disease: a cautionary note. *Conserv. Biol.* 8, 256–262. doi: 10.1046/j.1523-1739.1994.08010256.x

Hoban, S. (2018). Integrative conservation genetics: Prioritizing populations using climate predictions, adaptive potential and habitat connectivity. *Mol. Ecol. Resour.* 18, 14–17. doi: 10.1111/1755-0998.12752

Hoffmann, A. A., and Sgro, C. M. (2011). Climate change and evolutionary adaptation. *Nature* 470, 479–485.

Holderegger, R., Kamm, U., and Gugerli, F. (2006). Adaptive vs. neutral genetic diversity: implications for landscape genetics. *Landsc. Ecol.* 21, 797–807. doi: 10.1007/s10980-005-5245-9

Holl, S. A., Bleich, V. C., and Torres, S. G. (2004). Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967–2002. *Wildl. Soc. Bull.* 32, 412–426. doi: 10.2193/0091-7648(2004)32[412:pdobsi]2.0.co;2

Ikeda, D. H., Max, T. L., Allan, G. J., Lau, M. K., Shuster, S. M., and Whitham, T. G. (2017). Genetically informed ecological niche models improve climate change predictions. *Glob. Chang. Biol.* 23, 164–176. doi: 10.1111/gcb.13470

Jaeger, J. R., and Wehausen, J. D. (2012). *Development of a Habitat Management Plan to Maintain Viability of the Desert Bighorn Sheep Population in the River Mountains, Nevada: Analysis of Mitochondrial DNA Diversity and Connectivity. Final Report to the National Park Service*. Las Vegas, NV: University of Nevada.

Jahner, J. P., Matocq, M. D., Malaney, J. L., Cox, M., Wolff, P., Gritts, M. A., et al. (2019). The genetic legacy of 50 years of desert bighorn sheep translocations. *Evol. Appl.* 12, 198–213. doi: 10.1111/eva.12708

Janes, J. K., Miller, J. M., Dupuis, J. R., Malenfant, R. M., Gorrell, J. C., Cullingham, C. I., et al. (2017). The K = 2 conundrum. *Mol. Ecol.* 26, 3594–3602.

Johnson, K. A. (2014). *Climate Change Vulnerability Assessment for Natural Resources Management: Toolbox of Methods with Case Studies, version 2.0*. Arlington, VA: U.S. Fish and Wildlife Service.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24, 1403–1405. doi: 10.1093/bioinformatics/btn129

Jombart, T., Devillard, S., and Balloux, F. (2010). Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genet.* 11:94. doi: 10.1186/1471-2156-11-94

Kalinowski, S. T. (2011). The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulations and implications for human population structure. Heredity 106, 625–632. doi: 10.1038/hdy.2010.95

Leberg, P. L. (2002). Estimating allelic richness: effects of sample size and bottlenecks. *Mol. Ecol.* 11, 2445–2449. doi: 10.1046/j.1365-294x.2002.01612.x

Linløkken, A. N. (2018). "Genetic diversity in small populations," in *Genetic Diversity and Disease Susceptibility*, ed. Y. Liu (London: IntechOpen), 43–55.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., and Ackerly, D. D. (2009). The velocity of climate change. *Nature* 462, 1052–1055.

Longshore, K., and Thompson, D. B. (2013). Detecting short-term responses to weekend recreation activity: desert bighorn sheep avoidance of hiking trails. *Wildl. Soc. Bull.* 37, 698–706. doi: 10.1002/wsb.349

Longshore, K. M., Lowrey, C., and Thompson, D. B. (2009). Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. *J. Arid Environ.* 73, 280–286. doi: 10.1016/j.jaridenv.2008.09.021

Lowe, W. H., and Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Mol. Ecol.* 19, 3038–3051. doi: 10.1111/j.1365-294x.2010.04688.x

Malaney, J. L., Feldman, C. R., Cox, M., Wolff, P., Wehausen, J. D., and Matocq, M. D. (2015). Translocated to the fringe: genetic and niche variation in bighorn sheep of the Great Basin and northern Mojave deserts. *Divers. Distrib.* 21, 1063–1074. doi: 10.1111/ddi.12329

McRae, B. H., and Kavanagh, D. M. (2011). *Linkage Mapper*. Available online at: http://www.circuitscape.org/linkagemapper (accessed January 1, 2016).

Meirmans, P., and Hedrick, P. (2011). Assessing population structure: FST and related measures. *Mol. Ecol. Resour.* 11, 5–18. doi: 10.1111/j.1755-0998.2010.02927.x

Merilä, J., and Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.* 7, 1–14. doi: 10.1111/eva.12137

Miller, J. M., Malenfant, R. M., David, P., Davis, C. S., Poissant, J., Hogg, J. T., et al. (2014). Estimating genome-wide heterozygosity: effects of demographic history and marker type. *Heredity* 112, 240–247. doi: 10.1038/hdy.2013.99

Nickerson, B. S. (2014). *Effects of Genetic Drift, Natural Selection, and Population Connectivity on Adaptive-Linked Genetic Diversity of Desert Bighorn Sheep*. Master's thesis, Oregon State University, Corvallis, OR.

Nicotra, A. B., Beever, E. A., Robertson, A. L., Hofmann, G. E., and O'Leary, J. (2015). Assessing the components of adaptive capacity to improve conservation and management efforts under global change. *Conserv. Biol.* 29, 1268–1278. doi: 10.1111/cobi.12522

Pacifici, M., Foden, W., Visconti, P., Watson, J., Butchart, S., Kovacs, K., et al. (2015). Assessing species vulnerability to climate change. *Nat. Clim. Chang.* 5, 215–225.

Parmesan, C., and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. doi: 10.1038/nature01286

Pearson, R. G., Stanton, J. C., and Shoemaker, K. T. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim.* 4, 217–221. doi: 10.1038/nclimate2113

Perez, M. F., Franco, F. F., Bombonato, J. R., Bonatelli, I. A. S., Khan, G., Romeiro-Brito, M., et al. (2018). Assessing population structure in the face of isolation by distance: Are we neglecting the problem? *Divers. Distrib.* 24, 1883–1889. doi: 10.1111/ddi.12816

Petit, R. J., El Mousadik, A., and Pons, O. (2008). Identifying populations for conservation on the basis of genetic markers. *Conserv. Biol.* 12, 844–855. doi: 10.1111/j.1523-1739.1998.96489.x

Pierson, J. C., Coates, D. J., Oostermeijer, J. G. B., Beissinger, S. R., Bragg, J. G., Sunnucks, P., et al. (2016). Genetic factors in threatened species recovery plans on three continents. *Front. Ecol. Environ.* 14, 433–440. doi: 10.1002/fee.1323

Porfirio, L. L., Harris, R. M. B., Lefroy, E. C., Hugh, S., Gould, S. F., Lee, G., et al. (2014). Improving the use of species distribution models in conservation planning and management under climate change. *PLoS One* 9:e113749. doi: 10.1371/journal.pone.0113749

Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155, 945–959.

Prugh, L. R. (2009). An evaluation of patch connectivity measures. *Ecol. Appl.* 19, 1300–1310. doi: 10.1890/08-1524.1

Prunier, J., Laroche, J., Beaulieu, J., and Bosquet, J. (2011). Scanning the genome for gene SNPs related to climate adaptation and estimating selection at the molecular level in boreal black spruce. *Mol. Ecol.* 20, 1702–1716. doi: 10.1111/j.1365-294x.2011.05045.x

R Development Core Team (2017). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Razgour, O., Forester, B., Taggart, J. B., Bekaert, M., Juste, J., Ibáñez, C., et al. (2019). Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proc. Natl. Acad. Sci. U.S.A.* 116, 10418–10423. doi: 10.1073/pnas.1820663116

Razgour, O., Taggart, J. B., Manel, S., Juste, J., Ibáñez, C., Rebelo, H., et al. (2018). An integrated framework to identify wildlife populations under threat from climate change. *Mol. Ecol. Resour.* 18, 18–31. doi: 10.1111/1755-0998.12694

Reed, D. H., and Frankham, R. (2001). How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55, 1095–1103. doi: 10.1111/j.0014-3820.2001.tb00629.x

Reed, D. H., and Frankham, R. (2003). Correlation between fitness and genetic diversity. *Conserv. Biol.* 17, 230–237. doi: 10.1046/j.1523-1739.2003.01236.x

Renaud, L.-A., Pigeon, G., Festa-Bianchet, M., and Pelletier, F. (2019). Phenotypic plasticity in bighorn sheep reproductive phenology: from individual to population. *Behav. Ecol. Sociobiol.* 73:50.

Rominger, E. M., Whitlaw, H. A., Weybright, D. L., Dunn, W. C., and Ballard, W. B. (2004). The influence of mountain lion predation on bighorn sheep translocations. *J. Wildl. Manage.* 68, 993–999. doi: 10.2193/0022-541x(2004)068[0993:tiomlp]2.0.co;2

Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145, 1219–1228.

Sappington, J. M., Longshore, K. M., and Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* 71, 1419–1426. doi: 10.2193/2005-723

Schwalm, D., Epps, C. W., Rodhouse, T. J., Monahan, W. B., Castillo, J. A., Ray, C., et al. (2016). Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. *Glob. Chang. Biol.* 22, 1572–1584. doi: 10.1111/gcb.13189

Sexton, J. P., Strauss, S. Y., and Rice, K. J. (2011). Gene flow increases fitness at the warm edge of a species' range. *Proc. Natl. Acad. Sci. U.S.A.* 108, 11704–11709. doi: 10.1073/pnas.1100404108

Sgro, C. M., Lowe, A. J., and Hoffmann, A. A. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* 4, 326–337. doi: 10.1111/j.1752-4571.2010.00157.x

Simberloff, D., and Cox, J. (1987). Consequences and costs of conservation corridors. *Conserv. Biol.* 1, 63–71. doi: 10.1111/j.1523-1739.1987.tb00010.x

Singer, F. J., and Gudorf, M. A. (1999). *Restoration of Bighorn Sheep Metapopulations in and Near 15 National Parks: Conservation of a Severely Fragmented Species. Volume I: Planning, Problem Definition, Key Findings, and Restoration*. Fort Collins, CO: U.S. Geological Survey.

Smith, A. B., Beever, E. A., Kessler, A. E., Johnston, A. N., Ray, C., Epps, C. W., et al. (2019). Alternatives to genetic affinity as a context for within-species response to climate. *Nat. Clim. Chang.* 9, 787–794.

Smith, C. T., Adams, B., Bartron, M., Burnham-Curtis, M. K., Monroe, E., Olsen, J. B., et al. (2016). Comment on Haig et al. (2016): the conservation genetics juggling act: integrating genetics and ecology, science and policy. *Evol. Appl.* 9, 635–637. doi: 10.1111/eva.12374

Staudinger, M., Morelli, T., and Bryan, A. (2015). *Integrating Climate Change into Northeast and Midwest State Wildlife Action Plans*. Amherst, MA: Northeast Climate Science Center.

Summers, D. M., Bryan, B. A., Crossman, N. D., and Meyer, W. S. (2012). Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Glob. Chang. Biol.* 18, 2335–2348. doi: 10.1111/j.1365-2486.2012.02700.x

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., et al. (2004). Extinction risk from climate change. *Nature* 427, 145–148.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science* 348, 571–573. doi: 10.1126/science.aaa4984

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., et al. (2016). Improving the forecast for biodiversity under climate change. *Science* 353:aad8466.

Utah Division of Wildlife Resources (2013). *Utah Bighorn Sheep Statewide Management Plan*. Salt Lake City, UT: Utah Department of Natural Resources.

van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al. (2011). The representative concentration pathways: an overview. *Clim. Change* 109, 5–31. doi: 10.1007/s10584-011-0148-z

Weeks, A. R., Sgro, C. M., Young, A. G., Frankham, R., Mitchell, N. J., Miller, K. A., et al. (2011). Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evol. Appl.* 4, 709–725. doi: 10.1111/j.1752-4571.2011.00192.x

Wehausen, J. D. (1996). Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. *Wildl. Soc. Bull.* 24, 471–479.

Wehausen, J. D., Bleich, V. C., Blong, B., and Russi, T. L. (1987). Recruitment dynamics in a Southern California mountain sheep population. *J. Wildl. Manage.* 51, 86–98.

Wehausen, J. D., Kelley, S. T., and Ramey, R. R. (2011). Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. *Calif. Fish Game* 97, 7–24.

Wehausen, J. D., and Ramey, R. R. (2000). Cranial morphometric and evolutionary relationships in the northern range of *Ovis canadensis*. *J. Mammal.* 81, 145–161. doi: 10.1093/jmammal/81.1.145

Wehausen, J. D., Ramey, R. R., and Epps, C. W. (2004). Experiments in DNA extraction and PCR amplification from bighorn sheep feces: the importance of DNA extraction method. *J. Hered.* 95, 503–509. doi: 10.1093/jhered/esh068

Weir, B. S., and Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* 38, 1358–1370. doi: 10.1111/j.1558-5646.1984.tb05657.x

Whittaker, D. G., Ostermann, S. D., and Boyce, W. M. (2004). Genetic variability of reintroduced California bighorn sheep in Oregon. *J. Wildl. Manage.* 68, 850–859. doi: 10.2193/0022-541x(2004)068[0850:gvorcb]2.0.co;2

Wiedmann, B. P., and Bleich, V. C. (2014). Demographic responses of bighorn sheep to recreational activities: a trial of a trail. *Wildl. Soc. Bull.* 38, 773–782. doi: 10.1002/wsb.463

Wiedmann, B. P., and Sargeant, G. A. (2014). Ecotypic variation in recruitment of reintroduced bighorn sheep: implications for translocation. *J. Wildl. Manage.* 78, 394–401. doi: 10.1002/jwmg.669

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., and Snyder, M. A. (2009). Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. U.S.A.* 106, 19729–19736. doi: 10.1073/pnas.0901639106

Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biol.* 14:e2001104. doi: 10.1371/journal.pbio.2001104

Wild Sheep Working Group (2015). *Records of Wild Sheep Translocations - United States and Canada, 1922-Present*. Available online at: https://www.wafwa.org/DocumentsandSettings/37/SiteDocuments/WorkingGroups/WildSheep/Publications/RecordsofWildSheepTranslocations-United~StatesandCanada,1922-Present-Reduced.pdf (accessed January 1, 2016).

Williams, A. P., Allen, C. D., Millar, C. I., Swetnam, T. W., Michaelsen, J., Still, C. J., et al. (2010). Forest responses to increasing aridity and warmth in the southwestern United States. *Proc. Natl. Acad. Sci. U.S.A.* 107, 21289–21294. doi: 10.1073/pnas.0914211107

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., and Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* 6:e325. doi: 10.1371/journal.pbio.0060325

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 16 September 2020
doi: 10.3389/fevo.2020.521767

Capital-Income Breeding in Male Ungulates: Causes and Consequences of Strategy Differences Among Species

Marco Apollonio[1†], Enrico Merli[2†], Roberta Chirichella[1], Boštjan Pokorny[3,4*], Ajša Alagić[4], Katarina Flajšman[4] and Philip A. Stephens[5]

[1] Department of Veterinary Medicine, University of Sassari, Sassari, Italy, [2] Agriculture and Wildlife Service, Piacenza, Italy, [3] Environmental Protection College, Velenje, Slovenia, [4] Slovenian Forestry Institute, Ljubljana, Slovenia, [5] Department of Biosciences, Durham University, Durham, United Kingdom

OPEN ACCESS

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Lin Zhang,
Hangzhou Normal University, China
Petter Kjellander,
Swedish University of Agricultural
Sciences, Sweden

***Correspondence:**
Boštjan Pokorny
bostjan.pokorny@vsvo.si;
bostjan.pokorny@gmail.com

†These authors have contributed
equally to this work

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 19 December 2019
Accepted: 26 August 2020
Published: 16 September 2020

Citation:
Apollonio M, Merli E, Chirichella R,
Pokorny B, Alagić A, Flajšman K and
Stephens PA (2020) Capital-Income
Breeding in Male Ungulates: Causes
and Consequences of Strategy
Differences Among Species.
Front. Ecol. Evol. 8:521767.
doi: 10.3389/fevo.2020.521767

The capital and income breeding concept links energy resources used during reproduction to the timing of their acquisition. During reproduction, capital breeders rely on resources gained previously and accumulated for reproductive investment. By contrast, income breeders use mainly resources collected during the period of reproductive activity. Most commonly, this concept is applied to females; relatively few studies have considered males. Moreover, there has been little attention to the link between the capital-income divide and other aspects of mating strategy. We studied adult males of three wild ungulates with different levels of polygyny. A large dataset (4,264 red deer, 53,619 roe deer, and 13,537 Alpine chamois, respectively) was obtained during 2007–2017 in the whole territory of Slovenia and in the Trento province, Italy. During the rut, body mass loss of males in highly polygynous species was more than twice that of weakly polygynous species: on average, red deer stags lost 19.5%; chamois bucks 16.0%; and roe deer bucks 7.5% of their body mass. This indicates potential for a hitherto unrecognized link between the degree of intrasexual competition and the degree of capital mating. The variability in body mass at the end of the rut was clearly reduced in both highly polygynous species (from 15.1 to 9.4% in red deer, and from 12.5 to 10.5% in chamois), but did not change in roe deer. Finally, roe deer bucks had recovered body mass to that of the pre-rut period by just 2 months after the rut, while red deer stags did not manage to compensate the loss of weight until the end of the year. We suggest that, at least in ungulates, there is a link between the degree of polygyny and that of capital breeding. Males of capital and income breeders underwent body mass changes resulting from different reproductive investment during the rut. Capital breeders lost considerably more weight, and invested a variable amount of energy among individuals or among years, possibly to cope with different environmental or body conditions. In so doing, they ended the rut with poorer but more even condition among individuals.

Keywords: capital-income breeding, male reproductive investment, *Capreolus capreolus*, *Cervus elaphus*, *Rupicapra rupicapra*

INTRODUCTION

Capital and income breeding concepts were developed to help differentiate broad strategies for "financing" the costs of reproduction in animal species: "capital breeding" describes the situation in which reproduction is financed using stored capital; by contrast, "income breeding" refers to the use of concurrent intake to pay for a reproductive attempt (Drent and Daan, 1980; Jönsson, 1997). Recently, these strategies have been recognized to lie toward either end of a continuum of capital-to-income approaches to reproduction, and that placement along that continuum can vary among age classes of the same sex (Houston et al., 2007; Jaatinen et al., 2016; Williams et al., 2017).

Initially, most of the effort to understand both capital and income breeding and the differences between them was devoted to studying females at different phases of breeding from conception to egg laying, incubation and offspring-rearing in birds, and from conception to embryonic development, birth and lactation in mammals (Drent and Daan, 1980; Andersen et al., 2000; Boyd, 2000; Connan et al., 2019). Far fewer studies, however, considered males (but see Soulsbury, 2019), for which the contribution to reproduction is usually lower than for females. Despite this, reproduction may be demanding for males of some species, especially those – like ungulates – characterized by high polygyny (Mysterud et al., 2004). In male ungulates, which show no parental care, the relevant time period of reproductive investment is obviously the rut, because once conception is ensured, males have no further involvement in reproduction. In this context, the obvious metric to estimate the investment of rutting males is their loss of weight during the rut (Mysterud et al., 2005).

In ungulates, adult males show the highest loss of body mass during the rut, whereas younger males that have yet to reach social maturity show more limited loss, if any (for Alpine chamois *Rupicapra rupicapra*: Mason et al., 2011; for moose *Alces alces*: Mysterud et al., 2005; for American bison *Bison bison*: Komers et al., 1994; for red deer *Cervus elaphus*: Bobek et al., 1990; Milner et al., 2002; Yoccoz et al., 2002; for fallow deer *Dama dama*: McElligott et al., 2003; for reindeer *Rangifer tarandus*: Kojola, 1991; Mysterud et al., 2003). Moreover, adult males are the age class in which hypophagia is more evident (in moose: Miquelle, 1990; fallow deer: Apollonio and Di Vittorio, 2004; reindeer: Barboza et al., 2004; Alpine ibex: Brivio et al., 2010; American bison: Bergman et al., 2001; bighorn sheep *Ovis canadensis*: Pelletier et al., 2005; Alpine chamois: Willisch and Ingold, 2007).

The hypothesis that gradation from income to capital breeding, reflecting the importance of foraging strategies for reproduction in adults, has gained acceptance. Moreover, the degree of capital (vs. income) breeding is correlated with various ecological, morphological, and physiological traits (Stephens et al., 2009 for review). As yet, however, mating systems – and, more specifically, the degree of polygyny associated with different systems – have not been recognized as potential drivers of the adoption of capital or income breeding strategies. This is the case, despite the likelihood that mating systems could play a strong role, especially for males in systems with a defined breeding period and no paternal care. Socially adult males are ideal candidates for testing this hypothesis, because they are fully involved in bearing the costs of reproduction during rut (Mysterud et al., 2004).

In mammalian polygynous mating systems, male mating success is strongly linked to the level of monopolization of females and is related to the amount of energy devoted to intra-male competition (Clutton-Brock, 1989). In those systems, the major cost of reproduction for males must be associated with mating and the acquisition of mates. Moreover, given that high polygyny is associated with high competition, the intensity of competition is likely to favor the suppression of feeding (i.e., capital breeding) in highly polygynous males. By contrast, if there is low polygyny and low competition, males can continue to feed (i.e., income breeding). Alternatively, the low potential gains in systems characterized by low levels of polygyny will reduce the incentive to cease eating (and vice versa for high polygyny).

Our reasoning suggests that the degree of polygyny associated with different mating systems could be a powerful predictor of the adoption of either capital or income breeding. To test such hypotheses, a group of species that vary in their degree of polygyny, and for which reproductive investment can be determined whilst accounting for competing predictors of apparent investment must be identified. European ungulates present a useful opportunity for this analysis, exhibiting wide variability in polygyny with, as a result of the climatic range across which they occur, the simultaneous opportunity to compare effects of the environment on patterns of mass gain and loss.

Different levels of polygyny are shown by different standardized variances in male lifetime reproductive success or by different degrees of sexual dimorphism. At present, reliable data on variance in male lifetime reproductive success in mammals are limited (in red deer: Pemberton et al., 1992; Marshall et al., 1998; in bighorn sheep: Coltman et al., 2002; in Soay sheep *Ovis aries*: Coltman et al., 1999; in roe deer *Capreolus capreolus*: Vanpé et al., 2009). Degree of polygyny also can be shown by a relationship with sexual size dimorphism (SSD), especially in those polygynous species in which fighting between males involves wrestling or ramming. This outcome occurs because species with high SSD tend to have highly polygynous mating systems (for a review, see Alexander et al., 1979; and for ungulates, see: Loison et al., 1999; Vanpé et al., 2008). Associations between the degree of capital breeding and the phenotypic difference between males and females (i.e., secondary sex characteristics, body size, physical strength and morphology, ornamentation, and other bodily traits) can therefore be evaluated.

We analyzed a substantial sample of >65,000 individual males, belonging to three common European ungulate species: red deer, roe deer, and Alpine chamois. Males of those species differ in size, with undressed body weights (mean ± ES) of adult males from our sample of 163.0 ± 1.5 kg for red deer, 27.2 ± 0.1 kg for Alpine chamois, and 18.7 ± 0.03 kg for roe deer. More importantly for our study, clear differences exist in the mating systems adopted by the three species. Specifically, in the social red deer and Alpine chamois, males monopolize access to female groups, whilst in the more solitary roe deer, males guard only one female at any time.

Red deer adopt a mating system in which a harem or territory-holding male monopolizes from 1 to 22 females (mean 3.6 per day) (Clutton-Brock et al., 1982) and territorial males up to a mean of 2.8 females per day (Carranza et al., 1990). In Alpine chamois, territorial and non-territorial males vie to monopolize groups of three to five females per hour during the rut (Corlatti et al., 2013b; Chirichella et al., unpublished). In contrast, roe deer bucks are long-term territory holders, but females are solitary, so territorial males have access only to one female at any time, i.e., only to the females either present in their territory (Kurt, 1991; Lieberg et al., 1998) or females that visit them during reproductive excursions (Debeffe et al., 2014).

Our objectives were as follows: (i) to test if species with a higher degree of polygyny are characterized by a capital breeding strategy, whilst the less polygynous roe deer is an income breeder; (ii) to evaluate the seasonal dynamics of weight loss in males of all three studied species, examining variance of body mass before and after the rut; and (iii) to assess the roles of location and year of sampling in determining variation in apparent investment among adult males.

MATERIALS AND METHODS

Study Areas and Sampling

Data were collected in Italy, in the Central-Eastern Italian Alps, across a 6,207 km^2 area in the Trento province (46°04'N, 11°07'E), and throughout Slovenia, across a 20,273 km^2 area (46°03'N, 14°30'E). All individuals used in the study were legally hunted during the regular hunting activity prescribed by the state of Slovenia and Italy within yearly hunting-management plans. We used only data on dead individuals; therefore, no animal was shot or killed by any other means for the purposes of the research.

Slovenia is located in the transition zone between four macrogeographical units (Sub-Mediterranean, Alpine and Pre-Alpine, Karst-Dinaric, Pre-Pannonian), therefore it has a mixture of temperate continental, mountain (moderate Alpine), and Sub-Mediterranean climates (Ogrin, 1996; Perko, 1998; Lovenčak, 1999). Considering presence-abundance and ecological differentiation among populations of studied species (for red deer: Hafner, 2008; roe deer: Flajšman, 2017; chamois: Bužan et al., 2013) we located each individual in one of those macrogeographical units. In the Sub-Mediterranean region, vegetation is dominated by deciduous tree and shrub species. Mean temperature of the coldest month (mean January temperature) is above 0°C, and mean temperature of the warmest month (mean July temperature) is above 20°C. Mean annual precipitation is between 1,000 and 1,700 mm. The Alpine and Pre-Alpine region covers high mountains, lower hills and plains. Up to the tree line, there is mostly mixed forest. Mean temperature of the coldest month is below -3°C, whereas mean temperature of the warmest month depends on the altitude: in lower altitudes, it is above 10°C, and in higher altitudes [>1,500 m above sea level (asl)] below 10°C. Mean annual precipitation is between 1,100 and 3,000 mm. The Karst-Dinaric region consists of Dinaric plateaus and valley systems and is mainly covered by large complexes of beach-fir forest. The Pre-Pannonian region covers hilly and lowland area that extends toward the Pannonian plain. This region is mostly covered with cultivated land and broadleaf forests. In both Karst-Dinaric and Pre-Pannonian regions, there is a continental climate. Mean temperature of the coldest month is between 0 and -3°C, and the mean temperature of the warmest month is between 15 and 20°C. Mean annual precipitation in the Karst-Dinaric region is between 1,300 and 2,800 mm, and in the Pre-Pannonian region between 800 and 1,000 mm.

Variability in the climate of Trento province is similar, because of its geographical position and rich variety of landscapes. The climate in this area can be defined as a transition between the semi-continental and the Alpine climate. Temperature and rain are influenced by the Mediterranean climate in the southern part, while the northern part has a more continental climate. Average winter temperatures are between -5 and -10°C in January, and average summer temperatures are 20–25°C or more. Average annual rainfall is 815 mm. Nonetheless, rainfall varies according to the altitude and exposition of the relief. In general, the greatest rainfall falls on the highest peaks and in the southern and western sectors, where the western and southern winds that accompany the passage of the Atlantic disturbances bring humidity: here, rainfall amounts to 1,200–1,400 mm/year. The peaks of rainfall generally occur during autumn and spring whereas in winter, snowfall prevails. A large part of the Trento province is at relatively high average altitude (about 77% above 1,000 m asl; slightly <20% above 2,000 m asl); snow cover has an extremely irregular pattern (with some very snowy and other very dry years), and has exhibited a decrease in snow depth from the late 1980s. This decrease is more evident in the pre-Alpine areas and can have high variation based on the exposure (data from Forecasts and Organization Office – Civil Protection Infrastructures Department of the Trento province)[1].

Around 58% of Slovenia is covered by forest (1.2 million ha), and its elevation ranges from sea level to 2,864 m asl. Slovenia is divided into 15 hunting management districts (HMD), subdivided into 411 hunting grounds managed by hunting clubs, and 12 hunting grounds with special purposes managed by the public organizations (i.e., Slovenia Forest Service, State Protocol, and the Triglav National Park). Roe deer are abundant throughout Slovenia, while abundances of red deer and Alpine chamois in Sub-Mediterranean are too low to be included in the analyses (**Table 1**).

Trento province has an elevation that ranges from 52 to 3,558 m asl, with about 77% of the province over 1,000 m asl. The province is forested up to treeline at about 2,000 m, above which it consists of Alpine meadows, rocky outcrops, scree fields, and open rock faces. Alpine chamois hunting is subdivided between 28 hunting districts, which are further subdivided into 209 municipal reserves (hunting management units).

Italy: Alpine Chamois Dataset

In Italy, chamois are culled with rifles from mid-September to mid-December. This time period encompasses a pre-rut period as well as the entire rut (Mason et al., 2011). Hunting

---

[1] www.meteotrentino.it

TABLE 1 | Sample size (n) subdivided by species and area.

Species	Area					
	Alpine and Pre-Alpine (SI)	Karst–Dinaric (SI)	Pre-Pannonian (SI)	Sub-Mediterranean (SI)	Trentino (IT)	Total
Roe deer	16,584	14,726	18,940	3,369	–	53,619
Red deer	1,031	2,931	302	–	–	4,264
Chamois males	1,841	445	105	–	4,831	7,222
Chamois females	–	–	–	–	6,315	6,315

is controlled through licenses issued by local wildlife boards. Area-wide hunting quotas are set for specific age classes in each sex. Data were collected on the undressed body mass (i.e., weighed without viscera and flowing blood), sex, age, and the harvesting date of 27,629 Alpine chamois (14,769 males and 12,860 females) harvested over 10 consecutive hunting seasons between 2007 and 2016. Age was estimated by counting horn growth annuli (Schröder and Von Elsner-Schak, 1985). Male age varied between 1 and 20 years, and female age between 1 and 21 years, respectively.

Slovenia: Roe Deer, Red Deer, and Chamois Datasets

In Slovenia, the roe deer rut starts around mid-July and finishes around mid-August. Male roe deer rifle hunting encompasses that period, extending from the beginning of May to the end of October. Data were collected on the undressed body mass, age category (yearlings, adults) and the harvesting date of all roe deer males culled throughout Slovenia over 11 consecutive hunting seasons between 2007 and 2017. Determination of age category of roe deer bucks was made by local hunting authorities using macroscopic inspection of dentition development of premolars and molars in the left hemimandibles accompanying each individual, which is a routine method enabling yearlings and adults to be distinguished reliably (Ratcliffe and Mayle, 1992; Pokorny and Jelenko Turinek, 2017). Because of uncertainty in age assessment of adult roe deer by macroscopic inspection of tooth wear (Hewison et al., 1999) all adults were pooled into one group.

Red deer stags were harvested with rifles from mid-August till the end of December. The rut typically starts in the mid-September and lasts for less than 1 month. Data were collected on the undressed body mass, age category (yearlings, 2–4-years, 5–9-years, and 10+ years old), and the harvesting date of all red deer stags shot over 11 consecutive hunting seasons between 2007 and 2017. Age category of red deer stags was estimated post-mortem on the basis of tooth wear of the left hemimandibles evaluated by experienced and authorized wildlife managers.

Chamois sample set included all adult males harvested in the same study period (2007–2017); also for this species, data on undressed body mass, age (assessed by counting horn grown annuli), and date of harvest were available in the Central Slovene hunting information system.

Data Analysis

Data collected from hunting-management districts were grouped with respect to main area (population) and year. We focused only on age classes of males that had reached social maturity and were fully involved in the rut. Threshold ages for social maturity, i.e., the age at which males are not only sexually mature but also able to sustain intersexual competition having reached full body development, were based on published data on rutting activities and hypophagia of male age classes (Mysterud et al., 2005). For roe deer, senescent individuals (assessed age >10 years) were discarded (Hewison et al., 2011). Male age classes, considered in our paper, were as follows: roe deer: 3–10 years old (Vanpé et al., 2008; Hewison et al., 2011); red deer ≥ 5 years old (Clutton-Brock, 1984; Mysterud et al., 2008); and chamois ≥ 5 years old (von Hardenberg et al., 2000; Corlatti et al., 2012). The final sample set considered for the analysis consisted of 71,420 ungulates (6,315 of which were chamois females, analyzed with the aim to remove seasonal effect of body-mass decline in this species), subdivided by areas provided in **Table 1**.

To determine reproductive investment, we quantified the reduction of body mass of males from the beginning to the end of the rut as a measure of the cost of reproduction. To compare body mass loss among different species and among populations of the same species, we standardized the protocol as follows: (i) a time series was created by computing the average (undressed) body mass of each consecutive day of the year; (ii) an intervention analysis (Box and Tiao, 1975) identified break points in the series, defining the beginning of the decline in body mass, which indicates the beginning of the rut; (iii) in each population, each animal's weight was standardized as a percentage of the body mass observed at the beginning of the rut; (iv) populations with standardized body masses were grouped by synchronizing the beginning of the rut (aligning the time series to the onset of rut as a common start point). Note that the analysis in step (ii) comprises a group of techniques that aims to find changes in time series data, including changes in the overall trend or in the amplitude after an event occurred (intervention). In time series, data are often autocorrelated and there may be seasonality and high variability around the mean, confounding efforts to recognize changes in patterns. To take into account these properties, ARIMA models iteratively evaluate the likelihood of alternative models with different dates of changes of time series properties, finally finding the model that best explains the patterns.

All computations were conducted in the R system for statistical computing (R Development Core Team, 2019 – version 3.6.0). Intervention analysis was performed with package strucchange 1.5–1, that uses the Bayesian Information Criterion to select the best number of breakpoints in a time series (Zeileis et al., 2002).

Start and end dates of body-mass decline were slightly different among populations of the same species. Thus, population time series were aligned to the beginning of the rut (assumed, for our purposes, to be identified by the beginning of body mass decline) by using the mean value among populations, to preserve as much as possible of each time series (and of the aggregated series).

To facilitate comparisons across populations, body-mass values also were standardized. New values were represented by percentages of the average value of the body mass in the 15 days before the beginning of the rut. In this way, the initial standardized body mass for all populations was equal to 100, and body mass on a given day was expressed as a percentage of that initial value.

Standardized body masses and Julian dates enabled us to group all data for each species, creating a unified time series on which a further intervention analysis was used to identify the end point of body-mass declines. An index of the loss of body mass resulting from reproduction was estimated as the difference between 100 (initial standardized body mass) and average standardized body mass of individuals 15 days after the end of the weight decline. To describe the pattern of body mass after reproduction, for roe deer and red deer (chamois data were lacking) the same computation was made 1 and 2 months after the end of the rut.

Because the chamois rut takes place in the second half of autumn and a decline in body mass is observed in females resulting from seasonal rather than reproductive factors, we also estimated body-mass changes of adult females (for this species only). Body mass decline observed in chamois females was then subtracted from that of males, to consider only the reproductive component of body mass variation in males.

Environmental variability is important in shaping life-history traits in ungulates (Gaillard et al., 2003). Consequently, we estimated for each species the variance in body mass loss because of sample differences in areas and years. We estimated variability of body-mass loss in each area and year by resampling 1,000 times (R package “boot” 1.3–23 – Davison and Hinkley, 1997; Canty and Ripley, 2019) the initial and final sample of body mass measurements. To evaluate relative importance of area and year in shaping loss of body mass, we built afterward for each species three Generalized Linear Models. Two models included as fixed factors either area or year as single independent predictors, and the third one included both predictors. Model-selection used AIC and AIC weights (Burnham and Anderson, 2002). Finally, we preformed variance components analysis using the VCA package (version 1.4.0 – Searle et al., 1992; Schuetzenmeister and Dufey, 2019) that allows unbalanced designs in computing the variance of variance components.

RESULTS

In the best time series model determined by intervention analysis, the trend in roe deer standardized body mass exhibited three break points (**Figure 1**). The first identified the beginning of the decline, on days 194–195 of the combined Julian date (13–14 July). At that time, observed mean body mass was 18.69 kg (*SE* = 0.029; *n* = 6,100). The second break-point corresponded to a steady change in the steepness of the decline on days 228–229 (16–17 August), when the observed mean body mass was 17.24 kg (*SE* = 0.030; *n* = 4,584). The third

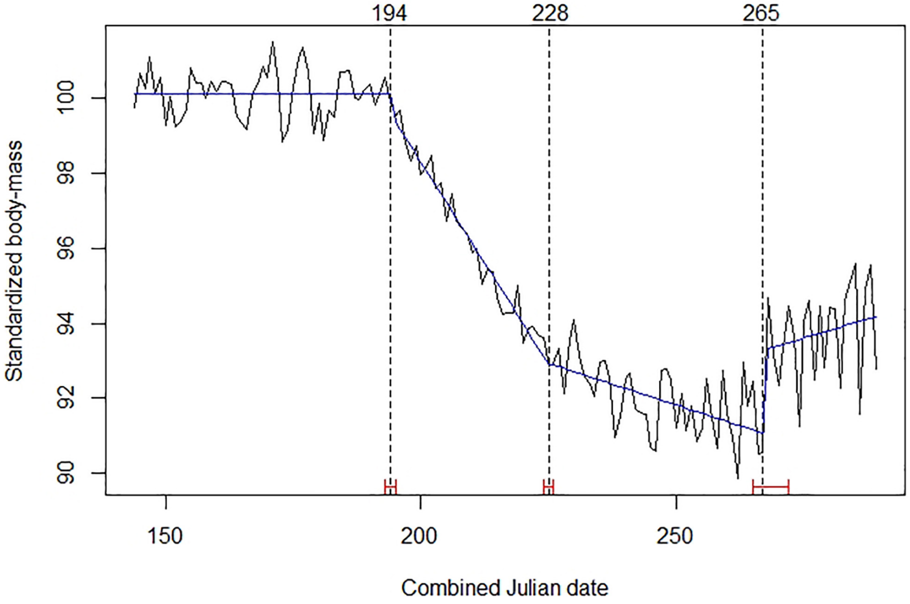

FIGURE 1 | Mean daily standardized body mass of roe deer (black broken line), trends (blue line), Julian date of estimated structural changes (dashed lines, labeled at the top), and 95% confidence intervals of estimated structural change date (red bars). **Table 1** provides details about sample size and origin of data.

break-point, on days 265–266 (24–25 September), indicated the start of a period of fat gain, possibly related to storage and preparation for winter.

A model with two break points provided the best explanation for the body mass time series of red deer (**Figure 2**). The first break point was on days 245–246 (2–3 September), when the trend became strongly negative. Red deer observed mean body mass at that first breakpoint was 163.0 kg (*SE* = 1.531; *n* = 293). The second break was on days 272–273 (29–30 September), when decline in body mass significantly reduced its steepness; mean body mass at that second breakpoint was 131.1 kg (*SE* = 0.756; *n* = 475).

The best-fitting model of the time series for chamois body mass involved three break-points (**Figure 3**). Those of interest, because of their role in defining the end of the rut, were the last two points. The second was set on days 297–298 (24–25 October), at the start of a strong decline in body mass that was initially observed equal to 28.39 kg (*SE* = 0.131; *n* = 758) on average. The third break point was on days 343–344 (9–10 December), when the decline significantly reduced and chamois mean observed body mass was 21.36 kg (*SE* = 0.157; *n* = 366). Comparing time series of body mass for male and female chamois allowed us to estimate the seasonal reduction of body mass of 1.6 kg after the end of October also in females, corresponding to 7.5% of their standardized body mass (**Figure 4**). This weight loss was not considered as a reproductive cost for males; consequently, we excluded this percentage of body mass loss from calculations for males.

The decline in standardized body mass at the beginning and the end of the rut exhibited pronounced differences among the three species of ungulates. Decreases in body mass were the highest in red deer (19.5%), and the lowest in roe deer (7.5%). In roe deer, the body mass decrease was, on average, less than one-half that of chamois (16.0%) (**Table 2**). Body mass of red deer continued to decline 2 months after the rut (additional 3.4% of reduction). By contrast, 2 months after the rut, roe deer average body mass had increased by 2.4%.

Red deer showed the greatest differences in body-mass variability between the beginning and the end of the rut, while roe deer showed the smallest ones (**Table 2**). In red deer, body mass dispersion around the mean value was larger at the beginning of the rut than at the end. In chamois, the observed pattern was similar to red deer although differences were smaller. In roe deer, body mass variability was similar before and after the rut.

For the three species, area and year differed in their importance for explaining changes in proportional mass loss (**Table 3**). In roe deer, variability in body mass loss was mainly because of spatial differences, with differences between years explaining little of the variation in mass loss. Although slight effects of area and year were evident for both red deer and chamois, these were overwhelmed by residual variance for both species.

DISCUSSION

The ecological and evolutionary drivers of the placement of a species on the capital-income breeding continuum have been the focus of considerable interest (Jönsson, 1997; Bonnet et al., 1998; Stephens et al., 2009). In this context, explanations have tended to focus on three broad classes of drivers: aspects of food supply, morphological or physiological constraints, and habitat characteristics (Stephens et al., 2009). Here, by contrast, we argue that a behavioral factor might favor the adoption of a particular capital or income breeding strategy. Specifically, we argue that high levels of male-male competition, resulting from high degrees of polygyny, are likely to favor a strong focus on competitive interactions during the mating period, with a consequent reduction in foraging. This pattern, in turn, indicates that high levels of polygyny will necessitate a heavy

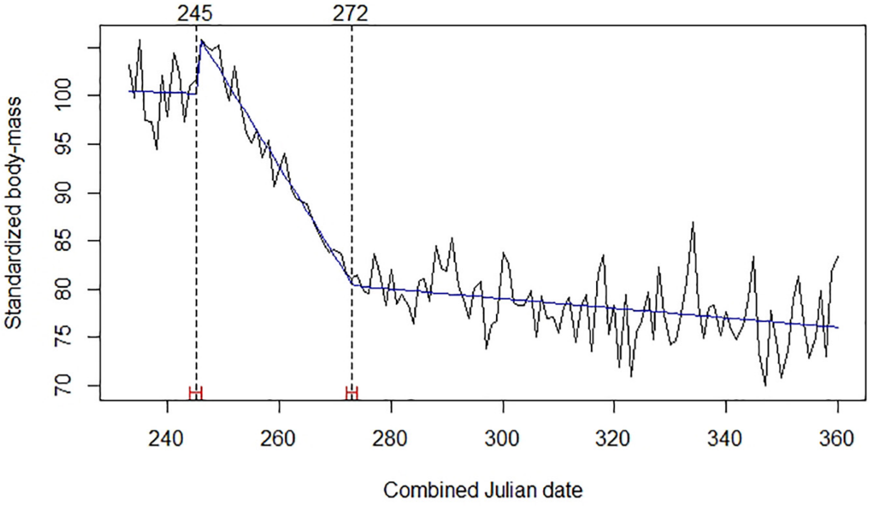

FIGURE 2 | Mean daily standardized body mass of red deer (black broken line), trends (blue line), Julian date of estimated structural changes (dashed lines, labeled at the top), and 95% confidence intervals of estimated structural change date (red bars). **Table 1** provides details about sample size and origin of data.

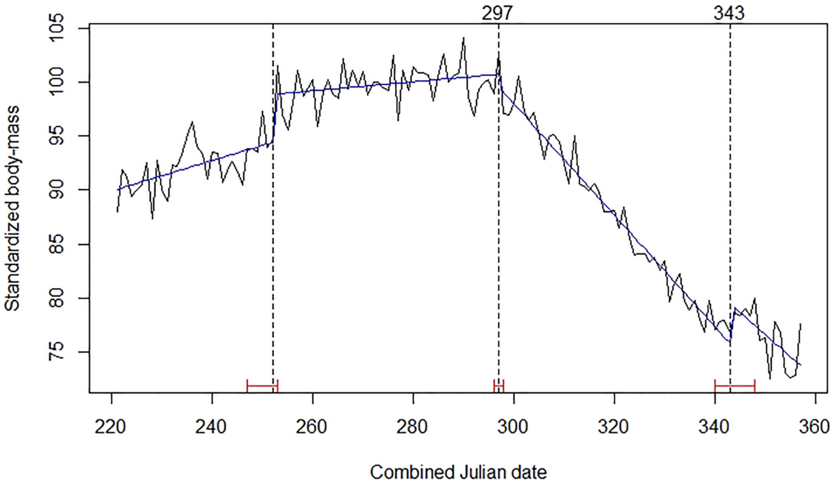

FIGURE 3 | Mean daily standardized body mass of Alpine chamois (black broken line), trends (blue line), Julian date of estimated structural changes (dashed lines, labeled at the top), and 95% confidence intervals of estimated structural change date (red bars). **Table 1** provides details about sample size and origin of data.

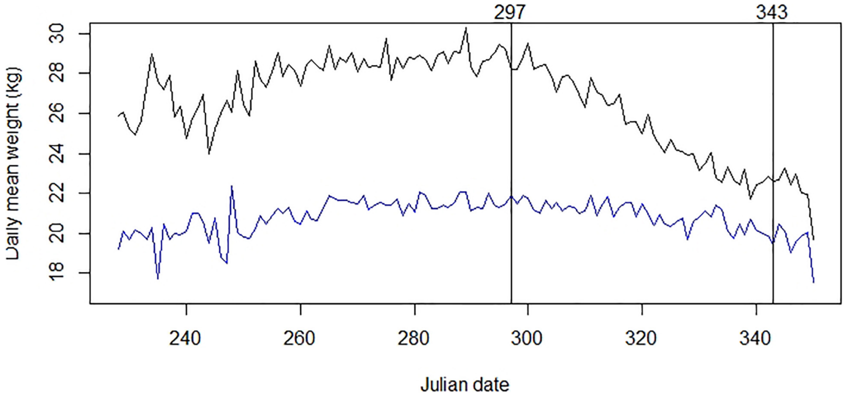

FIGURE 4 | Males (black) and females (blue) chamois average daily body mass and rut period (defined by the two labeled black lines). **Table 1** provides details about sample size and origin of data.

TABLE 2 | Changes (%) in standardized body mass of social mature male in three ungulate species.

Species	Changes in standardized body mass (%)			Body mass SD	
	Decline during the rut*	A month after the end of the rut	2 months after the end of the rut	Pre-rut	Post-rut
Roe deer	7.5	−0.5	+2.4	12.063	11.183
Red deer	19.5	−2.4	−3.4	15.150	9.416
Alpine chamois	16.0*	*n.a.*	*n.a.*	12.486	10.541

*Table 1 provides details about sample size and origin of data. *Values for chamois males were corrected for seasonal effect as determined by body mass changes in adult females.*

reliance on stored capital during the mating period. High levels of polygyny in our species also correspond to different group sizes during the mating season: red deer and Alpine chamois adult males can have access to groups of females, as females of these species, in particular, are social; by contrast, roe deer adult males can have access only to solitary females at any time, and inside their territory only. Our very large dataset of carcass weights of three common and widespread ungulate species, obtained from two European countries, is consistent with our hypothesis: male roe deer, a species exhibiting low levels of polygyny and therefore limited variance in lifetime reproductive success (Vanpé et al., 2008), lose a relatively small proportion of body mass during the rut, indicating a low reliance on stored energetic capital during that period; by contrast, male red deer and Alpine chamois, both of which are known to have either high levels of polygyny (red deer) or at least high male-male competition (both species) (Kramer, 1969; Clutton-Brock, 1984; Pemberton et al., 1992; Marshall et al., 1998; Garel et al., 2009;

TABLE 3 | GLM models of body mass loss ranking and evaluation and variance components analysis.

Species	GLM model	P	AIC	Δ AIC	AIC weight	Variance factor	VC	% (SD)
Roe deer	Area + year	<0.001	172,963	–	1.000			
	Area	<0.001	176,170	3,207	0.000	Area	5.464	62.84 (2.337)
	Year	<0.001	211,009	38,046	0.000	Year	0.249	2.86 (0.499)
						Error	2.982	34.30 (1.727)
						Total	8.695	100.00
Red deer	Area + year	<0.001	169,110	–	1.000			
	Year	<0.001	169,694	584	0.000	Year	6.171	13.19 (2.484)
	Area	<0.001	172,333	3,223	0.000	Area	1.542	3.29 (1.242)
						Error	39.077	83.52 (6.251)
						Total	46.790	100.00
Alpine chamois	Area + year	<0.001	227,143	–	1.000			
	Area	<0.001	230,000	2,857	0.000	Area	22.218	26.29 (4.714)
	Year	<0.001	234,754	7,611	0.000	Year	5.204	6.16 (2.281)
						Error	57.098	67.55 (7.556)
						Total	84.520	100.00

P, probability Chi-sq value. VC, single observation variance component; %, percentage of variability (SD) imputed to the factor. ***Table 1*** *provides details about sample size and origin of data.*

Rughetti and Festa-Bianchet, 2011; Corlatti and Bassano, 2014), show much larger levels of body-mass loss during the rut, suggesting a high reliance on stored energetic capital. We discuss these findings in relation to two main issues: the broader ecology and life-history of our focal species, and the limitations on identifying cause and effect in an observational life-history study, with potential directions for future research.

Capital and Income Breeding and the Life-Histories of Male Ungulates

Our hypothesis relating proximity to the capital end of the capital-income breeder continuum to the degree of polygyny of mating systems was entirely consistent with the outcomes of our comparison between the two deer species. Red deer showed a decrease in body weight during the rut that was 2.5-times larger than in roe deer. We argue that this is associated with a much larger variance in lifetime breeding success (Im) in red deer stags ($Im \geq 3.0$) than in roe deer bucks ($Im \sim 0.75$) (Pemberton et al., 1992; Marshall et al., 1998; Vanpé et al., 2008).

Alpine chamois bucks demonstrated a marked loss of body mass during the rut, losing about 16% of the initial weight, which is more than twice the mass loss experienced by roe deer bucks. In that sense, chamois seem to be closer to the capital rather than to the income end of the breeding continuum. This is surprising because, owing to their unbiased sex-specific survival (Rughetti and Festa-Bianchet, 2011; Corlatti et al., 2012), they are not considered to be strongly polygynic (Corlatti et al., 2013a). The high similarity of male and female body size, however, does not constitute a useful diagnostic of their level of polygyny. Indeed, in male chamois physical competition is related to agility and not just to body mass, which is the dominant factor for most deer species that use fighting strategies based on wresting or ramming (Kramer, 1969; Clutton-Brock et al., 1979; Festa-Bianchet et al., 1990). As a related example, horses are nearly monomorphic but are recognized to be highly polygynous (Berger, 1986; Rubenstein, 1986). Notably, despite the lack of dimorphism in the average body masses of male and female chamois, evidence exists of seasonal changes in the degree of dimorphism. Specifically, male chamois body weight is about 40% greater than that of females before the rut but that difference declines to only about 6% in January (Garel et al., 2009; Rughetti and Festa-Bianchet, 2011). This is probably because chamois bucks have to gain energy in order to cope with intense energy expenditure of a late autumn rut in a harsh mountain environment.

However, seasonal change in the degree of body-mass dimorphism in Alpine chamois is also consistent with the potential for high energy expenditure by males, linked to a higher level of polygyny than expected from overall levels of dimorphism alone. The rationale behind the link between the level of polygyny and condition of capital-income breeders is provided by the differential opportunities of mating for adult males in scarcely vs. highly polygynic mating systems. More mating opportunities imply higher competition and the need for higher energy expenditure to cope with intrasexual conflicts that, in turn, lead to a capital breeder strategy relying on long term energy storage. By contrast, limited mating opportunities do not justify year-long (or season-long) accumulation of large amounts of stored energy that, for various reasons, can be detrimental to survival (see, for instance, Varpe and Ejsmond, 2018). Measures of lifetime breeding success for chamois would help to bolster confidence in this suggestion.

In mammals, the energy costs for males of acquiring mating opportunities can often exceed those of lactating females (Lane et al., 2010). Energy storage to meet the costs of future reproduction could also represent an advanced payment of reproductive costs (e.g., in term of predation risk) that can be justified only if the outcome overcomes the investment. A further difference between males belonging to opposite ends of the capital-income breeder continuum seems to be the seasonal dynamic of the pre- and post-rut variance in body mass variability among males. For income breeders (i.e., roe deer males), there was a minimal change in the standard deviation of body mass before and after the rut, demonstrating that rutting activities did not modify body-mass variance among adult males. This outcome is consistent with the delayed implantation that characterizes this species, allowing the choice of optimal timing for mating, placed in the least-limiting season (Sandell, 1990). In contrast, the capital breeding red deer stags exhibited a considerable decrease of variance in body mass at the end of the rut, indicating that differential investment by males of different body mass and quality led to a more even condition among them at the end of the rut. This result implies that there is some body mass threshold, below which stags cannot decrease their weight without compromising their survival during the following winter. Although the effect is less pronounced than in red deer, the same seems to be true for Alpine chamois.

Where possible (i.e., within both deer species), we also evaluated changes in body mass after the intense effort connected with the rut. We documented that the capital-breeding red deer continued to lose body mass after the rut, whilst the income-breeding roe deer males were able to recover part of the loss suffered during the rut within 2 months of the end of the mating season. This result is likely to be related to two different factors: (i) the timing of the rut that, in the case of roe deer, occurred in the middle of summer, in contrast to red deer that, after the rut, have to face a limiting time both in resources and climate like the last part of autumn and then winter; and (ii) the lower level of energy expenditure of roe deer, leading to a greater ability to recover rut losses.

The reduced post-rut variability among males in capital breeders and a fast recovery of body mass of an income breeder can be interpreted in the light of the differential ability of capital and income breeders to cope with a variable environment in a number of taxa (Pélisson et al., 2012). Income breeders seem to be more susceptible to sudden environmental changes, and rutting in summer seems to be a strategy that allows roe deer males efficiently to buffer the loss of body condition during reproduction.

Our models to explain variation in male body mass loss among areas and years suggest that interindividual differences are the major factors for red deer and chamois, whilst area is the dominant factor dictating weight loss for roe deer (Gaillard et al., 1993; Linnell and Andersen, 1998; Raganella-Pelliccioni et al., 2007; Plard et al., 2014). This is consistent with the idea that capital breeders are less dependent on environmental factors linked to different resource availability in space (area) or time (year) than income breeders like roe deer. As noted by Kerby and Post (2013), the capital-breeder strategy seems to be more suitable to cope with a changing environment as it relies on long-term accumulation of energy rather than on the immediate conditions preceding the start and the development of rutting activities. Long-term accumulation gives the potential to buffer against sudden losses of resources due to extreme climatic events, and therefore constitutes a better strategy to guarantee the sustainability of high energy expenditure linked to strong polygyny and the connected high opportunity of gaining reproduction success. Moreover, capital breeders seem more able to cope with human induced disturbance, a further element of environmental unpredictability (for evidence that the effect of disturbance is greater for income than capital breeders, see also McHuron et al., 2017).

Limitations and Future Directions

Our findings are consistent with a link between capital and income breeding in males, and the degree of polygyny they express. Our results challenge ecologists to consider mating systems as a further axis of variation that could push species toward one or the other end of the capital-income spectrum. Inevitably, however, our findings do not "prove" a causal link between mating systems and degree of reliance on stored capital for male mating. This is because of both the nature of correlational data vs. experimentation, and the complexity of life-history systems.

Although our sample sizes for carcass weights are large, they represent transverse observational data on only three species. Despite the difficulty of obtaining large sample sizes, longitudinal data are often preferred for life-history studies (Gaillard et al., 2003). In this instance, data on individuals that breed in some years but not in others would be ideal for estimating the true body mass loss associated with reproduction alone. Nevertheless, such data would be difficult to obtain in the wild, as most male ungulates attempt to breed in all years (Loison et al., 1999), thereby incurring some costs. In captivity, it would be possible to conduct experimental manipulations of the potential to breed, but this would be confounded by the very different food regimes available in those situations. All metrics would be improved by simultaneous observations of the extent of feeding, which would enable estimates of the relative contributions of stores and intake to finance the costs of reproduction. In general, however, insights into the costs of reproduction have been as a rule obtained from transverse data in the past (Mysterud et al., 2008; Mason et al., 2011); because of a very large sample set used in our study, such insights are likely sufficiently accurate to characterize the broad differences between populations and species of interest.

Here, we presented data on three heavily hunted species for which large data sets are available. These include only one species toward the income breeding end of the spectrum and two toward the capital breeding extreme. Certainly, these species vary in many aspects of ecology and life-history, not just in their degree of polygyny. This rightly prevents us from attributing cause and effect in the system. Nevertheless, our main purpose was to demonstrate that the hypothesis on the relation between the level of polygyny and position of ungulate males within the capital-income breeding spectrum is consistent with observation in three data-rich species. Further research could take this forward on several fronts. First, other species are also heavily hunted and could yield similar data (e.g., moose, fallow deer, mouflon *Ovis gmelini musimon,* reindeer, and wild boar *Sus scrofa* among European ungulates). It would be interesting to determine whether those species, broadly characterized as showing high or low degrees of polygyny, are also consistent with our expectations. With a large enough sample of populations and species, and given a measure of variance in lifetime reproductive success of males within them, more quantitative phylogenetic comparisons would also be possible. Given the likely link between seasonal gluts of food availability and capital breeding as well as our posited link between capital breeding and polygyny, we might expect populations in more seasonal environments to exhibit greater polygyny and greater reliance on stored capital as substantial seasonal differences exist in energy financing opportunities. Finally, although life-history traits do not evolve in strictly linear causal chains (Stephens et al., 2009), theoretical models can shed light on the correlations expected between capital and income breeding and other aspects of organism-environment interactions (Houston et al., 2007; Stephens et al., 2014). Our purposes would be well-served by models that alter only female dispersion, thus modifying an important part of the potential for polygyny (Emlen and Oring, 1977), and allow variation in energy storage strategies as well as the extent of polygyny. Distinct emergent optima arising from covariation in these two attributes would be strongly supportive of the link that we propose in this paper.

CONCLUSION

Here, we suggest that – owing to the high demands of time and energy that polygynous males face during the reproductive period – it is likely that males in highly polygynous species are more likely to be reliant on capital breeding than are those in relatively monogamous species. Our data on seasonal patterns of body mass change in three ungulate species are consistent with this hypothesis, indicating that mating systems should be considered as a further factor driving variation on the capital-income breeding spectrum. Both empirical and theoretical approaches should cast further light on the validity of our hypothesis, which should provide new insights and help advance the field of ungulate ecology.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because all individuals used in the study were hunted during the regular hunting activity prescribed by the state of Slovenia and Italy within the yearly hunting management plans. We used only data on dead individuals therefore no animal was shot or killed by any other means for the purposes of the research.

AUTHOR CONTRIBUTIONS

MA, BP, EM, and RC conceived and planned the experiment. EM analyzed the data. RC, KF, and AA collected and prepared data. MA, EM, RC, BP, and PS contributed to the interpretation of the results. MA and EM took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

FUNDING

Slovene co-authors acknowledge the financial support from the Ministry of Agriculture, Forestry and Food (project V4–1825) and the Slovenian Research Agency (ARRS), which funded KF and BP through the programme group P4–0107. ARRS was also foreseen to fund the Open Access publication fee.

ACKNOWLEDGMENTS

We are grateful to the Hunters Association of Slovenia for developing on-line available hunting information system enabling us the access to all needed data on all harvested ungulates in Slovenia, and to the Trento Province and the Trentino Hunters' Association for supplying Italian chamois data. We also thank the associate editor, RB, and the reviewers, LZ, and PK, for very helpful comments improving the first version of the manuscript.

REFERENCES

Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., and Sherman, P. W. (1979). "Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans," in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, eds N. A. Chagnon and W. Irons (Scituate, MA: Duxbury Press), 402–435.

Andersen, R., Gaillard, J. M., Linnell, J. D., and Duncan, P. (2000). Factors affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.* 69, 672–682. doi: 10.1046/j.1365-2656.2000.00425.x

Apollonio, M., and Di Vittorio, I. (2004). Feeding and reproductive behaviour in fallow bucks (*Dama dama*). *Naturwissenschaften* 91, 579–584. doi: 10.1007/s00114-004-0574-0

Barboza, P. S., Hartbauer, D. W., Hauer, W. E., and Blake, J. E. (2004). Polygynous mating impairs body condition and homeostasis in male reindeer (*Rangifer tarandus tarandus*). *J. Comp. Physiol. B* 174, 307–317. doi: 10.1007/s00360-004-0416-6

Berger, J. (1986). *Wild Horses of the Great Basin: Social Competition and Population Size*. Chicago: The University of Chicago Press.

Bergman, C. M., Fryxell, J. M., Gates, C. C., and Fortin, D. (2001). Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* 70, 289–300. doi: 10.1111/j.1365-2656.2001.00496.x

Bobek, B., Perzanowski, K., and Weiner, J. (1990). Energy expenditure for reproduction in male red deer. *J. Mammal.* 71, 230–232. doi: 10.2307/1382171

Bonnet, X., Bradshaw, D., and Shine, R. (1998). Capital versus income breeding: an ectothermic perspective. *Oikos* 83, 333–342. doi: 10.2307/3546846

Box, G. E., and Tiao, G. C. (1975). Intervention analysis with applications to economic and environmental problems. ıJ. *Am. Stat. Assoc.* 70, 70–79. doi: 10.1080/01621459.1975.10480264

Boyd, I. L. (2000). State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Funct. Ecol.* 14, 623–630. doi: 10.1046/j.1365-2435.2000.t01-1-00463.x

Brivio, F., Grignolio, S., and Apollonio, M. (2010). To feed or not to feed? Testing different hypotheses on rut−induced hypophagia in a Mountain ungulate. *Ethology* 116, 406–415. doi: 10.1111/j.1439-0310.2010.01753.x

Burnham, K. P., and Anderson, D. R. (2002). *Model Section and Multimodel Inferences: A Practical-Theoretic Approach*, 2nd Edn. New York, NY: Springer-Verlag.

Bužan, E., Bryja, J., Zemanová, B., and Kryštufek, B. (2013). Population genetics of chamois in the contact zone between the Alps and the Dinaric mountains: uncovering the role of habitat fragmentation and past management. *Cons. Genet.* 14, 401–412. doi: 10.1007/s10592-013-0469-8

Canty, A., and Ripley, B. D. (2019). *Boot: Bootstrap r (s-plus) Functions. R Package Version 1.3-23*. Cambridge: Cambridge University Press.

Carranza, J., Alvarez, F., and Redondo, T. (1990). Territoriality as a mating strategy in red deer. *Anim. Behav.* 40, 79–88. doi: 10.1016/s0003-3472(05)80667-0

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* 123, 212–229. doi: 10.1086/284198

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. R. Soc. Lond. Ser. B* 236, 339–372. doi: 10.1098/rspb.1989.0027

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., and Guinness, F. E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* 27, 211–225. doi: 10.1016/0003-3472(79)90141-6

Clutton-Brock, T. H., Guinness, F., and Albon, S. (1982). *Red Deer Behaviour and Ecology of Two Sexes*. Cambridge: Cambridge University Press.

Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T., and Strobeck, C. (2002). Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. Lond. B* 269, 165–172. doi: 10.1098/rspb.2001.1851

Coltman, D. W., Pilkington, J. G., Smith, J. A., and Pemberton, J. M. (1999). Parasite−mediated selection against inbred Soay sheep in a free−living island population. *Evolution* 53, 1259–1267. doi: 10.1111/j.1558-5646.1999.tb04538.x

Connan, M., Dilley, B. J., Whitehead, T. O., Davies, D., McQuaid, C. D., and Ryan, P. G. (2019). Multidimensional stable isotope analysis illuminates resource partitioning in a sub−Antarctic island bird community. *Ecography* 42, 1948–1959. doi: 10.1111/ecog.04560

Corlatti, L., and Bassano, B. (2014). Contrasting alternative hypotheses to explain rut-induced hypophagia in territorial male chamois. *Ethology* 120, 32–41. doi: 10.1111/eth.12177

Corlatti, L., Bassano, B., Valencak, T. G., and Lovari, S. (2013a). Foraging strategies associated with alternative reproductive tactics in a large mammal: foraging strategies of male chamois. *J. Zool.* 291, 111–118. doi: 10.1111/jzo.12049

Corlatti, L., Béthaz, S., von Hardenberg, A., Bassano, B., Palme, R., and Lovari, S. (2012). Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs. *Anim. Behav.* 84, 1061–1070. doi: 10.1016/j.anbehav.2012.08.005

Corlatti, L., Caroli, M., Pietrocini, V., and Lovari, S. (2013b). Rutting behaviour of territorial and nonterritorial male chamois: is there a home advantage? *Behav. Proc.* 92, 118–124. doi: 10.1016/j.beproc.2012.11.008

Davison, A. C., and Hinkley, D. V. (1997). *Bootstrap Methods and Their Applications*. Cambridge: Cambridge University Press.

Debeffe, L., Focardi, S., Bonenfant, C., Hewison, A. J. M., Morellet, N., Vanpé, C., et al. (2014). A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. *Oecologia* 176, 431–443. doi: 10.1007/s00442-014-3021-8

Drent, R. H., and Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68, 225–252. doi: 10.5253/arde.v68.p225

Emlen, S. T., and Oring, L. W. O. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215–223. doi: 10.1126/science.327542

Festa-Bianchet, M., Apollonio, M., Mari, F., and Rasola, G. (1990). Aggression among lekking male fallow deer (*Dama dama*): territory effects and relationship with copulatory success. *Ethology* 85, 236–246. doi: 10.1111/j.1439-0310.1990.tb00403.x

Flajšman, K. (2017). *Effects of Individual, Population and Environmental Factors on Parameters of Reproductive Success of Female Roe Deer (Capreolus capreolus* L.). Doctoral dissertation, University of Ljubljana, Biotechnical faculty, Ljubljana.

Gaillard, J. M., Delorme, D., Boutin, J. M., Van Laere, G., Boisaubert, B., and Pradel, R. (1993). Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* 62, 778–791. doi: 10.2307/5396

Gaillard, J. M., Loison, A., and Toïgo, C. (2003). "Variation in life history traits and realistic population models for wildlife management," in *Animal Behavior and Wildlife Conservation*, eds M. Festa-Bianchet and M. Apollonio (Washington, DC: Island Press), 115–132.

Garel, M., Loison, A., Jullien, J. M., Dubray, D., Maillard, D., and Gaillard, J. M. (2009). Sex-specific growth in Alpine chamois. *J. Mammal.* 90, 954–960. doi: 10.1644/08-MAMM-A-287.1

Hafner, M. (2008). *Jelenjad*. Ljubljana: Lovska zveza Slovenije.

Hewison, A. J. M., Gaillard, J. M., Delorme, D., Van Laere, G., Amblard, T., and Klein, F. (2011). Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size allometry in roe deer. *Oikos* 120, 1217–1226. doi: 10.1111/j.1600-0706.2011.19316x

Hewison, A. J. M., Vincent, J. P., Angibault, J. M., Delorme, D., Van Laere, G., and Gaillard, J. M. (1999). Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. *Can. J. Zool.* 77, 58–67. doi: 10.1139/z98-183

Houston, A. I., Stephens, P. A., Boyd, I. L., Harding, K. C., and McNamara, J. M. (2007). Capital or income breeding? A theoretical model of female reproductive strategies. *Behav. Ecol.* 18, 241–250. doi: 10.1093/beheco/arl080

Jaatinen, K., Öst, M., and Hobson, K. A. (2016). State-dependent capital and income breeding: a novel approach to evaluating individual strategies with stable isotopes. *Front. Zool.* 13:24. doi: 10.1186/s12983-016-0157-x

Jönsson, K. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78, 57–66. doi: 10.2307/3545800

Kerby, J., and Post, E. (2013). Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Phil. Trans. R. Soc. B* 368:20120484. doi: 10.1098/rstb.2012.0484

Kojola, I. (1991). Influence of age on the reproductive effort of male reindeer. *J. Mammal.* 72, 208–210. doi: 10.2307/1382001

Komers, P. E., Messier, F., Flood, P. F., and Gates, C. C. (1994). Reproductive behavior of male wood bison in relation to progesterone level in females. *J. Mammal.* 75, 757–765. doi: 10.2307/1382527

Kramer, A. (1969). Soziale organisation und Sozialverhalten einer gemspopulation *Rupicapra rupicapra* der Alpen. *Z. Tierpsychol.* 26, 889–964. doi: 10.1111/j.1439-0310.1969.tb01983.x

Kurt, F. (1991). *Das Reh in der Kulturlandschaft. Sozialverhalten und Ökologie eines Anpassers*. Hamburg: Verlag Paul Parey.

Lane, J. E., Boutin, S., Speakman, J. R., and Humphries, M. M. (2010). Energetic costs of male reproduction in a scramble competition mating system. *J. Anim. Ecol.* 79, 27–34. doi: 10.1111/j.1365-2656.2009.01592.x

Lieberg, O., Johansson, A., Andersen, R., and Linnell, J. (1998). "Mating system, mating tactics and the function of male territoriality in roe deer," in *The European Roe Deer: The Biology of Success*, eds R. Andersen, P. Duncan, and J. Linnell (Oslo: Scandinavian University Press), 221–256.

Linnell, J. D. C., and Andersen, R. (1998). Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*. *J. Zool.* 244, 497–504. doi: 10.1111/j.1469-7998.1998.tb00055.x

Loison, A., Gaillard, J. M., Pélabon, C., and Yoccoz, N. G. (1999). What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* 1, 611–633.

Lovenčak, F. (1999). *Naravnogeografske Značilnosti kot Možnost Razvoja Slovenije*. Ljubljana: Univerza v Ljubljani.

Marshall, T. C., Slate, J., Kruuk, L. E. B., and Pemberton, J. M. (1998). Statistical confidence for likelihood−based paternity inference in natural populations. *Mol. Ecol.* 7, 639–655. doi: 10.1046/j.1365-294x.1998.00374.x

Mason, T. H. E., Chirichella, R., Richards, S. A., Stephens, P. A., Willis, S. G., and Apollonio, M. (2011). Contrasting life histories in neighbouring populations of a large mammal. *PLoS One* 6:e28002. doi: 10.1371/journal.pone.0028002

McElligott, A. G., Naulty, F., Clarke, W. V., and Hayden, T. J. (2003). The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* 5, 1239–1250. doi: 10.5167/uzh-402

McHuron, E. A., Costa, D. P., Schwarz, L., and Mangel, M. (2017). State-dependent behavioural theory for assessing the fitness consequences of anthropogenic disturbance on capital and income breeders. *Methods Ecol. Evol.* 8, 552–560. doi: 10.1111/2041-210X.12701

Milner, J. M., Alexander, J., and Griffin, C. (2002). *A Highland Deer Herd and Its Habitat*. London: Red Lion House.

Miquelle, D. G. (1990). Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27, 145–151. doi: 10.1007/BF00168458

Mysterud, A., Bonenfant, C., Loe, L. E., Langvatn, R., Yoccoz, N. G., and Stenseth, N. C. (2008). Age-specific feeding cessation in male red deer during rut. *J. Zool.* 275, 407–412. doi: 10.1111/j.1469-7998.2008.00453.x

Mysterud, A., Holand, Ø, Røed, K. H., Gjøstein, H., Kumpula, J., and Nieminen, M. (2003). Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *J. Zool.* 261, 341–344. doi: 10.1017/S0952836903004114

Mysterud, A., Langvatn, R., and Stenseth, N. C. (2004). Patterns of reproductive effort in male ungulates. *J. Zool.* 264, 209–215. doi: 10.1017/S0952836904005618

Mysterud, A., Solberg, E. J., and Yoccoz, N. G. (2005). Ageing and reproductive effort in male moose under variable levels of intrasexual competition. *J. Anim. Ecol.* 74, 742–754. doi: 10.1111/j.1365-2656.2005.00965.x

Ogrin, D. (1996). Podnebni tipi v Sloveniji. *Geog. Vest.* 68, 39–56.

Pélisson, P. F., Bel-Venner, M. C., Rey, B., Burgevin, L., Martineau, F., Fourel, F., et al. (2012). Contrasted breeding strategies in four sympatric sibling insect species: when a proovigenic and capital breeder copes with a stochastic environment. *Funct. Ecol.* 26, 198–206. doi: 10.1111/j.1365-2435.2011.01925.x

Pelletier, F., Page, K. A., Ostiguy, T., and Festa−Bianchet, M. (2005). Fecal counts of lungworm larvae and reproductive effort in bighorn sheep, *Ovis canadensis*. *Oikos* 110, 473–480. doi: 10.1111/j.0030-1299.2005.14120.x

Pemberton, J. M., Albon, S. D., Guinness, F. E., Clutton-Brock, T. H., and Dover, G. A. (1992). Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* 3, 66–75. doi: 10.1093/beheco/3.1.66

Perko, D. (1998). The regionalization of Slovenia. *Geog. Zb.* 38, 12–57.

Plard, F., Gaillard, J. M., Coulson, T., Hewison, A. M., Delorme, D., Warnant, C., et al. (2014). Long−lived and heavier females give birth earlier in roe deer. *Ecography* 37, 241–249. doi: 10.1111/j.1600-0587.2013.00414.x

Pokorny, B., and Jelenko Turinek, I. (2017). *Čeljustnice Prostoživečih Parkljarjev*. Ljubljana: Lovska zveza Slovenije.

R Development Core Team (2019). *R: A Language and Environment for Statistical Computing. Version 3.6.0*. Vienna: R Foundation for Statistical Computing.

Raganella-Pelliccioni, E., Scremin, M., and Toso, S. (2007). Phenology and synchrony of roe deer breeding in northern Italy. *Acta Theriol.* 52, 95–100. doi: 10.1007/BF03194204

Ratcliffe, P. R., and Mayle, B. A. (1992). Age determination of roe deer. *For. Comm. Bull.* 105, 26–28.

Rubenstein, D. I. (1986). "Ecology and sociality in horses and zebras," in *Ecological Aspects of Social Evolution: Birds and Mammals*, eds D. I. Rubenstein and R. W. Wrangham (Princeton: Princeton University Press), 282–302. doi: 10.2307/j.ctt7zvwgq.17

Rughetti, M., and Festa-Bianchet, M. (2011). Seasonal changes in sexual size dimorphism in northern chamois: sexual dimorphism. *J. Zool.* 284, 257–264. doi: 10.1111/j.1469-7998.2011.00800.x

Sandell, M. (1990). The evolution of seasonal delayed implantation. *Q. Rev. Biol.* 65, 23–42. doi: 10.1086/416583

Schröder, W., and Von Elsner-Schak, I. (1985). "Correct age determination in chamois," in *The Biology and Management of Mountain Ungulates*, ed. S. Lovari (London: Croom Helm), 65–70.

Schuetzenmeister, A., and Dufey, F. (2019). *VCA: VarianceComponents Analysis. R package version 1.4.0*. Available online at: https://cran.r-project.org/web/packages/VCA/VCA.pdf

Searle, S. R., Casella, G., and McCulloch, C. E. (1992). *Variance Components*. New York, NY: Wiley.

Soulsbury, C. D. (2019). Income and capital breeding in males: energetic and physiological limitations on male mating strategies. *J. Exp. Biol.* 222:jeb184895. doi: 10.1242/jeb.184895

Stephens, P. A., Boyd, I. L., McNamara, J. M., and Houston, A. I. (2009). Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* 90, 2057–2067. doi: 10.1890/08-1369.1

Stephens, P. A., Houston, A. I., Harding, K. C., Boyd, I. L., and McNamara, J. M. (2014). Capital and income breeding: the role of food supply. *Ecology* 95, 882–896. doi: 10.1890/13-1434.1

Vanpé, C., Gaillard, J. M., Morellet, N., Kjellander, P., Liberg, O., Delorme, D., et al. (2009). Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J. Mammal.* 90, 661–665. doi: 10.1644/08-MAMM-A-137R.1

Vanpé, C., Kjellander, P., Galan, M., Cosson, J. F., Aulagnier, S., Liberg, O., et al. (2008). Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behav. Ecol.* 19, 309–316. doi: 10.1093/beheco/arm132

Varpe, Ø, and Ejsmond, M. J. (2018). Trade-offs between storage and survival affect diapause timing in capital breeders. *Evol. Ecol.* 32, 623–641. doi: 10.1007/s10682-018-9961-4

von Hardenberg, A., Bassano, B., Peracino, A., and Lovari, S. (2000). Male Alpine chamois occupy territories at hotspots before the mating season. *Ethology* 106, 617–630. doi: 10.1046/j.1439-0310.2000.00579.x

Williams, C. T., Klaassen, M., Barnes, B. M., Buck, C. L., Arnold, W., Giroud, S., et al. (2017). Seasonal reproductive tactics: annual timing and the capital-to-income breeder continuum. *Phil. Trans. R. Soc. B* 372:20160250. doi: 10.1098/rstb.2016.0250

Willisch, C. S., and Ingold, P. (2007). Feeding or resting? The strategy of rutting male Alpine chamois. *Ethology* 113, 97–104. doi: 10.1111/j.1439-0310.2006.01301.x

Yoccoz, N. G., Mysterud, A., Langvatn, R., and Stenseth, N. C. (2002). Age- and density-dependent reproductive effort in male red deer. *Proc. R. Soc. Lond. Ser. B* 269, 1523–1529. doi: 10.1098/rspb.2002.2047

Zeileis, A., Leisch, F., Hornik, K., and Kleiber, C. (2002). Strucchange: an R package for testing for structural change in linear regression models. *J. Stat. Softw.* 7, 1–38. doi: 10.18637/jss.v007.i02

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 29 October 2020
doi: 10.3389/fevo.2020.535715

Fragmentation and Translocation Distort the Genetic Landscape of Ungulates: Red Deer in the Netherlands

Joost F. de Jong[1]*, Pim van Hooft[1], Hendrik-Jan Megens[2], Richard P. M. A. Crooijmans[2], Gerard Arjen de Groot[3], Josephine M. Pemberton[4], Jisca Huisman[4], Luděk Bartoš[5], Laura Iacolina[6], Sip E. van Wieren[1], Ronald C. Ydenberg[7] and Herbert H. T. Prins[1]

[1] Wildlife Ecology and Conservation Group, Wageningen University & Research, Wageningen, Netherlands, [2] Animal Breeding and Genomics Group, Wageningen University & Research, Wageningen, Netherlands, [3] Wageningen Environmental Research, Wageningen University & Research, Wageningen, Netherlands, [4] Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, United Kingdom, [5] Institute of Animal Science, Prague, Czechia, [6] Faculty of Agriculture, University of Zagreb, Zagreb, Croatia, [7] Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

OPEN ACCESS

Edited by:
R. Terry Bowyer,
University of Alaska Fairbanks,
United States

Reviewed by:
Kris Hundertmark,
University of Alaska Fairbanks,
United States
Javier Pérez-González,
University of Extremadura, Spain

****Correspondence:***
Joost F. de Jong
joost.dejong@wur.nl

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *17 February 2020*
Accepted: *29 September 2020*
Published: *29 October 2020*

Citation:
de Jong JF, van Hooft P, Megens H-J, Crooijmans RPMA, de Groot GA, Pemberton JM, Huisman J, Bartoš L, Iacolina L, van Wieren SE, Ydenberg RC and Prins HHT (2020) Fragmentation and Translocation Distort the Genetic Landscape of Ungulates: Red Deer in the Netherlands. Front. Ecol. Evol. 8:535715. doi: 10.3389/fevo.2020.535715

Many ungulate populations have a complex history of isolation and translocation. Consequently, ungulate populations may have experienced substantial reductions in the level of overall gene flow, yet simultaneously have augmented levels of long-distance gene flow. To investigate the effect of this dual anthropogenic effect on the genetic landscape of ungulates, we genotyped 35K SNPs in 47 red deer (*Cervus elaphus*) of Netherlands, including putative autochthonous relic populations as well as allochthonous populations established in private estates and rewilding areas. We applied F_{ST} and ordination analyses to determine the meta-population genetic structure and thereby the occurrence of hybridization. At population level, we investigated levels of inbreeding through individual-based diversity measures, including Runs of Homozygosity. We documented that both spatial genetic structure and within-population genetic variation differed markedly from patterns assumed from present-day abundance and distribution. Notwithstanding the small spatial scale, red deer populations formed distinct genetic clusters, and some had higher genetic similarity to distant than to nearby populations. Moreover, the putative autochthonous relic deer populations had much reduced levels of polymorphism and multi-locus heterozygosity, despite relatively large current population sizes. Accordingly, genomes of these deer contained a high proportion of long (>5 Mb) Runs of Homozygosity. Whereas the observed high levels of inbreeding warrant defragmentation measures, the presence of adjacent autochthonous and allochthonous genetic stocks imply that facilitation of gene flow would cause genetic homogenization. Such distortions of the genetic landscape of ungulates creates management dilemmas that cannot be properly anticipated without baseline genetic monitoring.

Keywords: red deer, ungulate, gene flow, translocation, single nucleotide polymorphisms, genetic monitoring

INTRODUCTION

In the Anthropocene, ungulates are subject to both population isolation and translocation. Because of eradication and overexploitation, many ungulates occur in small or bottlenecked autochthonous population relics that are further isolated by anthropogenic barriers (Linnell and Zachos, 2011; Deinet et al., 2013; Ripple et al., 2015). Being such iconic elements of the 'the world around us,' ungulates have a long history of translocation (Iacolina et al., 2019). Translocations may come in the form of supplementation of existing populations or (re)introduction of new populations, and frequently involve immigrants from non-native, distant stocks (Seddon et al., 2012; Iacolina et al., 2018, 2019). The dual anthropogenic influences of isolation and translocation have contrasting effects on the key evolutionary process of gene flow, as it is both impeded as well as augmented. This means that the genetic landscape (e.g., Söderquist et al., 2017 and Wang et al., 2019) of ungulate populations is altered by inbreeding (i.e., mating among closely related individuals) as well as outbreeding (i.e., mating among distantly related individuals). Consequently, ungulate populations are at risk of inbreeding depression (i.e., lowered fitness of inbred individuals) on the one hand (Ralls et al., 2018) and outbreeding depression (i.e., lowered fitness of hybrids) on the other (Frankham et al., 2011). Furthermore, outbreeding results in loss of genetic integrity and in genetic homogenization, i.e., an increase of genetic similarity of populations (Kolodny et al., 2019).

The occurrence of inbreeding depression in isolated wildlife populations is now well established (Hasselgren and Norén, 2019). This outcome is especially true for ungulates, for which genomic approaches developed for domestic counterparts could be adopted. The genomes of over 20 ungulates have now been assembled (Martchenko et al., 2018). The genomic consequences of population isolation have been investigated in a variety of species, showing that many populations have individuals with genomes containing frequent and long Runs of Homozygosity (e.g., wild boar (*Sus scrofa*), ibex (*Capra ibex*), bighorn sheep (*Ovis canadensis*), Soay sheep (*Ovis aries*), and red deer (*Cervus elaphus*); Bérénos et al., 2016; Grossen et al., 2018, 2019; Hasselgren and Norén, 2019). A negative relationship between inbreeding and individual survival and reproductive performance was reported in red deer of the Isle of Rum, Scotland (Huisman et al., 2016). Moreover, in a recent study involving 26 European ibex populations, growth rate appeared to be substantially lower in inbred than in non-inbred populations (Bozzuto et al., 2019).

The general consensus is that in contemporary ungulate populations outbreeding, and the consequences thereof, is less adverse and pressing than inbreeding (Edmands, 2007; Pekkala et al., 2014, Bell et al., 2019). Recently, however, the debate began on whether the consequences of outbreeding are underestimated (Kolodny et al., 2019; Bell et al., 2019). There is equivocal evidence that hybrids may have lowered relative fitness (Marshall and Spalton, 2000; Bell et al., 2019). Such outbreeding depression may arise because of genetic incompatibility and reduced local adaptation. Apart from this, genetic homogenization may reduce the genetic diversity at a species-wide scale (Kolodny et al., 2019), in particular when migrants swamp the genetic variation of the native stock (Bell et al., 2019; Harris et al., 2019). Species exhibit geographic variation in phenotypic traits. Ungulates, in particular, have substantial regional variation in morphology (body size, size of horns and antlers, coat pattern and coloration) and behavior (timing of mating season, vocalization) (e.g., Putman and Flueck, 2011; Castelló, 2016). Underlying this geographic variation in phenotypes may be a complex and often little understood spatial genetic structuring (e.g., Moodley and Bruford, 2007). Translocation and subsequent hybridization of ungulates therefore may have both genetic and conspicuous phenotypic effects.

In practice, ungulate management policies often account poorly for both inbreeding and outbreeding. "Genetic legislation" or guidelines on inbreeding and outbreeding are absent or non-normative (Hoban et al., 2013; Ralls et al., 2018). The main genetic guideline, the 100/1000 Ne rule (or 50/500, Frankham et al., 2014), has gained a foothold, but in practice actual effective population sizes are seldom estimated. Indeed, genetic diversity measures are not incorporated in IUCN assessments (Vitorino et al., 2019). Similarly, the IUCN guidelines on translocation ("Guidelines for Reintroductions and Other Conservation Translocations") do not contain normative or quantitative targets (IUCN/SSC, 2013). Although recommended (e.g., IUCN/SSC, 2013), genetic monitoring, whether pre- or post-intervention, is rarely applied (Hoban et al., 2013). Considering the long history of diverse anthropogenic impacts, the demographic history of contemporary ungulate populations is often complex. Present-day abundance and distribution may therefore give little indication of genetic status.

The simultaneous risk of inbreeding and outbreeding in contemporary ungulate populations is exemplified by the red deer of Netherlands. After a complex and partially known history of eradication, overexploitation, fragmentation and translocation, red deer of Netherlands now occur in remnant populations with different genetic ancestry. By 1900, the red deer population was likely reduced to perhaps a few tens of individuals, which occurred in the pastoral lands of the Veluwe moraine forest and heaths. To improve hunting opportunities, Dutch royalty and local landlords translocated red deer from across the European continent to estates (Rijk and Pelzers, 1991; van den Hoorn, 1992). Fences around the estates, and later busy provincial and national roads, probably hindered gene flow between the introduced allochthonous estate population and the presumably relic, autochthonous population. Within the framework of the "rewilding movement", red deer were introduced in a disjunct area of The Oostvaardersplassen around 1990. This area was in a newly reclaimed polder about 30 km removed from the Veluwe area. These deer were translocated from various stocks, predominantly Scotland and Czechia. Across the species range, deer including red deer show considerable phenotypic variation in morphology (body size, antler size and shape) and behavior (e.g., male rutting roars) (Mystkowska, 1966; Geist, 1998, pp. 170-222; Putman and Flueck, 2011; Volodin et al., 2018). This phenotypic variation is partially heritable (Kruuk et al., 2002; Coulson et al., 2003; Flueck and Smith-Flueck, 2011). In Netherlands, hunters maintain that up until today the allochthonous and autochthonous red deer populations differ in timing of mating activity and morphology (in particular, body and antler size; **Figure 1**). These differences may, however, also be caused by local variation in population density as well as in resource quality the latter because of contrasting soils and management regimes (including forage improvement and supplementary feeding). For example, the Oostvaardersplassen area has very fertile marine clay soils while the Veluwe area is on nutrient-poor leached Pleistocene cover sands.

To what extent gene flow may have homogenized the populations with distinct genetic ancestry, or whether anthropogenic barriers still prevent this homogenization is unknown. In addition, the level of inbreeding in the various populations is poorly understood. The various red deer populations underwent bottlenecks or founder effects, and today vary from a few hundred to thousands of animals. All populations accord with Dutch nature legislation based on European directives, which prescribes that to guarantee a 'favorable conservation status', ungulate populations should have a minimum size of 150 (assuming a minimum effective population size of 50, and an effective to census population size ratio of 0.33; Groot Bruinderink et al., 2000). The first microsatellite study was suggestive of the existence of separate genetic clusters, but did not detect genetic erosion (Groot et al., 2016). Concerns about inbreeding have triggered defragmentation measures in the past few decades, including the removal of fences and the construction of highway wildlife overpasses. The need for such measures, as well as the potential hybridization consequences, are poorly understood. In Dutch ungulate management, the allochthonous ancestry of some red deer populations is not part of the decision-making process (Spek, 2014).

FIGURE 1 | Difference in the shape of red deer antlers of relic and estate populations of Netherlands. **Above:** Antlers characteristic for deer of the allochthonous estate Hoge Veluwe (outside) and the autochthonous relic population. The antlers are from deer that are approximately seven years old. The antlers differ, inter alia, in the shape of the crown, which is a fork in the relic population, but tends to form palms in the estate. **Below:** Antlers collected in the estate Hoge Veluwe in 1985 **(left)** and 2013 (estimated age of the deer: both eight years). The characteristic shape of tines and palms is retained over generations.

Here, we report on a case study of the alteration of the genetic landscape of ungulates caused by population isolation and translocation, through analyses of 35K SNPs of red deer populations of Netherlands. Specifically, at meta-population level, we applied genetic ordination to study the occurrence of hybridization and assess its potential. At the population level, we investigated levels of inbreeding through Runs of Homozygosity. We expected a distortion of the null model of Isolation by Distance, as evidenced by (i) distinct genetic clusters at small spatial scales, and (ii) genetic similarity between distant, rather than nearby, populations. Furthermore, we expected (iii) relic autochthonous populations to be inbred, because of their bottlenecked history. In contrast, we expected allochthonous populations, which were established by founders of diverse genetic ancestry, to be outbred. Nontheless, if fences around estates cause isolation, then autochthonous estate populations also would be expected to have relatively low genetic variation. We test the overall hypothesis that genetic status of red deer can be derived from contemporary abundance and distribution patterns in a human-dominated landscape.

MATERIALS AND METHODS

Sample Collection, DNA Extraction and Genotyping

We assembled a SNP dataset from red deer populations from Netherlands with Czechia and Scotland as references (**Figure 2A** and **Supplementary Table 1**). Within Netherlands, we sampled red deer of the two main populations: the Veluwe and the Oostvaardersplassen (**Figure 2C**). In the Veluwe, we sampled two allochthonous populations from (formerly) fenced estates (NP Hoge Veluwe, Kroondomeinen), and two relic autochthonous populations, in the southwest (Planken Wambuis) and southeast (Veluwezoom and Deelerwoud, referred to as Veluwezoom). In addition, we sampled deer from the rewilding population at the Oostvaardersplassen. To avoid potential sampling bias, we excluded 1st and 2nd degree relatives (following Anderson et al., 2010, see subsequent calculation). This resulted in the following sample sizes: 15 deer from the Oostvaardersplassen, 13 from the Veluwe estate populations and 19 from the relic Veluwe populations. In additional 10, 36 and 100 samples were used for the reference populations of Czechia, mainland Scotland and Isle of Rum, respectively (**Supplementary Table 1**). To decrease the bias due to unequal sample size, a maximum of 25 samples from the Scottish populations were randomly selected for some of the analyses (PCoA, rarefaction, F_{ST}).

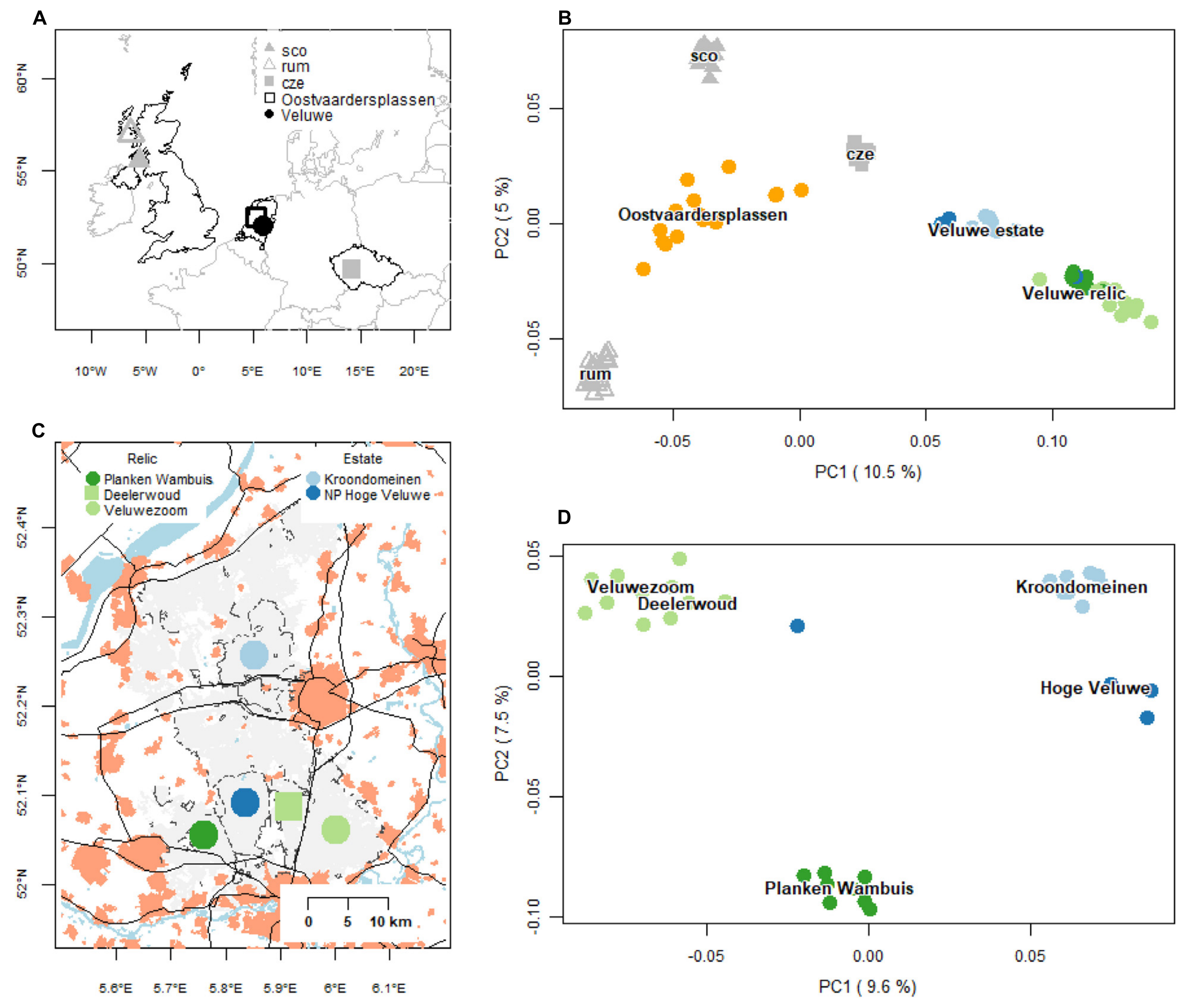

FIGURE 2 | Geography and genetic structure of red deer samples. **(A)** Geographic distribution of the red deer populations of Netherlands, and reference populations of Czechia and Scotland (mainland and Isle of Rum). Oostvaardersplassen is an allochthonous rewilding population, established in the early 1990s. Kroondomeinen and Hoge Veluwe are allochthonous Veluwe estate populations, established the early 1900s. Planken Wambuis (Southwest Veluwe) and Veluwezoom/Deelerwoud (Southeast Veluwe) are relic autochthonous populations. Abbreviations of the reference populations are: sco, mainland Scotland; rum, Isle of Rum; cze, Czechia. **(B)** First two axis of a PCoA of pairwise Hamming genetic distances of all populations (based on a maximum of 25 deer per population). Labels are positioned at the median ordination axis scores. **(C)** Geographic distribution of subpopulations of the focal populations in the Veluwe. Based on demographic history, red deer populations of the Veluwe can be distinguished as either relic populations, i.e., continuously present (color: green) and estate populations, which were founded at the beginning of the 20th century and are fenced (color: blue). Filled light gray areas are forests and heaths, light red areas cities and towns, black lines roads and black dashed lines fences. **(D)** PCoA biplot of the focal Veluwe populations. Labels are positioned at the median ordination values.

Collection and SNP genotyping of the Scottish deer is described in Senn and Pemberton (2009) and Huisman et al. (2016). Samples of red deer of Netherlands and Czechia were SNP genotyped specifically for this study. These samples, mostly tongue and ear tissue, were obtained shortly after death from animals that were culled for population management purposes, died from traffic collisions or because of natural mortality (the latter in the Oostvaardersplassen). Samples were genotyped with the cervine 50 K Illumina Infinium iSelect HD Custom BeadChip (Brauning et al., 2015; Rowe et al., 2015). Chromosome and chromosome positions of SNP loci were based on the linkage map by Johnston et al. (2017). After quality control, which included filtering on a minimum individual and SNP call rate of 0.98 and a minor allele frequency of > 0.01, 35,522 SNPs remained, of which 33,688 were autosomal. These remaining SNPs had a median density of one SNP per 53Kbp. For all analyses except ROH detection, we excluded SNPs that were in Linkage Disequilibrium (LD; $r^2 > 0.2$) (Anderson et al., 2010). After LD pruning, the number of remaining autosomal SNPs was 27,396 (median spacing of 55Kbp).

Genome-Wide SNP Analyses

Data management and standard genetic analyses were conducted with a combination of the software PLINK1.9 (Purcell et al., 2007) and R (R Core Team, 2019), specifically the package Adegenet (Jombart and Ahmed, 2011). To ensure independence of markers, we pruned SNPs with PLINK using a LD threshold of $r^2 = 0.2$. We used the PLINK pairwise IBD estimator to calculate pi_hat, which is the proportion of IBD between pairs of individuals (Purcell et al., 2007). We did this for various genetic clusters separately because the method assumes that samples do not show population stratification. We pruned individuals such that the maximum estimated pi_hat was 0.1.

To study genetic structure, we estimated genetic dissimilarity at the individual and population level. As individual measure we used the Hamming genetic distance estimator, which we calculated with the R package poppr (Kamvar et al., 2015). The Hamming genetic distance measure is simply the inverse of the proportion of alleles that are shared (i.e., that are Identical-by-State). For dissimilarity at the population level, we calculated the fixation index F_{ST} (Weir and Cockerham, 1984) with the R package StAMPP (Pembleton *et al.,* 2013). The F_{ST} estimator used by this program is accurate even when sample size is small (minimally 5 individuals), provided that the number of markers is large (~10,000 loci or more) and differentiation is weak ($F_{ST} < 0.10$) (Willing et al., 2012). Significance of F_{ST}-values was tested by bootstrapping loci 1,000 times (Pembleton et al., 2013). To study the main genetic partitioning among samples, we applied multidimensional reduction of the pairwise genetic distance matrices by use of PCoA (Principal Coordinate Analysis) as implemented in the R package Ape (Paradis et al., 2004). Furthermore, we evaluated the most likely number of clusters and estimated individual ancestry coefficients using the least-square method incorporated in the R package LEA (function 'snmf'; Frichot and Francois, 2015). We used the aforementioned PCoA and LEA ancestry analysis for direct gene flow estimationthrough the proportion of misassignments (Paetkau et al., 2004). The medium-density SNP dataset gave resolution to detect first generation hybrids. Hence, we calculated migration rates for the current and previous generation (i.e., parents). We calculated 95% confidence intervals around migration rates using the binomial distribution (R base package function 'binom.test').

To study inbreeding, we calculated Multilocus Heterozygosity. MLH estimates based on 10,000 or more SNPs correlates near to perfect with whole genome MLH estimations ($r^2 \approx 0.99$ from a ROH study on wolves (*Canis lupus*), by Kardos et al., 2018). In addition to MLH, we detected Runs of Homozygosity (ROHs). The fraction of the genome that contains ROHs (F_{ROH}) has been shown to be the best estimator for inbreeding (Keller et al., 2011; Kardos et al., 2015), especially when sample size is small (Gazal et al., 2014). Moreover, in contrast to other inbreeding estimators, this metric is comparable among different populations and species, provided that similar segment sizes and variation because of recombination rate are considered. Kardos et al. (2018) reported a high correlation between F_{ROH} estimates based on whole-genome sequences and estimates based on 10,000 SNP markers. Nevertheless, SNP estimations of F_{ROH} tend to be biased upwards. Specifically, for whole genome sequence F_{ROH} values of 0.0625, SNP based F_{ROH} estimates ranged from 0.05 to 0.10; for whole genome sequences F_{ROH} values of 0.125, SNP based F_{ROH} estimates ranged from 0.10 to 0.20. Following recommendations of Howrigan et al. (2011) we defined the number and length of ROHs with PLINK1.9 as a tract of at least 50 completely homozygous, moderately pruned SNPs (i.e., LD $r^2 > 0.5$, heterozygote loci not allowed); 50 such SNPs is equivalent to approximately 5 Mb. We restricted ourselves to quantification of ROHs longer than 5Mb, so as to minimize the chance of false positives (Howrigan et al., 2011; Kardos et al., 2018). Following McQuillan et al. (2008) and Keller et al. (2011) we distinguished ROHs of > 20 Mb, 10–20 Mb, and 5–10 Mb. Given that the length of ROHs is related to the number of generations since the shared ancestor as 1/2 g M, with g and M representing generations and Morgan, respectively (Howrigan et al., 2011), and assuming that 1 Morgan ≈ 1 Mb, these classes roughly correspond with a shared ancestor < 2, 2–5, and 5–10 generations ago (Ceballos et al., 2018).

RESULTS

Genetic Structure

PCoA and ancestry analyses showed that the Dutch red deer populations formed discrete genetic clusters, with little to no gene flow (**Figures 2B,D,3**). Deer of the same source populations had distinct ordination scores and ancestry coefficients. For all population comparisons, F_{ST}-values were significantly different from zero, and ranged from 0.04 to 0.15, with the highest values observed in the Veluwe estate populations ($P = 0.001$; **Supplementary Table 2**).

Nevertheless, an apparent scattered (rather than a clumped) ordination for deer of the rewilding Oostvaardersplassen population as well as the relic Veluwezoom population occurred (**Figure 2B**). Oostvaardersplassen deer had relatively high within-population genetic distances, as well as strong variation in genetic distances to other populations (**Supplementary Figure 3A**) – the latter causing the scatter (**Supplementary Figure 3A**). In the relic Veluwezoom population, in contrast, deer were genetically similar to each other (low within-population genetic distances), and strongly dissimilar to deer of other populations (high among-population genetic distances) (**Supplementary Figure 3B**). Here, the scatter was caused by variation in both the within-population genetic distances (low vs. very low) as well as in the among-population genetic distances (high vs. very high) – as illustrated in **Supplementary Figure 3D**. Furthermore, whereas genomes of deer of Oostvaardersplassen were characterized by a high proportion of heterozygote genotypes, genomes of deer of Veluwezoom had high proportion of genotypes that were homozygous for the major or minor allele (**Supplementary Figure 3E**). Hence, the scattered ordination of the Oostvaardersplassen and Veluwezoom population were caused by contrasting genetic properties.

Despite the existence of genetic clusters within the Veluwe area, there was a single animal with a dispersal history among

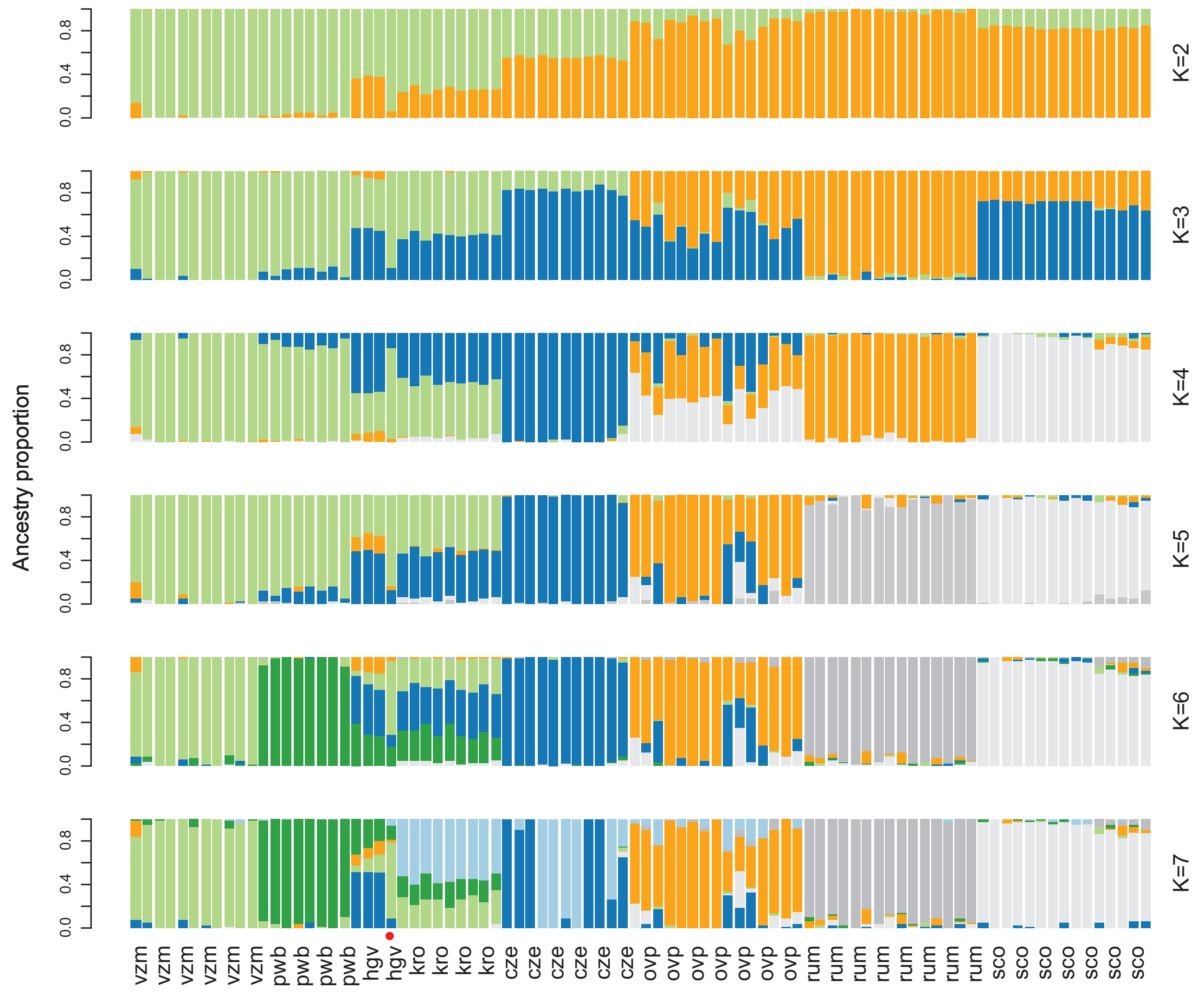

FIGURE 3 | Ancestry analysis of red deer focal and reference populations, at $K = 2$ to $K = 7$. The most likely number of K clusters lies within the range 2 to 4 (**Supplementary Figure 6**). Each vertical bar represents one individual. The red dot indicates the putative migrant. Population abbreviations and sample sizes are as follows: Of the autochthonous relic populations: vzm, Veluwezoom (11); pwb, Planken Wambuis (8); of the allochthonous estate populations: hgv, Hoge Veluwe (4) and kro, Kroondomeinen (9), of the allochthonous rewilding population: ovp, Oostvaardersplassen (15); and the reference populations: cze, Czechia (11), rum, Isle of Rum (15), sco, mainland of Scotland (15). For populations with more than 15 samples, 15 individuals were randomly selected.

the neighboring deer populations of the Veluwe: this animal was sampled within the estate Hoge Veluwe, but had a genetic signature in between its source population and the relic population Veluwezoom (based on the first two axes of PCoA of Veluwe deer, **Figure 2D**, and the ancestry analysis, **Figure 3**). Most probably, this individual was the first generation offspring of a disperser. None of the other 34 Veluwe samples indicated dispersal events. Considering zero dispersal events of 35 sampled deer, and one dispersal events of 70 parents, the estimated migration rate was 0.009 (95% CI: 0.000 – 0.052, Binomial exact calculation).

PCoA and ancestry analysis showed that the genetic clusters of Dutch red deer had diverse ancestry. First, the allochthonous Oostvaardersplassen population had higher genetic similarity to Scottish and Czechian reference populations than to other Dutch populations (**Figures 2B**, **3**). The Oostvaardersplassen population additionally showed a high degree of within-population heterogeneity (high within-population Hamming genetic distance, **Supplementary Figures 2, 3**; and scattered ordination, **Figure 2B**). Indeed, some individuals were most similar to deer from other populations (**Supplementary Figure 4**). Second, the autochthonous and allochthonous deer of the Veluwe had a partially shared genetic ancestry (**Figure 3**; green cluster). A signal of allochthonous ancestry also occurred—the allochthonous estate populations were genetically more similar to each other than to surrounding autochthonous relic populations (PCoA; **Figures 2B,D**). The allochthonous estate populations had high ancestry scores for the genetic cluster allocated to the Czechia reference population (**Figure 3**; blue cluster). This genetic signature was small or absent in the autochthonous relic populations Planken Wambuis and Veluwezoom, respectively.

Inbreeding

We observed strong variation in the Multilocus heterozygosity (MLH) of red deer of Netherlands. The most heterozygous individual (maximum MLH = 0.40, from the allochthonous rewilding population) had a 54% higher MLH than the least heterozygous individual (minimum MLH = 0.26, from the autochthonous relic population). Median multilocus heterozygosity differed significantly among the Dutch red deer populations (**Figure 4A**; Kruskal Wallis $\chi^2 = 100.4$, d.f. = 7, $P < 0.001$). Deer from the autochthonous relic populations had a lower median MLH than deer from both the allochthonous

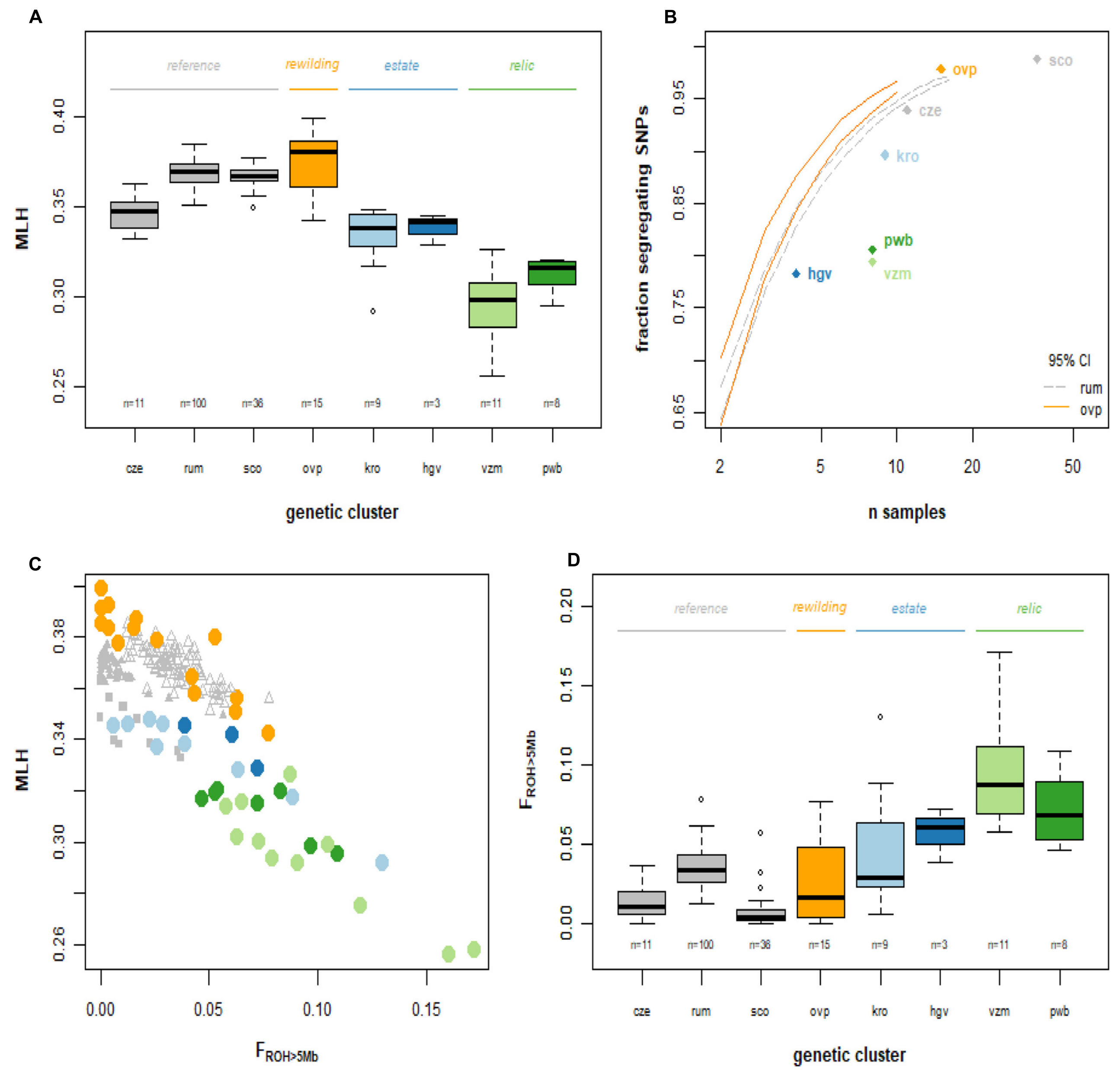

FIGURE 4 | Genetic diversity of the red deer study populations. Abbreviations as in **Figures 1**, **2**. **(A)** Boxplot of observed multilocus heterozygosity. **(B)** Fraction of monomorphic SNPs, at population level, in relation to sample size. The relic populations of the Veluwe have relatively many monomorphic SNPs. Lines represent the bootstrapped 95% confidence intervals for Rum (dashed gray line) and the allochthonous Oostvaardersplassen (unbroken, orange line) deer populations (i.e., rarefaction curves). **(C)** Individual F_{ROH} vs. multilocus observed heterozygosity. F_{ROH} is the genomic fraction of all ROHs longer than 5 Mb. **(D)** Fraction of the genome containing ROH segments > 5 Mb, per individual, grouped over genetic clusters. ROH segments with a length of 5 Mb stem from a common ancestor of maximum 10 generations ago.

rewilding and estate populations, and also lower than deer from European reference populations (Wilcoxon rank pairwise comparison test, $P < 0.001$, **Supplementary Table 3**). Among the allochthonous populations, deer from the estate populations had lower median MLH than the rewilding population, and also lower than the two Scottish populations. Furthermore, the autochthonous relic populations, and to a lesser degree also the allochthonous estate populations, had a high proportion of non-segregating SNPs (**Figure 3B**).

Multilocus heterozygosity was strongly and positively correlated with the fraction of the genome containing ROH segments larger than 5Mb ($F_{ROH > 5Mb}$; **Figure 3C**; Spearman rank correlation, r_s = -0.54, d.f. = 256, $P < 0.001$). Among the red deer populations of Netherlands, there were significant differences in $F_{ROH > 5Mb}$ (Kruskal Wallis $\chi^2 = 106.1$, d.f. = 7, $P < 0.001$; **Figure 3D**). Notwithstanding substantial individual variation (with maximum $F_{ROH > 5Mb}$ of 0.08), the rewilding population had the lowest median $F_{ROH > 5Mb}$ values. Conversely, red deer of the autochthonous relic populations had a significantly higher median $F_{ROH > 5Mb}$ than the allochthonous rewilding population as well as European reference populations (Wilcoxon rank pairwise comparison test, $P < 0.05$; **Supplementary Table 4** and **Supplementary Figure 5**). Red deer of these two relic populations had a minimum $F_{ROH > 5Mb}$ of 0.05, and a median $F_{ROH > 5Mb}$ of 0.07 (Planken Wambuis) and 0.09 (Veluwezoom). Most of the detected FROH segments had a length of 5–10 Mb, corresponding to a shared ancestor 5–10 generations back in time (**Supplementary Figure 5**). Despite having few individuals with high $F_{ROH > 5Mb}$, the median $F_{ROH > 5Mb}$ of the allochthonous rewilding and estate deer populations did not differ from reference populations.

DISCUSSION

Using genome-wide SNP analysis we showed that because of historic and contemporary human impacts, red deer populations of Netherlands differ greatly, and sometimes unexpectedly, in genetic composition. Population isolation (because of anthropogenic barriers) and translocation resulted in adjacent red deer populations having little gene flow and, consequently, discrete genetic clusters with diverse ancestry. Concurrently, red deer populations were shown to vary widely in genetic diversity. In particular, autochthonous relic populations were substantially inbred, despite their relatively large contemporary population size. Altogether, the genetic landscape of red deer of Netherlands can be characterized as a complex mosaic of patches with distinct, uncorrelated properties.

The findings illustrate the substantial distortion that humans can cause to the natural spatial pattern of genetic variation of red deer specifically and ungulates in general. Earlier microsatellite studies indicated that historic and contemporary anthropogenic interventions affect the genetic diversity of red deer populations in, inter alia, Scotland, Iberia, Belgium and Germany (Nussey et al., 2006; Pérez-Espona et al., 2013; Queiros et al., 2014; Hoffmann et al., 2016; Frantz et al., 2017). Recently, there has been a growing attention on the effects of translocation for genetic variation in ungulates (e.g., Iacolina et al., 2018; Gille et al., 2019; Jahner et al., 2019). Our SNP study on the main extant red deer populations of the human-dominated and fine-grained landscape of Netherlands, improves the resolution of our understanding of the human-caused alteration of the genetic landscape. We demonstrate that the genetic differences among deer populations come in the form of sharp discontinuities, and at a spatial scale much smaller than typical male red deer dispersal distances (around 10 km and up to 50 km, Pérez-Espona et al., 2008). This is in contrast to a recent study on red deer and wild boar in the human-dominated landscape of Belgium (Frantz et al., 2017). The study of Frantz et al. (2017) was based on many (thousands) individuals, but few (tens) of markers – the opposite of the study design of our research. Next to showing fine-scale genetic structure, we are the first to apply Runs of Homozygosity as a means to assess genetic effects of human interventions on red deer, revealing hitherto unnoticed substantial inbreeding. Given that in a preceding microsatellite study (Groot et al., 2016) other red deer populations of Northwestern Europe (not included in this research) had much lower levels of genetic diversity than Dutch populations, we presume that SNP genotyping of other red deer populations will reveal similar or even higher levels of inbreeding.

The observed substantial distortion of the genetic landscape of the Dutch red deer populations highlights the limitations of landscape genetics null models of panmixia (gene flow is ubiquitous), Isolation by Distance (gene flow decreases over geographic distance), and even Isolation by Resistance (gene flow is impeded by barriers) (Manel et al., 2003) for managed ungulate populations. None of these models captures the gene flow patterns of populations that are fragmented, because of human interventions, but also supplemented through translocation, practices common for the management of many ungulates (Seddon et al., 2012), prompting the need for the development of specific approaches.

The relevance of historical human interventions was highlighted by our finding that alterations of the genetic landscape may be long-lasting. In the Veluwe the height of the anthropogenic impact is therefore long past. Bottleneck and translocation events date back to beginning of the 20th century, which, assuming a generation time of 7 years (Coulson et al., 1998) is 14 deer generations in the past. Before this study we therefore assumed that gene flow between the putative Veluwe autochthonous and allochthonous Veluwe populations would have resulted in homogenization. This would predict that presently there should be little genetic structure, and that levels of genetic variation would be similar between subpopulations by now. The detected migrant offspring provided evidence that gene flow is not absent., The allochthonous estate populations, however, were shown to still have low genetic similarity to adjacent autochthonous populations. The partial shared ancestry indicates that there has been some admixture between the estate and relic populations (possibly because of few occasional breakouts, for example during World War II, Rijk and Pelzers (1991)), but that at large fences around estates have prevented gene flow and admixture, and hence have maintained the segregation of allochthonous estate and autochthonous relic populations. The significance of this finding is that anthropogenic barriers do not merely cause genetic differentiation – they also may preserve the signatures of historical anthropogenic interventions. Hence, in landscapes with anthropogenic barriers, historic anthropogenic effects on ungulates may be maintained much longer than anticipated.

The implication of our study is that present-day abundance and distribution is a poor predictor of the genetic status of ungulates. The autochthonous relic Veluwezoom population is a good case in point. This population is currently the largest of all the Veluwe subpopulations sampled (spring census since 2000: more than 700 animals; Spek, 2014). Moreover, because of highway overpasses this area should be well connected to the other Veluwe subpopulations. Nevertheless, all diversity indicators show this population to be the most isolated and most inbred. We thus posit that the poor genetic status is a legacy of the historic bottleneck combined with an effective absence of genetic exchange. When we shared our findings about inbreeding with them, managers of the Veluwezoom red deer population were surprised. After all, the main bottleneck is thought to have occurred approximately one century ago, though is poorly documented (Rijk and Pelzers, 1991). Even recent demographic events may quickly be forgotten, as we realized when we contacted a retired employee to discover the origin of the founders of the Oostvaardersplassen red deer population (established early 1990s). Furthermore, the management of the autochthonous Veluwe populations was attempting to follow best conservation genetic practices. The management was not aware that conservation geneticists have recently altered the recommendation of minimum inbreeding effective population size to 100 (Frankham et al., 2014). Second, the management was advised an optimistic Ne/Nc-ratio of 0.33 - a ratio universally adopted by ungulate managers in Netherlands (Groot Bruinderink et al., 2000; Spek, 2014), but one that does not account for historic bottlenecks (Vucetich et al., 1997).

A complicating factor is that genetic consequences of historic anthropogenic impacts may be strong yet difficult to detect. In the autochthonous relic populations Veluwezoom and Planken Wambuis the median observed values of $F_{ROH} > 5$ Mb were larger than 0.0625. Using medium-density SNP data, we may have slightly overestimated $F_{ROH} > 5$ Mb (see section "MATERIALS AND METHODS"). The F_{ROH} values are above levels expected for offspring of third order relatives, and among the highest reported for a non-insular ungulate population (Hasselgren and Norén, 2019). Such a level of inbreeding was associated with lowered survival and reproductive performance (lowered calf survival on the Isle of Rum, reduced ibex population growth; Walling et al., 2011; Huisman et al., 2016; Bozzuto et al., 2019). In red deer, inbreeding also may be expressed through the occurrence of overbites (shortened lower jaw, or brachygnathy; Zachos et al., 2007). Typically however, inbreeding depression effects (if any) are subtle, and conditional on stressful environments (Keller and Waller, 2002; Pemberton et al., 2016). Phenotypically, deer of the relic inbred Veluwezoom population do not show signs of inbreeding depression. The population has a high growth rate, deer appear to be in good condition, and health issues are not reported (Spek, 2014). Furthermore, even the preceding microsatellite study, involving nine molecular markers, had not detected inbreeding (Groot et al., 2016).

Our study also pinpointed the dilemma between inbreeding and outbreeding. In the introduced deer of the rewilding area Oostvaardersplassen, we detected inbreeding as well as admixture within the same population, and even in genomes of the same individual. In addition, the finding that autochthonous and allochthonous populations are still differentiated and have different genetic ancestry, shows that in areas with a population translocation history, the option of alleviating inbreeding through facilitation of gene flow would lead to admixture. We agree with the current consensus among conservation geneticists that inbreeding should be treated with more concern than outbreeding (Bell et al., 2019). Nontheless, for ungulates the natural spatial genetic structure is substantially affected by fragmentation and translocation, and may, peculiarly, be further altered by defragmentation measures. In the Veluwe, where interpopulation phenotypic differences are allegedly persistent (**Figure 1**), it is not unlikely that such admixture will affect antler size and shape of autochthonous populations, and thus have more conspicuous phenotypic effects than inbreeding (though not negative). A potential scenario is swamping of allochthonous genetic variation into the gene pool of autochthonous deer (Bell et al., 2019). Irrespective of whether such phenotypic variation is adaptive in many ungulates, managers may influence the genetic integrity and phenotypic traits such as the shape of horns and antlers and coat coloration. The recent rewilding movement has embraced the concept of ecological substitutes, thereby implicitly ignoring intra- and interspecific phenotypic variation (Lorimer et al., 2015). Yet, many translocations of ungulates have been and are being dictated by aesthetic considerations (Seddon et al., 2012), thereby deliberately modifying local phenotypic variation. The consequence is potential disruption of local adaptation, and homogenization of geographic variation (Gippoliti et al., 2018; Kolodny et al., 2019).

The multitude and diversity of anthropogenic impacts and the consequential genetic complex of the genetic landscape pose a challenge for ungulate managers to effectively account for inbreeding and outbreeding consequences. We argue that for ungulate populations historically and presently subject to anthropogenic impact (i) genetic variation cannot be inferred from contemporary distribution and abundance, and (ii) assessment of genetic status is necessary to enable appropriate management. Given that genetic variation may bear the 'marks' of unknown or underestimated anthropogenic effects in the past, we recommend managers of ungulate populations to start with a baseline-assessment of standing genetic variation using modern genomic approaches. Ungulate managers may imagine they can slow down loss of genetic variation sufficiently in a population by ensuring high population census size (with little fluctuation, equal sex ratio, etc.) and by connecting subpopulations in the landscape. Historical impacts on population demography, however, may have had such adverse effects that these positive interventions do not suffice and the poor genetic status of a population is not alleviated (at least not on a time scale of decades). Conversely, managers may be unaware of the presence and extent of allochthonous genetic ancestry, and hence of the potential admixture and homogenization effects of their interventions. For genetic monitoring purposes, we recommend the use of genome-wide SNP data or, if affordable, whole genome sequences. The relatively high costs may, at the present, still constrain sample size and cause a trade-off between population coverage and individual width. Yet, as illustrated by our study, SNP data enable the determination of fine-scale genetic structure, the direct estimation of migration rates, and the precise assessment of genetic status. In particular, genomic approaches facilitate the use of accurate, individual-based measures (e.g., MLH, F_{ROH}), rather than indirect measures that are equilibrium-based and averaged over populations (e.g., population-level heterozygosity with a few loci, allelic richness). The high levels of inbreeding in the autochthonous red deer populations underline the argument that continuation to ignore genetic factors may severely hamper conservation efforts. We advocate that genetic monitoring has to be made integral to ungulate management and policy making.

In our study we illustrate that genetic variation of present-day ungulates is much affected by ongoing and historic human interventions, and put forward that this likely effects ecological interactions as well. Whereas fragmentation and the associated loss of genetic variation may reduce adaptive potential to future environmental change, translocation possibly causes distortion of ongoing local adaptation processes. A first step towards understanding the ecology of present-day ungulate populations of human-dominated landscapes is therefore a genetic investigation of the often unknown and complex demographic history.

DATA AVAILABILITY STATEMENT

The data are located on the Dryad repository: https://doi.org/10.5061/dryad.hqbzkh1dp.

ETHICS STATEMENT

Samples of deer of Isle of Rum were collected and used following approval of the Animal Welfare and Ethical Review Body of the University of Edinburgh, and under appropriate United Kingdom Home Office licenses (Johnston et al., 2017). For the other deer samples, an ethical review process was not required, because samples were collected from deer already culled as part of population management programs. The samples of mainland Scotland were collected by hunters of the Forestry Commission Scotland. Red deer samples of Netherlands were collected from animals culled as part of population control programs regulated by Faunabeheereenheid Gelderland and Faunabeheereenheid Flevoland. In Czechia, samples were collected from deer culled according to the law No. 449/2001 Sb. Hence, in Czechia, Netherlands, and Mainland Scotland no animal was specifically killed for this research.

AUTHOR CONTRIBUTIONS

JJ, PH, H-JM, LI, RY, SW, and HP contributed to the conception and design of the study. GG, LB, JH, and JP provided samples. RC coordinated the laboratory genetic analysis. JJ performed the statistical analysis, in consultation with PH, H-JM, JH, JP, RY, SW, and HP. JJ wrote the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

FUNDING

This research was funded by 'Stichting De Eijk,' the 'Koninklijke Nederlandse Jagervereniging,' and by 'BIJ12'. Genotyping of the Rum and Mainland Scotland samples was funded by an ERC grant to JP.

ACKNOWLEDGMENTS

The photos of red deer antlers of estates and relic populations is mediated by the park management of National Park Hoge Veluwe. Furthermore, we are thankful for insightful discussions with wildlife managers of the estate populations Kroondomeinen and National Park Hoge Veluwe, and the relic populations Veluwezoom and Planken Wambuis.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.535715/full#supplementary-material

REFERENCES

Anderson, C. A., Pettersson, F. H., Clarke, G. M., Cardon, L. R., Morris, A. P., and Zondervan, K. T. (2010). Data quality control in genetic case-control association studies. *Nat. Protoc.* 5, 1564–1573. doi: 10.1038/nprot.2010.116

Bell, D. A., Robinson, Z. L., Funk, W. C., Fitzpatrick, S. W., Allendorf, F. W., Tallmon, D. A., et al. (2019). The exciting potential and remaining uncertainties of genetic rescue. *Trends Ecol. Evol.* 34, 1070–1079. doi: 10.1016/j.tree.2019.06.006

Bérénos, C., Ellis, P. A., Pilkington, J. G., and Pemberton, J. M. (2016). Genomic analysis reveals depression due to both individual and maternal inbreeding in a free-living mammal population. *Mol. Ecol.* 25, 3152–3168. doi: 10.1111/mec.13681

Bozzuto, C., Biebach, I., Muff, S., Ives, A. R., and Keller, L. F. (2019). Inbreeding reduces long-term growth of Alpine ibex populations. *Nat. Ecol. Evol.* 3, 1359–1364. doi: 10.1038/s41559-019-0968-1

Brauning, R., Fisher, P. J., McCulloch, A. F., Smithies, R. J., Ward, J. F., Bixley, M. J., et al. (2015). Utilization of high throughput genome sequencing technology for large scale single nucleotide polymorphism discovery in red deer and Canadian elk. *bioRxiv* 1, 1. doi: 10.1101/027318

Castelló, J. R. (2016). *Bovids of the World.* Princeton, NJ: Princeton University Press.

Ceballos, F. C., Joshi, P. K., Clark, D. W., Ramsay, M., and Wilson, J. F. (2018). Runs of homozygosity: windows into population history and trait architecture. *Nat. Rev. Genet.* 19, 220–234. doi: 10.1038/nrg.2017.109

Coulson, T., Kruuk, L. E. B., Tavecchia, G., Pemberton, J. M., and Clutton-Brock, T. H. (2003). Selection on neonatal traits in red deer. *Evolution* 57, 2879–2892. doi: 10.1111/j.0014-3820.2003.tb01528.x

Coulson, T. N., Pemberton, J. M., Albon, S. D., Beaumont, M., Marshall, T. C., Slate, J., et al. (1998). Microsatellites reveal heterosis in red deer. *Proc. Biol. Sci.* 22, 489–495. doi: 10.1098/rspb.1998.0321

Deinet, S., Ieronymidou, C., Burfield, I. J., Foppen, R. P., Collen, B., and Böhm, M. (2013). *Wildlife Comeback in Europe: The Recovery of Selected Mammal and Bird Species*. London: ZSL.

Edmands, S. (2007). Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding depression for conservation and management. *Mol. Ecol.* 16, 463–475. doi: 10.1111/j.1365-294x.2006.03148.x

Flueck, W. T., and Smith-Flueck, J. M. (2011). Intraspecific phenotypic variation in deer: the role of genetic and epigenetic processes. *Anim. Prod. Sci.* 51, 365–374. doi: 10.1071/an10169

Frankham, R., Ballou, J. D., Eldridge, M. D. B., Lacy, R. C., Ralls, K., Dudash, M. R., et al. (2011). Predicting the probability of outbreeding depression. *Conserv. Biol.* 25, 465–475. doi: 10.1111/j.1523-1739.2011.01662.x

Frankham, R., Bradshaw, C. J. A., and Brook, B. W. (2014). Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biol. Conserv.* 170, 56–63. doi: 10.1016/j.biocon.2013.12.036

Frantz, A. C., Zachos, F. E., Bertouille, S., Eloy, M. C., Colyn, M., and Flamand, M. C. (2017). Using genetic tools to estimate the prevalence of non-native red deer (*Cervus elaphus*) in a western European population. *Ecol. Evol.* 7, 7650–7660. doi: 10.1002/ece3.3282

Frichot, E., and Francois, O. (2015). LEA: an R package for landscape and ecological association studies. *Methods Ecol. Evol.* 6, 925–929. doi: 10.1111/2041-210x.12382

Gazal, S., Sahbatou, M., Perdry, H., Letort, S., Genin, E., and Leutenegger, A. L. (2014). Inbreeding coefficient estimation with dense SNP data: comparison of strategies and application to HapMap III. *Hum. Hered.* 77, 49–62.

Geist, V. (1998). *Deer of the World*. Mechanicsburg, PA: Stackpole Book.

Gille, D. A., Buchalski, M. R., Conrad, D., Rubin, E. S., Munig, A., Wakeling, B. F., et al. (2019). Genetic outcomes of translocation of bighorn sheep in Arizona. *J. Wildl. Manage.* 83, 838–854. doi: 10.1002/jwmg.21653

Gippoliti, S., Cotterill, F. P. D., Groves, C. P., and Zinner, D. (2018). Poor taxonomy and genetic rescue are possible co-agents of silent extinction and biogeographic homogenization among ungulate mammals. *Biogeographia* 33, 41–54.

Groot, G. A. D., Spek, G. J., Bovenschen, J., Laros, I., Meel, T. V., and Jansman, H. A. H. (2016). *Herkomst en Migratie van Nederlandse Edelherten en Wilde Zwijnen: een Basiskaart van de Genetische Patronen in Nederland en Omgeving*. Wageningen.

Groot Bruinderink, G. W. T. A., Lammertsma, D. R., and Pouwels, R. (2000). *De geschiktheid van Natuurgebieden in Noord-Brabant en Limburg als Leefgebied voor Edelhert en Wild Zwijn*. Wageningen: Research Instituut voor de Groene Ruimte.

Grossen, C., Biebach, I., Angelone-Alasaad, S., Keller, L. F., and Croll, D. (2018). Population genomics analyses of European ibex species show lower diversity and higher inbreeding in reintroduced populations. *Evol. Appl.* 11, 123–139. doi: 10.1111/eva.12490

Grossen, C., Guillaume, F., Keller, L. F., and Croll, D. (2019). Accumulation and purging of deleterious mutations through severe bottlenecks in ibex. *bioRxiv* [Preprint]. doi: 10.1101/605147

Harris, K., Zhang, Y., and Nielsen, R. (2019). Genetic rescue and the maintenance of native ancestry. *Conserv. Genet.* 20, 59–64. doi: 10.1007/s10592-018-1132-1

Hasselgren, M., and Norén, K. (2019). Inbreeding in natural mammal populations: historical perspectives and future challenges. *Mamm. Rev.* 49, 369–383. doi: 10.1111/mam.12169

Hoban, S., Hauffe, H., Perez-Espona, S., Arntzen, J. W., Bertorelle, G., Bryja, J., et al. (2013). Bringing genetic diversity to the forefront of conservation policy and management. *Conserv. Genet. Resour.* 5, 593–598. doi: 10.1007/s12686-013-9859-y

Hoffmann, G. S., Johannesen, J., and Griebeler, E. M. (2016). Population dynamics of a natural red deer population over 200 years detected via substantial changes of genetic variation. *Ecol. Evol.* 6, 3146–3153. doi: 10.1002/ece3.2063

Howrigan, D. P., Simonson, M. A., and Keller, M. C. (2011). Detecting autozygosity through runs of homozygosity: a comparison of three autozygosity detection algorithms. *BMC Genomics* 12:460. doi: 10.1186/1471-2164-12-460

Huisman, J., Kruuk, L. E. B., Ellis, P. A., Clutton-Brock, T., and Pemberton, J. M. (2016). Inbreeding depression across the lifespan in a wild mammal population. *Proc. Natl. Acad. Sci. U.S.A.* 113, 3585–3590. doi: 10.1073/pnas.1518046113

Iacolina, L., Corlatti, L., Buzan, E., Safner, T., and Šprem, N. (2019). Hybridization in European ungulates: a review of the current status, causes and consequences. *Mamm. Rev.* 49, 45–59. doi: 10.1111/mam.12140

Iacolina, L., Pertoldi, C., Amills, M., Kusza, S., Megens, H. J., Bâlteanu, V. A., et al. (2018). Hotspots of recent hybridization between pigs and wild boars in Europe. *Sci. Rep.* 8:17372.

IUCN/SSC (2013). *Guidelines for Reintroductions and Other Conservation Translocations. Version* 1.0. Gland: IUCN Species Survival Commission.

Jahner, J. P., Matocq, M. D., Malaney, J. L., Cox, M., Wolff, P., Gritts, M. A., et al. (2019). The genetic legacy of 50 years of desert bighorn sheep translocations. *Evol. Appl.* 12, 198–213. doi: 10.1111/eva.12708

Johnston, S. E., Huisman, J., Ellis, P. A., and Pemberton, J. M. (2017). A high density linkage map reveals sexual dimorphism in recombination landscapes in red deer (*Cervus elaphus*). *G3* 7, 2859–2870. doi: 10.1534/g3.117.044198

Jombart, T., and Ahmed, I. (2011). adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* 27, 3070–3071. doi: 10.1093/bioinformatics/btr521

Kamvar, Z. N., Brooks, J. C., and Grünwald, N. J. (2015). Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Front. Genet.* 6:208. doi: 10.3389/fgene.2015.00208

Kardos, M., Åkesson, M., Fountain, T., Flagstad, Ø., Liberg, O., Olason, P., et al. (2018). Genomic consequences of intensive inbreeding in an isolated wolf population. *Nat. Ecol. Evol.* 2, 124–131. doi: 10.1038/s41559-017-0375-4

Kardos, M., Luikart, G., and Allendorf, F. W. (2015). Measuring individual inbreeding in the age of genomics: marker-based measures are better than pedigrees. *Heredity* 115, 63–72. doi: 10.1038/hdy.2015.17

Keller, L. F., and Waller, D. M. (2002). Inbreeding effects in wild populations. *Trends Ecol. Evol.* 17, 230–241. doi: 10.1016/s0169-5347(02)02489-8

Keller, M. C., Visscher, P. M., and Goddard, M. E. (2011). Quantification of inbreeding due to distant ancestors and its detection using dense single nucleotide polymorphism data. *Genetics* 189, 237–249. doi: 10.1534/genetics.111.130922

Kolodny, O., McLaren, M. R., Greenbaum, G., Ramakrishnan, U., Feldman, M. W., Petrov, D., et al. (2019). Reconsidering the management paradigm of fragmented populations. *bioRxiv* [Preprint]. doi: 10.1101/649129

Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F., and Clutton-Brock, T. (2002). Antler size in red deer: heritability and selection but no evolution. *Evolution* 56, 1683–1695. doi: 10.1111/j.0014-3820.2002.tb01480.x

Linnell, J. D. C., and Zachos, F. E. (2011). "Status and distribution patterns of European ungulates: genetics, population history and conservation," in *Ungulate Management in Europe: Problems and Practices*, eds R. Putman, M. Apollonio, and R. Andersen (Cambridge: Cambridge University Press), 12–53. doi: 10.1017/cbo9780511974137.003

Lorimer, J., Sandom, C., Jepson, P., Doughty, C. E., Barua, M., and Kirby, K. J. (2015). Rewilding: science, practice, and politics. *Annu. Rev. Environ. Resour.* 40, 39–62. doi: 10.1146/annurev-environ-102014-021406

Manel, S., Schwartz, M. K., Luikart, G., and Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* 18, 189–197. doi: 10.1016/s0169-5347(03)00008-9

Marshall, T. C., and Spalton, J. A. (2000). Simultaneous inbreeding and outbreeding depression in reintroduced Arabian oryx. *Anim. Conserv.* 3, 241–248. doi: 10.1111/j.1469-1795.2000.tb00109.x

Martchenko, D., Prewer, E., Latch, E. K., Kyle, C. J., and Shafer, A. B. A. (2018). "Population genomics of ungulates," *Population Genomics*, ed. O. P. Rajora (Cham: Springer).

McQuillan, R., Leutenegger, A.-L., Abdel-Rahman, R., Franklin, C. S., Pericic, M., Barac-Lauc, L., et al. (2008). Runs of homozygosity in European populations. *Am. J. Hum. Genet.* 83, 359–372.

Moodley, Y., and Bruford, M. W. (2007). Molecular biogeography: towards an integrated framework for conserving pan-African biodiversity. *PLoS One* 2:e454. doi: 10.1371/journal.pone.0000454

Mystkowska, E. T. (1966). Morphological variability of the skull and body weight of the red deer. *Acta Theriol.* 11, 129–194. doi: 10.4098/at.arch.66-5

Nussey, D. H., Pemberton, J., Donald, A., and Kruuk, L. E. B. (2006). Genetic consequences of human management in an introduced island population of red deer (*Cervus elaphus*). *Heredity* 97, 56–65. doi: 10.1038/sj.hdy.6800838

Paetkau, D., Slade, R., Burden, M., and Estoup, A. (2004). Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Mol. Ecol.* 13, 55–65. doi: 10.1046/j.1365-294x.2004.02008.x

Paradis, E., Claude, J., and Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290. doi: 10.1093/bioinformatics/btg412

Pekkala, N., Knott, K. E., Kotiaho, J. S., Nissinen, K., and Puurtinen, M. (2014). The effect of inbreeding rate on fitness, inbreeding depression and heterosis over a range of inbreeding coefficients. *Evol. Appl.* 7, 1107–1119. doi: 10.1111/eva.12145

Pemberton, J. M., Ellis, P. E., Pilkington, J. G., and Bérénos, C. (2016). Inbreeding depression by environment interactions in a free-living mammal population. *Heredity* 118, 64–77. doi: 10.1038/hdy.2016.100

Pembleton, L. W., Cogan, N. O., and Forster, J. W. (2013). StAMPP: an R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Mol. Ecol. Resour.* 13, 946–952. doi: 10.1111/1755-0998.12129

Pérez-Espona, S., Hall, R. J., Pérez-Barbería, F. J., Glass, B. C., Ward, J. F., and Pemberton, J. M. (2013). The impact of past introductions on an iconic and economically important species, the red deer of Scotland. *J. Hered.* 104, 14–22. doi: 10.1093/jhered/ess085

Pérez-Espona, S., Pérez-Espona, F. J., McLeod, J. E., Jiggins, C. D., Gordon, I. J., and Pemberton, J. M. (2008). Landscape features affect gene flow of Scottish highland red deer (*Cervus elaphus*). *Mol. Ecol.* 17, 981–996. doi: 10.1111/j.1365-294x.2007.03629.x

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., et al. (2007). PLINK: a toolset for whole-genome association and population-based linkage analysis. *Am. J. Hum. Genet.* 81, 559–575. doi: 10.1086/519795

Putman, R., and Flueck, W. T. (2011). Intraspecific variation in biology and ecology of deer: magnitude and causation. *Anim. Prod. Sci.* 51, 277–291. doi: 10.1071/an10168

Queiros, J., Vicente, J., Boadella, M., Gortazar, C., and Alves, P. C. (2014). The impact of management practices and past demographic history on the geneticdiversity of red deer (*Cervus elaphus*): an assessment of population and individual fitness. *Biol. J. Linn. Soc.* 111, 209–223. doi: 10.1111/bij.12183

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ralls, K., Ballou, J. D., Dudash, M. R., Eldridge, M. D. B., Fenster, C. B., Lacy, R. C., et al. (2018). Call for a paradigm shift in the genetic management of fragmented populations. *Conserv. Lett.* 11:e12412. doi: 10.1111/conl.12412

Rijk, J. D., and Pelzers, E. (1991). Geschiedenis van het edelhert in Nederland. *Het Edelhert* 26, 1–32. doi: 10.1007/978-94-011-9335-1_1

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., et al. (2015). Collapse of the world's largest herbivores. *Sci. Adv.* 1:e1400103. doi: 10.1126/sciadv.1400103

Rowe, S. J., Clarke, S. M., Van Stijn, T. C., Hyndman, D. L., Ward, J. F., McEwan, K. M., et al. (2015). Brief communication: developing genomic tools in the New Zealand deer industry. *Proc. N.Z. Soc. Anim. Prod.* 75, 91–93.

Seddon, P. J., Strauss, W. M., and Innes, J. (2012). "Animal translocations: what are they and why do we do them?," in *Reintroduction Biology: Integrating Science and Management*, eds J. G. Ewen, D. P. Armstrong, K. A. Parker, et al. (West Sussex: Wiley-Blackwell).

Senn, H. V., and Pemberton, J. M. (2009). Variable extent of hybridization between invasive sika (*Cervus nippon*) and native red deer (*C. elaphus*) in a small geographical area. *Mol. Ecol.* 18, 862–876. doi: 10.1111/j.1365-294x.2008.04051.x

Söderquist, P., Elmberg, J., Gunnarsson, G., Thulin, C. G., Champagnon, J., and Guillemain, M. (2017). Admixture between released and wild game birds: a changing genetic landscape in European mallards (*Anas platyrhynchos*). *Eur. J. Wildl. Res.* 63:98. doi: 10.1007/s10344-017-1156-8

Spek, G. J. (2014). *Faunabeheerplan grofwild FBE Gelderland 2014-2019*. Arnhem: Faunabeheereenheid Gelderland.

van den Hoorn, D. (1992). Sinds vele eeuwen weer edelherten buiten de Veluwe. *Het Edelhert* 27, 6–8.

Vitorino, L. C., Borges Souza, U. J., Jardim, T. P. F. A., and Ballesteros-Mejia, L. (2019). Towards inclusion of genetic diversity measures into IUCN assessments: a case study on birds. *Anim. Biodivers. Conserv.* 42, 317–335. doi: 10.32800/abc.2019.42.0317

Volodin, I. A., Nahlik, A., Tari, T., Frey, R., and Volodina, E. V. (2018). Rutting roars in native Pannonian red deer of Southern Hungary and the evidence of acoustic divergence of male sexual vocalization between Eastern and Western European red deer (*Cervus elaphus*). *Mamm. Biol.* 94, 54–65. doi: 10.1016/j.mambio.2018.10.009

Vucetich, J. A., Waite, T. A., and Nunney, L. (1997). Fluctuating population size and the ratio of effective to census population size. *Evolution* 51, 2017–2021. doi: 10.1111/j.1558-5646.1997.tb05123.x

Walling, C. A., Nussey, D. H., Morris, A., Clutton-Brock, T. H., Kruuk, L. E. B., and Pemberton, J. M. (2011). Inbreeding depression in red deer calves. *BMC Evol. Biol.* 11:318. doi: 10.1186/1471-2148-11-318

Wang, D., Yao, H., Li, Y., Xu, Y., Ma, X., and Wang, H. (2019). Global diversity and genetic landscape of natural populations and hatchery stocks of largemouth bass *Micropterus salmoides* across American and Asian regions. *Sci. Rep.* 9:16697. doi: 10.1038/s41598-019-53026-3

Weir, B. S., and Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* 38, 1358–1370. doi: 10.2307/2408641

Willing, E. M., Dreyer, C., and van Oosterhout, C. (2012). Estimates of genetic differentiation measured by F(ST) do not necessarily require large sample sizes when using many SNP markers. *PLoS One* 7:e42649. doi: 10.1371/journal.pone.0042649

Zachos, F., Althoff, C., Steynitz, Y., Eckert, I., and Hartl, G. (2007). Genetic analysis of an isolated red deer (*Cervus elaphus*) population showing signs of inbreeding depression. *Eur. J. Wildl. Res.* 53, 61–67. doi: 10.1007/s10344-006-0065-z

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 23 November 2020
doi: 10.3389/fevo.2020.564567

Pronounced Fidelity and Selection for Average Conditions of Calving Area Suggestive of Spatial Memory in a Highly Migratory Ungulate

Matthew D. Cameron[1,2]*, Kyle Joly[2], Greg A. Breed[1,3], Christa P. H. Mulder[1,3] and Knut Kielland[1,3]

[1] Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK, United States, [2] Gates of the Arctic National Park and Preserve, Arctic Inventory and Monitoring Network, National Park Service, Fairbanks, AK, United States, [3] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, United States

A distinguishing characteristic of many migratory animals is their annual return to distinct calving (birthing) areas in the spring, yet the navigational mechanisms employed during migration that result in this pattern are poorly understood. Effective conservation of these species requires reliable delineation of such areas, quantifying the factors that influence their selection, and understanding the underlying mechanisms resulting in use of calving areas. We used barren-ground caribou (*Rangifer tarandus granti*) as a study species and identified calving sites of the Western Arctic Herd in Alaska using GPS collar data from 2010–2017. We assessed variability in calving areas by comparing spatial delineations across all combinations of years. To understand calving area selection at a landscape scale, we performed a resource selection analysis comparing calving sites to available locations across the herd's range and incorporated time-varying, remotely sensed metrics of vegetation quality and quantity. We found that whereas calving areas varied from year to year, this annual variation was centered on an area of recurring attraction consistent with previous studies covering the last six decades. Calving sites were characterized by high-quality forage at the average time of calving, but not peak calving that year, and by a narrow range of distinct physiographic factors. Each year, calving sites were located on areas of above-average conditions based on our predictive model. Our findings indicate that the pattern of spring migration for pregnant females was to migrate to areas that consistently provide high-quality forage when averaged across years, and then upon arriving at this calving ground, refine selection using their perception of annually varying conditions that are driven by environmental stochasticity. We suggest that the well-documented and widespread pattern of fidelity to calving grounds by caribou is supportive of a navigational mechanism based on spatial memory at a broad scale to optimize foraging and energy acquisition at a critical life-history stage. The extent to which migrants depend on memory to reach their spring destinations has implications for the adaptability of populations to changing climate and human impacts.

Keywords: Alaska, calving grounds, caribou, migration, NDVI, *Rangifer tarandus*

OPEN ACCESS

Edited by:
Vernon Bleich,
University of Nevada, Reno,
United States

Reviewed by:
Inger Suzanne Prange,
Appalachian Wildlife Research
Institute, United States
Carl Soulsbury,
University of Lincoln, United Kingdom

****Correspondence:***
Matthew D. Cameron
matthew_cameron@nps.gov

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *12 June 2020*
Accepted: *30 October 2020*
Published: *23 November 2020*

Citation:
Cameron MD, Joly K, Breed GA,
Mulder CPH and Kielland K (2020)
Pronounced Fidelity and Selection
for Average Conditions of Calving
Area Suggestive of Spatial Memory
in a Highly Migratory Ungulate.
Front. Ecol. Evol. 8:564567.
doi: 10.3389/fevo.2020.564567

INTRODUCTION

Migration is a behavioral adaptation to seasonal environmental conditions and resource availability (Alerstam et al., 2003; Avgar et al., 2014). How animal movement relates to resource conditions is scale dependent (Bailey et al., 1996), such that movements within patches of resources (MacArthur and Pianka, 1966; Charnov, 1976) can scale up to landscape-scale use patterns and can result in the dramatic movements characteristic of migratory animals (Shaw and Couzin, 2013). A current challenge in the field of animal ecology is to understand the influence of the navigational mechanisms responsible for large-scale movements such as migration. These mechanisms broadly fall into two domains: perception-based movements, where animals follow immediately perceived resource gradients to track high-quality resources as they arise, or memory-based movements, where animals use previous experience to direct their movements to areas of high-quality resources outside of the immediately perceptible zone (Avgar et al., 2013; Fagan et al., 2013). Examples of perception-based movement include animals "surfing a green wave" of high-quality forage as it moves across a spatial gradient (van der Graaf et al., 2006; Merkle et al., 2016; Aikens et al., 2017), whereas memory-based movements are characterized by animals moving independently of proximal resource gradients and moving to distant areas of high-quality resources (Howery et al., 1999; Polansky et al., 2015; Bracis and Mueller, 2017). Because these navigational processes cannot be directly measured in wild animals, inferring their relative influence from movement data requires integrating empirical observations with theoretical and experimental findings (Fagan et al., 2013).

Spring migration of females in many migratory ungulate species culminates with parturition (hereafter calving), with females often aggregating on calving areas. Such species include blue wildebeest (*Connochaetes taurinus*; Estes, 1976), Tibetan antelope (*Pantholops hodgsonii*; Schaller et al., 2006), Saiga antelope (*Saiga tatarica*; Bekenov et al., 1998), and barren-ground caribou (*Rangifer tarandus*; Kelsall, 1968). Calving begins a period of heightened nutritional demand for pregnant females caused by the high energetic cost of lactation (Chan-McLeod et al., 1994). Owing to this demand, females are hypothesized to synchronize calving with periods of high vegetative quality (Oftedal, 1985; Miller-Rushing et al., 2010) and, indeed, selection for calving areas has been linked to vegetative productivity for some species [Tibetan antelope, Ganzorig et al., 2011; Mongolian gazelle (*Procapra gutturosa*), Leimgruber et al., 2001]. Spring vegetative productivity has also been positively associated with offspring condition (Pettorelli et al., 2005b, 2006). An alternative explanation for calving area selection is that females attempt to space away from predators (Bergerud, 1996; Creel et al., 2005), but testing the influence of these two hypotheses is often difficult.

Calving aggregations are typically highly vulnerable to human disturbance because a large percentage of the population is concentrated in relatively small areas at calving and anthropogenic influences can strongly alter female behavior (Nellemann and Cameron, 1998; Joly et al., 2004; Singh et al., 2010). Survival of neonates is a critical factor in population dynamics (Gaillard et al., 2000) and lactation performance directly affects offspring growth (White, 1992; Crête and Huot, 1993), meaning conservation of calving areas is likely a key component to managing these populations (Taillon et al., 2012). Considering that calving areas typically exhibit some level of annual variability (Lent, 1966; Skoog, 1968; Griffith et al., 2002), documenting annual use at decadal scales and understanding the mechanistic processes driving selection of these areas are critical for effective, long-term conservation (Singh and Milner-Gulland, 2011; Wilson et al., 2012). Understanding these processes before anthropogenic development has taken place is essential; inferences about calving selection after development has taken place will likely be confounded by risk effects and avoidance behavior, introducing potentially large and unknown biases to calving site selection (Harju et al., 2011).

To address these issues in a unified approach, we used migratory barren-ground caribou as a study species and investigated the use of calving areas across 8 years for the Western Arctic Herd (WAH) in Alaska, one of the largest caribou herds in the world. Barren-ground caribou are an excellent study species for this approach, for calving marks the destination of long-distance migration in the spring for pregnant females, which aggregate around calving and generally exhibit inter-annual fidelity to their calving grounds (Kelsall, 1968). We defined three scales of calving: individual calving sites in a given year (first scale) comprise an annual calving area (second scale), that in turn constitute a calving ground when considered across numerous years (third scale; **Figure 1**; Gunn and Miller, 1986). Our goals were to (1) document spatial trends in the calving areas of the WAH, (2) investigate the landscape-level factors influencing selection for calving sites to better understand the emergent spatial patterns of calving areas, and (3) interpret our findings to better understand what navigational mechanisms could explain the phenomenon of fidelity of caribou to their calving grounds. We hypothesized that if females exhibited primarily perception-based selection, calving sites would be characterized by low interannual consistency and track high-quality vegetation for each year. Alternatively, if selection were primarily memory-based, calving sites would be characterized by high interannual consistency and high-quality vegetation, as averaged across the study period, but not necessarily the best site in any given year.

MATERIALS AND METHODS

Study Species

The WAH utilizes over 350,000 km^2 of northwestern Alaska, typically migrating from wintering areas in the south, which vary by year and individual, to the calving ground and summer range in the north (**Figure 2**; Lent, 1966; Dau, 2015, Joly and Cameron, 2019). Calving generally occurs May 31–June 13 (Cameron et al., 2018). Beginning in 2009, GPS collars (Telonics, Mesa, AZ) were deployed annually on adult female caribou ($\geq$2years old) as they swam across the Kobuk River during fall migration (Dau, 1997; Joly et al., 2012). Captures were conducted using procedures approved by the State of

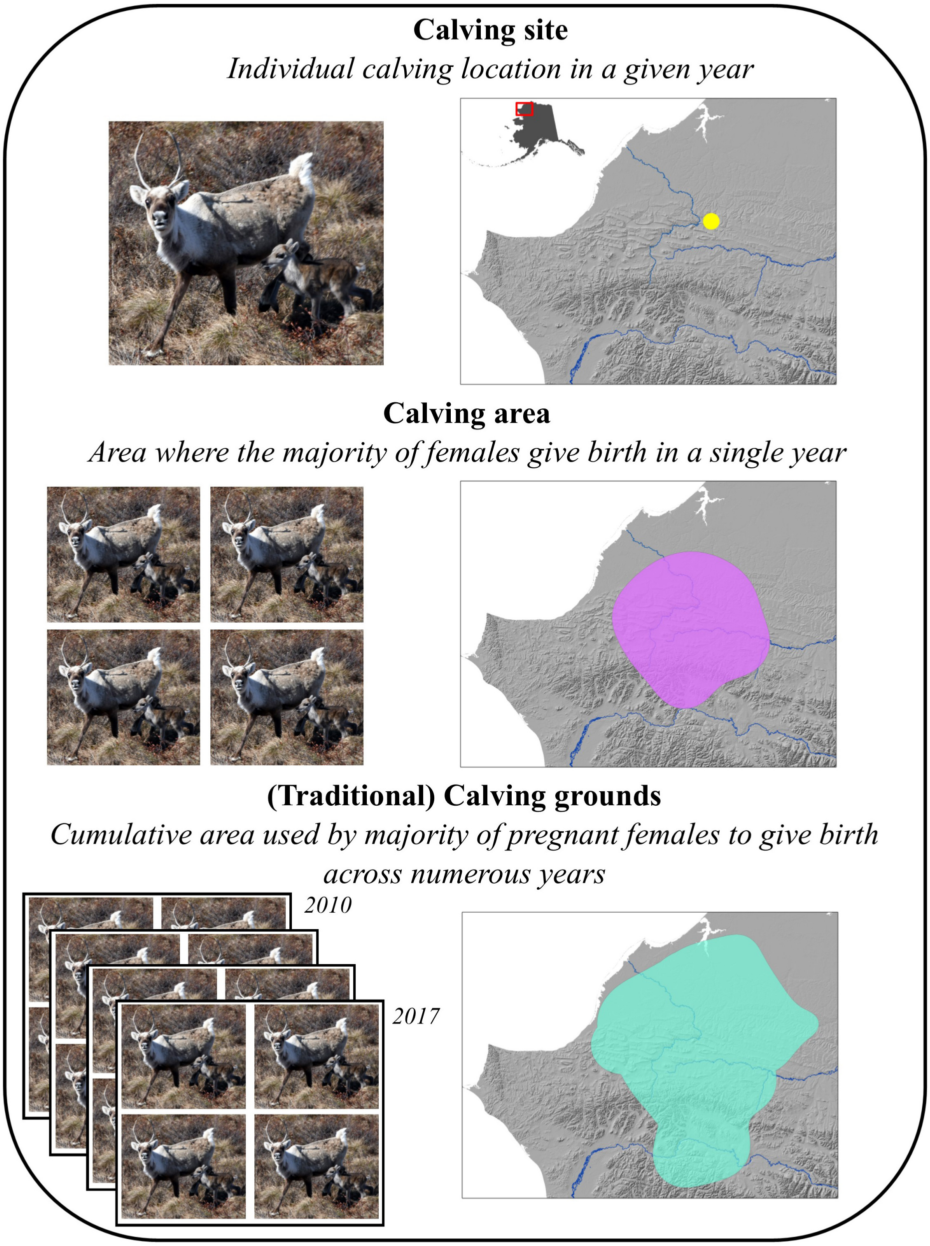

FIGURE 1 | The scales and definitions of calving considered in this analysis of the Western Arctic Herd. The calving location (yellow point) was from an individual in 2010, the calving area (purple polygon) was based on all detected calving events in 2010, and the calving ground (teal polygon) was the extent of all calving areas from 2010–2017 combined. Definitions adapted from Gunn and Miller (1986).

Alaska Institutional Animal Care and Use Committee (IACUC; 0040-2017-40). Collars were programmed to record locations every 8 h and by 2017, 203 collars had been deployed. From 2003 to 2016, the herd decreased from a high of 490,000 to 201,000 caribou and then increased to 244,000 in 2019 (Alaska Department of Fish and Game, 2019). Caribou populations are known to fluctuate at decadal time scales, and this is generally linked with large-scale climate patterns (Gunn, 2003; Joly et al., 2011). The northeast extent of the WAH range overlaps with the neighboring Teshekpuk Herd, and individuals between the two herds have been known to mix (Mager et al., 2013; Prichard et al., 2020).

Identifying Calving Events

We applied two different approaches to infer calving events from the 2010–2017 GPS data: an individual-based method and a population-based method (DeMars et al., 2013; Cameron et al., 2018). The former fit two *a priori* movement models (parturient and non-parturient) to movement rate data and model fit was evaluated using information criteria. The second

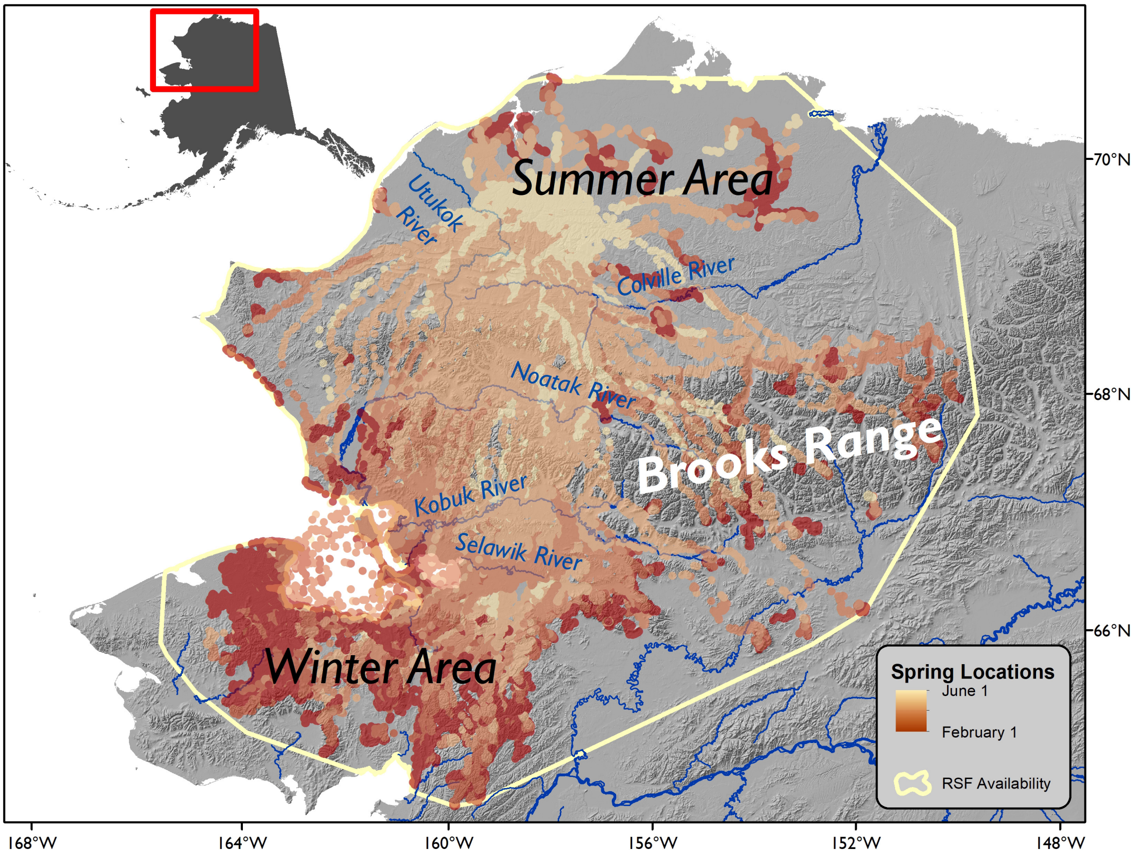

FIGURE 2 | Annual range of Western Arctic Herd caribou, Alaska. All GPS points from February 1 (dark red) to June 1 (yellow) are displayed from 2009–2017. The 100% minimum convex polygon, indicating the extent of the available area for the resource selection function (RSF), is presented as a pale yellow line and was generated using all annual locations in the same span of years.

method established a herd-specific movement rate threshold for calving from known events and then analyzed movement rates for individuals that dropped below the threshold using a 3-day smoothing parameter (DeMars et al., 2013). Using instances when the two methods agreed resulted in accurately classifying calving events 89% of the time ($n = 119$) when compared to aerial observation data (Cameron et al., 2018).

For data spanning 2010–2015, we used the calving events as reported in Cameron et al. (2018), in which aerial data were used to validate identified calving events from the movement-based approaches. For the data spanning the calving period of 2016–2017, we followed the procedures outlined in Cameron et al. (2018) to identify calving events without relying on supporting aerial data. However, because there was a record number of non-migratory individuals during the winter of 2016–2017 (Joly and Cameron, 2019) and the individual-based method is ill-suited for individuals not exhibiting migration movements prior to calving (Cameron et al., 2018), we incorporated a designation of migratory and non-migratory for each individual and adjusted the analysis as follows. For individuals that migrated (identified as crossing at least one of the three major rivers separating summer and wintering areas), we used the calving events from instances of method agreement. For individuals that did not migrate to a southern wintering area that year and that the two model results disagreed, we used calving events identified by the population-based method. For calving sites, we used the GPS location that corresponded with the identified calving event from the population-based method, because the individual-based method appeared to label events one GPS interval early (Cameron et al., 2018).

Spatial Patterns in Calving Areas

To address our first goal of spatial trends in calving areas, we defined an annual calving area as the area used by the majority (>80%) of individuals for calving in the herd in a given year (Gunn and Miller, 1986). We calculated a kernel utilization distribution (Worton, 1989) based on the calving sites for each year using the package "adehabitatHR" version 0.4.14 (Calenge, 2006) in the R statistical program version 3.4.3 (R Core Team, 2017). In this approach, a bivariate normal probability distribution is centered over each calving site in a given year and averaged together, resulting in one distribution (the kernel) for each year. Kernels were generated using a 500 × 500 m grid in an Albers equal area projection, which minimizes distortion along the latitudinal gradient given the relatively high latitude of our study area and ensured valid comparisons between years (Snyder, 1987). All kernels were generated using the same bandwidth smoothing parameter ($h = 25{,}000$) and we used the 95% contour as they resulted in unbroken range delineations for all years (Hooten et al., 2017). This approach, which is based on the explicit calving sites, minimizes potential bias in delineating calving areas that can be introduced by mismatches between calving timing and aerial observation timing during traditional surveys (Gunn and Miller, 1986).

To test the null hypothesis that the spatial distribution of annual calving areas did not vary by year, we employed a kernel randomization analysis outlined by Breed et al. (2006). For comparisons between 2 years, we randomly assigned (without replacement) a year designation to each calving site. Then, kernels for both years were generated using the same grid and smoothing parameters as outlined above. The area of both randomized kernels was then computed, as well as the area of overlap between the two kernels. Last, we calculated the test statistic as the area of the kernel overlap divided by the largest area of the two kernel regions. We repeated this process 250 times without duplicating any random year assignments. The p-value was calculated as the proportion of random overlaps smaller than the observed overlap for the 2 years being considered, so that if the observed overlap was smaller than all observed overlap values, the p-value was <0.004 (see **Supplementary Figure 1** for illustration). We performed this analysis for all combinations of annual comparisons, ranging from sequential up to 7-year intervals, and considered our alpha level as 0.05 for a one-tailed test.

Range-Wide Calving Site Selection

Our other goals were to understand the biotic and abiotic factors driving caribou calving site selection at the landscape level and the navigational mechanisms caribou employ to arrive there. We performed a resource selection function analysis (RSF; Manly et al., 2002) using the calving sites each year and compared them with random locations from the herd's range, representing the third-order of selection (Johnson, 1980). To define range-wide availability, we drew a 100% minimum-convex polygon, constrained to the coastal boundary, around all GPS locations during the study period. Defining availability is a particular challenge for resource selection studies, with the implicit assumption that available points are unused and available to all individuals (Keating and Cherry, 2004; Aarts et al., 2008). We focused on a range-wide scale for this analysis because individuals in the herd used the polygon area throughout the 8 years of study and we detected calving events at the extreme southwestern and northeastern extent of the range, far outside of the traditionally defined calving area. For each of the 8 years from 2010 to 2017, we created 10,000 random locations within the polygon, for a total of 80,000 available points.

We attributed both used and available points with a combination of physiographic attributes and annually varying environmental indices. We attributed elevation values from a 5 m resolution digital terrain model derived from the Interferometric Synthetic Aperture Radar (U.S Geological Survey, 2017) and calculated a solar radiation index (Keating et al., 2007) for each point using slope and aspect derived from the terrain model. This index ranges from −1 to 1, with low index values corresponding to north-facing steep slopes, high values south-facing steep slopes, and flatter slopes around 0.35. We calculated a vector ruggedness measure (VRM; Sappington et al., 2007), which is a measure of the ruggedness of the terrain, for each point using the digital terrain model and a 15 × 15 m swath. We used a land cover classification map (Boggs et al., 2016) to attribute all points with land cover type and reduced the classifications into four categories from the original 20 based on diet categories of the predominant vegetation (forest, shrub, herbaceous, and lichen/sparse; **Supplementary Table 1**). We filtered points that occurred in pixels originally categorized as bare ground, fire scar, ice/snow, and water.

For environmental indices, we attributed the annual snow off date (day of year) specific to that year for each point as determined from Moderate Resolution Imaging Spectroradiometer (MODIS) data (Macander et al., 2015). We included two measures of primary productivity at multiple time intervals using the normalized difference vegetative index (NDVI, for review see Pettorelli et al., 2005a) acquired from the MODIS V6 and compiled into 7-day composites with 250 m resolution (data available from the U.S. Geological Survey; Jenkerson et al., 2010). For an index of forage quantity, we used the raw NDVI value at a weekly temporal resolution and as an index of forage quality we calculated the change in NDVI values between sequential NDVI composites (NDVI rate) for the same time period by calculating the difference between sequential coverages (denoted "ΔNDVI"). ΔNDVI has been used in prior studies as an index for forage quality, including in Africa (Boone et al., 2006) and Alaska (Griffith et al., 2002), and also used to calculate a similar measure, the Instantaneous Rate of Green-up (Bischof et al., 2012). For arctic vegetation, a positive change in NDVI during spring corresponds with phenological periods of high nutrient concentrations and rapid vegetation growth (Finstad, 2008; Gustine et al., 2017).

We included five temporal windows (1 week before peak calving, the week of the peak, and the following 3 weeks after peak calving) for both NDVI metrics to assess at what temporal scale caribou may be responding to vegetation signals. To evaluate support for perception-based selection, we assigned the five temporal windows for both NDVI metrics relative to peak calving for that specific year, with the effect that the week of peak calving NDVI values differed between years and corresponded to the timing of calving observed the given year (perception of current conditions). To evaluate the potential for memory-based selection, we assigned these temporal windows relative to the herd's average peak calving across all 8 years (June 3, see section "Results"), such that regardless of when peak calving was in a given year, both NDVI metrics represented consistent weeks across years (average conditions). This framework is similar to work assessing the influence of perception and memory in zebra (*Equus burchelli*) migration (Bracis and Mueller, 2017).

We tested the influence of these biotic and abiotic factors on caribou calving site selection using mixed-effects logistic regression, with use of a calving site as the response. We log-transformed elevation and VRM to approximate a normal distribution and standardized continuous covariates (mean centered and divided by the standard deviation) for model fitting. Correlation coefficients among physiographic attributes were under 0.5, and they all were under 0.2 when compared with environmental variables. We included a random intercept term for year to account for sampling across time and considered random slope terms for the environmental variables to account for stochastic annual variability (Gillies et al., 2006). We performed model selection at two stages – the first to select a random effect structure and the second to select fixed effect variables and structures (Bolker et al., 2009) using model selection based on Akaike's Information Criterion corrected for small sample sizes (AICc; Hurvich and Tsai, 1989; Burnham and Anderson, 2002). For all NDVI, ΔNDVI, and snow-free variables, we fitted full fixed-effects models with a random slope term for each environmental covariate (including a random intercept for year) and compared performance with an intercept-only random effects model. In the second stage of model selection, we proceeded with fixed-effects selection using the top-performing random effect structure from the previous stage and included all biologically justifiable interactions and combinations. All analyses were performed in the R statistical program using the package "lme4" (Bates et al., 2015). We used our top model to generate a predictive map for calving sites by averaging the selected environmental covariate raster across the 8 years, as well as generated year-specific predictive maps with the corresponding environmental data for that year. We calculated the average of the year-specific predictive values within each annual calving area and compared these with the calving site values for the given year.

RESULTS

Identifying Calving Events

From 2010 to 2017, we detected 214 total calving events, ranging from 15 to 52 in a given year, and the average calving date was June 3 (**Table 1**). We identified calving in one non-migratory individual in 2016 and 14 in 2017 for which we used results from only the population-based model. We detected four calving events outside of the historical calving grounds: one in 2012 for an individual that remained on the winter range of the Seward Peninsula and three in 2017 for WAH individuals that calved in the Teshekpuk Herd calving area to the east. For the subsequent analyses of calving area trends and selection, we excluded these four events because they greatly skewed calving distribution estimates, leaving us with 210 total calving events across 8 years.

TABLE 1 | Detected calving events based on movement data for the Western Arctic Herd (WAH), 2010–2017, Alaska.

Year	Calving events	WAH only	Median calving date	Calving area (km^2)
2010	15	15	4-Jun	27,313
2011	23	23	5-Jun	24,261
2012	17	16	6-Jun	24,913
2013	20	20	8-Jun	33,487
2014	26	26	1-Jun	18,196
2015	30	30	3-Jun	19,110
2016	31	31	30-May	24,269
2017	52	49	3-Jun	26,630
	214	210	3-Jun	24,772

We excluded four events from the subsequent analyses (used "WAH Only") because they were far outside of the typical calving area. Area of annual calving areas was determined from kernel densities generated from detected calving events. The bottom rows provide totals for calving events and the average median parturition date and calving area across all 8 years.

Spatial Patterns in Calving Areas

Across the 8 years we analyzed, the WAH calving areas exhibited variation at the annual scale, but the general area was characterized by remarkable fidelity. The average extent of the calving area for the herd in a given year was 24,772 km^2 (**Table 1**). Calving areas exhibited both latitudinal and longitudinal variation across years, with calving occurring in the Brooks Range and as far south as the Noatak River in some years (**Figure 3**). On an annual basis, calving areas had significantly less overlap than expected by chance three out of seven times ($p < 0.05$; **Table 2**). This trend of significant differentiation among years was evident at all further levels of comparison: at 2-year ($p < 0.05$ for five out of six), 3-year ($p < 0.05$ for four out of five), 4-year ($p < 0.05$ for three out of four), 5-year ($p < 0.05$ for one out of three), 6-year ($p < 0.05$ for one out of two), and 7-year intervals ($p < 0.05$ for the one comparison). When considered across years, the calving area of WAH females always shared a 7,281 km^2 core area of overlapping extent that was used every year of the study, with calving areas of less frequent use stretching as far away as the Noatak River (**Figure 4**) for a total calving ground extent of 53,330 km^2.

Range-Wide Calving Site Selection

The selection of calving sites was characterized by mostly flat tundra within a band of elevation that was greening up at the time of average calving for the herd across all years of the study. The environmental covariate that explained the most variance in calving site selection was ΔNDVI at the average peak calving date for the study ("ΔNDVI.148"), from May 21–27 to May 28–June 3 every year (day of year 141–147 to 148–154; **Supplementary Table 2**) and substantially outperformed the next best model in random effect selection, which included a random slope for ΔNDVI at peak calving specific to each year (ΔNDVI.Calve; Δ AICc = 29.2). In model selection for fixed effects, the top performing model included terms for land cover, quadratic terms for elevation and solar radiation that indicate selection for intermediate values for both, an interaction between elevation and ΔNDVI.148, and terrain ruggedness (**Supplementary Table 3**). Females strongly selected for sites with high ΔNDVI at the time of peak calving (**Table 3**).

Calving sites were associated with a band of low elevation areas, indicating selection of elevations between approximately 50–600 m above sea level. Elevation and ΔNDVI exhibited an interactive effect, with females most strongly selecting for elevations approximately 100–175 m that were experiencing the fastest green-up at the time of peak calving. Of the four land cover classes we considered, we did not detect calving in any forested sites and found the strongest selection for herbaceous

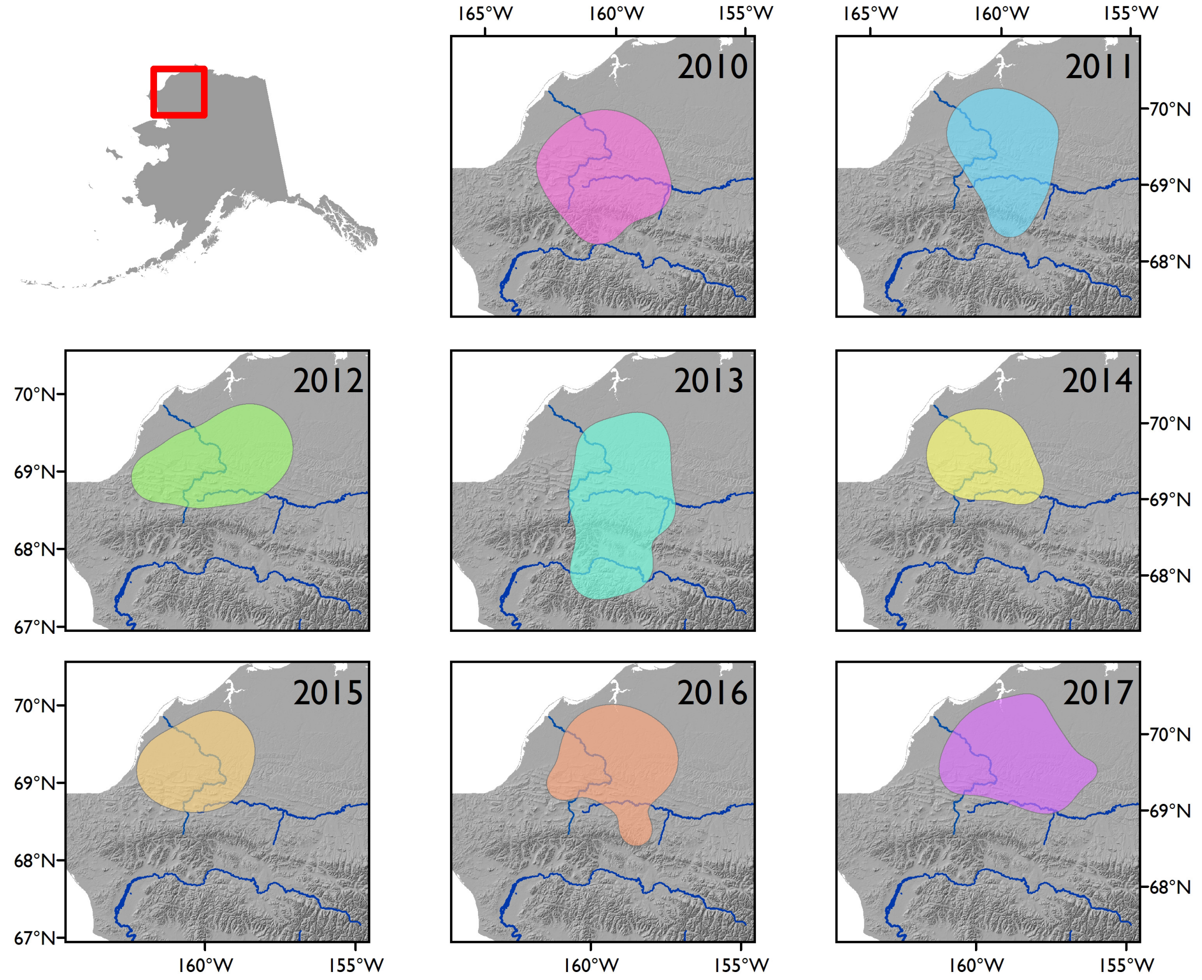

FIGURE 3 | Annual calving areas of the Western Arctic Herd, 2010–2017, Alaska. Calving areas were delineated using the 95% contour of a kernel utilization distribution generated from parturition locations, which were inferred from GPS data.

TABLE 2 | Kernel overlap tests comparing annual calving areas of Western Arctic Herd caribou, 2010–2017, Alaska.

	2011	2012	2013	2014	2015	2016	2017
2010	0.096	0.064	0.160	**0.004**	**<0.004**	**0.008**	**<0.004**
2011		0.340	**0.048**	**<0.004**	**<0.004**	0.612	0.08
2012			**0.008**	**0.004**	**<0.004**	0.556	0.136
2013				**<0.004**	**<0.004**	**<0.004**	**0.004**
2014					0.112	**0.004**	**<0.004**
2015						**<0.004**	**<0.004**
2016							0.608

Comparisons were performed for every interval ranging from 1 to 7-years apart, and the results for each interval can be read along the diagonal. A significant result ($p < 0.05$, one-tailed test; bold text) indicates less overlap than expected by random chance.

cover at calving (**Table 3**). The solar radiation index also exhibited a quadratic relationship for calving site selection (**Table 3**), indicating selection of sites with a positive index ranging from approximately 0.15 to 0.5, which correspond to lower angle slopes and encompass nearly all aspects. The negative linear coefficient for terrain ruggedness supported this result, indicating that females selected for less rugged terrain (**Table 3**). Our predictive map of calving habitat indicates that calving for the WAH occurs in the largest, continuous expanse of habitat characterized by these unique factors within their range, and that the attributes associated with calving sites extend to the east beyond documented calving areas (**Figure 5**). Importantly, calving occurred on sites with higher predicted value from the top model compared to the average of the calving area in the given year (**Supplementary Figure 2**).

DISCUSSION

Mounting evidence indicates that animals use memory to make movement decisions that improve resource acquisition in a heterogeneous landscape (Bailey et al., 1996; Fagan et al., 2013; Bracis et al., 2015; Abrahms et al., 2019; Merkle et al., 2019).

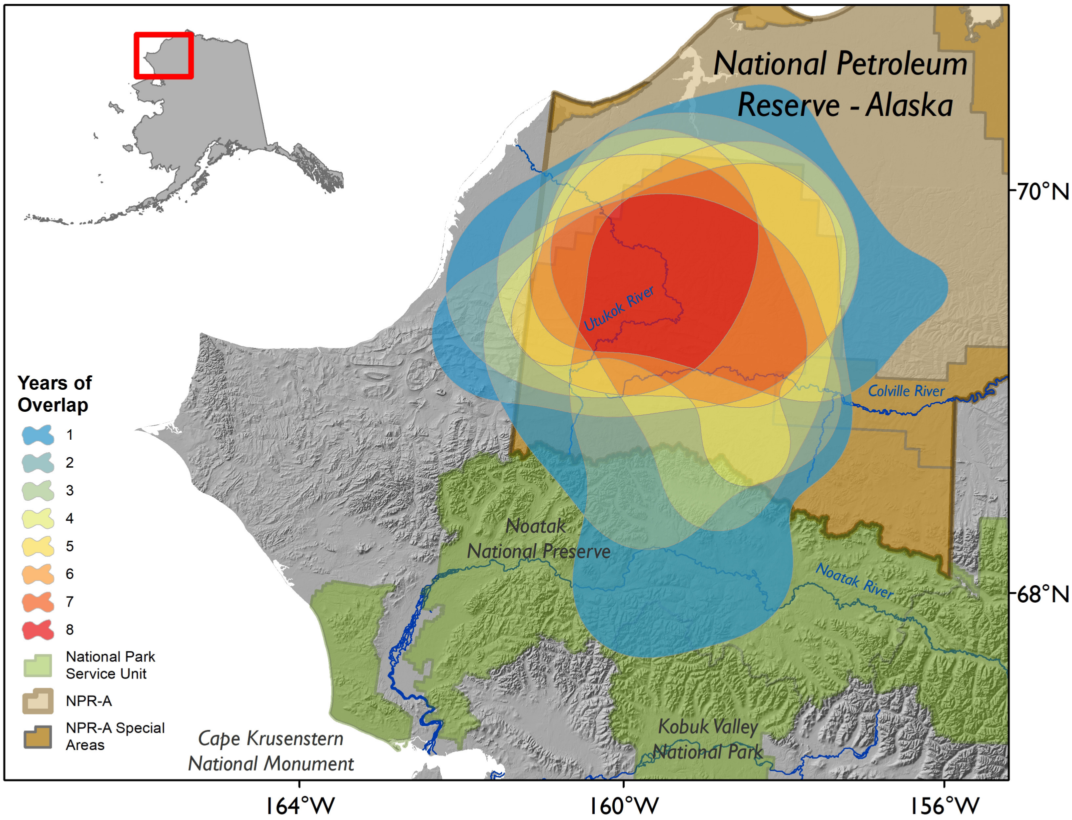

FIGURE 4 | Overlap of all observed annual calving areas for caribou of the Western Arctic Herd, 2010–2017, Alaska. Calving areas were delineated using the 95% contour of a kernel utilization distribution generated from parturition locations, which were inferred from GPS data. Special Areas of the National Petroleum Reserve – Alaska (NPR-A; brown) include the Utukok River Uplands and Colville River Special Areas, as defined in the 2013 Integrated Activity Plan (BLM, 2012).

TABLE 3 | Coefficient estimates from the top RSF model for female caribou calving site selection, Western Arctic Herd, 2010–2017, Alaska.

	Variable	β	SE
Land cover	Forest	-21.78	53.40
	Herbaceous	-4.99	0.21
	Shrub	-6.19	0.30
	Sparse	-5.57	1.02
	Elevation	-0.44	0.16
	Elevation^2	-1.58	0.20
	SRI	-1.96	0.33
	SRI^2	-1.55	0.43
	VRM	-0.17	0.10
	ΔNDVI.148	0.47	0.20
	Elevation: ΔNDVI.148	-0.43	0.12

Elevation and terrain ruggedness were log transformed and all continuous variables were standardized (mean = 0; SD = 1). "SRI" is the solar radiation index, "VRM" is the vector ruggedness measure, and "ΔNDVI.148" is the difference in NDVI values from the week prior to and the week of average peak calving for the study (May 21–June 3). Coefficients presented in logit-space and from a no-intercept model (no reference class).

For example, bison (*Bison bison*) base foraging on their memory of patch location and quality that result in observed home-range spatial patterns (Merkle et al., 2014). Elephants (*Loxodonta africana*) rely on spatial memory to minimize long-distance travel to perennial waterholes in an arid environment (Polansky et al., 2015). In an explicit test of the relative importance of memory versus perception using zebras, simulations of migration paths based on memory mechanisms reached the actual migration destination more accurately than simulations based on perception mechanisms, even when the perceptual range was increased to omniscience (Bracis and Mueller, 2017). Considering that less productive regions are associated with longer annual movements of large terrestrial mammals (Joly et al., 2019), the extreme variability of arctic conditions could conceivably promote an adaptation for memory-based capabilities in caribou.

Our results highlight the strong fidelity of a highly migratory ungulate to its calving ground within an extensive range across the nearly decade-long study period. Notably, pregnant females selected calving sites that were characterized by high-quality forage at the average time of peak calving. High fidelity is particularly impressive considering the highly variable winter ranges of individuals in this (Joly and Cameron, 2019) and other herds (Schaefer et al., 2000; Faille et al., 2010; Peignier et al., 2019), and thus females must routinely travel different routes between winter ranges and the calving area (Kelsall, 1968; Nicholson et al., 2016; Baltensperger and Joly, 2019). Spring

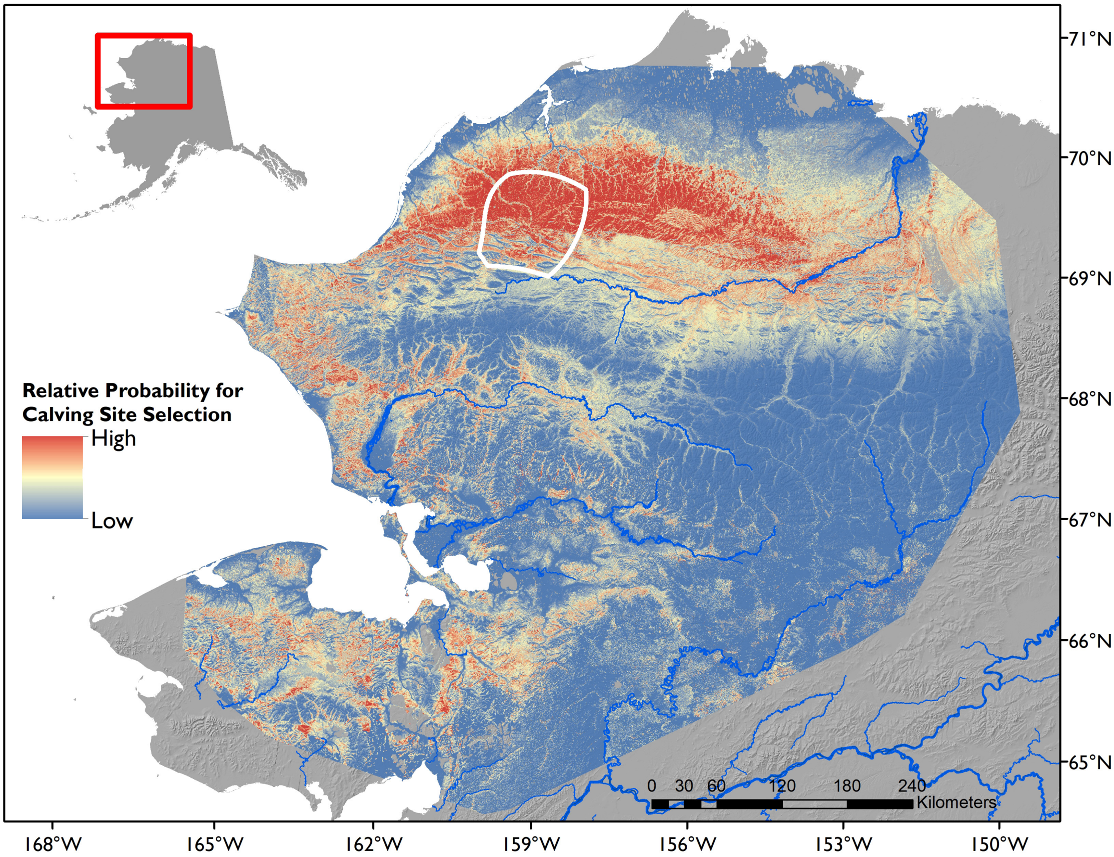

FIGURE 5 | Predictive map of high-quality calving habitat for caribou of the Western Arctic Herd, Alaska. Map was made from the top performing resource selection function model including land cover, elevation, solar radiation, terrain ruggedness, and rate of NDVI increase from the week before to the week of average peak calving. Data for NDVI rate at peak calving were averaged across the 8 years of NDVI composites from the analysis for map generation. White polygon indicates the core area in which calving was detected for all 8 years in the study.

migration routes for pregnant females are typically snow covered (Boelman et al., 2019; Gurarie et al., 2019), so these segments of the migration occur well before green-up and are unlikely to be a product of perception-based movement along the way used by other ungulates (e.g., Merkle et al., 2016). Considering the spatial consistency of use and selection for average conditions, we suggest that the fidelity of caribou to their calving grounds is supportive of memory-based movement at the landscape scale.

The use of perception-based versus memory-based movement are not necessarily mutually exclusive and may depend on the scale being considered (Bailey et al., 1996). Trial studies with sheep (*Ovis* spp.) revealed that individuals can remember the locations of resources between trials and use spatial memory to improve foraging efficiency. Impressively, sheep could also associate a cue with resource locations, such that when a resource patch was moved between trials, the sheep went to the original location first, then directed movement to the cue (and thus the resource; Edwards et al., 1996). Spatial consistency in calving areas for the WAH did not appear to be driven exclusively by memory of a specific place – calving sites for individuals were approximately 55 km apart across years on average (Joly et al., in preparation), which is similar to findings for other herds (Fancy and Whitten, 1991; Schaefer et al., 2000). Our finding that specific calving sites had higher forage quality than the overall average for that year's calving area suggests that females refine calving site selection based on updated information perceived after arriving on the calving ground. In other words, our results suggest that memory guides pregnant female caribou to the general calving grounds during spring migration but then the individual's perception of local, contemporary conditions each year refines their movement, resulting in the annual variability in calving sites and thus the characteristic annual variability of the calving areas of many herds.

Weather conditions, such as precipitation (Le Corre et al., 2017), can influence spring arrival timing, and deeper snow increases the cost of movement for caribou (Fancy and White, 1987) and is hypothesized to delay migration in other arctic caribou herds (Duquette, 1988; Gurarie et al., 2019). We suspect some of the southerly calving sites reported here were caused by such snowy spring conditions impeding migratory movement and delaying arrival to the main calving ground, which resulted in birth en route. The spring of 2013 had unusually cold temperatures and heavy late spring snowfall (Sousanes and Hill, 2013), as well as the most southerly calving sites of our study.

Such snow-related delays have occurred before: some calves were born south of the Brooks Range during the unseasonably late spring of 1962 (Lent, 1966), and late snowmelt has correlated with southerly calving events in the nearby Teshekpuk Herd (Carroll et al., 2005). Based on the influence of forage quality to calving sites we detected, we attribute the observed east-west spatial variation to caribou adjusting their calving sites to annual vegetative conditions they found upon arriving to the calving ground. Variability in the annual calving area has been linked to variation in forage quality for the Porcupine Herd (Griffith et al., 2002), as well as variation in snow conditions (Fancy and Whitten, 1991). Considered cumulatively, WAH caribou utilized an area seven times larger than the core calving area across nearly a decade, likely responding to experienced annual environmental stochasticity.

Our finding of selection for an index of vegetation phenology (NDVI rate from weekly composites) supports previous studies documenting selection for ΔNDVI after calving (Kelleyhouse, 2001; Griffith et al., 2002) and aligns with recent work suggesting that raw NDVI is a poor metric of forage nutrients (Johnson et al., 2018). For many ungulates, calving and subsequent lactation are the most energetically demanding periods of the year (Clutton-Brock et al., 1989; Barboza and Parker, 2008). Female caribou exhibit a strong preference for immature floral heads of cottongrass (*Eriophorum vaginatum)* at calving (Kuropat and Bryant, 1980; Thompson and McCourt, 1981; Griffith et al., 2002), which offers one of the greatest sources of digestible nitrogen and protein at the beginning of the arctic growing season (Kuropat and Bryant, 1980; Johnstone et al., 2002; Cebrian et al., 2008; Gustine et al., 2017). Cottongrass is adapted to early spring growth relative to other tundra plant communities (Chapin et al., 1979), with initiation of the floral heads the autumn before allowing elongation to resume shortly after snow ablation (Wein, 1973; Cebrian et al., 2008). Considering the dominance of tussock-tundra communities (of which cottongrass is the primary component) in the foothills north of the Brooks Range (Boggs et al., 2016), we posit that the forage quality signal we identified in calving site selection by the WAH is largely influenced by cottongrass flowering, though early leaf flush of deciduous shrubs such as willow species (such as *Salix pulchra*) may also occur during the calving period (Borner et al., 2008). The absence of calving in the large area of predicted high-quality habitat to the east of the calving ground (**Figure 5**) is notable. One explanation is that following calving, the herd reliably moves to the southwest and toward the coast to avoid insect harassment, an activity that exerts large energetic costs as well as lost foraging opportunities (Witter et al., 2012; Dau, 2015; Joly and Cameron, 2019; Joly et al., 2020). Potentially, the selection of calving sites balances the nutritional need for access to high-quality resources at calving with distance to insect relief areas that will be critical in July. If so, this would suggest that selection of calving sites can also be influenced by the expectation of conditions to come after calves are born.

Another possible interpretation for our results of calving area consistency, and the most widely accepted alternative explanation for migratory ungulates to synchronously give birth in distinct calving areas, is to escape predation (Bergerud, 1974, 1996; Estes, 1976; Fancy and Whitten, 1991). The principal predators for caribou calves are wolves (*Canis lupus*), brown bears (*Ursus arctos*), and golden eagles (*Aquila chrysaetos*; Whitten et al., 1992). If predation risk primarily motivates selection of the calving area, then we would expect calving to occur in areas of the lowest predator densities across the range. Indeed, coarse estimates indicate that densities of wolves and brown bears are higher south of the Brooks Range compared to the north. However, in the northern portion of the herd's range, densities for both predators are greater in the Brooks Range foothills, where WAH calving is centered, compared to the coastal plain to the north (**Supplementary Table 4**). Thus, the location of the core WAH calving ground is not consistent with predation risk as the primary driver of calving site selection. Our findings support the alternative hypothesis that migratory species match the increased metabolic demands of calving with favorable foraging conditions (Baker, 1938), and fit within a growing body of literature that links bottom-up signals to calving area selection by migratory ungulates. In Mongolia, calving areas for Mongolian gazelles exhibited higher NDVI values than the rest of the range at the time of use (Leimgruber et al., 2001). In Kazakhstan, Saiga antelope calving was found to be synchronized with peak productivity based on NDVI, and calving areas were characterized by low variability, and thus high reliability, of vegetative productivity (Singh et al., 2010). A preliminary study on the Tibetan Plateau suggested that Tibetan antelopes synchronize use of calving areas with peaks in primary productivity as well (Ganzorig et al., 2011). Whereas none of these studies directly tested for predator avoidance effects, there is mounting evidence from around the globe that bottom-up forces influence calving site selection for ungulates and that the motivation of selection cannot be simplified without considering scale and the potential that predation risk plays a lesser role than has been previously suggested (Fancy and Whitten, 1991; Bergerud, 1996).

Recent studies indicate that animal movement is strongly affected by social interactions when animals are in groups, termed collective movement (Westley et al., 2018). In a collective movement framework, individual group members may hold different levels of information about the environment (Couzin et al., 2005) and more informed individuals can act as group leaders in movement processes (Huse et al., 2002; Couzin et al., 2005; Guttal and Couzin, 2010; Berdahl et al., 2018). Given that caribou migrate in the spring in groups, we speculate that collective movement processes are likely at play (Duquette and Klein, 1987). This concept has a long history with local indigenous knowledge about caribou, which recommends "let the leaders pass" during migration (Padilla and Kofinas, 2014). If so, determining at what level information is held in caribou groups (such as age classes) and what proportion of informed individuals are necessary to result in the observed calving patterns, are promising avenues for future research.

Management Implications

Migratory ungulates rely on large expanses of range to maximize fitness (Hebblewhite et al., 2008; Joly et al., 2019) and migration routes of animals that rely on spatial memory are more susceptible to disturbance as they are likely more inflexible (Bracis and Mueller, 2017). Once lost, migratory patterns can take many generations for a population to learn and re-establish (Jesmer et al., 2018). Previous studies recommend that to fully conserve calving grounds for species such as caribou, managers should consider the full extent of calving at a decadal scale as the goal (Carroll et al., 2005; Taillon et al., 2012). Across 8 years of study, the WAH used an approximately 7,000 km^2 core area along the Utukok River for calving and a broader area of 53,330 km^2 to respond to environmental variability experienced each year on the calving ground. Comparing our findings with previous studies of the WAH up to six decades prior highlights the remarkable fidelity of this herd to its general calving ground (**Supplementary Figure 3**; Lent, 1966; Kelleyhouse, 2001) and local indigenous knowledge suggests this pattern extends before the 20th century (Lent, 1966; Burch, 2012). We recommend managers adopt the extent of the calving ground as the management goal for migratory caribou herds such as the WAH to ensure adequate space to respond to the annual environmental variability faced by caribou populations. We expect this recommendation has immediate utility for WAH management, for the area where the majority of calving occurs is on the National Petroleum Reserve – Alaska and specifically within the Utukok River Special Area. The Bureau of Land Management is currently revising the Integrated Activity Plan, which will designate conservation areas within the Reserve and stipulations on development in the greater area, and decisions made now have the potential to impact the WAH calving grounds for decades.

DATA AVAILABILITY STATEMENT

Movement data used in this manuscript is stored in a public repository called IRMA, but access is restricted due to the sensitivity of a harvestable species' location data. Contact authors for access. https://irma.nps.gov/Datastore/Reference/Profile/2260262.

ETHICS STATEMENT

The animal study was reviewed and approved by the State of Alaska Institutional Animal Care and Use Committee (IACUC; 0040-2017-40).

AUTHOR CONTRIBUTIONS

MC and KJ managed the data. MC, KJ, GB, CM, and KK analyzed and interpreted the data, and contributed to manuscript revision. MC wrote the first draft of the manuscript. All authors read and approved the submitted version.

FUNDING

National Park Service (NPS) and Alaska Department of Fish and Game fund the on-going caribou monitoring program and NPS funded personnel time for this project.

ACKNOWLEDGMENTS

We thank Lincoln Parrett and Alex Hansen of the Alaska Department of Fish and Game (ADF&G), as well as their colleagues, for their continued efforts and collaboration in the long-term monitoring of the Western Arctic Herd, as well as countless insightful discussions on caribou. We also thank Regan Sarwas of the National Park Service (NPS) for his invaluable contributions to data management as well as Dave Swanson of NPS for his input and numerous discussions on remote sensing data. We are indebted to Lincoln Parrett, Luke Sanford, Julia McMahon, Eric Wald, and our reviewers for their insightful input on previous versions of this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.564567/full#supplementary-material

REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., and Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31, 140–160. doi: 10.1111/j.2007.0906-7590.05236.x

Abrahms, B., Hazen, E. L., Aikens, E. O., Savoca, M. S., Goldbogen, J. A., and Bograd, S. J. (2019). Memory and resource tracking drive blue whale migrations. *Proc. Natl. Acad. Sci. U.S.A.* 116, 5582–5587. doi: 10.1073/pnas.1819031116

Aikens, E. O., Kauffman, M. J., Merkle, J. A., Dwinnell, S. P. H., Fralick, G. L., and Monteith, K. L. (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.* 20, 741–750. doi: 10.1111/ele.12772

Alaska Department of Fish and Game (2019). *Western Arctic Caribou Herd Working Group – 2019 Meeting Summary*. Available online at: https://westernarcticcaribou.net/wp-content/uploads/2020/03/2019-WACH-WG-Meeting-Summary-DRAFT-for-WACH-WG-approval-at-2020-mtg.pdf (accessed April 15, 2020).

Alerstam, T., Hedenström, A., and Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos* 103, 247–260.

Avgar, T., Deardon, R., and Fryxell, J. M. (2013). An empirically parameterized individual based model of animal movement, perception, and memory. *Ecol. Modell.* 251, 158–172. doi: 10.1016/j.ecolmodel.2012.12.002

Avgar, T., Street, G., and Fryxell, J. M. (2014). On the adaptive benefits of mammal migration. *Can. J. Zool.* 92, 481–490. doi: 10.1139/cjz-2013-0076

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., et al. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manag.* 49, 386–400. doi: 10.2307/4002919

Baker, J. R. (1938). "The evolution of breeding seasons," in *Evolution: Essays on Aspects of Evolutionary Biology Presented to Professor E. S. Goodrich*, ed. G. R. de Beer (Oxford: Clarendon), 161–177.

Baltensperger, A. P., and Joly, K. (2019). Using seasonal landscape models to predict space use and migratory patterns of an arctic ungulate. *Mov. Ecol.* 8, 1–19.

Barboza, P. S., and Parker, K. L. (2008). Allocating protein to reproduction in arctic reindeer and caribou. *Physiol. Biochem. Zool.* 81, 835–855. doi: 10.1086/590414

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Bekenov, A. B., Grachevand, I. A., and Milner-Gulland, E. J. (1998). The ecology and management of the Saiga antelope in Kazakhstan. *Mamm. Rev.* 28, 1–52.

Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A. H., Codling, E. A., Couzin, I. D., et al. (2018). Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philos. Trans. R. Soc. B Biol. Sci.* 373:20170009. doi: 10.1098/rstb.2017.0009

Bergerud, A. T. (1974). "The role of the environment in the aggregation, movement and disturbance behaviour of caribou," in *The Behaviour of Ungulates and Its Relation to Management*, Vol. 2, eds V. Gesit and F. Walther (Gland: International Union for Conservation of Nature and Natural Resources), 552–584.

Bergerud, A. T. (1996). Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer* 16, 95–116. doi: 10.7557/2.16.4.1225

Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., and Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *Am. Nat.* 180, 407–424. doi: 10.1086/667590

BLM (2012). *National Petroleum Reserve-Alaska Integrated Activity Plan/Environmental Impact Statement*. Available online at: https://eplanning.blm.gov/epl-front-office/projects/nepa/5251/41003/43153/Vol1_NPR-A_Final_IAP_FEIS.pdf (accessed April 15, 2020).

Boelman, N., Liston, G. E., Gurarie, E., Meddens, A. J. H., Mahoney, P. J., Kirchner, P. B., et al. (2019). Integrating snow science and wildlife ecology in Arctic-boreal North America. *Environ. Res. Lett.* 14:010401. doi: 10.1088/1748-9326/aaeec1

Boggs, K., Flagstad, L., Boucher, T., Kuo, T., Fehringer, D., Guyer, S., et al. (2016). *Vegetation Map and Classification: Northern, Western, and Interior Alaska - Second Edition*. Anchorage: Alaska Center for Conservation Science, University of Alaska Anchorage.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135. doi: 10.1016/j.tree.2008.10.008

Boone, R. B., Thirgood, S. J., and Hopcraft, J. G. C. (2006). Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology* 87, 1987–1994.

Borner, A. P., Kielland, K., and Walker, M. D. (2008). Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan arctic tundra. *Arctic Antarct. Alp. Res.* 40, 27–38. doi: 10.1657/1523-0430(06-099)

Bracis, C., Gurarie, E., Van Moorter, B., and Goodwin, R. A. (2015). Memory effects on movement behavior in animal foraging. *PLoS One* 10:e0136057. doi: 10.1371/journal.pone.0136057

Bracis, C., and Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proc. R. Soc. B Biol. Sci.* 284:20170449. doi: 10.1098/rspb.2017.0449

Breed, G. A., Bowen, W., McMillan, J., and Leonard, M. (2006). Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc. R. Soc. B Biol. Sci.* 273, 2319–2326. doi: 10.1098/rspb.2006.3581

Burch, E. S. (2012). *Caribou Herds of Nothwest Alaska, 1850-2000*. Fairbanks, AK: University of Alaska Press.

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197, 516–519.

Cameron, M. D., Joly, K., Breed, G. A., Parrett, L. S., and Kielland, K. (2018). Movement-based methods to infer parturition events in migratory ungulates. *Can. J. Zool.* 96, 1187–1195. doi: 10.1139/cjz-2017-0314

Carroll, G. M., Parrett, L. S., George, J. C., and Yokel, D. A. (2005). Calving distribution of the Teshekpuk caribou herd, 1994-2003. *Rangifer* 16, 27–35. doi: 10.7557/2.25.4.1767

Cebrian, M. R., Kielland, K., and Finstad, G. (2008). Forage quality and reindeer productivity: multiplier effects amplified by climate change. *Arctic Antarct. Alp. Res.* 40, 48–54. doi: 10.1657/1523-0430(07-069)

Chan-McLeod, A. C. A., White, R. G., and Holleman, D. F. (1994). Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. *Can. J. Zool.* 72, 938–947. doi: 10.1139/z94-127

Chapin, F. S. III, van Cleve, K., and Chapin, M. C. (1979). Soil temperature and nutrient cycling in the tussock growth form of Eriophorum vaginatum. *J. Ecol.* 67, 169–189. doi: 10.2307/2259343

Charnov, E. L. (1976). Optimal foraging theory: the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136.

Clutton-Brock, T. H., Albon, S. D., and Guiness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature* 337, 260–262. doi: 10.1038/337260a0

Couzin, I. D., Krause, J., Franks, N. R., and Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature* 433, 513–516. doi: 10.1038/nature03236

Creel, S., Winnie, J. Jr., Maxwell, B., Hamlin, K., and Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397.

Crête, M., and Huot, J. (1993). Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Can. J. Zool.* 71, 2291–2296. doi: 10.1139/z93-321

Dau, J. R. (1997). "Units 21D, 22A, 22B, 23, 24, 26A caribou management report," in *Caribou Management Report of Survey-Inventory Activities 1 July 1994-1930 June 1996*, ed. M. V. Hicks (Alaska: Alaska Department Fish and Game, Division of Wildlife Conservation).

Dau, J. R. (2015). "Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A. Chapter 14, pages 14-1 through 14-89," in *Caribou Management Report of Survey And Inventory Activities 1 July 2012-2030 June 2014*, eds P. Harper and L. A. McCarthy (Alaska: Alaska Department of Fish and Game).

DeMars, C. A., Auger-Méthé, M., Schlägel, U. E., and Boutin, S. (2013). Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecol. Evol.* 3, 4149–4160. doi: 10.1002/ece3.785

Duquette, L. S. (1988). Snow characteristics along caribou trails and within feeding areas during spring migration. *Arctic* 41, 143–144.

Duquette, L. S., and Klein, D. R. (1987). Activity budgets and group size of caribou during spring migration. *Can. J. Zool.* 65, 164–168. doi: 10.1139/z87-023

Edwards, G. R., Newman, J. A., Parsons, A. J., and Krebs, J. R. (1996). Use of cues by grazing animals to locate food patches: an example with sheep. *Appl. Anim. Behav. Sci.* 50, 147–160. doi: 10.1016/S0168-1591(96)01095-7

Estes, R. D. (1976). The significance of breeding synchrony in the wildebeest. *East Afr. Wildl. J.* 14, 135–152.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G. A., et al. (2013). Spatial memory and animal movement. *Ecol. Lett.* 16, 1316–1329. doi: 10.1111/ele.12165

Faille, G., Dussault, C., Ouellet, J. P., Fortin, D., Courtois, R., St-Laurent, M. H., et al. (2010). Range fidelity: the missing link between caribou decline and habitat alteration? *Biol. Conserv.* 143, 2840–2850. doi: 10.1016/j.biocon.2010.08.001

Fancy, S. G., and White, R. G. (1987). Energy expenditures for locomotion by barren-ground caribou. *Can. J. Zool.* 65, 122–128. doi: 10.1139/z87-018

Fancy, S. G., and Whitten, K. R. (1991). Selection of calving sites by Porcupine herd caribou. *Can. J. Zool.* 69, 1736–1743. doi: 10.1139/z91-242

Finstad, G. L. (2008). *Applied Range Ecology of Reindeer (Rangifer tarandus tarandus) on the Seward Peninsula, Alaska*. Available online at: https://search.proquest.com/docview/304684271?accountid=43793 (accessed April 15, 2020).

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Ganzorig, S., Hoshino, B., Manaeva, K., and Igota, H. (2011). Seasonal migration of Tibetan antelope (*Pantholops hodgsonii*) and its relation with spatial patterns of relative primary productivity (NDVI). *Proceeding 32nd Asian Conf. Remote Sens.* 3, 1493–1497.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898. doi: 10.1111/j.1365-2656.2006.01106.x

Griffith, B., Douglas, D. C., Walsh, N. E., Young, D. D., McCabe, T. R., Russell, D. E., et al. (2002). "The porcupine caribou herd," in *Arctic Refuge Coastal Plain Terrestrial Wildlife Research Summaries*, eds D. C. Douglas, P. E. Reynolds, and E. B. Rhode (Reston: U. S. Geological Survey), 8–37.

Gunn, A. (2003). Voles lemmings and caribou - population cycles revisited? *Rangifer* 23, 105–111. doi: 10.7557/2.23.5.1689

Gunn, A., and Miller, F. L. (1986). Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. *Rangifer* 6, 151–158. doi: 10.7557/2.6.2.640

Gurarie, E., Hebblewhiteb, M., Joly, K., Kelly, A. P., Adamczewski, J., Davidson, S. C., et al. (2019). Tactical departures and strategic arrivals: divergent effects of climate and weather on caribou spring migrations. *Ecosphere* 10:e02971. doi: 10.1002/ecs2.2971

Gustine, D. D., Barboza, P. S., Adams, L., Griffith, B., Cameron, R., and Whitten, K. (2017). Advancing the match-mismatch framework for large herbivores in the Arctic: evaluating the evidence for a trophic mismatch in caribou. *PLoS One* 12:e0171807. doi: 10.1371/journal.pone.0171807

Guttal, V., and Couzin, I. D. (2010). Social interactions, information use, and the evolution of collective migration. *Proc. Natl. Acad. Sci. U.S.A.* 107, 16172–16177. doi: 10.1073/pnas.1006874107

Harju, S. M., Dzialak, M. R., Osborn, R. G., Hayden-Wing, L. D., and Winstead, J. B. (2011). Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. *Anim. Conserv.* 14, 502–511. doi: 10.1111/j.1469-1795.2011.00456.x

Hebblewhite, M., Merrill, E. H., and McDermid, G. J. (2008). A multi-scale test of the forage maturation hypothesis in a partially migrating ungulate population. *Ecol. Monogr.* 78, 141–166. doi: 10.1890/06-1708.1

Hooten, M. B., Johnson, D. S., Mcclintock, B. T., and Morales, J. M. (2017). *Animal Movement: Statistical Models for Telemetry Data*. Boca Raton, FL: CRC Press, Inc.

Howery, L. D., Bailey, D. W., and Laca, E. A. (1999). Impact of spatial memory on habitat use. *Grazing Behav. Livest. Wildl.* 3, 91–100.

Hurvich, C. M., and Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika* 76, 297–307.

Huse, G., Railsback, S., and Fernö, A. (2002). Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *J. Fish Biol.* 60, 571–582. doi: 10.1006/jfbi.2002.1874

Jenkerson, C., Maiersperger, T., and Schmidt, G. (2010). *eMODIS: A User-Friendly Data Source*. Reston: U. S. Geological Survey Open-File Report.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., et al. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* 361, 1023–1025. doi: 10.1126/science.aat0985

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. doi: 10.2307/1937156

Johnson, H. E., Gustine, D. D., Golden, T. S., Adams, L. G., Parrett, L. S., Lenart, E. A., et al. (2018). NDVI exhibits mixed success in predicting spatiotemporal variation in caribou summer forage quality and quantity. *Ecosphere* 9:e02461. doi: 10.1002/ecs2.2461

Johnstone, J., Russell, D. E., and Griffith, B. (2002). Variations in plant forage quality in the range of the Porcupine caribou herd. *Rangifer* 22, 83–91. doi: 10.7557/2.22.1.693

Joly, K., and Cameron, M. D. (2019). *Caribou vital sign annual report for the Arctic Network Inventory and Monitoring Program: September 2018-August 2019*. Fort Collins, CO: Collins.

Joly, K., Couriot, O., Cameron, M. D., and Gurarie, E. (2020). Behavioral, physiological, demographic and ecological impacts of hematophagous and endoparasitic insects on an arctic ungulate. *Toxins* 12:334. doi: 10.3390/toxins12050334

Joly, K., Gurarie, E., Sorum, M. S., Kaczensky, P., Cameron, M. D., Jakes, A. F., et al. (2019). Longest terrestrial migrations and movements around the world. *Sci. Rep.* 9:15333. doi: 10.1038/s41598-019-51884-5

Joly, K., Klein, D. R., Verbyla, D. L., Rupp, T. S., and Chapin, F. S. (2011). Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography* 34, 345–352. doi: 10.1111/j.1600-0587.2010.06377.x

Joly, K., Miller, S. D., and Shults, B. S. (2012). *Caribou Monitoring Protocol for the Arctic Network Inventory and Monitoring Program*. Natural Resource Report NPS/ARCN/NRR—2012/564. Fort Collins, CO: National Park Service.

Joly, K., Nellemann, C., and Vistnes, I. (2004). A reevaluation of caribou distribution near an oilfield road on Alaska's North Slope. *Wildl. Soc. Bull.* 34, 866–869.

Keating, K. A., and Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. *J. Wildl. Manage.* 68, 774–789.

Keating, K. A., Gogan, P. J. P., Vore, J. M., and Irby, L. R. (2007). A simple solar radiation index for wildlife habitat studies. *J. Wildl. Manage.* 71, 1344–1348. doi: 10.2193/2006-359

Kelleyhouse, R. A. (2001). *Calving Ground Selection and Fidelity: Teshekpuk Lake and Western Arctic Caribou Herds*. Fairbanks, AK: University of Alaska Fairbanks.

Kelsall, J. P. (1968). *The Migratory Barren-Ground Caribou of North America*. Ottawa: Queen's Printer.

Kuropat, P., and Bryant, J. P. (1980). "Foraging behavior of cow caribou on the Utukok calving grounds in Northwestern Alaska," in *Proceedings of the Second International Reindeer/Caribou Symposium 17-21 September 1979, Roros, Norway*, eds E. Reimers, E. Gaare, and S. Skjenneberg (Røros: Direktoratet for Vilt og Ferskvannsfisk), 64–70.

Le Corre, M., Dussault, C., and Côté, S. D. (2017). Weather conditions and variation in timing of spring and fall migrations of migratory caribou. *J. Mammal.* 98, 260–271. doi: 10.1093/jmammal/gyw177

Leimgruber, P., McShea, W. J., Brookes, C. J., Bolor-Erdene, L., Wemmer, C., and Larson, C. (2001). Spatial patterns in relative primary productivity and gazelle migration in the Eastern Steppes of Mongolia. *Biol. Conserv.* 102, 205–212. doi: 10.1016/S0006-3207(01)00041-6

Lent, P. C. (1966). Calving and related social behavior in the barren-ground caribou. *Z. Tierpsychol.* 23, 701–756. doi: 10.1111/j.1439-0310.1966.tb01707.x

Macander, M. J., Swingley, C. S., Joly, K., and Raynolds, M. K. (2015). Landsat-based snow persistence map for northwest Alaska. *Remote Sens. Environ.* 163, 23–31. doi: 10.1016/j.rse.2015.02.028

MacArthur, R., and Pianka, E. R. (1966). On optimal use of a patchy environment. *Am. Nat.* 100:603. doi: 10.1086/282454

Mager, K. H., Colson, K. E., and Hundertmark, K. J. (2013). High genetic connectivity and introgression from domestic reindeer characterize northern Alaska caribou herds. *Conserv. Genet.* 14, 1111–1123. doi: 10.1007/s10592-013-0499-2

Manly, B. F. J., McDonald, L. L., Thomas, D. L., Mcdonald, T. L., and Erickson, W. P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, Second Edn. Dordrecht: Springer.

Merkle, J. A., Fortin, D., and Morales, J. M. (2014). A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecol. Lett.* 17, 924–931. doi: 10.1111/ele.12294

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., et al. (2016). Large herbivores surf waves of green-up in spring. *Proc. R. Soc. B Biol. Sci.* 283:20160456. doi: 10.1098/rspb.2016.0456

Merkle, J. A., Sawyer, H., Monteith, K. L., Dwinnell, S. P. H., Fralick, G. L., and Kauffman, M. J. (2019). Spatial memory shapes migration and its benefits: evidence from a large herbivore. *Ecol. Lett.* 22, 1797–1805. doi: 10.1111/ele.13362

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., and Post, E. (2010). The effects of phenological mismatches on demography. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 3177–3186. doi: 10.1098/rstb.2010.0148

Nellemann, C., and Cameron, R. D. (1998). Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. *Can. J. Zool.* 76, 1425–1430. doi: 10.1139/z98-078

Nicholson, K. L., Arthur, S. M., Horne, J. S., Garton, E. O., and Del Vecchio, P. A. (2016). Modeling caribou movements: seasonal ranges and migration routes of the Central Arctic Herd. *PLoS One* 11:e0150333. doi: 10.1371/journal.pone.0150333

Oftedal, O. T. (1985). "Pregnancy and lactation," in *Bioenergetics of Wild Herbivores*, eds R. J. Hudson and R. G. White (Boca Raton, FL: CRC Press, Inc), 215–238.

Padilla, E., and Kofinas, G. P. (2014). "Letting the leaders pass": barriers to using traditional ecological knowledge in comanagement as the basis of formal hunting regulations. *Ecol. Soc.* 19:7. doi: 10.5751/ES-05999-190207

Peignier, M., Webber, Q. M. R., Koen, E. L., Laforge, M. P., Robitaille, A. L., and Vander Wal, E. (2019). Space use and social association in a gregarious ungulate:

testing the conspecific attraction and resource dispersion hypotheses. *Ecol. Evol.* 9, 5133–5145. doi: 10.1002/ece3.5071

Pettorelli, N., Gaillard, J., Mysterud, A., Duncan, P., Stenseth, N. C., Delorme, D., et al. (2006). Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos* 112, 565–572.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., and Stenseth, N. C. (2005a). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20, 503–510. doi: 10.1016/j.tree.2005.05.011

Pettorelli, N., Weladji, R. B., Holand, Ø, Mysterud, A., Breie, H., and Stenseth, N. C. (2005b). The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. *Biol. Lett.* 1, 24–26. doi: 10.1098/rsbl.2004.0262

Polansky, L., Kilian, W., and Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proc. R. Soc. B Biol. Sci.* 282:20143042. doi: 10.1098/rspb.2014.3042

Prichard, A. K., Parrett, L. S., Lenart, E. A., Caikoski, J. R., Joly, K., and Person, B. T. (2020). Interchange and overlap among four adjacent arctic caribou herds. *J. Wildl. Manage.* 84, 1500–1514. doi: 10.1002/jwmg.21934

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Sappington, J. M., Longshore, K. M., and Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* 71, 1419–1426. doi: 10.2193/2005-723

Schaefer, J. A., Bergman, C. M., and Luttich, S. N. (2000). Site fidelity of female caribou at multiple spatial scales. *Landsc. Ecol.* 15, 731–739. doi: 10.1023/A:1008160408257

Schaller, G. B., Kang, A., Xinbin, C. A. I., and Schaller, G. B. (2006). Migratory and calving behavior of Tibetan antelope population. *Acta Theriol. Sin.* 26, 105–113.

Shaw, A. K., and Couzin, I. D. (2013). Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *Am. Nat.* 181, 114–124. doi: 10.1086/668600

Singh, N. J., Grachev, I. A., Bekenov, A. B., and Milner-Gulland, E. J. (2010). Saiga antelope calving site selection is increasingly driven by human disturbance. *Biol. Conserv.* 143, 1770–1779. doi: 10.1016/j.biocon.2010.04.026

Singh, N. J., and Milner-Gulland, E. J. (2011). Conserving a moving target: planning protection for a migratory species as its distribution changes. *J. Appl. Ecol.* 48, 35–46. doi: 10.1111/j.1365-2664.2010.01905.x

Skoog, R. O. (1968). *Ecology of the Caribou (Rangifer Tarandus Granti) in Alaska*. Fairbanks, AK: University of Alaska Fairbanks.

Snyder, J. P. (1987). *Map Projections: A Working Manual*, Vol. 1395. Washington, D.C: US Government Printing Office.

Sousanes, P., and Hill, K. (2013). *Western Arctic Parklands Spring 2013 Weather Summary*. Available online at: https://irma.nps.gov/DataStore/DownloadFile/473401 (accessed April 15, 2020).

Taillon, J., Festa-Bianchet, M., and Côté, S. D. (2012). Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. *Biol. Conserv.* 147, 163–173. doi: 10.1016/j.biocon.2011.12.027

Thompson, D. C., and McCourt, K. H. (1981). Seasonal diets of the porcupine caribou herd. *Am. Midl. Nat.* 105, 70–76.

U.S Geological Survey (2017). *5 Meter Alaska Digital Elevation Models (DEMs) - USGS National Map 3DEP Downloadable Data Collection*. Reston: U.S. Geological Survey.

van der Graaf, S., Stahl, J., Klimkowska, A., Bakker, J. P., and Drent, R. H. (2006). Surfing on a green wave – how plant growth drives spring migration in the barnacle goose *Branta leucopsis*. *Ardea* 94, 567–577.

Wein, R. W. (1973). *Eriophorum vaginatum* L. *J. Ecol.* 61, 601–615. doi: 10.1016/j.colsurfb.2011.03.013

Westley, P. A. H., Berdahl, A. M., Torney, C. J., and Biro, D. (2018). Collective movement in ecology: from emerging technologies to conservation and management. *Philos. Trans. R. Soc. B Biol. Sci.* 373:20170004. doi: 10.1098/rstb.2017.0004

White, R. G. (1992). "Nutritional in relation to season, lactation, and growth of north temperate deer," in *The Biology of Deer*, ed. R. D. Brown (New York, NY: Springer), 407–417.

Whitten, K. R., Garner, G. W., Mauer, F. J., and Harris, R. B. (1992). Productivity and early calf survival in the Porcupine caribou herd. *J. Wildl. Manage.* 56, 201–212. doi: 10.2307/3808814

Wilson, R. R., Prichard, A. K., Parrett, L. S., Person, B. T., Carroll, G. M., Smith, M. A., et al. (2012). Summer resource selection and identification of important habitat prior to industrial development for the Teshekpuk Caribou Herd in Northern Alaska. *PLoS One* 7:e48697. doi: 10.1371/journal.pone.0048697

Witter, L. A., Johnson, C. J., Croft, B., Gunn, A., and Gillingham, M. P. (2012). Behavioural trade-offs in response to external stimuli: time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. *J. Anim. Ecol.* 81, 284–295. doi: 10.1111/j.1365-2656.2011.01905.x

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168. doi: 10.2307/1938423

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 17 December 2020
doi: 10.3389/fevo.2020.531027

The Importance of Environmental Variability and Transient Population Dynamics for a Northern Ungulate

Sophie L. Gilbert[1]*, Kris J. Hundertmark[2], Mark S. Lindberg[2], David K. Person[3] and Mark S. Boyce[4]

[1] Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, United States, [2] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, United States, [3] Alaska Department of Fish and Game, Braintree, VT, United States, [4] Department of Biological Sciences, Faculty of Science, University of Alberta, Edmonton, AB, Canada

The pathways through which environmental variability affects population dynamics remain poorly understood, limiting ecological inference and management actions. Here, we use matrix-based population models to examine the vital rate responses to environmental variability and individual traits, and subsequent transient dynamics of the population in response to the environment. Using Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Southeast Alaska as a study system, we modeled effects of inter-annual process variance of covariates on female survival, pregnancy rate, and fetal rate, and summer and winter fawn survival. To examine the influence of environmental variance on population dynamics, we compared asymptotic and transient perturbation analysis (elasticity analysis, a life-table response experiment, and transience simulation). We found that summer fawn survival was primarily determined by black bear (*Ursus americanus*) predation and was positively influenced by mass at birth and female sex. Winter fawn survival was determined by malnutrition in deep-snow winters and was influenced by an interaction between date of birth and snow depth, with late-born fawns at greater risk in deep-snow winters. Adult female survival was the most influential vital rate based on classic elasticity analysis, however, elasticity analysis based on process variation indicated that winter and summer fawn survival were most variable and thus most influential to variability in population growth. Transient dynamics produced by non-stable stage distributions produced realized annual growth rates different from predicted asymptotic growth rates in all years, emphasizing the importance of winter perturbations to population dynamics of this species.

Keywords: transient population dynamics, ungulate, Sitka black-tailed deer, winter severity, environmental stochasticity, survival, population growth

Edited by:
Paul Richard Krausman,
University of Arizona, United States

Reviewed by:
Inger Suzanne Prange,
Appalachian Wildlife Research Institute, United States
Lin Zhang,
Hangzhou Normal University, China

****Correspondence:***
Sophie L. Gilbert
sophiegilbert@uidaho.edu

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *30 January 2020*
Accepted: *09 October 2020*
Published: *17 December 2020*

Citation:
Gilbert SL, Hundertmark KJ, Lindberg MS, Person DK and Boyce MS (2020) The Importance of Environmental Variability and Transient Population Dynamics for a Northern Ungulate. Front. Ecol. Evol. 8:531027. doi: 10.3389/fevo.2020.531027

INTRODUCTION

Identifying key environmental factors that dictate animal population dynamics is a primary goal of ecologists, yet linking changes in environmental conditions to population-level responses remains a central challenge (Gamelon et al., 2014; Maldonado-Chaparro et al., 2018). Environments are complex and many features vary across time and space. Consequently, the effects of environmental variables on dynamics of populations can differ annually, seasonally, and spatially in magnitude and direction (Coulson et al., 2005). Moreover, those effects may be manifested differently in life history stages within the population, dependent on the species' biology (Gamelon et al., 2014). Because of difficulties in measuring population responses to environmental influences across all life history stages, inference regarding population responses to environmental change is frequently drawn from studies of a single important life history phase, and important covariates of fitness for this life history phase are then assumed to also be the primary factors influencing population dynamics. Yet even strong effects of the environment on life history phase may not matter in the context of population dynamics if those vital rates are relatively unimportant in determining population growth (Gaillard et al., 1998). Likewise, highly influential life-history phases in theory may not vary much in the real world due to evolutionary canalization of life-history patterns (i.e., reduced phenotypic variation due to unknown developmental mechanisms; Gaillard and Yoccoz, 2003).

Animal populations going through an abrupt change in size due to environmental or management actions often have different proportions of animals of each age (i.e., population stage) than populations not going through such perturbations, because the effects of the perturbation on age-specific vital rates often differs. Yet long-standing approaches to prospective and retrospective population analysis (i.e., sensitivity and elasticity analysis and life table response experiments), which are often used to analyze the effects of perturbations on population growth rates, assume the population has reached an asymptotic equilibrium where proportions of population stages are constant (i.e., stable age distribution). Importantly, perturbed populations with a non-stable age distribution often can result in very different annual population growth rates and population abundance than predicted by asymptotic analysis, which is referred to as population momentum (Koons et al., 2006).

Advances in modeling have led to substantial progress in understanding the effects of covariates on vital rates, such as survival (Pollock et al., 1989; Tsai et al., 1999; Blums et al., 2005; Monteith et al., 2013) and reproductive success (Delgiudice et al., 2007; Therrien et al., 2008; Tollefson et al., 2010). In parallel, our understanding of how vital rates affect population dynamics in variable environments has also improved dramatically with the advent of stochastic and density-dependent population models (Grant and Benton, 2000; Hunter et al., 2010; Boyce et al., 2012), life table response experiments (LTREs; Caswell, 2001, 2010), integrated population models (Schaub and Abadi, 2011), and increasingly in recent years, transient population analysis (Koons et al., 2005; Caswell, 2007; Ezard et al., 2010; Maldonado-Chaparro et al., 2018). Yet for many species, such analyses remain elusive due to data limitations, because data on all important life-history phases are required.

In this study, we examined the response of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) vital rates to environmental and individual-level predictor variables, then compare asymptotic and transient analysis of population dynamics to better understand the importance of transience for this population. Sitka black-tailed deer in the coastal temperate rainforest of North America provide an excellent system for such an examination of transience in response to the environment. Like many ungulates inhabiting temperate and higher latitudes, they are strongly influenced by seasonality and winter stochasticity. As expected for a sub-species of mule deer, Sitka black-tailed deer breed in fall (primary rut occurs in late October through early November, although secondary and tertiary rut cycles can occur for females not bred during the initial cycle), and produce 1 or 2 offspring per litter the following spring, first fawning as 2-year-olds (Johnson, 1987). They are the primary herbivore in the coastal temperate rainforest of Southeast Alaska, and an important source of protein for subsistence hunters, wolves (*Canis lupus*), and black bears (*Ursus americanus*). Winter is thought to limit deer populations in this system (Klein and Olson, 1960; Doerr et al., 2005; Farmer et al., 2006; Person et al., 2009), and industrial-scale timber harvest creates even-aged seral stands with poor winter forage (Alaback, 1982; Farmer and Kirchhoff, 2007), reducing the resilience of deer populations to severe winters, and possibly to predation as well (Farmer et al., 2006; Person et al., 2009). Previous studies have focused almost exclusively on adult female survival (Farmer et al., 2006; Person et al., 2009), without studying reproduction and subsequent fawn survival. This is a troubling gap in knowledge, because juvenile survival drives most observed variation in population growth rates for ungulates (Gaillard et al., 1998, 2000).

Here, we ask the following questions: Which environmental and individual variables are most predictive of survival for adult females and fawns? How do transient versus asymptotic population dynamics differ? And what do environmental effects and the resulting transient population dynamics imply for Sitka black-tailed deer ecology and management, and for ungulate populations in stochastic environments more generally? To answer these questions, we tested a series of hypotheses (**Table 1**) for each adult vital rate (pregnancy, fetal rate, and annual

TABLE 1 | Hypothesized effects of covariates on vital rates for Sitka black-tailed deer, Prince of Wales Island, AK, United States (2010–2013).

	Predicted Vital Rate Response				
Variable	**Pregnancy**	**Fetal rate**	**Fawn S(t), summer**	**Fawn S(t), winter**	**Adult S(t)**
Female age	+	+	+	+	+
Female mass (spring)	+	+	+	+	+
Female fat (spring)			+		+
Fawn birth mass			+	+	
Fawn birth date			+	–	
Fawn birth synchrony			+		
Litter size			–		
Sex (female)			+	+	
Winter severity (t)				–	–
Winter severity (t-1)	–	–	–	–	–
Winter(t)*Birthdate				–	
Timber harvest	–	–	–	–	–

Plus (+) signs indicate a hypothesized positive effect on each vital rate, while negative signs (–) indicate a hypothesized negative effect on that vital rate.

survival), and fawn vital rate (summer and winter survival). For fawn vital rates, we hypothesized that fawn survival should be influenced by maternal quality, and thus maternal age, mass, and body fat should increase fawn survival in summer and winter. Likewise, mass at birth should increases summer survival by reducing predation risk (Lomas and Bender, 2007; Johnstone-Yellin et al., 2009; Hurley et al., 2011), and increase winter survival if early mass deficits persist (Loison et al., 1999; Whiting et al., 2010). Similarly, litter size should reduce summer survival through decreased maternal investment, or potentially increased vulnerability to predation (Johnstone-Yellin et al., 2009; Van Vuren et al., 2013). In addition, birth synchrony should increase summer survival through reduced predation risk (but could have a negative effect instead; Sinclair et al., 2000) and enhanced overlap with peak plant nutrition (Langvatn et al., 2004; Parker et al., 2009). W also hypothesized that female fawns would survive at higher rates than males due to less-conspicuous behavior and slower growth rates (Jackson et al., 1972; Loison et al., 1999). In contrast, late-born fawns should be less vulnerable to bear predation as bears focus on salmon in late summer (Hilderbrand et al., 2004), but more vulnerable to winter starvation due to small body size (Loison et al., 1999; Whiting et al., 2010). Finally, we hypothesized that timber harvest would reduce summer fawn survival by concentrating deer and bears in young productive clearcuts; and winter severity and timber harvest could interactively reduce winter fawn survival, as young clearcuts with deep snow provide poor forage, while older clearcuts support little plant biomass (Alaback, 1982; Hanley, 2005; Farmer and Kirchhoff, 2007). For adult female deer, we predicted that all vital rates would respond positively to age, body mass, and body fat (Mueller and Sadleier, 1979; Delgiudice et al., 2006, 2007; Johnstone-Yellin et al., 2009), and negatively to timber harvest and winter severity, with potential lagged negative effects of winter in following years (Robinette et al., 1957; Verme, 1977; Fryxell et al., 1991). In terms of overall population dynamics, we expected that adult female survival would have the largest relative influence on population dynamics based on classic elasticity analysis, but that process variation in juvenile survival (i.e., recruitment) should be the highest of all the vital rates, and have the greatest influence on observed population fluctuations between years. Moreover, we predicted that non-stable stage distributions would result in transient dynamics that are quite different than those predicted by asymptotic growth rates.

MATERIALS AND METHODS

Study Area

Our study was conducted from 2010 to 2013, on central Prince of Wales Island, the largest among the many islands of the Alexander Archipelago of Southeast Alaska (**Figure 1**). The ∼420 km^2 study area is typical of the coastal temperate rainforest of the region, although with gentler topography, milder winter conditions (**Figure 2**), and more productive forests than many other islands. Nevertheless, topography can be quite rugged due to the limestone and granite bedrock underlying much of the landscape, ranging from 0 to 1200 m above sea level. Due to moderate annual temperature variation, year-round plentiful precipitation ($>$3 m per year) falls as rain in summer, and as rain and snow in winter, dependent on temperatures that often fluctuate around freezing. As a result, winter snowfall is highly variable, sometimes persisting at depths $<$ 1 m for weeks at a time even at sea level, but more often quite low at sea-level and increasing with elevation (White et al., 2009; Shanley et al., 2015). Relative to these long-term trends, our study period represented typical summer conditions in all summers (2010, 2011, and 2012), and a mild, moderately severe, and mild series of winters (2010–2011, 2011–2012, and 2012–2013, respectively). Natural habitat types are widely varied, including old-growth forest, numerous lakes, rivers and estuaries, alpine and subalpine vegetation above ∼400 m, and muskeg heaths (Alaback and Saunders, 2013).

The favorable environmental conditions relative to the region as a whole have traditionally supported abundant populations of key species, such as Sitka black-tailed deer, black bears, wolves, bald eagles (*Haliaeetus leucocephalus*), and salmon (*Oncorhynchus* spp.) that comprise a predator-prey system that also includes human hunters. In addition, central Prince of Wales continues to be the focus for industrial timber harvest in the Tongass National Forest, including in the study area (U.S. Forest Service, 2008), resulting in disproportionate harvest of productive old-growth forests via large-scale industrial clearcuts, particularly in our study area (Albert and Schoen, 2013). Historical patterns of timber harvest in our study area have produced a fragmented landscape, with some watersheds consisting entirely of old-growth forest, but most watersheds consisting of forest in a variety of seral stages. Timber harvest produces even-aged stands that gradually gain canopy cover and correspondingly lose forage biomass through successional stages, regaining old-growth properties after more than 200 years (Alaback, 1982; Alaback and Saunders, 2013). Of particular importance for deer in our study area is the abundance and large total area of seral stands $>$ 30 years old, now in the stem exclusion stage, resulting in reductions to deer nutritional carrying capacity that are likely to persist for decades across forest management scenarios (Albert and Schoen, 2013; Gilbert et al., 2015). Notably, on northern Prince of Wales Island, where our study area is located, contiguous patches of high-quality old-growth forest have been reduced by over 90%, with average patch size of these contiguous old-growth patches reduced from 264 ha in 1954 to 73 ha in 2004 (Albert and Schoen, 2013), an area comparable to the average female deer's home range (Schoen and Kirchhoff, 1985; Yeo and Peek, 1992).

Deer Capture and Monitoring

All animal capture and handling was carried out in accordance with the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC #136040-14) regulations.

From 2010 to 2012, 61 adult female deer (age 2 years and older) were captured from mid-April through mid-May of each year, and from July 5–25th during 2010 (n = 20 in 2010, n = 20 in 2011, and n = 21 in 2012). We did not capture yearling (age 1 year) animals during this study, but

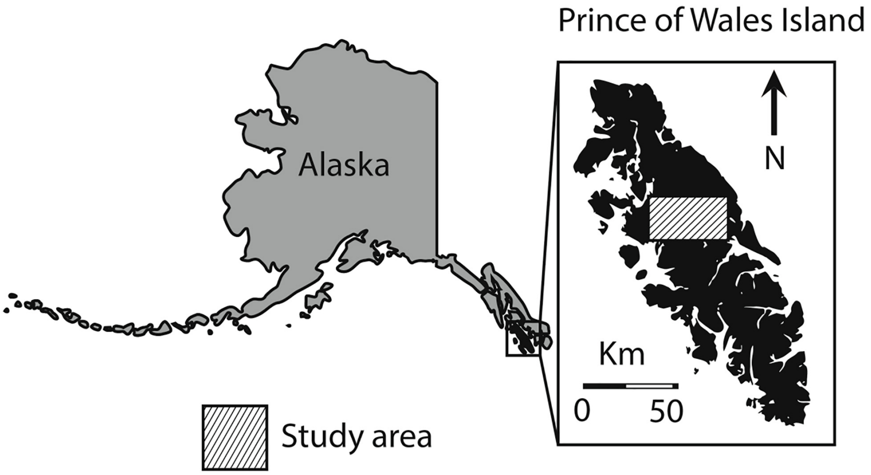

FIGURE 1 | The study area for Sitka black-tailed deer monitored from 2010 to 2013, located in the central portion of Prince of Wales Island in Southeast Alaska within the Tongass National Forest, United States.

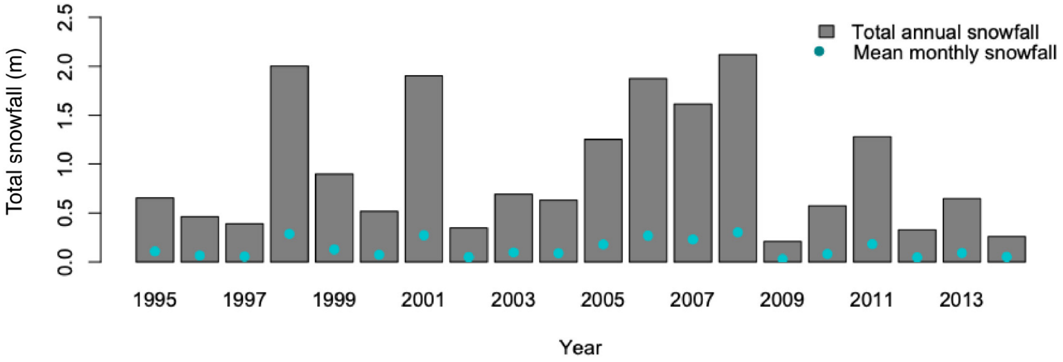

FIGURE 2 | Total annual snowfall recorded at Annette Island, the closest long-term weather station to the study area in Southeast Alaska, United States, where Sitka black-tailed deer were monitored from 2010 to 2013.

Farmer et al. (2006) and Person et al. (2009) studied deer in adjacent and overlapping study areas and found no difference in survival or causes of mortality between adult and yearling females. At capture, morphological measurements (i.e., heart girth, body length, hind foot length) were measured, blood collected, and body condition and pregnancy assessed using a portable ultrasound machine (Sonosite Titan®, Sonosite, Bothel, WA, United States). We estimated female body mass based on measured hearth girth (Parker, 1987), and ingesta-free body fat based on body mass and measurements from ultrasonography (Cook et al., 2010). Adult females were classified as 2, 3, and 4-plus years old based on tooth wear (Hamlin et al., 2000), but we collapsed 3 and 4-plus year-old animals into a single, adult age class. Adult survival was monitored weekly in summer (April–August 1) and every 2 weeks during the remainder of the year.

If adult females captured pre-parturition ($n = 53$) were pregnant, we attempted to fit them with vaginal implant transmitters (VITs; Advanced Telemetry Systems, Isanti, MN), allowing us to monitor females with VITs daily prior to parturition, locate the birth site, and capture neonates (Carstensen et al., 2003; Gilbert et al., 2014). Of the adult females successfully fitted with VITs ($n = 49$), we attempted to capture neonates by searching the birth site until 2 fawns were located, or for ≥2 h if fewer fawns were located. Neonates were gently restrained with eyes covered to reduce agitation, and were weighed, gendered, measured, and fitted with VHF (all years) and GPS (2012) break-away expandable collars, which fell off after approximately 1–1.5 years. Fawns were subsequently monitored 1-2 times per day from birth until August 1, then every 2 weeks until 1 year of age. The mortality signal was activated after 5 h of collar inactivity, and mortality events were investigated promptly (within 24 h of discovery during monitoring) to determine cause of death.

In total, 45 neonatal deer were captured at birth, while an additional 109 neonates were captured opportunistically along roads and trails and when spotted in meadows and clearcuts. Because mortality is highly age-dependent for neonatal deer, resulting in more vulnerable animals dying at birth or shortly thereafter, we excluded opportunistically captured neonates from

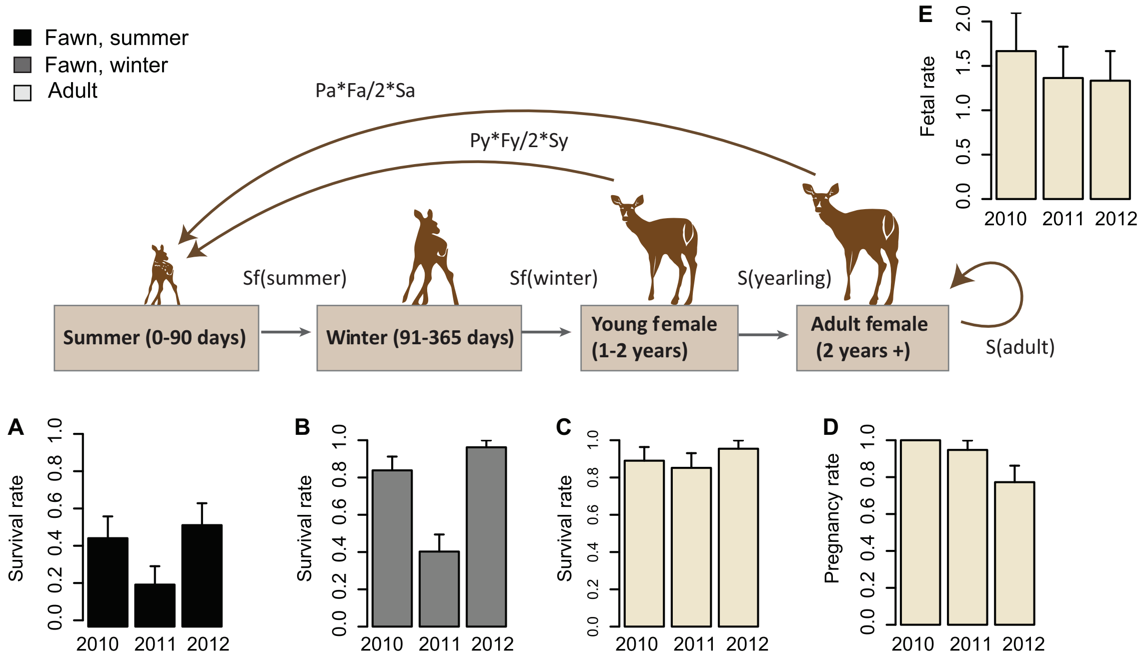

FIGURE 3 | Interannual variability in vital rates throughout the life cycle of Sitka black-tailed deer (monitored 2010–2013). Inter-annual variability in vital rates, with standard error bars, is shown for 2010–2012, comprised of **(A)** summer survival rate of fawns (0–90 days old); **(B)** winter survival rate of fawns (91–365 days old); **(C)** annual survival rate of adult females, **(D)** pregnancy rate of adult and yearling females, and **(E)** fetal rate of adult and yearling females. The study was conducted on Prince of Wales Island, AK, United States.

our analysis of summer survival to avoid left truncation of data (Gilbert et al., 2014). In addition, we lacked information on maternal covariates such as maternal age, body mass, and body fat for opportunistically captured fawns. Therefore, because daily survival rates and thus left truncation bias converge in our system at approximately 30 days of age, we included opportunistically captured fawns in our winter fawn survival estimates, increasing our winter sample size to 81 individuals.

Effects of Covariates on Vital Rates

We estimated vital rates, including mean rates across the 3 years of the study and for each year. Vital rates estimated were pregnancy and fetal rates (i.e., number of neonatal fawns per female), summer and winter survival rates for fawns, and annual survival rates for adults. Pregnancy and fetal rate were modeled using generalized linear models in program R (R Core Development Team, 2019) and were treated as binomial and Poisson response variables, respectively (Caswell, 2001; Morris and Doak, 2002).

Only 6 adult female deer died among the 63 monitored over 3 years. This low number of events limited the number of parameters that could be tested simultaneously. Models with fewer than 10 events per variable can produce biased model estimates and Type I predictor selection error (Vittinghoff and McCulloch, 2006). As a result, we only examined the univariate effects of age, mass, bodyfat, and timber harvest regime on adult survival.

Responses of fawn and adult female survival to environmental and individual covariates were modeled using known-fates survival models, implemented in the RMark package in program R (Laake, 2013). We modeled fawn survival in separate summer and winter periods, because vulnerability to predation, sources of mortality, and therefore effects of covariates change from birth through the first year of life. The neonatal period began at birth and continued to 90 days of age, by which age most summer fawn mortality had occurred (**Figure 3**). During this period, survival was modeled in weekly intervals, with a linear effect of time as survival increases markedly with fawn age (Gilbert et al., 2014). The fall and winter period, henceforth referred to as the over-winter period, extended from 91 to 365 days of age, and survival was considered in 2-week intervals, without an effect of time.

We did not consider adult female body fat as a covariate for pregnancy or fetal rate because body condition was measured in early spring, after pregnancy and fetal rate had already been determined. In addition, we did not have any measures of nutritional condition of fawns prior to winter because they were not re-captured. Therefore, with respect to winter survival of fawns, we included an effect of mass at birth, and back-calculated mass at birth for opportunistically captured fawns by assuming a universal age of 5 days at capture. Many studies age opportunistically captured fawns based on new hoof growth (Sams et al., 1996; Haskell et al., 2007); however, existing hoof growth equations were recently demonstrated to be inaccurate for mule deer (Grovenburg et al., 2014). Instead, we empirically generated a potential capture age window by re-capturing fawns caught at birth up until the age at which they could no longer be recaptured (11 days), and assigned the median of this period (5 days) as the age at capture (Johnson et al., 2004; Gilbert et al., 2014).

To identify top and competing models for inference, we began with a global covariate model for each vital rate, based on hypothesized ecological relationships described previously. We reduced the global model for each vital rate into subset models with a maximum of 3 covariates per model for fawns and 1 covariate per model for adult females due to our limited sample sizes and numbers of mortality events. Variables that were highly correlated with each other ($r > |0.6|$) were not included in the same sub-models to prevent coefficient bias. For each vital rate, a competitive model set was formed of models with Akiake's Information Critereon adjusted for small sample size (AICc) scores that differed ≤ 2 from the model with the lowest AICc score. We then discarded models with uninformative covariates from the competing model set (Arnold, 2010), defined as models where the model was simply an hierarchical expansion by a single covariate of the top-ranked model with no reduction in log likelihood (Burnham and Anderson, 2002; Arnold, 2010). We did not conduct model validation, as hypothesis-testing rather than prediction was the primary goal of this study, and sample size was limited.

Estimation of Process Variance in Vital Rates and Predictive Variables

Temporal process variation in the vital rates was estimated by fitting a model without covariates for each vital rate, but with a group (strata) effect of year, which we then used to estimate the mean and standard error for each vital rate in each year (i.e., raw variation in vital rates across years; Morris and Doak, 2002; White, 2000). Then, we followed the approach proposed by White (2000) to partition process from sampling variance, implemented in program R. The resulting mean vital rates, with variance partitioned into sampling and process components, were used in subsequent matrices. Temporal process variance in covariates of vital rates was estimated using different approaches for environmental and individual covariates. Variation in individual covariates between years was assumed to contain both process and sampling variance, as estimates depended on the animals sampled. For individual-level predictive variables, we estimated the inter-annual process variance by constructing generalized linear models of each covariate with an effect of year in the model, then used the maximization approach of White (2000) to partition process from sampling variance, as before. To quantify winter severity, we examined variation in total annual snowfall at Annette Island from 1995 to 2014 (**Figure 2**) as a measure of inter-annual variability and assumed that all observed variance was process variance.

Effects of Vital Rates and Covariates on Population Dynamics

To determine the effects of each covariate on vital rates, we used the fitted relationships from the top model for each vital rate identified based on AICc score to generate predicted vital rates across a range of each of two times the standard deviation of each predictive variable (calculated as the square root of process variance). If a variable occurred in more than one vital rate model, we perturbed all vital rates affected by that variable simultaneously so that the combined effects of each variable were incorporated into covariate elasticity calculations. For each variable perturbation, we then used the predicted vital rate responses as inputs into a matrix-based population model. The post-breeding model structure included 3 age classes (**Figure 3**), fawns, yearlings, and adults, with the transition probability for the first age class composed of multiplicative summer and winter survival rates, as discussed above. The matrix structure was specified as follows:

$$\begin{bmatrix} N_{f(t+1)} \\ N_{y(t+1)} \\ N_{a(t+1)} \end{bmatrix} = \begin{bmatrix} 0 & P_y * \frac{F_y}{2} * S_y & P_a * \frac{F_a}{2} * S_a \\ S_{f(s)} * S_{f(w)} & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} \begin{bmatrix} N_{f(t)} \\ N_{y(t)} \\ N_{a(t)} \end{bmatrix} \quad (1)$$

Where N_j is the number of individuals in age class j at time t, $N_{j(t+1)}$, is the number of individuals in age class j at time $t + 1$, S_j is the survival probability of age class j, and P_j and F_j are the pregnancy rate and fecundity (as females per female) respectively, of an individual of age class j. Because we did not capture any yearling individuals, we assumed that survival of yearlings was equal to that of adult females, as found in a previous study adjacent to our study area (Farmer et al., 2006). Pregnancy and fecundity of yearlings was measured during the course of this study, despite the fact that no yearlings were captured, because animals that were captured in the spring and aged as 2 years old were primiparous yearlings about to turn 2 (**Figure 3**).

For comparison with the perturbed matrix for each variable, we constructed a baseline matrix, with mean vital rates calculated from the top-ranked models and covariates held at mean values. We then calculated the covariate elasticity of each vital rate as the percent difference in the dominant eigenvalues (i.e., growth rates, λ) of the two matrices:

$$Ec = \frac{\lambda_{\text{pert}} - \lambda_{\text{base}}}{\lambda_{\text{base}}} \quad (2)$$

Where Ec is the covariate elasticity, λ_{base} is the dominant eigenvalue of the baseline matrix, and λ_{pert} is the dominant eigenvalue of the perturbed matrix [which is wonderfully dynamic like transient abundances]. We examined the effects of a positive versus negative perturbation to each covariate, resulting in positive and negative changes to λ_{pert} depending on the sign of the covariate coefficient. We calculated elasticities of the vital rates, and contributions of vital rates to observed inter-annual variability in growth rate (LTRE; Caswell, 2001; Morris and Doak, 2002), using the popbio package (Stubben et al., 2012) in program R. Elasticities of vital rates were calculated from the baseline matrix, λ_{base}. Contributions of vital rates to variation in growth rate (i.e., LTRE; Caswell, 2001) were based on sensitivity analysis of vital rates within the mean matrix between a treatment matrix and the baseline matrix. In this case, the vital rates for the treatment matrix where simply baseline vital rates reduced by 2 standard deviations, with SDs calculated from estimated process

TABLE 2 | Estimates of vital rates for across the period of the study (2010–2013) for Sitka black-tailed deer, Prince of Wales Island, AK, United States.

Vital Rate	Estimate	*Total* σ^2	*Process* σ^2	*N*
Pregnancy Rate	0.89	0.03	0.004	53
Fetal rate (fawns per female)	1.45	0.07	<0.001	32
Fawn survival, 1–90 days	0.41	0.06	0.01	45
Fawn survival, 91–365 days	0.73	0.17	0.08	82
Adult survival, 1–365 days	0.90	0.005	<0.001	61

Estimates are shown as means with total variance, process variance, and sample size (N).

variance for each vital rate (**Table 2**). If a vital rate had zero estimated process variance, it was not perturbed.

Sex was a covariate of fawn survival, yet we used a single-sex, all-female model for prediction of the effects of covariates, including sex. Perturbing the frequency of male versus female fawns would affect fawn survival and would therefore change the fecundity terms in our population model (i.e., number of female fawns per female at birth) in our population model. Because as we found no process variance (<0.001) in sex ratio between the years of our study, we not vary the sex ratio of fawns in our models.

Transient Analysis

Because our population was thought to be strongly affected by winter severity, which differentially affects stage class, and because we do not know how density dependence affects vital rates included in our population matrices, it is highly unlikely that the population ever achieves the stable stage distributions dictated by asymptotic analysis of our three annual Leslie matrices. To better understand how important such non-stable-stage effects on population growth might be, we conducted transient analysis. First we, constructed a simulation, in which we stochastically generated 10,000 initial stage distributions for the first year of our study (2008-09, a mild winter year following 3 successive severe winters), then projected this population structure through the subsequent annual matrices, which represented a year with a mild winter in year *t* (2010–2011), followed by a year with a severe winter (2011–2012), followed by a year with a mild winter (2012–2013). For each population run, we calculated population size for each stage in each year, transient population growth [simply $N(t{+}1)/N(t)$], reactivity (a measure of population density in the first year following perturbation, calculated as transient growth divided by asymptotic growth of the annual matrix), and inertia, a similar metric indicating the ratio of maximum population size achieved due to both transient and population dynamics compared to that achieved via asymptotic growth alone (Koons et al., 2007; Stott et al., 2012). Following initial analysis, inertia was revealed to be equivalent to reactivity for this population, since maximum transient population size relative to asymptotic dynamics was achieved in year $t = 1$, and inertia was therefore not included in our final analysis. These resulting distributions of population size, transient growth, and reactivity were used to generate the median and 95% confidence intervals for these metrics. In addition, we examined the minimum and maximum potential influences of transient dynamics for each annual matrix using the minimum attenuation and maximum amplification metrics described in Stott et al. (2012), which also allows for calculation of which population stage contributed most to attenuation and amplification relative to asymptotic dynamics.

RESULTS

Vital Variability and Response to Predictive Variables

Pregnancy and Fetal Rate

The average pregnancy rate for adult female deer was 0.89 (Total variance = 0.03, process variance = 0.009). Vital rates varied across years (**Table 2** and **Figure 3**). Females had pregnancy rates of 1.0 in 2010, 0.95 in 2011, and 0.77 in 2012.

The average fertility rate for pregnant females was 1.45 fawns per female (total variance = 0.07, process variance < 0.001), implying a rate of 0.72 female fawns per female if a 1:1 gender ratio is assumed. The rate of female fawns per female measured from our captured fawns was 0.625 female fawns per female (*SE* = 0.10), with an upper 95% confidence interval of 0.82, leading us to accept the 1:1 gender ratio assumption. Among years, the fertility rate was 1.67 fawns per female (*SE* = 0.43) in 2010, 1.36 (*SE* = 0.35) in 2011, and 1.33 (*SE* = 0.33) in 2012.

Variables that affected probability of pregnancy were the severity of the proceeding winter as measured by total snowfall [winter(*t*-1)], adult female age, and timber harvest of the watershed, with the best-supported model including winter (*t*-1) and timber harvest (**Table 3**). Adult female age had a positive effect on probability of pregnancy, as did occupancy of a timber-harvested watershed, while a winter with greater total snowfall reduced the probability of pregnancy in the following spring. Fetal rate was not strongly affected by any covariates; the null model was top-ranked, although a positive effect of female age ($\Delta AICc = 1.24$; **Table 3**) and female mass ($\Delta AICc = 1.83$) also received support. Female age and female mass were positively correlated for pregnant females ($r = 0.60$, $p < 0.01$) and for females where fawns were captured ($r = 0.57$, $p < 0.01$), and as a result, female age and female mass were not simultaneously included as covariates in any vital rate models. Based on the univariate analysis of covariates of female survival, there was support for negative effects of female mass and age on survival (i.e., younger, lighter-weight females survived with higher probability; **Table 3**).

Adult Survival Rate

As previously discussed, annual adult survival was high and showed little process variance, averaging 0.90 (total variance = 0.005, process variance < 0.001) for the study period, and varying little between years, and was estimated as 0.89 (*SE* = 0.07) in 2010, 0.85 (*SE* = 0.08) in 2011), and 0.95 (*SE* = 0.04) in 2012. The largest source of mortality ($n = 3$) was from hunting, with an average mortality rate of 0.05 (*SE* = 0.03), followed by a 0.03 (*SE* = 0.02) mortality rate from malnutrition ($n = 2$), and a 0.02 mortality rate form black bear predation ($n = 1$, *SE* = 0.02). Wolf mortality was not recorded for any

TABLE 3 | Ranked vital rate models within 2 *AICc* units of the top models of vital rates for Sitka black-tailed deer during the period of the study (2010–2013), Prince of Wales Island, AK, United States.

Model Equation	β_1	β_2	β_3	Δ *AICc*
Probability of pregnancy				
$P \sim \beta_1(Logged) + \beta_2\ (Winter_{(t-1)})$	2.49 (1.19)	-3.07 (1.55)	–	0
$P \sim \beta_1(Logged) + \beta_2\ (Winter_{(t-1)}) + \beta_3\ (Age)$	2.27 (1.22)	−2.99 (1.57)	1.24 (0.90)	0.12
Number of fetuses per female				
$F \sim 1$	–	–	–	0
$F \sim \beta_1(Age)$	0.20 (0.19)	–	–	1.24
$F \sim \beta_1(Mass)$	0.01 (0.02)	–	–	1.83
Fawn survival summer, 1–90 days				
$S(t)_S \sim \beta_1(Mass) + \beta_2(Sex)$	2.48 (0.97)	0.90 (0.56)	–	0
$S(t)_S \sim \beta_1(Mass)$	2.12 (0.92)	–	–	0.51
$S(t)_S \sim \beta_1(Mass) + \beta_2(Winter_{(t-1)})$	2.34 (0.95)	0.74 (0.62)	–	1.18
$S\ (t)_S \sim \beta_1(Mass) + \beta_2(B.date)$	2.08 (0.92)	0.03 (0.03)		1.65
$S(t)_S \sim \beta_1(Mass) + \beta_2(Sync)$	2.12 (0.91)	0.33 (0.40)	–	1.91
Fawn survival winter, 91–365 days				
$S(t)_w \sim \beta_1(Winter_t) + \beta_2(B.date)$	−3.27 (0.69)	−0.06 (0.02)	–	0
$S\ (t)_w \sim \beta_1\ (Winter_t) + \beta_2\ (B.date)\ + \beta_3(B.date * Winter_t)$	−1.60 (1.34)	0.02 (0.06)	−0.08 (0.06)	0.14
Adult survival 1–365 days				
$S(t) \sim \beta_1(Mass)$	−0.19 (0.07)	–	–	0
$S(t) \sim \beta_1(Age)$	−1.67 (0.74)	–	–	1.77

Competitive models are shown with parameter estimates and (standard errors), and difference in AICc score from top-ranked model.

adult deer monitored during this study, despite wolf predation acting as a major source of mortality for deer monitored in the same study area 10 years previously (Person et al., 2009; Alaska Department of Fish and Game, unpublished data). Wolves were at low numbers and restricted distributions during the course of this study due to high harvest pressure (Gilbert et al., 2015; Alaska Department of Fish and Game, 2017).

Fawn Survival Rate

Fawn survival was lowest during the summer, due primarily to predation by black bears, and highly variable between years. Average survival in summer was 0.41 across years (total variance = 0.06, process variance = 0.01), and annual summer survival rates were 0.47 in 2010 (SE = 0.13), 0.23 in 2011 (SE = 0.11), and 0.54 in 2012 (SE = 0.13). Across all years, mortality rates were 0.46 (n = 21, SE = 0.08) due to black bear predation, and 0.11 (n = 6, SE = 0.05) due to other causes. Other causes of mortality included unknown predation (n = 1), eagle predation (n = 1), drowning (n = 1), and premature birth (n = 3). As before, because maternal mass and age were correlated among the fawns sampled (r = 0.56), they were not included in the same models. In addition, synchrony of births was lower in timber harvested watersheds (p = 0.015), although the two variables were only moderately correlated (r = 0.36).

Summer fawn survival, from birth through 90 days of age, was affected by gender and birth mass. In the top-ranked survival model, female fawns had a higher survival probability male fawns, as did fawns that weighed more at birth (**Table 3** and **Figure 4A**). Other competitive models included a positive effect of birth asynchrony on survival, indicating that fawns born more synchronously survived at lower rates, and a positive effect of winter severity in the previous year, indicating that fawns produced following a severe winter survived better. While there were no strongly correlated covariates, there was a statistical relationship between timber harvest of watershed and birth synchrony, with more asynchronous births in timber harvested watersheds (r = 0.34, p = 0.015).

During the winter months, fawn survival was determined primarily by malnutrition-caused mortality, which occurred only during the winter of 2011. Across the three years of the study, the average winter survival rate was 0.73 (total variance = 0.17, process variance = 0.08), due to a mortality rate of 0.21 (n = 16, SE = 0.05) from malnutrition, 0.03 (n = 2, SE = 0.02) from wolf predation, 0.02 (n = 1, SE = 0.02) from bear predation (in late September), and 0.03 (n = 2, SE = 0.02) due to other causes (n = 1 car collision, n = 1 illegal hunting). Among years, winter survival rates were high in 2010 (M = 0.84, SE = 0.07) and 2012 (M = 0.96, SE = 0.04), and quite low in 2011 (M = 0.40, SE = 0.09).

Winter fawn survival, from 91 through 365 days of age, was strongly affected by winter severity and birthdate. The top-ranked model supported negative effects of winter severity and birthdate, indicating that late-born fawns were at greater risk of mortality, as were fawns during high-snowfall winters. In addition, a competing model supported an interactive, negative effect of winter severity and birthdate, indicating lower survival during severe winters and for late-born fawns (**Table 3** and **Figure 4B**).

Effects of Vital Rates on Asymptotic Population Dynamics

Analysis of the baseline population model indicated that the average population growth rate for the study period was

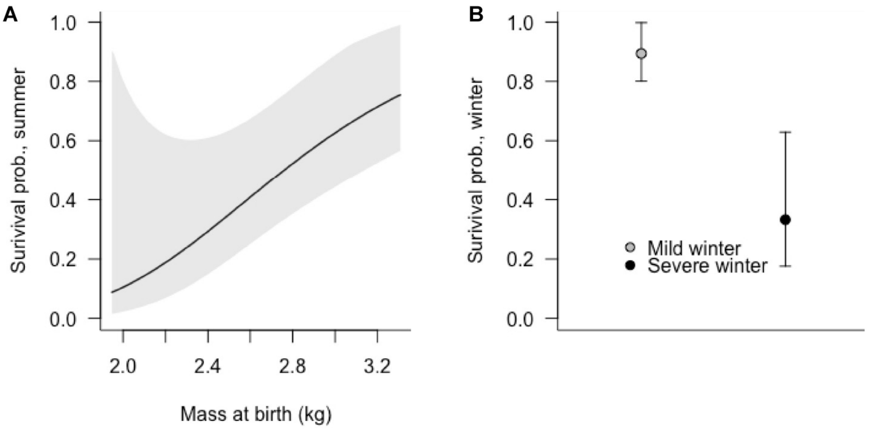

FIGURE 4 | The effects of **(A)** birth mass of Sitka black-tailed deer fawns on summer survival (0–90 days old), and of **(B)** occurrence of a severe winter on fawn winter survival (91–365 days old), shown with 95% confidence intervals. The study was conducted 2010–2013, on Prince of Wales Island, AK, United States.

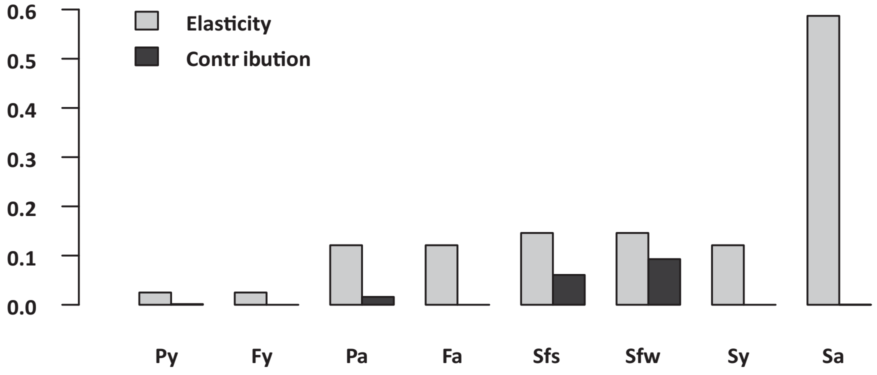

FIGURE 5 | Sitka black-tailed deer vital rate elasticity versus contributions to observed annual variability in asymptotic growth rate, where *Py* and *Fa* denotes pregnancy of yearlings and adults, *Fy* and *Fa* denoted fertility (females per fawn) of yearling and adults, and *Sf(s), Sf(w)*, *Sy*, and *Sa* denote survival of age classes fawn (days 1–90), fawn (days 91–365), yearling, and adults. The study was conducted 2010–2013, on Prince of Wales Island, AK, United States.

distinctly positive, with λ = 1.08, despite the harsh winter of 2011. Annual estimates of deterministic population growth rates were 1.17 in 2010, 0.92 in 2011, and 1.18 in 2012. The most influential vital rate based on deterministic elasticity values (**Figure 5** and **Supplementary Table 1**) was adult female survival, followed by summer and winter fawn survival, survival of yearlings, fertility of adults and yearling, and pregnancy of adults and yearlings. In contrast, when vital rates were perturbed based on process variation, relatively high levels of process variation resulted in winter fawn survival contributing most to variation in inter-annual growth rate, followed closely by summer fawn survival, then by adult and yearling pregnancy rate, with other vital rates contributing much less due to almost no process variation (**Figure 5** and **Supplementary Table 1**).

Transient Population Dynamics

Transient simulation analysis indicated that initial stage structure can cause differences in realized growth compared to growth predicted from asymptotic analysis (**Figure 5**). Realized median growth rate was 1.29 (95% CI = 1.13, 1.43) in 2010, 0.92 (95% CI = 0.89, 0.95) in 2011, and 1.12 (95% CI = 1.11, 1.12) in 2012, indicating that the initial uncertainty we included in stage structure attenuated with time. These transient growth rates were different from those predicted by asymptotic dynamics, resulting in reactivity ratios relative to asymptotic dynamics of 1.10 (95% CI = 0.96, 1.22) in 2010, 0.99 (95% CI = 0.97, 1.04) in 2011, and 0.93 (95% CI = 0.93, 0.94) in 2012. This simulation did not include uncertainty in yearly vital rate values, so potential variability of growth rates could be considerably higher. Analysis of population inertia indicated that both maximum attenuation and amplification relative to asymptotic growth rate occurred in the first time-step following perturbation of all annual matrices. For the 2010, 2011, and 2012 annual matrices, maximum attenuation was 1.49, 1.73, and 1.36 respectively, resulting in a realized growth rate of 1.75, 1.58, and 1.62, and with the adult female stage, fawn stage, and fawn stage contributing most to amplification differences. Yearly matrix maximum attenuations for 2010, 2011, and 2012 were 0.34, 0.08, and 0.41 respectively, resulting in realized growth rates of 0.40, 0.07, and 0.49, and

TABLE 4 | Maximum possible amplifications and attenuations of Sitka black-tailed deer population projection matrices observed during this study (2010–2013), along with number achieved at max/min [N(t)], and stage making the greatest contribution.

Matrix	$A_{Mild(t-1)Mild\ (t)}$	$A_{Mild(t-1)Severe\ (t)}$	$A_{Severe(t-1)Mild\ (t)}$
Max amplification	1.49	1.73	1.36
N(t)	1.75	1.58	1.63
Stage	Adult female	Fawn	Adult female
Max attenuation	0.34	0.08	0.41
N(t)	0.40	0.07	0.49
Stage	Fawn	Fawn	Fawn

All min/max values were achieved within one timestep. The study was conducted on Prince of Wales Island, AK, United States.

with the highest level of contributions coming from fawns for all matrices (**Table 4**).

DISCUSSION

Winter severity emerged as a dominant influence on population dynamics for Sitka black-tailed deer, based on vital rate models and analysis of population dynamics, and resulting from high vulnerability of fawns to mortality in severe winter conditions. While many of our hypotheses regarding the primary influences on deer vital rates and population dynamics followed expectations for a northern ungulate, there were also some intriguing and unexpected outcomes from our analyses. For adult females, probability of pregnancy and fetal rate were higher for older females, as predicted, while adult female mass positively affected fetal rate. These results agree with life-history theory, in which older and larger females of long-lived species typically produce more offspring at more frequent intervals (Hamel et al., 2009; Lindberg et al., 2013). While reproductive senescence is thought to occur in Sitka black-tailed deer (Johnson, 1987), our study was not longitudinal across the lifetime of a deer, so the importance of senescence was not possible to determine. Interestingly, there was a mild positive effect of the binary timber harvest variable on probability of pregnancy; in addition, synchrony of births was negatively affected by timber harvest, indicating that some feature of these altered watersheds affected deer conception probability and timing and suggesting the need for further inquiry. Based on our univariate analysis of covariates of adult survival, female mass negatively affected survival of adult females, likely because hunters selected for larger individuals. Hunting was the primary cause of death for adult females in our study, and larger animals are typically preferred by hunters (Milner et al., 2007; Brinkman et al., 2009). Thus, large body mass could decrease adult female risk from natural causes (as has been documented in many other systems) but increase risk from human hunting.

Summer fawn survival was the lowest survival rate, with more than half of all fawns dying before 3 months of age on average (**Table 2**), primarily from black bear predation. Summer fawn mortality risk was negatively affected by birth mass and fawn gender, with larger fawns and female fawns surviving with higher probability. Behavioral differences between male and female fawns have been observed, with male fawns engaging in more conspicuous behaviors (i.e., active more of the time; Jackson et al., 1972), likely increasing detection probability by bears. In addition, synchrony of birth decreased summer survival, possibly because bears actively search for fawns only during the peak of births. Surprisingly, the severity of the previous winter positively affected summer fawn survival, possibly because low-quality adult females were selectively removed from the population, along with their unborn offspring, or lost fetuses prematurely and did not give birth at all (as evidenced by the low pregnancy rate in 2012). Bear predation risk appears to be linked to nutrition of fawns, given the strong effect of fawn mass at birth on summer survival, and thus is likely partially compensatory. Yet other expected nutritional effects were not supported; maternal spring body fat did not predict subsequent fawn survival, suggesting that perhaps females conserve body fat at the expense of fawn mass at birth (i.e., the “selfish cow” hypothesis, Clutton-Brock et al., 1989; Therrien et al., 2008; Parker et al., 2009).

In contrast, overwinter fawn mortality varied greatly from year to year, and was almost entirely driven by malnutrition in the single harsh winter, with very high fawn survival during the other years, beyond our expectations. Late-born fawns, which enter winter at smaller sizes and with fewer body reserves, were at greater risk of malnutrition during the harsh winter but not during other winters. Intriguingly, we recorded no effect of birth mass, demonstrating that fawns were likely able to recover from early deficits in body mass. While there was no support for an effect of timber harvest regime of watershed on winter survival, the connection between timber harvest and birth asynchrony indicates that timber harvest can affect birth timing, and merits further investigation given the importance of birthdate for surviving harsh winters.

While timber harvest did have a negative effect on fawn and adult female survival based on coefficient values in models in which it occurred, the standard errors of the term were high, leading to the exclusion of the term from final models. Timber harvest regime of watersheds is a very coarse variable, homogenizing variation in seral stage and corresponding nutrition within deer home ranges. In addition, deer select habitat from within the home range (Johnson, 1980), and may be able to increase access to nutrition through selection (Parker, 2003). Age and configuration of harvested stands, and quality and size of remaining old-growth forest patches, interactively drive deer selection in this study area in winter (Gilbert et al., 2017), and are likely important in determining winter survival. For example, Brinkman et al. (2011) found that deer density declined by 30% after 3 successive severe winters, using a study area overlapping ours and with largest declines in timber-harvested watersheds. A detailed analysis of winter habitat selection that included stand-level variation in seral stage, biomass, and snow depth was conducted in 2017 (Gilbert et al., 2017), and efforts to better characterize timber-harvested habitat and its effects on deer are ongoing (Shanley et al., in review; Gilbert et al., 2015), but linking habitat selection or use to fitness outcomes and population dynamics is an important next step.

Major limitations of this study are its relatively short duration compared to the lifetime of a deer, the correspondingly small

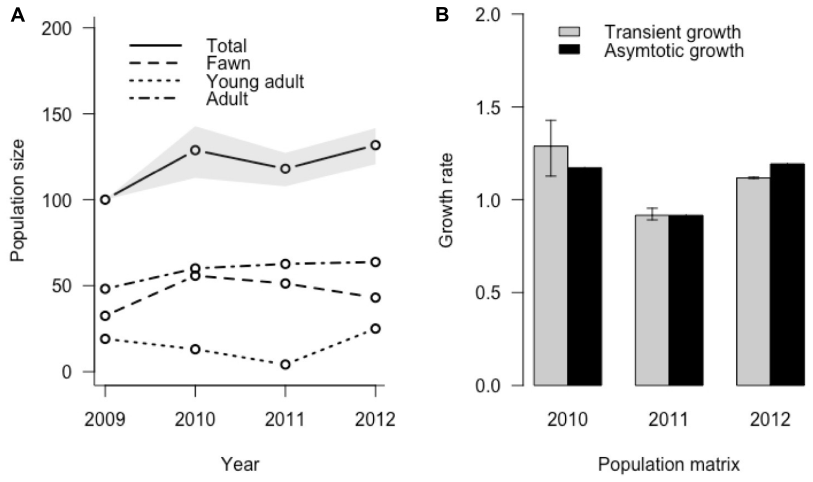

FIGURE 6 | Realized population change for the Sitka black-tailed deer population, incorporating simulated uncertainty in initial stage distribution in 2009 and based on a starting size of 100 individuals; **(A)** shows population size in total and in each stage, and **(B)** shows transient versus asymotic growth rate produced by each year's projection matrix, during the years of the study (2010–2013) on Prince of Wales Island, AK, United States.

number of winters observed, the lack of knowledge regarding population structure or density, and the lack of detailed information available regarding timber harvest for the different age classes sampled. The negative effects of winter we document here are the result of only 3 years of study, which were by no means as extreme as previously documented severe winters (Brinkman et al., 2011). In such very severe winters, adult female survival can be greatly reduced (Alaska Department of Fish and Game, 2013), whereas we documented only 2 deaths from malnutrition during the severe winter in our study, with no statistical effect on adult female survival. For example, Brinkman et al. (2011) documented a 30% decline in deer density over 3 years, equivalent to a mean annual growth rate of 0.89, lower than our lowest calculated annual growth rate of 0.92. In addition, winter severity could interact with deer density relative to carrying capacity to influence survival and growth rate response (Bowyer et al., 2014), which we were not able to measure during the course of this study. Therefore, it is likely that the effects of severe winters on population growth can be much greater than documented here, due to reduced adult female survival, a highly influential vital rate in the population, and also dependent on stage structure entering the winter, as indicated by a minimum possible transient growth rate from our harsh winter matrix of 0.07 (i.e., drastic population decline). Likewise, a larger wolf population, typical during years prior to our study, likely would reduce winter survival of fawns and adults, particularly during severe winters, but we were unable to document such winter-predation interactions due to a greatly reduced wolf population size during our study (Person et al., 2009; Gilbert et al., 2015; Alaska Department of Fish and Game, 2017). Wolf abundance also may affect the influence of habitat covariates on vital rates if deer alter behavior and select lower-nutrition habitats to avoid risk of predation at higher wolf densities (Chamaillé-Jammes et al., 2014). In addition, while timber harvest is the dominant disturbance mechanism in the temperate rainforest ecosystem of our study area, which has been disproportionately harvested compared to other parts of the region (Albert and Schoen, 2013), our sampling methods did not allow us to conduct detailed analysis of habitat use for all deer included in the study (e.g., fawns sampled opportunistically did not have GPS-collared mothers to provide spatial locations). As a result, we were only able to include timber harvest as a binary, watershed-level predictive variable in our models, which undoubtedly greatly reduces our ability to make inference about how this important source of disturbance affects deer.

Both asymptotic and transient analysis of growth yielded broadly similar pictures of depressed growth during harsh winters (**Figure 6**), but with differences in stage structure contributing to considerable divergence in transient versus predicted asymptotic growth. While adult female survival is highly influential in determining inter-annual differences in asymptotic population growth in theory, it is neither highly variable nor highly responsive to environmental influences in our system, nor does it contribute substantially to variability in population growth rate. This conforms to other studies of ungulate population dynamics (Gaillard et al., 1998, 2000). In contrast, juvenile survival is strongly influenced by environmental and individual covariates, primarily by mass at birth and thus presumably nutrition during summer and early fall, and winter severity during the winter. Thus, variation in environmental covariates can influence population growth rate most strongly through changes in fawn survival rather than adult survival. It is important to note, however, that when an extreme event (i.e., very deep, persistent snow in winter) does reduce adult survival, the same event is likely to reduce juvenile survival and pregnancy rates much more, resulting in a compounded negative impact to the transient population growth rate via a change in stage structure and a change in vital rates (Coulson et al., 2005; **Figure 5**).

We were unable to fully investigate the demographic impact of extreme weather events in this study, because such an extreme event did not occur during the three years of this work. Given projections for increased stochasticity and severity of weather under future climate change scenarios, such compounding, multi-vital-rate effects of stochastic weather should prove highly influential for ungulate populations. In this ecosystem, average winter snowfall is projected to decrease, while severity of stochastically occurring major storms may increase (Shanley et al., 2015), potentially leading to greater swings in deer population size as series of mild winters lead to high population densities, which then experience density-dependent negative impacts of occasional severe winters. Although survival of adult female ungulates is evolutionarily canalized against environmental variation (Gaillard and Yoccoz, 2003), extreme events can overwhelm the resilience of this key vital rate (Brinkman et al., 2011), causing large demographic impacts through joint reductions of adult and juvenile survival. Understanding and predicting the effects of increased frequency of extreme events, and the interactive role that other environmental influences such an anthropogenic habitat change could play in determining population response, is therefore an emerging challenge for population ecology and management.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care and Use Committee University of Alaska Fairbanks.

AUTHOR CONTRIBUTIONS

All authors carried out the study design. SG and DP carried out the data collection. SG carried out the data analysis with planning and feedback from all other authors. SG wrote the manuscript with editing by all other authors.

FUNDING

This work was funded primarily by a grant from the Alaska Department of Fish and Game. Additional support came from the National Science Foundation, in the form of an NSF GK-12 graduate fellowship. Publication of this article was funded in part by the University of Idaho – Open Access Publishing Fund, and in part by the Institute of Arctic Biology Director's Fund at the University of Alaska Fairbanks.

ACKNOWLEDGMENTS

We thank the Alaska Department of Fish and Game, the U.S. Forest Service, and the National Science Foundation's GK-12 Fellowship program for support of this work. In addition, we thank Jim Baichtal, Ray Slayton, Kris Larsen, Doug Larsen, Rod Flynn, Casey Pozzanghera, Kathleen Miles, Tess Ruswick, and Moira Hughes for their invaluable assistance with field data collection. This manuscript was originally a chapter in the dissertation of SG, but has not been published in peer-reviewed form elsewhere, and is accessible online (Gilbert, 2015).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.531027/full#supplementary-material

REFERENCES

Alaback, P. B. (1982). Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63, 1932–1948. doi: 10.2307/1940131

Alaback, P. G., and Saunders, S. (2013). "Disturbance ecology of the temperate rainforests of Southeast Alaska and adjacent British Columbia," in *North Temperate Rainforests: Ecology and Conservation*, eds J. W. Shoen and G. Orians (Seattle, WA: University of Washington Press), 73–88.

Alaska Department of Fish and Game (2013). *Operational Plan for Intensive Management of Sitka Black-Tailed Deer in a Portion of Game Management Unit 3*. Juneau, AK: Alaska Department of Fish and Game.

Alaska Department of Fish and Game (2017). *GMU 2 Wolf Population Update, Autumnt 2016*. Juneau, AK: Alaska Department of Fish and Game.

Albert, D. M., and Schoen, J. W. (2013). Use of historical logging patterns to identify disproportionately logged ecosystems within temperate rainforests of southeastern Alaska. *Conserv. Biol.* 27, 774–784. doi: 10.1111/cobi.12109

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *J. Wildl. Manage.* 74, 1175–1178. doi: 10.1111/j.1937-2817.2010.tb01236.x

Blums, P., Nichols, J. D., Hines, J. E., Lindberg, M. S., and Mednis, A. (2005). Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia* 143, 365–376. doi: 10.1007/s00442-004-1794-x

Bowyer, R. T., Bleich, V. C., Stewart, K. M., Whiting, J. C., and Monteith, K. L. (2014). Density dependence in ungulates: a review of causes, and concepts with some clarifications. *J. Wildl. Manage.* 100, 550–572.

Boyce, M. S., Baxter, P. W. J., and Possingham, H. P. (2012). Managing moose harvests by the seat of your pants. *Theor. Popul. Biol.* 82, 340–347. doi: 10.1016/j.tpb.2012.03.002

Brinkman, T. J., Chapin, T., Kofinas, G., and Person, D. K. (2009). Linking hunter knowledge with forest change to understand changing deer harvest opportunities in intensively logged landscapes. *Ecol. Soc.* 14:36. Available online at: http://www.ecologyandsociety.org/vol14/iss1/art36/

Brinkman, T. J., Person, D. K., Chapin, F. S. III, Smith, W., and Hundertmark, K. J. (2011). Estimating abundance of Sitka black-tailed deer using DNA from fecal pellets. *J. Wildl. Manage.* 75, 232–242. doi: 10.1002/jwmg.22

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd Edn. New York, NY: Springer.

Carstensen, M., Delgiudice, G. D., and Sampson, B. A. (2003). Using doe behavior and vaginal-implant transmitters to capture neonate white-tailed deer in north-central Minnesota. *Wildl. Soc. Bull.* 31, 634–641.

Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd Edn. Sunderland, MA: Sinauer Associates, Inc.

Caswell, H. (2007). Sensitivity analysis of transient population dynamics. *Ecol. Lett.* 10, 1–15. doi: 10.1111/j.1461-0248.2006.01001.x

Caswell, H. (2010). Life table response experiment analysis of the stochastic growth rate. *J. Ecol.* 98, 324–333. doi: 10.1111/j.1365-2745.2009.01627.x

Chamaillé-Jammes, S., Malcuit, H., Le Saout, S., and Martin, J. L. (2014). Innate threat-sensitive foraging: black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. *Oecologia* 174, 1151–1158. doi: 10.1007/s00442-013-2843-0

Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature* 337, 260–262. doi: 10.1038/337260a0

Cook, R. C., Cook, J. G., Stephenson, T. R., Myers, W. L., Mccorquodale, S. M., Vales, D. J., et al. (2010). Revisions of rump fat and body scoring indices for deer, elk, and moose. *J. Wildl. Manage.* 74, 880–896. doi: 10.2193/2009-031

Coulson, T., Gaillard, J. M., and Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *J. Anim. Ecol.* 74, 789–801. doi: 10.1111/j.1365-2656.2005.00975.x

Delgiudice, G. D., Fieberg, J., Riggs, M. R., Carstensen Powell, M., and Pan, W. (2006). A long-term age-specific survival analysis of female white-tailed deer. *J. Wildl. Manage.* 70, 1556–1568. doi: 10.2193/0022-541X(2006)70[1556:ALASAO]2.0.CO;2

Delgiudice, G. D., Lenarz, M. S., and Carstensen Powell, M. (2007). Age-specific fertility and fecundity of northern free-ranging white-tailed deer: evidence for reproductive senescence? *J. Mammal.* 88, 427–435. doi: 10.1644/06-MAMM-A-164R.1

Doerr, J. G., Degayer, E. J., and Ith, G. (2005). Winter habitat selection by Sitka black-tailed deer. *J. Wildl. Manage.* 69, 322–331. doi: 10.2193/0022-541X(2005)069<0322:WHSBSB>2.0.CO;2

Ezard, T. H. G., Bullock, J. M., Dalgleish, H. J., Millon, A., Pelletier, F., Ozgul, A., et al. (2010). Matrix models for a changeable world: the importance of transient dynamics in population management. *J. Appl. Ecol.* 47, 515–523. doi: 10.1111/j.1365-2664.2010.01801.x

Farmer, C. J., and Kirchhoff, M. D. (2007). Ecological classification of deer habitat in the Tongass National Forest, Alaska. *Northwest. Nat.* 88, 73–84. doi: 10.1898/1051-1733(2007)88[73:ECODHI]2.0.CO;2

Farmer, C. J., Person, D. K., and Bowyer, R. T. (2006). Risk factors and mortality of black-tailed deer in a managed forest landscape. *J. Wildl. Manage.* 70, 1403–1415. doi: 10.2193/0022-541X(2006)70[1403:RFAMOB]2.0.CO;2

Fryxell, J. M., Hussell, D. J. T., Lambert, A. B., and Smith, P. C. (1991). Time lags and population fluctuations in white-tailed deer. *J. Wildl. Manage.* 55, 377–385. doi: 10.2307/3808963

Gaillard, J. M., Festa-Bianchet, M., and Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* 13, 58–63. doi: 10.1016/S0169-5347(97)01237-8

Gaillard, J.-M., Festa-Bianchet, N. G., Yoccoz, N. G., Loison, A., and Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., and Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84, 3294–3306. doi: 10.1890/02-0409

Gamelon, M., Gimenez, O., Baubet, E., Coulson, T., Tuljapurkar, S., and Gaillard, J. (2014). Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. *Am. Nat.* 184, 673–683. doi: 10.1086/677929

Gilbert, S. L. (2015). *Environmental Drivers of Deer Population Dynamics and Spatial Selection in Southeast Alaska*. Available online at: http://hdl.handle.net/11122/6088 (accessed August 2015).

Gilbert, S. L., Haynes, T., Lindberg, M. S., Albert, D. M., and Kissling, M. (2015). *Future Population Trends and Drivers of change for Alexander Archipelago Wolves on and Near Prince of Wales Island, Alaska*. Final Report for Cooperative Agreement No. F15AC000206. Anchorage, AK: Alaska Department of Fish and Game. doi: 10.7287/peerj.preprints.1934

Gilbert, S. L., Hundertmark, K. J., Person, D. K., Lindberg, M. S., and Boyce, M. S. (2017). Behavioral plasticity in a variable environment?: snow depth and habitat interactions drive deer movement in winter. *J. Wildl. Manage.* 98, 246–259. doi: 10.1093/jmammal/gyw167

Gilbert, S. L., Lindberg, M. S., Hundertmark, K. J., and Person, D. K. (2014). Dead before detection: addressing the effects of left truncation on survival estimation and ecological inference for neonates. *Methods Ecol. Evol.* 5, 992–1001. doi: 10.5061/dryad.p1r40

Grant, A., and Benton, T. G. (2000). Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* 81, 680–693. doi: 10.1890/0012-9658(2000)081[0680:EAFDDP]2.0.CO;2

Grovenburg, T., Monteith, K., Jaques, C., Klaver, R., DePerno, C., Brinkman, T., et al. (2014). Re-evaluating neonatal age models for ungulates: does model choice affect survival estimates? *PLoS One* 9:e108797. doi: 10.1371/journal.pone.0108797

Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J. M., and Côté, S. D. (2009). Spring normalized difference vegetation index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J. Appl. Ecol.* 46, 582–589. doi: 10.1111/j.1365-2664.2009.01643.x

Hamlin, K. L., Pac, D. F., Sime, C. A., DeSimone, R. M., and Dusek, G. L. (2000). Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *J. Wildl. Manage.* 64, 441–449. doi: 10.2307/3803242

Hanley, T. A. (2005). Potential management of young-growth stands for understory vegetation and wildlife habitat in southeastern Alaska. *Landsc. Urban Plan.* 72, 95–112. doi: 10.1016/j.landurbplan.2004.09.015

Haskell, S. P., Ballard, W. B., Butler, D. A., Tatman, N. M., Wallace, M. C., Kochanny, C. O., et al. (2007). Observations on capturing and aging deer fawns. *J. Mammal.* 88, 1482–1487. doi: 10.1644/07-MAMM-A-004R.1

Hilderbrand, G. V., Farley, S. D., Schwartz, C. C., Charles, T., and Robbins, C. T. (2004). Importance of salmon to wildlife: implications for integrated management. *BioOne* 15, 1–9. doi: 10.2192/1537-6176(2004)015<0001:IOSTWI>2.0.CO;2

Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Armstrup, S., and Stirling, I. (2010). Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* 91, 2883–2897. doi: 10.1890/09-1641.1

Hurley, M. A., Unsworth, J. W., Zager, P., Hebblewhite, M., Garton, E. O., Montgomery, D. M., et al. (2011). Demographic response of mule deer to experimental reduction of coyotes and mountain lions in Southeastern Idaho. *Wildl. Monogr.* 178, 1–33. doi: 10.1002/wmon.4

Jackson, R. M., White, M., and Knowlton, F. F. (1972). Activity patterns of young white-tailed deer fawns in South texas. *Ecology* 53, 262–270. doi: 10.2307/1934080

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. doi: 10.2307/1937156

Johnson, D. S., Barry, R. P., and Bowyer, R. T. (2004). Estimating timing of life-history events with coarse data. *J. Mammal.* 85, 932–939. doi: 10.1644/BFW-009

Johnson, L. J. (1987). *Reproductive Potential of Sitka Black-Tailed Deer in Southeast Alaska*. Juneau, AK: Alaska Department of Fish and Game.

Johnstone-Yellin, T. L., Shipley, L. A., Myers, W. L., and Robinson, H. S. (2009). To twin or not to twin? Trade-offs in litter size and fawn survival in mule deer. *J. Mammal.* 90, 453–460. doi: 10.1644/08-MAMM-A-030.1

Klein, D. R., and Olson, S. T. (1960). Natural mortality patterns of deer in Southeast Alaska. *J. Wildl. Manage.* 24, 80–88. doi: 10.2307/3797359

Koons, D. N., Grand, J. B., Zinner, B., and Rockwell, R. F. (2005). Transient population dynamics: relations to life history and initial population state. *Ecol. Modell.* 185, 283–297. doi: 10.1016/j.ecolmodel.2004.12.011

Koons, D. N., Holmes, R. R., and Grand, J. B. (2007). Population inertia and sensitivity to changes in vital rates and population structure. *Ecology* 88, 2857–2867. doi: 10.1890/06-1801.1

Koons, D. N., Rockwell, R. F., and Grand, J. B. (2006). Population momentum: implications for wildlife management. *J. Wildl. Manage.* 70, 19–26. doi: 10.2193/0022-541X(2006)70[19:PMIFWM]2.0.CO;2

Laake, J. L. (2013). *RMark: an R Interface for Analysis of Capture-Recapture Data with MARK*. Silver Spring, MD: National Marine Fisheries Service, 1–25.

Langvatn, R., Mysterud, A., Stenseth, N. C., and Yoccoz, N. G. (2004). Timing and synchrony of ovulation in red deer constrained by short northern summers. *Am. Nat.* 163, 763–772. doi: 10.1086/383594

Lindberg, M. S., Sedinger, J. S., and Lebreton, J.-D. (2013). Individual heterogeneity in black brant survival and recruitment with implications for harvest dynamics. *Ecol. Evol.* 3, 4045–4056. doi: 10.1002/ece3.767

Loison, A., Langvatn, R., and Solberg, E. J. (1999). Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* 22, 20–30. doi: 10.1111/j.1600-0587.1999.tb00451.x

Lomas, L. A., and Bender, L. C. (2007). Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. *J. Wildl. Manage.* 71, 884–894. doi: 10.2193/2006-203

Maldonado-Chaparro, A., Blumstein, D. T., Armitage, K., and Childs, D. Z. (2018). Transient LTRE analysis reveals the demographic and trait- mediated processes that buffer population growth. *Ecol. Lett.* 21, 1693–1703. doi: 10.1111/ele.13148

Milner, J. M., Nilsen, E. B., and Andreassen, H. P. (2007). Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* 21, 36–47. doi: 10.1111/j.1523-1739.2006.00591.x

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2013). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildl. Monogr.* 186, 1–62. doi: 10.1002/wmon.1011

Morris, B., and Doak, D. (2002). *Quantitative Conservation Biology*. Sunderland, MA: Sinauer Associates, Inc.

Mueller, C. C., and Sadleier, R. M. F. S. (1979). Age at first conception in black-tailed deer. *Biol. Reprod.* 21, 1099–1104. doi: 10.1095/biolreprod21.5.1099

Parker, K. L. (1987). Body-surface measurements of mule deer and elk. *J. Wildl. Manage.* 51, 630–633. doi: 10.2307/3801281

Parker, K. L. (2003). Advances in the nutritional ecology of cervids at different scales. *Ecoscience* 10, 395–411. doi: 10.1080/11956860.2003.11682788

Parker, K. L., Barboza, P. S., and Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* 23, 57–69. doi: 10.1111/j.1365-2435.2008.01528.x

Person, D. K., Farmer, C., O'Connor, P., and Doerr, J. (2009). *Habitat use and Survivorship of Sitka Black-Tailed Deer in Southeast Alaska: a Regional Meta-Analysis and Synthesis*. Juneau, AK: Alaska Department of Fish and Game.

Pollock, K. H., Winterstein, S. R., Bunck, C. M., Curtis, P. D., The, S., Management, W., et al. (1989). Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* 53, 7–15. doi: 10.2307/3801296

R Core Development Team (2019). *R.: a Language and Environment for Statistical Computing*. Available online at: http://www.r-project.org (accessed August 1, 2019).

Robinette, W. L., Gashwiler, J. S., Low, J. B., and Jones, D. A. (1957). Differential mortality by sex and age among mule deer. *J. Wildl. Manage.* 21, 1–16. doi: 10.2307/3797671

Sams, M. G., Lochmiller, R. L., Hellgren, E. C., Warde, W. D., Varner, L. W., and Warde, D. (1996). Morphometric predictors of neonatal age for white-tailed deer. *Wildl. Soc. Bull.* 24, 53–57.

Schaub, M., and Abadi, F. (2011). Integrated population models?: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* 152, 227–237. doi: 10.1007/s10336-010-0632-7

Schoen, J. W., and Kirchhoff, M. D. (1985). Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, Southeast Alaska. *J. Wildl. Manage.* 49, 96–103. doi: 10.2307/3801852

Shanley, C. S., Pyare, S., Goldstein, M. I., Alaback, P. B., Albert, D. M., Beier, C. M., et al. (2015). Climate change implications in the northern coastal temperate rainforest of North America. *Clim. Change* 130, 155–170. doi: 10.1007/s10584-015-1355-9

Sinclair, A. R. E., Mduma, S. A. R., and Arcese, P. (2000). What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* 81, 2100–2111. doi: 10.1890/0012-9658(2000)081[2100:WDPASO]2.0.CO;2

Stott, I., Hodgson, D. J., and Townley, S. (2012). Popdemo: an R package for population demography using projection matrix analysis. *Methods Ecol. Evol.* 3, 797–802. doi: 10.1111/j.2041-210X.2012.00222.x

Stubben, C., Miligan, B., and Nantel, P. (2012). *Popbio: Construction and Analysis of Matrix Population Models*. Available online at: https://CRAN.R-project.org/package=popbio (accessed August 1, 2019)

Therrien, J.-F., Cote, S. D., Festa-Bianchet, M., and Ouellet, J.-P. (2008). Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction. *Anim. Behav.* 75, 235–243. doi: 10.1016/j.anbehav.2007.04.030

Tollefson, T. N., Shipley, L. A., Myers, W. L., Keisler, D. H., and Dasgupta, N. (2010). Influence of summer and autumn nutrition on body condition and reproduction of lactating mule deer. *J. Wildl. Manage.* 74, 974–986. doi: 10.2193/2008-529

Tsai, K., Pollock, K. H., and Brownie, C. (1999). Effects of violation of assumptions for survival analysis methods in radiotelemetry studies. *J. Wildl. Manage.* 63, 1369–1375. doi: 10.2307/3802856

U.S. Forest Service (2008). *Tongass Land and Resource Management Plan. R10-MB-338dd*. Juneau, AK: Alaska Department of Fish and Game.

Van Vuren, D. H., Bray, M. P., and Heltzel, J. M. (2013). Differential investment in twin offspring by female pronghorns (*Antilocapra americana*). *J. Mammal.* 94, 155–161. doi: 10.1644/12-MAMM-A-107.1

Verme, L. J. (1977). Assessment of natal mortality in upper Michigan deer. *J. Wildl. Manage.* 41, 700–708. doi: 10.2307/3799992

Vittinghoff, E., and McCulloch, C. E. (2006). Relaxing the rule of ten events per variable in logistic and Cox regression. *Am. J. Epidemiol.* 165, 710–718. doi: 10.1093/aje/kwk052

White, G. C. (2000). "Population viability analysis: data requirements and essential analyses," in *Research Techniques in Animal Ecology: Controversies and Consequences*, eds L. Boitani and T. K. Fuller (New York, NY: Columbia University Press), 288–331.

White, K. S., Pendleton, G. W., and Hood, E. (2009). Effects of snow on Sitka black-tailed deer browse availability and nutritional carrying capacity in southeastern Alaska. *J. Wildl. Manage.* 73, 481–487. doi: 10.2193/2007-499

Whiting, J. C., Stewart, K. M., Bowyer, R. T., and Flinders, J. T. (2010). Reintroduced bighorn sheep: do females adjust maternal care to compensate for late-born young? *Eur. J. Wildl. Res.* 56, 349–357. doi: 10.1007/s10344-009-0323-y

Yeo, J. J., and Peek, J. M. (1992). Habitat selection by female Sitka black-tailed deer in logged forests of southeastern Alaska. *J. Wildl. Manage.* 56, 253–261. doi: 10.2307/3808820

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 28 January 2021
doi: 10.3389/fevo.2020.522174

Detecting Resource Limitation in a Large Herbivore Population Is Enhanced With Measures of Nutritional Condition

Brendan A. Oates[1*†], *Kevin L. Monteith*[2], *Jacob R. Goheen*[3], *Jerod A. Merkle*[3], *Gary L. Fralick*[4] and *Matthew J. Kauffman*[5]

[1] Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, United States, [2] Haub School of Environment and Natural Resources, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, United States, [3] Department of Zoology and Physiology, University of Wyoming, Laramie, WY, United States, [4] Wyoming Game and Fish Department, Thayne, WY, United States, [5] U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, United States

Edited by:
Paul Richard Krausman,
University of Arizona, United States

Reviewed by:
Inger Suzanne Prange,
Appalachian Wildlife Research
Institute (United States), United States
John Alfred Bissonette,
Utah State University, United States

***Correspondence:**
Brendan A. Oates
baoates@gmail.com

†Present address:
Brendan A. Oates,
Washington Department of Fish
and Wildlife, Ellensburg, WA,
United States

Specialty section:
This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 21 December 2019
Accepted: 31 December 2020
Published: 28 January 2021

Citation:
Oates BA, Monteith KL,
Goheen JR, Merkle JA, Fralick GL and
Kauffman MJ (2021) Detecting
Resource Limitation in a Large
Herbivore Population Is Enhanced
With Measures of Nutritional
Condition.
Front. Ecol. Evol. 8:522174.
doi: 10.3389/fevo.2020.522174

Resource limitation at the population level is a function of forage quality and its abundance relative to its per capita availability, which in turn, determines nutritional condition of individuals. Effects of resource limitation on population dynamics in ungulates often occur through predictable and sequential changes in vital rates, which can enable assessments of how resource limitation influences population growth. We tested theoretical predictions of bottom-up (i.e., resource limitation) forcing on moose (*Alces alces*) through the lens of vital rates by quantifying the relative influence of intrinsic measures of nutritional condition and extrinsic measures of remotely sensed environmental data on demographic rates. We measured rates of pregnancy, parturition, juvenile, and adult survival for 82 adult females in a population where predators largely were absent. Life stage simulation analyses (LSAs) indicated that interannual fluctuations in adult survival contributed to most of the variability in λ. We then extended the LSA to estimate vital rates as a function of bottom-up covariates to evaluate their influence on λ. We detected weak signatures of effects from environmental covariates that were remotely sensed and spatially explicit to each seasonal range. Instead, nutritional condition strongly influenced rates of pregnancy, parturition, and overwinter survival of adults, clearly implicating resource limitation on λ. Our findings depart from the classic life-history paradigm of population dynamics in ungulates in that adult survival was highly variable and generated most of the variability in population growth rates. At the surface, lack of variation explained by environmental covariates may suggest weak evidence of resource limitation in the population, when nutritional condition actually underpinned most demographics. We suggest that variability in vital rates and effects of resource limitation may depend on context more than previously appreciated, and density dependence can obfuscate the relationships between remotely sensed data and demographic rates.

Keywords: bottom-up, life stage simulation analysis, survival, ungulate, density dependence, vital rate, moose, population

INTRODUCTION

Empirical evidence along with perceived declines in abundance of moose (*Alces alces*) across the southern distribution of their range has resulted in heightened interest in identifying factors limiting population growth. Recent studies indicate that nutritional limitation stemming from suboptimal habitat conditions, parasite abundance, and thermal stress associated with climatic warming and drying are contributing to poor population performance in the Intermountain West (Becker et al., 2010; Monteith et al., 2015), Minnesota (Murray et al., 2006; Lenarz et al., 2009; DelGiudice et al., 2011), Michigan (Peterson, 1999; Dodge et al., 2004), and in the northeastern United States (Musante et al., 2010; Bergeron et al., 2013). Confounding the evidence for nutritional limitation is the recolonization of large carnivores, namely, grizzly bears (*Ursus arctos horribilis*) and gray wolves (*Canis lupus*), which, in the Intermountain West, occurred concurrently with changes in temperature and precipitation patterns (Bangs and Fritts, 1996; Berger et al., 2001). The relative importance of predation and resource limitation (i.e., forage quality and abundance, its per capita availability) in structuring dynamics of animal populations has been debated for decades, which was catalyzed partially by the Green World Hypothesis (GWH; Hairston et al., 1960). For prey populations, the continuum of top-down and bottom-up forcing implies that trade-offs occur between acquisition of resources for survival and susceptibility to predation (McNamara and Houston, 1987), mediated by proximity to carrying capacity (*K*) (Sinclair and Krebs, 2002; Pierce et al., 2012; Bowyer et al., 2013). Nonetheless, declines in recruitment of young and abundance of moose are also apparent in regions where large carnivores are absent, further suggesting a predominant role of nutritional limitation in populations near the southern distribution of moose. The life-history paradigm (Eberhardt, 2002) exhibited by ungulates offers a useful predictive framework to assess the influence of resource limitation on animal populations (Gaillard et al., 2000; Eberhardt, 2002; Bonenfant et al., 2009; Monteith et al., 2014). Understanding how nutritional limitation is expressed in populations near *K* can enhance predictive models that aim to determine the relative influence of top-down and bottom-up forces on ungulate population dynamics.

The proximity of prey populations to *K* has considerable influence on the relative strength of top-down and bottom-up forces that structure ungulate demography (Kie et al., 2003; Bonenfant et al., 2009). For example, populations near *K* tend to be in poor nutritional condition with reduced fecundity and survival (McCullough, 1979; Simard et al., 2008). Nevertheless, predator populations can reduce density-dependent feedbacks by killing prey and reducing intraspecific competition (Boyce et al., 1999). Consequently, we expect vital rates and the factors that underpin them to differ between populations regulated by top-down and bottom-up forcing (Pierce et al., 2012). For example, in prey populations under strong top-down forcing, intraspecific competition should be reduced and nutritional condition should increase (Bowyer et al., 2014). In this instance, predation should dampen signals of resource limitation by pushing prey populations below *K* (Owen-Smith and Mills, 2006; Hopcraft et al., 2010). In contrast, most populations without predators should exhibit strong signals of resource limitation as density increases, and vital rates should respond accordingly (Coulson et al., 2001; Stewart et al., 2005; Monteith et al., 2014). Indeed, interactions between resource limitation and predation can obscure their relative influence at the population level. Thus, a hypothesis-driven approach to assessing variability in vital rates in populations exposed to few predators can help tease apart and detect the mechanisms of resource limitation, advancing our understanding of the influence of predators on ungulate prey (Gaillard et al., 2000; Bowyer et al., 2013).

Resource limitation on population dynamics in ungulates often occurs through predictable and sequential changes in vital rates: reduced survival of young followed by increased age at first reproduction, reduced rates of pregnancy, parturition, and reduced survival of prime-aged adults (i.e., the "Eberhardt Model"; Eberhardt, 2002). Typically, adult survival is high and largely invariant, and the greater variability in juvenile survival commonly drives population dynamics (Gaillard et al., 1998, 2000; Gaillard and Yoccoz, 2003; Raithel et al., 2007). With a reduced energetic buffer against the vagaries of weather, populations exposed to resource limitation may be more sensitive to weather (Portier et al., 1998; Kie et al., 2003; Hansen et al., 2019), and consequently, environmental variability can lead to dramatic changes in population growth rate (λ) for resource-limited populations (Coulson et al., 2001). In contrast, reduced intraspecific competition in response to top-down forcing can weaken environmental signatures on vital rates, because animals possess an energetic buffer against them (Bowyer et al., 2014).

Assessing nutritional status is critical for understanding the influence of habitat alterations on populations, because the nutritional condition of an individual is an integrated measure of energetic gains and losses relative to food quality and abundance (Cook et al., 2007; Monteith et al., 2014). Nutritional condition forms the foundation for life history of individuals and thus affects nearly every demographic component of a population leading to net effects on population growth (Monteith et al., 2014). Remotely sensed data [e.g., normalized difference vegetation index (NDVI) and standardized precipitation index] are increasingly being used as a proxy for assessing resource limitation in ungulate populations (Pettorelli et al., 2011; Monteith et al., 2015), and their accessibility, broad spatial and temporal availability makes them an attractive tool. Nevertheless, remotely sensed data do not discriminate between the species and quality of forage selected by the animal, and per capita availability is particularly difficult to quantify. Thus, linking relationships between resource limitation and remotely sensed data can be noisy or weak. Measures of nutritional condition inherently integrate density dependence because of its effect on per capita availability of food, which is realized in the nutritional status of an animal and not possible to measure through simple measures of habitat. Moreover, directly quantifying habitat quality is exceedingly difficult and often cost prohibitive (DeYoung et al., 2000; Stephenson et al., 2006). An integrated measure of habitat quality and food availability is possible by measuring nutritional status because animal condition is a direct product of its environment (Franzmann, 1977; Parker et al., 2009).

Predictive equations for estimating ingesta-free body fat (IFBFat) of moose based on ultrasonography measurements of maximum depth of rump fat are quite accurate (r^2 = 0.96; Stephenson et al., 1998), and thus represent a meaningful measurement of nutritional condition.

We sought to quantify how resource limitation influences population dynamics through the lens of variability in vital rates of moose in the Sublette Herd, located in a mountainous region of western Wyoming, United States. Further, we wanted to understand the relative context in which measures of nutritional condition would compare with remotely sensed environmental covariates in predicting vital rate responses. We estimated demographic rates of individuals to evaluate predictions of variability in vital rates and their relative influence on λ (Gaillard et al., 1998) in the context of Eberhardt's model (Eberhardt, 2002). We did not incorporate population size into demographic models, because annual minimum counts and juvenile ratios were stable before, during, and after the study period (Wyoming Game and Fish Department, unpublished data). Predators were largely absent and female harvest was low; therefore, we expected negative effects of density dependence to be operating and moose to be sensitive to environmental signals of resource limitation (i.e., summer drought and NDVI). Specifically, we expected (1) reductions in survival of young, and fecundity of adults if resource limitation was occurring (Eberhardt, 2002) and (2) invariant survival of adults, relative to other vital rates (Gaillard et al., 1998). Further, we used individual measures of nutritional condition and remotely sensed data to quantify the ability to detect resource limitation, should it occur. We then used deterministic matrix models and life stage simulation analysis (LSA; Wisdom et al., 2000) to assess vital rate contributions to population-level responses to metrics of resource limitation. Additionally, our study provides insight into the interplay among bottom-up forces as they manifest through the life-history characteristics of moose in a variable environment.

MATERIALS AND METHODS

Study Area

We monitored 82 adult female moose in the Sublette Herd from February 2011 until August 2014 in the Upper Green River basin and eastern foothills of the Wyoming Range (42.8653 degrees North, 110.0708 degrees West; **Figure 1**). Land ownership was 60% private and 40% public lands. During winter, moose occupied riparian areas at low to mid elevations (1866–2150 m), consisting mainly of willow (Salix spp.) interspersed with cottonwood (*Populus* spp.), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*). Homogenous and mixed forests of subalpine fir, lodgepole pine (*Pinus contorta*), aspen, Engelmann spruce (*Picea engelmannii*), and Douglas fir also occurred throughout higher elevations along the foothills of the Wyoming Range. Winter ranges of moose typically spanned the relatively flat floodplains of the Green River, as well as Cottonwood, Horse, and Beaver Creeks, which were dominated by willow and intermixed with cottonwoods. Approximately half of the moose were resident with overlapping summer and winter seasonal ranges, while migratory individuals traveled short distances (5–20 miles) to higher elevations or other tributaries of the Green and Hoback Rivers containing stands of willow, subalpine fir, lodgepole pine, and Douglas fir interspersed with stands of aspen, limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*). Residents occupied willow communities, aspen forests, or mixed-conifer and aspen forest throughout the year. The climate is characterized by short, dry summers and long, cold winters.

The study area was host to four wild ungulates, cougars (*Puma concolor*), and American black bears (Ursus *americanus*) (Buskirk, 2016). Elk (*Cervus canadensis*) were the most numerous ungulate. Mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) occurred throughout. Gray wolves (*C. lupus*) and grizzly bears (*U. arctos*) were rarely documented in the study area.

Captures

We captured moose via helicopter net-gunning (Native Range Capture Services, Inc.) without immobilization agents, and blindfolded, hobbled, and restrained in a sternal-recumbent position. We fit 72 moose with GPS store-on-board collars (TGW-3700 and -4700, Telonics, Inc., Mesa, AZ, United States), and fit 12 with GPS satellite-uplink collars (various D-cell models, North Star Science and Technology, LLC, King George, VA, United States). Telonics collars recorded hourly locations, and North Star collars recorded locations every 3–5 h, depending on the model. Both Telonics and North Star collars were programmed to release from the animal approximately 2 years after deployment. For 13 moose in 2013 with expiring GPS collars, we deployed VHF-collars (M2230B, Advanced Telemetry Systems, Isanti, MN, United States) to continue demographic monitoring. One experienced investigator (K. L. Monteith) collected all data on nutritional condition from 2012 to 2014 (n = 70 individuals; nutritional condition estimates were not available for 2011). We first assessed condition of animals by palpation and acquired a modified rBCS, which was based on the extent (cm) to which the index finger could be inserted on the caudal side of the sacro-sciatic ligament. This rBCS was analogous to that validated for elk (Cook et al., 2001) and mule deer (Cook et al., 2007), which were highly correlated with percent IFBFat ($r^2 > 0.88$). We measured depth of rump fat and thickness of the bicep femoris using the electronic calipers (±0.1 cm) of a Bantam II portable ultrasound device (E.I. Medical Imaging, Loveland, CO, United States) with a 5-MHz linear-array transducer. We measured maximum depth of subcutaneous rump fat (MAXFat) along a line parallel to the spine and cranial to the ischial tuber (pin bone), which occurred immediately adjacent to the cranial process of the ischial tuber (Stephenson et al., 1998). We used subcutaneous rump fat to estimate percent IFBFat for moose with measurable fat. For animals without subcutaneous fat, we used rBCS to estimate percent IFBFat using the linear relationship between IFBFat and rBCS of moose with measurable rump fat (Cook et al., 2010; Jesmer et al., 2017). During captures for years 2013–2014, we removed the right-incisiform canine to estimate age of each moose (Boertje et al., 2015). For study animals that died before

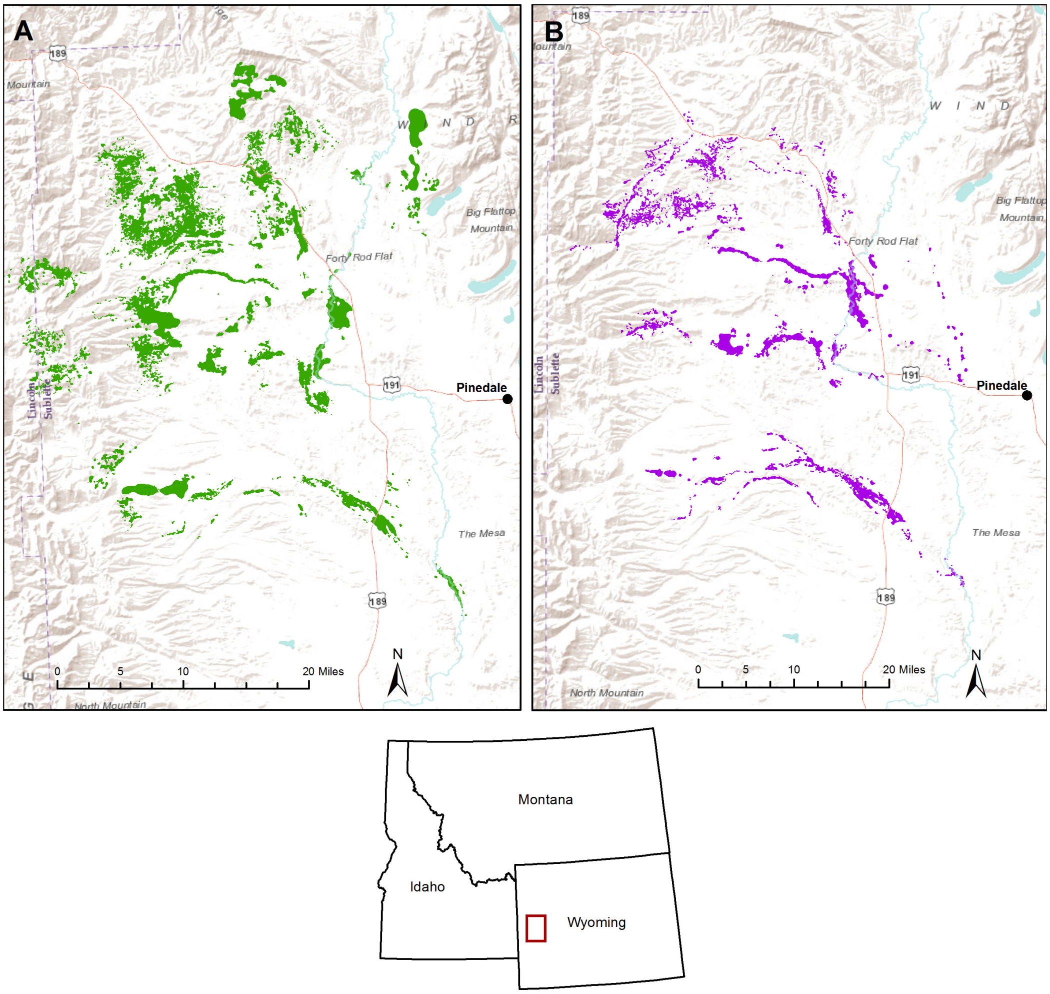

FIGURE 1 | Map of study area showing a sample (*n* = 63) of seasonal home ranges of adult (>2.5 years), GPS-collared moose from 2012 and 2013, derived from dynamic Brownian bridge movement models for summer **(A)** and winter **(B)** in Sublette County of western Wyoming, United States.

2013, we collected the I-1 incisor from the mortality site. All age estimates were conducted via cementum annuli by Matson's Laboratory, Milltown, MT, United States. We omitted yearlings from all analyses (<2 and ≥1 years), because their vital rates can be lower or more variable compared with reproductive adults (Gaillard et al., 2000; Bonenfant et al., 2009). We collected 20 ml of blood from each female by jugular venipuncture. For analyses, we omitted all mortalities that occurred within 2 weeks of capture (*n* = 4). The University of Wyoming Institutional Animal Care and Use Committee approved procedures for captures and handling (protocol number 20140124JG00057).

Seasonal Ranges of Moose

We delineated summer and winter ranges of each moose using characteristics of net squared displacement. First, we identified moose as migratory if they exhibited directional movement between distinct, non-overlapping winter and summer ranges. Second, we visually inspected plots of net squared displacement of migratory animals to identify start and end dates of migration. Migratory moose typically left winter ranges between late April and late May, and arrived on summer ranges between early and late June, returning to winter ranges around mid to late December. If seasonal ranges overlapped between winter and summer, we classified moose as residents and used the median start and end migration dates from migratory moose relative to year to define the temporal extent of winter and summer ranges. Net squared displacement calculations were derived from GPS-collar locations by calculating the squared distance between the first location identified from capture and every subsequent location along the annual travel path (Bunnefeld et al., 2011). After identifying migration dates, we delineated seasonal range polygons for moose with GPS collars using 95% contours derived from dynamic Brownian bridge movement models (dBBMMs; Kranstauber et al., 2012; see **Figure 1** for examples). We specified all dBBMMs with a location error of 20 m, raster cell size of 20 m, window size of 31 locations, and a margin of 11 locations. Fix rates of the GPS collars varied, depending on the year and season. For each of the 13 moose in our study that wore a VHF collar after wearing a GPS collar for two or more years, we used the extent of the seasonal range from the most recent year of the GPS collar to represent seasonal ranges during years the individual was fitted with a VHF collar.

Monitoring of Vital Rates

Pregnancy and Parturition

We separated red blood cells from serum collected at capture via centrifugation and submitted the latter to BioTracking LLC to determine pregnancy status using the presence of Pregnancy-Specific Protein B (PSPB; Huang et al., 2000). We used a PSPB cut-off value of $\geq$2.5 ng/ml to identify pregnant females with viable fetuses for each sample (Josh Branen, BioTracking LLC, personal communication). To identify parturition events, we evaluated females deemed pregnant during capture, observing collared moose aerially with a Bell-47 helicopter between 9 and 13 June, shortly after peak parturition (Schwartz, 1998, pp. 141–171; Poole et al., 2007). We calculated parturition rates as the proportion of pregnant individuals that were parturient. We calculated twinning rates as the proportion of parturient females observed with twins during the June survey.

Survival of Young

Ungulates are most vulnerable to mortality during the first 6 weeks of life (i.e., the neonatal phase), after which mortality typically decreases until winter (Ballard et al., 1991; Barber-Meyer et al., 2008). Thus, we distinguished between survival of neonates (parturition to mid-July) and survival of juveniles (mid-July to February). Approximately 4–8 weeks after parturition surveys, we relocated adult females from a helicopter to record presence and estimate survival of neonates at heel. The following February we estimated survival of juveniles by relocating females that had at least one neonate at heel in July from the air. We used Kaplan–Meier estimators (Pollock et al., 1989) to calculate annual survival rates of neonates and juveniles.

Adult Survival

We monitored the survival of collared moose with monthly fixed-wing flights and recovered collars from the field when logistically feasible. For GPS-collared moose, we verified date of death by visually inspecting fix locations relative to mortality site or dropped collar. We calculated annual survival rates at monthly intervals using a Kaplan–Meier estimator, with the biological year starting 1 June and ending 31 May.

Covariates

To evaluate the influence of metrics of resource limitation on each vital rate, we used IFBFat measurements and extracted a suite of covariates annually from seasonal ranges of each moose (**Table 1**). For newly captured moose (i.e., individuals for which the previous summer and winter ranges were not known), we used the seasonal range from the current year to represent the seasonal range for the previous year, because moose in the Greater Yellowstone Ecosystem are faithful to their seasonal ranges (Vartanian, 2011). For all environmental covariates, we used the spatially weighted mean of the raster value extracted from each seasonal range (i.e., polygon derived from the 95% isopleth of dBBMM from GPS-collared moose). Some moose died during the same winter they were first captured, and therefore, had no measurable summer range. To avoid bias associated with censoring these individuals because we lacked data for their summer range, we applied the annual mean value of each environmental covariate extracted from all other summer home ranges. We conducted all data extraction and modeling with R version 4.0.2 (R Core Team, 2020).

Resource Limitation

Length of spring and growing season can affect fecundity and survival in ungulates (Herfindal et al., 2006; Hamel et al., 2010; **Table 1**). As proxies for environmental effects and characteristics of summer ranges for moose, we used NDVI from the MODIS terra satellite (8-day temporal resolution) to calculate the annual length of spring (start to end of spring-green up of vegetation) and growing season (start of spring-green up until senescence of vegetation) in days (**Table 1**). We calculated NDVI annually from 2011 to 2014 using the MOD09Q1 data product from the MODIS terra satellite and followed the same protocol for processing NDVI as outlined in Merkle et al. (2016). We extracted length of spring and growing season in days from each summer range using the spatially-weighted mean of all cells overlapping the 95% dBBMM isopleth of the home range. We defined length of spring as the number of days from the start to end of vegetation green-up and length of the growing season from the start of vegetation green-up until the start of fall senescence of vegetation. Length of spring usually included the months of May and June, whereas the length of the growing season usually included months May to September. To evaluate responses of vital rates to NDVI metrics, we used either the value from current year, in addition to or in place of the previous year's value, depending on the vital rate. For example, pregnancy status was measured in February, so we used the value from the previous year to account for carry-over effects (Monteith et al., 2014, 2015). For survival of neonates (June–July), we evaluated length of spring from the current year and evaluated length of the growing season (calculated at the end of summer) from the previous year. We used the value from the previous year for length of spring and length of growing season to evaluate survival of juveniles (July–February). Although fires have occurred in Sublette, we did not assess their influence on vital rates because proportional overlap with home ranges was low.

We estimated drought using PRISM raster data of the Palmer Drought Severity Index (PDSI; Palmer, 1965; **Table 1**) extracted from the seasonal home range of each individual. Warm temperatures during late winter associated with reduced snow cover have been correlated with winter tick (*Dermacentor albipictus*) abundance the subsequent year (DelGiudice et al., 1997), which can decrease body condition of moose, especially juveniles, through loss of blood and hair (Samuel, 2007).

We estimated seasonal drought annually from the PDSI (Palmer, 1965) using rasters of 4-km^2 resolution from PRISM (Daly et al., 1994). The annual PDSI per summer home range of moose was calculated at the end of summer; therefore, we applied the PDSI value from the previous year to evaluate the influence of drought on pregnancy (February), parturition

TABLE 1 | Descriptions of covariates evaluated for their relative influence on probability of pregnancy, parturition, survival of juveniles (July–February), and overwinter adults (January–May) of Sublette moose from 2012 to 2014 moose in western Wyoming, United States.

Covariate (data source)	Spatial resolution (temporal resolution)	Influence	Description	Home range tested	Vital rates tested	Justification
Spring length (MODIS, NDVI[a])	250 m (8-day)	Forage quality and digestibility	Length of spring in days, from the start to end of spring green-up of vegetation from previous or current year	Summer	All	Pettorelli et al., 2007; Hebblewhite et al., 2008; Hamel et al., 2009b; Monteith et al., 2015
Growing season length (MODIS, NDVI[a])	250 m (8-day)	Forage quality and digestibility	Length of the growing season in days, from start of spring green-up to start of fall senescence of vegetation from previous or current year	Summer	All	Hjeljord and Histøl, 1999; Ericsson et al., 2002; Herfindal et al., 2006
Summer Palmer Drought Severity Index (PRISM[b])	4 km (Monthly)	Forage quality and digestibility	Home range value of Palmer Drought Severity Index experienced across all summer ranges from 1 June to 31 August from previous or current year	Summer	All	Owen-Smith et al., 2005; Pierce et al., 2012
Late-Winter Palmer Drought Severity Index (PRISM[b])	4 km (Monthly)	Correlated with tick abundance subsequent winter	Home range value of Palmer Drought Severity Index experienced across all winter home ranges during March and April from previous year	Winter	Juvenile and adult survival	DelGiudice et al., 1997; Samuel, 2007
Snow Water Equivalence (DAYMET[c])	1 km (Daily)	Winter severity	Cumulative amount of water kg/m^2 contained in the snowpack from 1 January to 31 May on winter home ranges from previous or current year	Winter	All[d]	Peterson and Allen, 1974; Keech et al., 2000; Parker et al., 2009
Ingesta-free-body fat (nutritional measurements at capture)	Individual (February)	Fecundity, survival	Ultrasound measurement of individual body fat levels for a percent-body fat estimate	None (nutritional measure)	All	Cook et al., 2004; Cook et al., 2013

[a] *Moderate resolution imaging spectroradiometer, normalized difference vegetation index.* [b] *Parameter-elevation regressions on independent slopes model.* [c] *Daily surface weather and climatological summaries.* [d] *Cumulative monthly values from 1 January to 31 May were used to assess overwinter survival of adults.*

(June), and overwinter (January–May) survival of adults. We used the PDSI value from the current year to evaluate survival of (July–February) juveniles. We evaluated the influence of late winter (March and April) drought on the survival of juveniles and adults. We did not evaluate the influence of late winter drought on pregnancy, because mating season for moose typically occurs during the early stages of tick loading, and it would be unlikely that an effect would be detected.

To relate the energetic costs of snow on moose vital rates, we used raster data of Snow Water Equivalent (SWE) from Daymet (Thornton et al., 1997). Although moose are well adapted to deep snow (Coady, 1974), harsh winters reduce mobility and increase energetic demands, negatively influencing survival of juveniles (Peterson, 1977; Keech et al., 2011) and adults (Peterson and Allen, 1974). Additionally, nutritional costs of moving through snow on maternal condition while calves are *in utero* could produce less viable neonates (Schwartz, 1998, pp. 141–171). We calculated cumulative values of daily SWE from moose winter ranges annually from 1 January to 31 May to evaluate the influence of snow on parturition, survival of neonates (SWE experienced while *in utero*), and survival of juveniles (*in utero*, and first winter as a juvenile). We calculated cumulative values of monthly SWE from January to May to evaluate the influence of winter severity on survival of adults.

Endogenous fat reserves are critical for survival and fecundity of ungulates (Cook et al., 2004, 2010; Monteith et al., 2014). We measured and evaluated the influence of IFBFat in addition to the aforementioned environmental covariates on pregnancy, parturition, and survival of juveniles and adults.

Ungulate populations that have senesced in age can confound estimates of survival and fecundity (Festa-Bianchet et al., 2003; Bonenfant et al., 2009). We included age as a covariate for all vital rate analyses, and determined whether a quadratic transformation was appropriate using residual diagnostics.

Statistical Analyses

Vital Rate Models

For probability of pregnancy, parturition, and survival of neonates and juveniles, we fit binomial GLMMs with the logit link function and individual animal as a random intercept. To assess monthly survival of adults, we used the Andersen–Gill formulation (Andersen and Gill, 1982) of Cox proportional hazards CPHs models (Cox, 1972). We used an information-theoretic approach to model selection by assessing all possible combinations of covariates (Doherty et al., 2012) selected *a priori* based on Akaike information criteria adjusted for small sample size (AIC_c), ΔAIC_c, and Akaike weights (w_i) (Burnham and Anderson, 2002). If Pearson correlation coefficients between each pair of covariates were $>| 0.5|$, we assessed univariate models between each pair and selected the covariate with the minimum AIC to use for model selection. Consequently, all variables that entered AIC_c model selection had Pearson correlation coefficients $< | 0.5|$. To improve convergence of the GLMMs and CPHs, we scaled all covariate values so that their mean was zero and their standard deviation was one. For all analyses, we omitted mortalities attributed to anthropogenic causes (e.g., harvest, poaching; $n = 4$). During model selection, we followed Babyak (2004), using approximately 10 events (i.e., failures or mortalities) per covariate (hereafter, "EPC") that entered a model. Model fit was assessed using area under the receiver operating characteristic curve (AUC; Hanley and McNeil, 1982).

We deemed covariates important if their 95% confidence intervals did not overlap zero within ΔAIC_c four of the top model.

In modeling monthly survival of adults, we assessed winter (January–May) and summer (June–December) separately, because we expected environmental covariates to affect moose survival differently with regard to season (Gaillard et al., 2000). We used the Andersen–Gill formulation of CPHs with each month representing a time interval (i.e., the counting process; Therneau and Grambsch, 2000), allowing for left-staggered entry (i.e., newly captured moose added to sample size) and right-censoring of adults (e.g., if the VHF transmitter failed, collar dropped from the individual, or the moose emigrated from study area). Coefficient estimates from CPHs specify the mortality hazard, where positive values increase mortality hazard (i.e., negatively relate to survival). Adults were allowed to contribute to the risk sample every year they were monitored; therefore, we used a robust "sandwich" estimator to account for correlated observations within individuals (Therneau and Grambsch, 2000). We chose a recurrent time-scale for seasonal CPHs based off of the biological year (i.e., 1 June–31 May), because adult mortality occurred largely during late winter (i.e., a strong seasonal hazard; Fieberg and DelGiudice, 2009). We allowed monthly SWE values to cumulatively increase over winter (e.g., a time-varying covariate; Therneau and Grambsch, 2000). Model fit of CPHs was assessed using concordance (Harrell, 2015), which is analogous to AUC. Diagnostic tests were performed on all CPH models to evaluate the proportional hazards assumption using Schoenfeld residuals (Therneau and Grambsch, 2000), but were not reported unless significant violations were detected (i.e., $P < 0.05$).

Life Stage Simulation Analysis

To assess the influence of interannual variation in vital rates on λ, we conducted LSA. We followed Morris and Doak (2002), and estimated vital rates separately by biological year and then derived a beta distribution of 10,000 estimates for each vital rate by randomly sampling the mean and variance estimated from each year. To derive the 10,000 estimates of λ from beta distributions, we used a 3 × 3 stage-structured, post-birth, female-based matrix model (Caswell, 2001) consisting of the following form:

$$\lambda = \begin{bmatrix} 0 & 0 & (S_a\,F\,T) \\ S_j & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} \tag{1}$$

The first stage calculates reproduction rates by multiplying adult survival (S_a) by fecundity (F = pregnancy rate × parturition rate), and probability of twinning [$T = (1{-}\text{t}) + (2\text{t})$].

The second stage is juvenile survival (S_j), calculated as the neonatal (June to July) survival rate × juvenile survival (July to

Feb) rate. Our surveys of juvenile survival were conducted during February; therefore, to correct for missed late-winter mortality of calves (Gaillard et al., 1998), we assumed that an additional 10% of mortality would occur between February and May 31. Effectively, this additional 10% did not change the variability of the vital rate in the LSA and only influenced estimates of λ. The third stage consists of yearling survival (S_y) and adult survival (S_a). Rates of yearling survival in the Sublette herd were unavailable, so we calculated a mean estimate from a range of yearling survival rates for moose reported in Kunkel and Pletscher (1999) and McLaren et al. (2000). On average, yearling survival was 6.43% lower than adult survival, thus our estimate was calculated as $S_y = S_a - 6.43\%$. We assumed no reproduction of yearlings in our model. The resulting beta distributions of each vital rate were randomly sampled for vital rate estimates to produce 10,000 matrix replicates, estimates of λ, elasticity and sensitivity. Elasticity analysis estimates the effect of a proportional change in the vital rates on population growth rate, whereas sensitivity analysis estimates the impact of an absolute change in vital rates on lambda. We then regressed λ on each vital rate, providing an estimate of the proportion of variation in λ explained by each vital rate (r^2). We were unable to account for sampling variance due to the limited time-frame of the study.

Covariate LSA

After assessing vital rate variability and its influence on λ, we evaluated the influence of the covariates on λ through their relative effect on vital rates. To estimate the strength and variability of covariates on vital rates, we extended the LSAs to incorporate the effects of covariates on the vital rates. We estimated rates of pregnancy, parturition, neonatal, juvenile, and overwinter adult survival as a function of the coefficient estimates of the covariates for 10,000 iterations, and populated the same 3 × 3 stage-structured, female-based, post-birth matrix models used in LSAs with these predicted values (hereafter, "covariate LSA"). For the covariate LSA, we used estimates of adult survival from the overwinter (January–May) model only, because summer models failed to converge due to small sample size of mortalities. We accounted for total annual mortality by subtracting the average rate of summer (June–December) mortality from each predicted estimate of overwinter survival. For vital rate responses that were not predicted by any covariate, we applied the beta distribution from the LSA to account for unexplained variation. Yearling survival was also set as a constant, estimated at 6.43% lower than adult survival ($S_y = S_a - 6.43\%$). Similar to the LSA, we then regressed λ on each covariate, providing an estimate of the amount of variation (r^2) in λ explained by the covariate.

RESULTS

Probabilities of pregnancy, parturition, and overwinter survival of adults were positively and strongly related to IFBFat (**Figures 2A–C** and **Table 3**). Drought conditions on summer home ranges from the previous year reduced probability of parturition (**Figure 2D** and **Table 3**). We did not detect important predictors of juvenile survival. Variation in survival of adults was a strong driver of interannual changes in λ ($r^2 = 0.70$; **Figures 3A,F**). Variation in neonate and juvenile survival, as well as rates of parturition, and pregnancy contributed comparatively little to population growth (**Figures 3B–F**). Elasticity values for fecundity and survival of juveniles were 0.12, compared with 0.64 for survival of adults. Sensitivity values for fecundity, survival of juveniles, and survival of adults were 0.30, 0.25, and 0.75, respectively. From the time period of the demographic rates measured, the Sublette moose population was increasing ($\lambda = 1.027$). Twinning rates were low, neonatal survival remained stable and high, and overwinter survival of juveniles was stable, but slightly reduced (**Table 2**). Although age competed with other predictors in top models for probability of parturition and pregnancy, all confidence intervals overlapped zero (**Table 3**). Age as a sole predictor of adult survival was important (CPH $\beta = 0.73$; 95% CI: 0.41–1.05), but was clearly outweighed by IFBFat (**Table 3**). Prime-aged (2–8 years) moose accounted for 63% (SE $\pm$ 0.10; $n = 15$) of total adult mortalities ($n = 24$), and 84% of all individuals were $\leq$ 8 years in age ($\bar{x} = 6$; range: 2.5–15 years).

The covariate LSA revealed a strong influence of IFBFat on population growth rate, explaining 82% of variation in λ through its combined influence on overwinter survival of adults, parturition, and pregnancy (**Figure 4**). Only 0.7% of the variation in λ was explained by drought conditions from the previous summer.

DISCUSSION

Our study illustrates how measurements of nutritional condition can better characterize degree of resource limitation in populations of a large herbivore than remotely sensed metrics of environmental variation. Although we did not measure density dependence directly, we suspect that the influence of nutritional condition at least partially reflects a key role of density dependence operating within a population of moose largely free of large predators with low female harvest—a conclusion that would have been impossible to draw based on inference from remotely sensed environmental measures as proxies of resource limitation. Lambda was explained almost entirely by nutritional condition of females, which clearly illustrated that this population was resource limited and likely experiencing density dependence at a level that obscured the effects of environmental variation detected from remotely sensed data. Moreover, response and variability of vital rates to resource limitation for a population of moose at the southern extent of its distribution conflicted with the Eberhardt paradigm of life history for long-lived ungulates. Despite the typical vulnerability of juveniles and robustness of adults to resource limitation (Gaillard and Yoccoz, 2003), nutritional condition of adults strongly influenced survival, yet survival of juveniles had little predictive power. Further, our LSA results depart from typical expectations for the life-history characteristics of ungulates, where variation in juvenile survival typically fluctuates

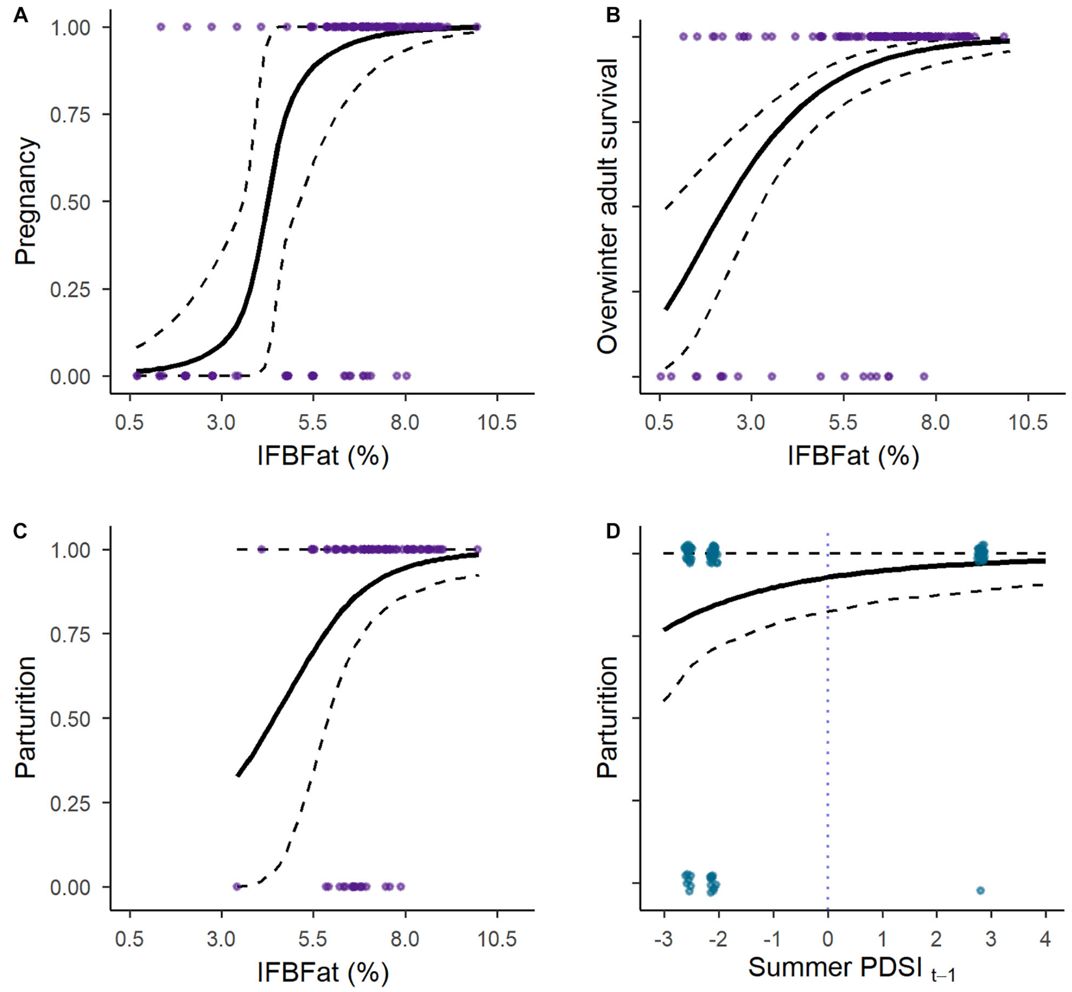

FIGURE 2 | Predicted probabilities (±95% CI) and observed values of **(A)** pregnancy, **(C,D)** parturition, and **(B)** overwinter adult (>2.5 years) survival as a function of percent IFBFat for moose in Sublette 2012–2014 in western Wyoming, United States.

TABLE 2 | Mean estimates (SE) and sample sizes of demographic rates from 2011 to 2014 for Sublette moose in western Wyoming, United States.

Study	**Year**	**Pregnancy**		**Parturition**		**Twinning**		**Neonate survival**		**Juvenile survival**		**Adult survival**	
		n	**$\bar{x}$ (±SE)**	***n***	**$\bar{x}$ (±SE)**	***n***	**$\bar{x}$ (±SE)**	***n***	**$\bar{x}$ (±SE)**	***n***	**$\bar{x}$ (±SE)**	***n***	**$\bar{x}$ (±SE)**
Sublette	2011	19	0.53 (0.12)	10	0.80 (0.13)	9	0	9	0.71 (0.17)	9	na	23	0.91 (0.06)
	2012	47	0.66 (0.07)	28	0.89 (0.06)	26	0.12 (0.06)	28	0.82 (0.07)	9	0.71 (0.17)	50	0.88 (0.05)
	2013	63	0.76 (0.05)	39	0.69 (0.07)	41	0	30	0.93 (0.05)	25	0.72 (0.09)	70	0.79 (0.05)
	2014	40	0.68 (0.08)	30	0.67 (0.09)	27	0.04 (0.04)	22	0.95 (0.04)	22	0.77 (0.09)	53	0.83 (0.06)
	All years	169	0.69 (0.03)	107	0.75 (0.04)	103	0.04 (0.19)	89	0.89 (0.03)	65	0.74 (0.06)	196	0.84 (0.02)

Rates of pregnancy, parturition, and twinning were calculated as proportions, and survival estimates of neonates, juveniles, and adults are from Kaplan–Meier analysis, with biological year starting 1 June and ending 31 May.

widely and underpins variation in population growth (Gaillard et al., 1998, 2000). In our study, annual changes in rates of population growth were driven mostly by variation in survival of adults, whereas survival of juveniles explained substantially less variation. Our findings serve as a reminder that the influences of top-down and bottom-up forces are context-dependent relative to a population's proximity to *K*, and that the relative influence of each factor is obscured or magnified depending on the strength of density dependence.

The detection of resource limitation in Sublette moose through the lens of vital rates more clearly revealed the potential for interacting relationships from top-down and bottom-up forces, and the importance of context dependence in ungulate demography. In our study, signals of drought influencing

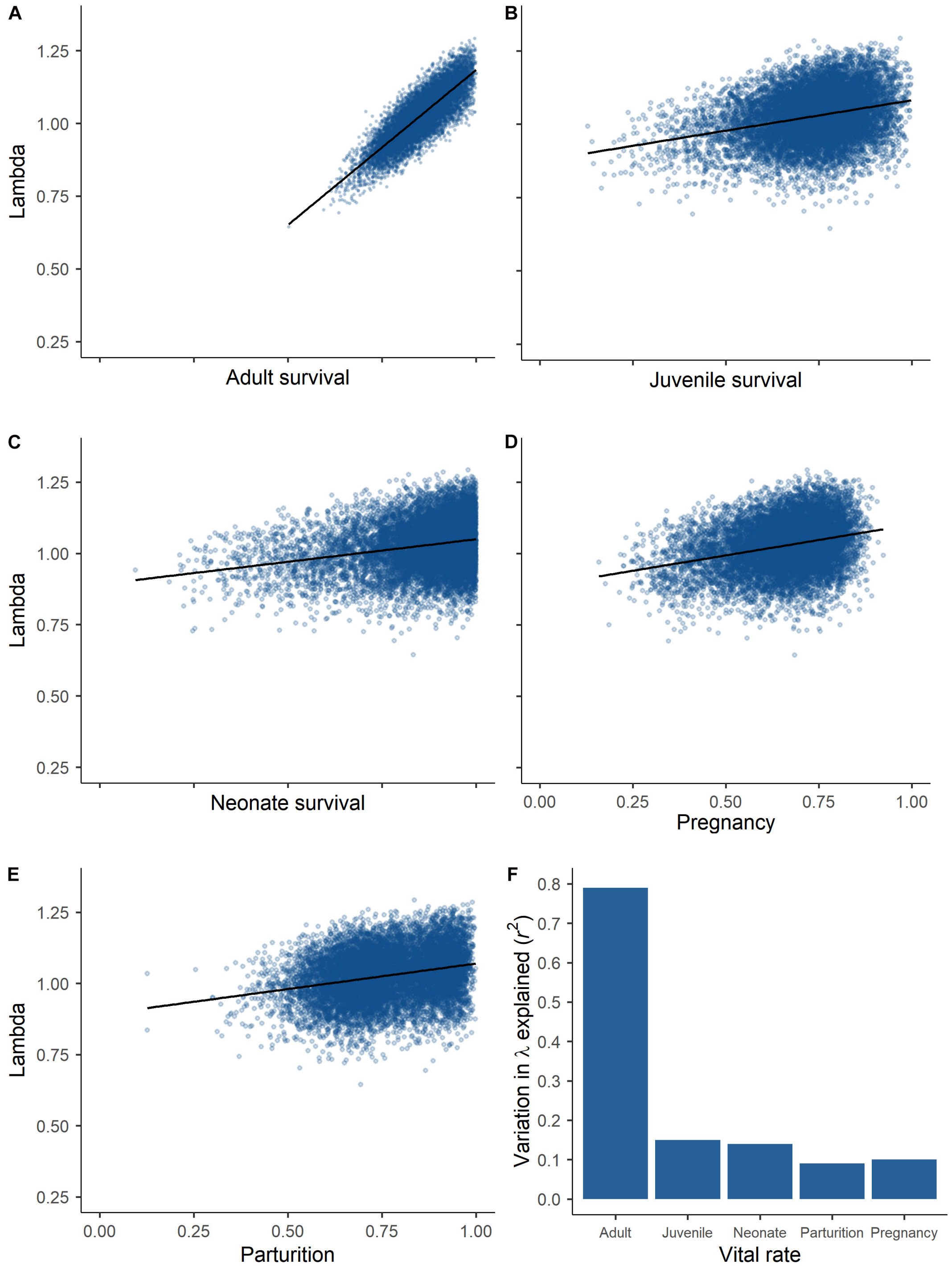

FIGURE 3 | Results from life stage simulation analysis for moose in Sublette from 2011 to 2014, showing the variation in lambda explained by **(A)** adult (>2.5 years) survival (r^2 = 0.70), **(B)** juvenile survival (r^2 = 0.08), **(C)** neonate survival (r^2 = 0.06), **(D)** pregnancy status (r^2 = 0.08), **(E)** parturition status (r^2 = 0.07), and **(F)** proportion of variation in λ explained by each vital rate (see **Table 2** for annual estimates) in western Wyoming, United States.

population growth rates were barely detected, yet we can logically infer that drought negatively influenced levels of body fat in moose. Warm temperatures during spring and summer reduce forage quality for ungulates (Hamel et al., 2009b), thereby limiting fat gains during the growing season that are necessary for reproduction and overwinter survival (Monteith et al., 2014). Indeed, in response to drought, Sublette moose experienced reduced rates of parturition, as well as low rates

TABLE 3 | Top models derived from AIC_c model selection with coefficient estimates and 95% confidence intervals (of all terms in model) that did not overlap zero for Sublette moose (*n* = 70 individuals) from 2012 to 2014.

Vital rate	Model	Parameter (β)	AICc	Δ	*wi*	95% CI	Model fit
Pregnancy	1	Fat [a] (2.39)	111.5	0	0.262	Fat (1.47, 27.15)	0.97
	2	Age [b] (−0.48) + Fat (2.13)	111.8	0.35	0.220		
	3	Fat (2.47) + GrowSeas [c] (−0.33)	112.7	1.23	0.142		
	4	Age (−0.51) + Fat (2.21) + GrowSeas (−0.34)	113	1.51	0.123		
	5	Fat (2.39) + SprLgth [d] (0.19)	113.3	1.82	0.106		
Parturition	1	Fat (0.88) + SmDroughtPY [e] (0.93)	84.7	0	0.585	Fat (0.25, 8.98), SmDroughtPY (0.19, 8.5)	0.89
	2	Fat (0.93)	87.7	3.07	0.126	Fat (0.27, 2.0)	0.89
	3	Age (−0.39) + Fat (0.84)	88.4	3.71	0.091		
	4	Age (−0.45) + SmDroughtPY (0.92)	89.1	4.48	0.062		
	5	SmDroughtPY (0.94)	89.3	4.66	0.057	SmDrought (0.21, 2.08)	
Adult	1	Fat (−1.01)	140.9	0	0.999	Fat (−1.4, −0.61)	0.82
	2	Age (0.73)	154.1	13.17	0.001	Age (0.41, 1.05)	0.73
	3	SmDroughtPY (−0.5426)	163.4	22.46	0		
	4	Intercept	164.7	23.79	0		
	5	GrowSeas (−0.29)	165.6	24.7	0		

[a] IFBFat calculated from rump fat measurements during February captures. [b] Age of individual, in years. [c] Length of the growing season, in days. [d] Length of the spring, in days. [e] Palmer Drought Severity Index from the previous summer's home range (positive values are wetter conditions). Model fit of generalized linear mixed-effects models (GLMMs) for probability of pregnancy and parturition was calculated using the area under the receiver operating characteristic curve. Model fit from Cox proportional hazards models (CPH) of adult survival was calculated via concordance. Negative beta coefficients from CPHs decrease the mortality hazard (i.e., positively relate to survival). We did not detect important covariates for juvenile survival of Sublette moose.

of twinning (**Table 2**), a symptom of resource limitation in moose (Boertje et al., 2007). A lack of predators combined with strong resource limitation revealed strong relationships between nutritional condition and vital rates. Measurements of nutritional condition thus simultaneously integrate disparate influences on resource limitation, and as a result, they are more informative than remotely sensed covariates in linking bottom-up effects to ungulate demography.

As prey populations approach *K* and competition for food increases, nutritional condition declines, and animals are consequently more sensitive to environmental variation (Aanes et al., 2000; Kie et al., 2003; Monteith et al., 2015), parasites, and disease. Effects of remotely sensed data on vital rate variability of moose in Sublette were subtle, and could have led to a conclusion of weak resource limitation in an area that was almost devoid of large predators. Nevertheless, measures of nutritional condition explained most of the variation in survival of adults, pregnancy, and parturition, leading to a cumulative explanation for 82% of the variation in λ (**Figure 4**). The striking connections between nutritional condition, and both individual and population performance were unequivocally indicative of a population regulated strongly by resource limitation and, presumably, density dependence which apparently obscured signals of environmental influence from remotely sensed data. In other words, measures of nutritional condition were a more precise representation of resource limitation when compared with remotely sensed proxies such NDVI and drought, even when those proxies were explicitly measured in a spatial and temporal context. There is increasing support for using remotely sensed data to detect resource limitation in ungulates (Tveraa et al., 2007; Pettorelli et al., 2011; Bastille-Rousseau et al., 2015; Monteith et al., 2015); however, our work provides evidence that these relationships can go undetected if integrative measures of resource limitation (e.g., nutritional condition) are not considered. Short-term studies such as ours are common for implementing management actions, and remotely sensed data might not be sufficient for detecting strong resource limitation. Similarly, Stewart et al. (2005) noted that signatures of resource limitation can be dampened in populations experiencing heightened density dependence. In Sublette moose, relationships between vital rates and environmental covariates were relatively weak compared with IFBFat, highlighting the potential for Type II errors in relating only remotely sensed covariates to ungulate demography. We recommend that future studies examining the effects of bottom-up forcing on ungulates carefully consider multiple pathways before declaring the absence of either pressure, and we also agree with others (Cook et al., 2004; Monteith et al., 2014; Stephenson et al., 2020) that nutritional condition is an effective indicator of resource limitation because it integrates both environmental variation and density dependence.

Our results depart from the life-history paradigm proposed by Eberhardt (2002), and deviate from life-history characteristics typical of ungulates (Gaillard et al., 2000). Juveniles are typically more sensitive to environmental variation than adults and are commonly the first stage class to experience declines as populations approach *K* (Eberhardt, 2002), ultimately driving interannual variability in λ (Gaillard et al., 2000). Nevertheless, adult survival was highly variable and explained the majority of variation in λ for our study population. Variable survival of adults is considered rare for ungulates, although exceptions have been noted in declining populations exposed to predators, including bighorn sheep (Johnson et al., 2010), mountain caribou

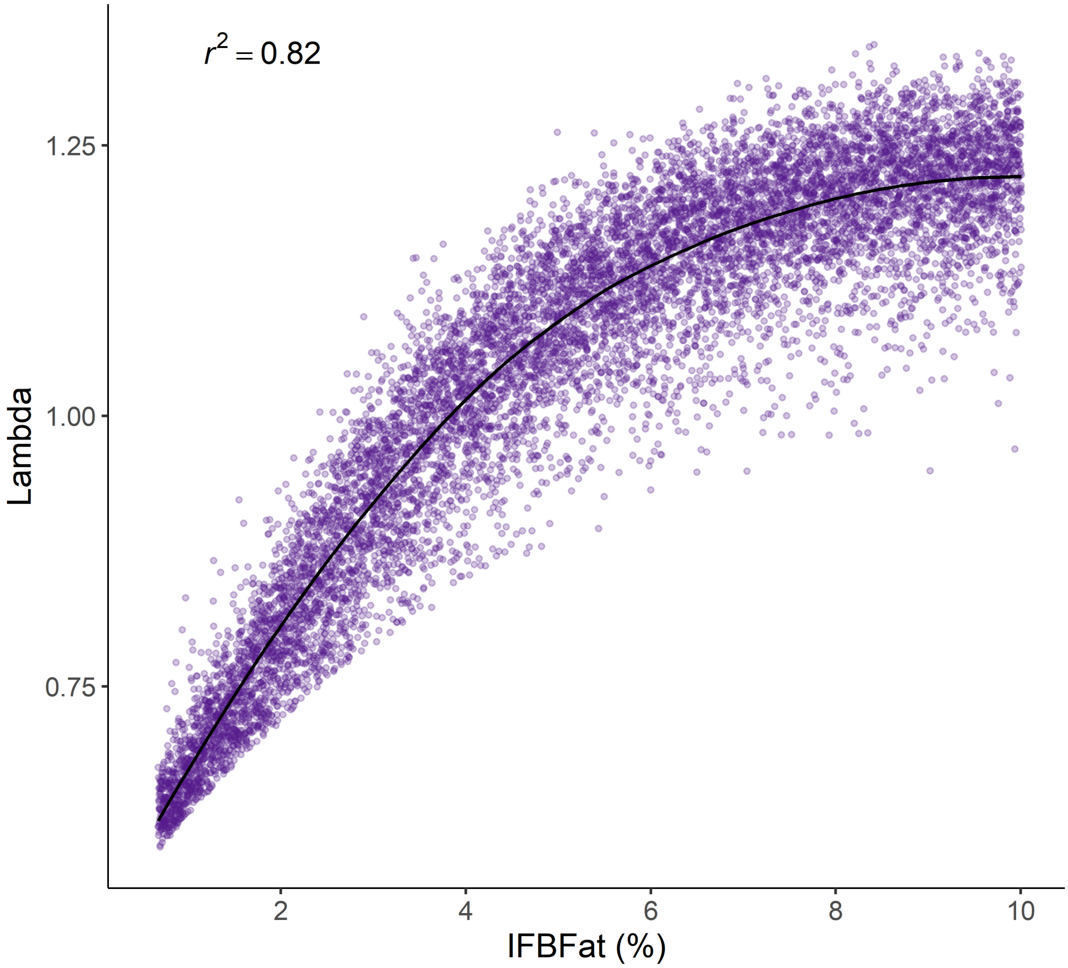

FIGURE 4 | The variation in λ (fitted with smoothing loess) explained by the cumulative effects of percent IFBFat on pregnancy, parturition, and overwinter survival of adult (>2.5 years) female moose in Sublette 2012–2014, western Wyoming, United States.

(*Rangifer tarandus*) (Hervieux et al., 2013), and tropical ungulates (Owen-Smith and Mason, 2005). Notably, variable survival of adults in Sublette in response to suppressed nutritional condition suggests that the population surpassed *K*, despite an estimated stable-to-increasing population growth rate. Moreover, survival of neonates and juveniles was not sensitive to nutritional condition. As intraspecific competition for resources increases, the detection of reproductive tradeoffs (lower juvenile survival) relative to environmental variation may be confounded by factors difficult to measure, such as experience in rearing young (Hamel et al., 2009a), heterogeneity of genotypic quality (van Noordwijk and de Jong, 1986), and immune function (Downs et al., 2015; Cheynel et al., 2017). There are multiple factors that can influence vital rates, and as such, their expected patterns (Gaillard et al., 2000) may be more context dependent than previously appreciated.

Our findings provide three important contributions that can help advance our understanding of resource limitation in ungulate populations. First, in our LSA, variation in adult survival strongly affected lambda, which is notable since adult survival is typically robust to environmental variation. Second, measurements of nutritional condition proved to be considerably more informative for detecting resource limitation compared with multiple proxies of environmental variation via remote sensing, indicating that seemingly intuitive relationships between proxies of resource limitation and vital rates can be obscured in ungulate populations experiencing strong density dependence. Finally, we documented low variability in survival of young that had little influence on λ, in contrast to expectations (Gaillard et al., 2000). Our results indicate that the life-history paradigm for long-lived ungulates may be more variable across taxa than originally proposed, and moose at the southern extent of their range may uniquely deviate from theoretical expectations.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The study was reviewed and approved by the University of Wyoming Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

BO, MK, KM, JG, and JM conceived the ideas and designed methodology. BO analyzed the data and led the writing of the manuscript. All authors collected the data, critically contributed to the drafts, and gave final approval for publication.

FUNDING

This study was funded by the US Forest Service (Bridger-Teton), Safari Club International Foundation, Sublette County Outfitters and Guides Association, Wyoming Outfitters and Guides Association, Wyoming Governor's Big Game License Coalition, the Wyoming Governor's Office, Plains Exploration and Production, Tim Delaney of Rolling Thunder Ranch LLC, Wyoming Game and Fish Department Commissioner Price (Commissioner license), Jim Finley of Finley Resources, Inc., Teton Conservation District, and Ricketts Conservation Foundation. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

ACKNOWLEDGMENTS

We thank Native Range Capture Services, Inc., Savage Air Services, Gallatin Flying Service, and Sky Aviation for safe piloting. We are indebted to landowners of Sublette County, Gary Hanvey (retired) of the Bridger-Teton National Forest, and personnel from Grand Teton National Park, and the Wyoming Game and Fish Department for logistical support. We thank T. McDonald of WEST, Inc. for statistical advice. This manuscript contains content that can also be referenced in Oates (2016).

REFERENCES

Aanes, R., Sæther, B.-E., and Øritsland, N. A. (2000). Fluctuations of an introduced population of *Svalbard reindeer*: the effects of density dependence and climatic variation. *Ecography* 23, 437–443. doi: 10.1111/j.1600-0587.2000.tb00300.x

Andersen, P. K., and Gill, R. D. (1982). Cox's regression model for counting processes: a large sample study. *Ann. Statist.* 10, 1100–1120. doi: 10.1214/aos/1176345976

Babyak, M. A. (2004). What you see may not be what you get: a brief, nontechnical introduction to overfitting in regression-type models. *Psychosomatic Med.* 66, 411–421. doi: 10.1097/01.psy.0000127692.23278.a9

Ballard, W. B., Whitman, J. S., and Reed, D. J. (1991). Population Dynamics of Moose in South-Central Alaska. *Wildlife Monographs* 55, 3–49.

Bangs, E. E., and Fritts, S. H. (1996). Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Soc. Bull.* 24, 402–413.

Barber-Meyer, S. M., Mech, L. D., and White, P. J. (2008). Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 2008, 1–30. doi: 10.2193/2008-2004

Bastille-Rousseau, G., Schaefer, J. A., Lewis, K. P., Mumma, M., Ellington, E. H., Rayl, N. D., et al. (2015). Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. *J. Anim. Ecol.* 85, 445–456. doi: 10.1111/1365-2656.12466

Becker, S. A., Kauffman, M. J., and Anderson, S. H. (2010). Nutritional condition of adult female *Shiras moose* in northwest Wyoming. *Alces* 46, 151–166.

Berger, J., Swenson, J. E., and Persson, I.-L. (2001). Recolonizing carnivores and naïve prey: conservation lessons from pleistocene extinctions. *Science* 291, 1036–1039. doi: 10.1126/science.1056466

Bergeron, D. H., Pekins, P. J., and Rines, K. (2013). Temporal assessment of physical characteristics and reproductive status of moose in New Hampshire. *Alces* 49, 39–48.

Boertje, R. D., Ellis, M. M., and Kellie, K. A. (2015). Accuracy of moose age determinations from canine and incisor cementum annuli. *Wildlife Soc. Bull.* 39, 383–389. doi: 10.1002/wsb.537

Boertje, R. D., Kellie, K. A., Seaton, C. T., Keech, M. A., Young, D. D., Dale, B. W., et al. (2007). Ranking alaska moose nutrition: signals to begin liberal antlerless harvests. *J. Wildlife Manag.* 71, 1494–1506. doi: 10.2193/2006-2159

Bonenfant, C., Gaillard, J. M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., et al. (2009). Empirical evidence of density-dependence in populations of large herbivores. *Adv. Ecol. Res.* 41, 313–357. doi: 10.1016/s0065-2504(09)00405-x

Bowyer, R. T., Bleich, V. C., Stewart, K. M., Whiting, J. C., and Monteith, K. L. (2014). Density dependence in ungulates: a review of causes, and concepts with some clarifications. *California Fish Game* 100, 550–572.

Bowyer, R. T., Kie, J. G., Person, D. K., and Monteith, K. L. (2013). Metrics of predation: perils of predator-prey ratios. *Acta Theriol.* 58, 329–340. doi: 10.1007/s13364-013-0133-131

Boyce, M. S., Sinclair, A. R. E., and White, G. C. (1999). Seasonal compensation of predation and harvesting. *Oikos* 87, 419–426. doi: 10.2307/3546808

Bunnefeld, N., Borger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., et al. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J. Anim. Ecol.* 80, 466–476. doi: 10.1111/j.1365-2656.2010.01776.x

Burnham, K., and Anderson, D. (2002). *Information and Likelihood Theory: a Basis for Model Selection and Inference*. New York, NY: Springer-Verlag.

Buskirk, S. W. (2016). *Wild Mammals of Wyoming and Yellowstone National Park*. Berkeley, CA: Univ of California Press.

Caswell, H. (2001). *Matrix Population Models*. Hoboken, NJ: Wiley Online Library.

Cheynel, L., Lemaître, J. F., Gaillard, J. M., Rey, B., Bourgoin, G., Ferté, H., et al. (2017). Immunosenescence patterns differ between populations but not between sexes in a long-lived mammal. *Sci. Rep.* 7:13700. doi: 10.1038/s41598-017-13686-13685

Coady, J. (1974). Influence of snow on behavior of moose. *Nat. Can.* 101, 417–436.

Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D., et al. (2004). Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155, 1–61. doi: 10.1002/wmon.1020

Cook, R. C., Cook, J. G., Murray, D. L., Zager, P., Johnson, B. K., and Gratson, M. W. (2001). Development of predictive models of nutritional condition for Rocky Mountain elk. *J. Wildlife Manag.* 65, 973–987. doi: 10.2307/3803046

Cook, R. C., Cook, J. G., Stephenson, T. R., Myers, W. L., McCorquodale, S. M., Vales, D. J., et al. (2010). Revisions of rump fat and body scoring indices for deer, elk, and moose. *J. Wildlife Manag.* 74, 880–896. doi: 10.2193/2009-2031

Cook, R. C., Cook, J. G., Vales, D. J., Johnson, B. K., McCorquodale, S. M., Shipley, L. A., et al. (2013). Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildlife Monographs* 184, 1–45. doi: 10.1002/wmon.1008

Cook, R. C., Stephenson, T. R., Myers, W. L., Cook, J. G., and Shipley, L. A. (2007). Validating predictive models of nutritional condition for mule deer. *J. Wildlife Manag.* 71, 1934–1943. doi: 10.2193/2006-2262

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J., Pemberton, J., Clutton-Brock, T. H., et al. (2001). Age, sex, density, winter weather, and population crashes in *Soay sheep*. *Science* 292, 1528–1531. doi: 10.1126/science.292.5521.1528

Cox, D. R. (1972). Regression models and life-tables. *J. R. Statist. Soc. Ser. B (Methodological)* 34, 187–220.

Daly, C., Neilson, R. P., and Phillips, D. L. (1994). A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *J. Appl. Meteorol.* 33, 140–158. doi: 10.1175/1520-0450(1994)033<0140:astmfm>2.0.co;2

DelGiudice, G. D., Rolf, O., Peterson, William, M., and Samuel. (1997). Trends of winter nutritional restriction, ticks and numbers of moose on Isle Royale. *J. Wildlife Manag.* 61, 895–903. doi: 10.2307/3802198

DelGiudice, G. D., Sampson, B. A., Lenarz, M. S., Schrage, M. W., and Edwards, A. J. (2011). Winter body condition of moose (alces Alces) in a declining population. *J. Wildlife Dis.* 47, 30–40. doi: 10.7589/0090-3558-47.1.30

DeYoung, R. W., Hellgren, E. C., Fulbright, T. E., Robbins, W. F., and Humphreys, I. D. (2000). Modeling nutritional carrying capacity for translocated desert bighorn sheep in Western Texas. *Restorat. Ecol.* 8, 57–65. doi: 10.1046/j.1526-100x.2000.80066.x

Dodge, W. B. Jr., Winterstein, S. R., Beyer, D. E. Jr., and Campa, H. III (2004). Survival, reproduction, and movements of moose in the western Upper Peninsula of Michigan. *Alces* 40, 71–85.

Doherty, P. F., White, G. C., and Burnham, K. P. (2012). Comparison of model building and selection strategies. *J. Ornithol.* 152, 317–323. doi: 10.1007/s10336-010-0598-595

Downs, C. J., Stewart, K. M., and Dick, B. L. (2015). Investment in constitutive immune function by North American Elk experimentally maintained at two different population densities. *PLoS One* 10:e0125586. doi: 10.1371/journal.pone.0125586

Eberhardt, L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* 83, 2841–2854. doi: 10.1890/0012-9658(2002)083[2841:apfpao]2.0.co;2

Ericsson, G., Ball, J. P., and Danell, K. (2002). Body mass of moose calves along an altitudinal gradient. *J. Wildlife Manag.* 66, 91–97. doi: 10.2307/3802875

Festa-Bianchet, M., Gaillard, J. M., and Côté, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *J. Anim. Ecol.* 72, 640–649. doi: 10.1046/j.1365-2656.2003.00735.x

Fieberg, J., and DelGiudice, G. D. (2009). What time is it? choice of time origin and scale in extended proportional hazards models. *Ecology* 90, 1687–1697. doi: 10.1890/08-0724.1

Franzmann, A. W. (1977). Condition assessment of *Alaskan moose*. *Proc. North Am. Moose Conf. Workshop* 13, 119–127.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N., Loison, A., and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Ann. Rev. Ecol. Systemat.* 31, 367–393. doi: 10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* 13, 58–63. doi: 10.1016/s0169-5347(97)01237-8

Gaillard, J.-M., and Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84, 3294–3306. doi: 10.1890/02-0409

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. *Am. Nat.* 94, 421–425. doi: 10.1086/282146

Hamel, S., Côté, S. D., and Festa-Bianchet, M. (2010). Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology* 91, 2034–2043. doi: 10.1890/09-1311.1

Hamel, S., Côté, S. D., Gaillard, J.-M., and Festa-Bianchet, M. (2009a). Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* 78, 143–151. doi: 10.1111/j.1365-2656.2008.01459.x

Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J.-M., and Côté, S. D. (2009b). Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J. Appl. Ecol.* 46, 582–589. doi: 10.1111/j.1365-2664.2009.01643.x

Hanley, J. A., and McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143, 29–36. doi: 10.1148/radiology.143.1.7063747

Hansen, B. B., Gamelon, M., Albon, S. D., Lee, A. M., Stien, A., Irvine, R. J., et al. (2019). More frequent extreme climate events stabilize reindeer population dynamics. *Nat Commun.* 10:1616. doi: 10.1038/s41467-019-09332-9335

Harrell, F. (2015). *Regression Modeling Strategies: with Applications to Linear Models, Logistic and Ordinal Regression, and Survival Analysis*. Berlin: Springer.

Hebblewhite, M., Merrill, E., and McDermid, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monographs* 78, 141–166. doi: 10.1890/06-1708.1

Hebblewhite, M., Whittington, J., Bradley, M., Skinner, G., Dibb, A., and White, C. A. (2007). Conditions for caribou persistence in the wolf-elk-caribou systems of the Canadian Rockies. *Rangifer* 27, 79–91. doi: 10.7557/2.27.4.322

Herfindal, I., Sæther, B. E., Solberg, E. J., Andersen, R., and Høgda, K. A. (2006). Population characteristics predict responses in moose body mass to temporal variation in the environment. *J. Anim. Ecol.* 75, 1110–1118. doi: 10.1111/j.1365-2656.2006.01138.x

Hervieux, D., Hebblewhite, M., DeCesare, N. J., Russell, M., Smith, K., Robertson, S., et al. (2013). Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Can. J. Zool.* 91, 872–882. doi: 10.1139/cjz-2013-0123

Hjeljord, O., and Histøl, T. (1999). Range-body mass interactions of a northern ungulate–a test of hypothesis. *Oecologia* 119, 326–339. doi: 10.1007/s004420050793

Hopcraft, J. G., Olff, H., and Sinclair, A. R. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends Ecol. Evol.* 25, 119–128. doi: 10.1016/j.tree.2009.08.001

Huang, F., Cockrell, D. C., Stephenson, T. R., Noyes, J. H., and Sasser, R. G. (2000). A serum pregnancy test with a specific radioimmunoassay for moose and elk pregnancy-specific protein B. *J. Wildlife Manag.* 64, 492–499. doi: 10.2307/3803246

Jesmer, B. R., Goheen, J. R., Monteith, K. L., and Kauffman, M. J. (2017). State-dependent behavior alters endocrine–energy relationship: implications for conservation and management. *Ecol. Appl.* 27, 2303–2312. doi: 10.1002/eap.1608

Johnson, H. E., Mills, L. S., Stephenson, T. R., and Wehausen, J. D. (2010). Population-specific vital rate contributions influence management of an endangered ungulate. *Ecol. Appl.* 20, 1753–1765. doi: 10.1890/09-1107.1

Keech, M. A., Bowyer, R. T., Jay, M., Hoef, V., Boertje, R. D., Dale, B. W., et al. (2000). Life-history consequences of maternal condition in *Alaskan moose*. *J. Wildlife Manag.* 64, 450–462. doi: 10.2307/3803243

Keech, M. A., Lindberg, M. S., Boertje, R. D., Valkenburg, P., Taras, B. D., Boudreau, T. A., et al. (2011). Effects of predator treatments, individual traits, and environment on moose survival in Alaska. *J. Wildlife Manag.* 75, 1361–1380. doi: 10.1002/jwmg.188

Kie, J. G., Bowyer, R. T., and Stewart, K. M. (2003). "Ungulates in western coniferous forests: habitat relationships, population dynamics, and ecosystem processes," in *Mammal Community Dynamics: Management and Conservation in the Coniferous forests of Western North America*, eds C. Zabel and R. G. Anthony (New York, NY: Cambridge University Press).

Kranstauber, B., Kays, R., LaPoint, S., Wikelski, M., and Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *J. Anim. Ecol.* 81, 738–746. doi: 10.1111/j.1365-2656.2012.01955.x

Kunkel, K., and Pletscher, D. H. (1999). Species-specific population dynamics of cervids in a multipredator ecosystem. *J. Wildlife Manag.* 63, 1082–1093. doi: 10.2307/3802827

Lenarz, M. S., Nelson, M. E., Schrage, M. W., and Edwards, A. J. (2009). Temperature mediated moose survival in Northeastern Minnesota. *J. Wildlife Manag.* 73, 503–510. doi: 10.2193/2008-2265

McCullough, D. R. (1979). *The George Reserve Deer Herd: Population Ecology of a K-selected Species*. Ann Arbor, MI: University of Michigan Press.

McLaren, B., McCarthy, C., and Mahoney, S. (2000). Extreme moose demographics in Gros Morne National Park. Newfoundland. *Alces* 36, 217–233.

McNamara, J. M., and Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology* 68, 1515–1519. doi: 10.2307/1939235

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., et al. (2016). Large herbivores surf waves of green-up during spring. *Proc. R. Soc. London B: Biol. Sci.* 283:20160456. doi: 10.1098/rspb.2016.0456

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., et al. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs* 186, 1–62. doi: 10.1002/wmon.1011

Monteith, K. L., Klaver, R. W., Hersey, K. R., Holland, A. A., Thomas, T. P., and Kauffman, M. J. (2015). Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia* 178, 1137–1148. doi: 10.1007/s00442-015-3296-3294

Morris, W. F., and Doak, D. F. (2002). *Quantitative Conservation Biology*. Sunderland, MA: Sinauer.

Murray, D. L., Cox, E. W., Ballard, W. B., Whitlaw, H. A., Lenarz, M. S., Custer, T. W., et al. (2006). Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs.* 166, 1–30. doi: 10.2193/0084-0173(2006)166[1:pndaci]2.0.co;2

Musante, A. R., Pekins, P. J., and Scarpitti, D. L. (2010). Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. *Wildlife Biol.* 16, 185–204. doi: 10.2981/09-014

Oates, B. A. (2016). *Effects of Predators and Resource Limitation on Demography and Behavior of Moose in the Greater Yellowstone Ecosystem*. MSc thesis, University of Wyoming: Laramie, WY.thesis

Owen-Smith, N., and Mason, D. R. (2005). Comparative changes in adult vs. juvenile survival affecting population trends of African Ungulates. *J. Anim. Ecol.* 74, 762–773. doi: 10.1111/j.1365-2656.2005.00973.x

Owen-Smith, N., Mason, D. R., and Ogutu, J. O. (2005). Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. *J. Anim. Ecol.* 74, 774–788. doi: 10.1111/j.1365-2656.2005.00974.x

Owen-Smith, N., and Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecol. Monographs* 76, 73–92. doi: 10.1890/04-1101

Palmer, W. C. (1965). *Meteorological Drought*. Washington, DC: US Department of Commerce.

Parker, K. L., Barboza, P. S., and Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* 23, 57–69. doi: 10.1111/j.1365-2435.2009.01528.x

Peterson, R. (1977). *Wolf Ecology and Prey Relationships on Isle Royale US National Park Service Scientific Monograph Series 11*. Washington, DC: US Government Printing Office.

Peterson, R. O. (1999). Wolf–moose interaction on isle royale: the end of natural regulation? *Ecol. Appl.* 9, 10–16. doi: 10.2307/2641163

Peterson, R. O., and Allen, D. (1974). Snow conditions as a parameter in moose-wolf relationships. *Nat. Can.* 101, 481–492.

Pettorelli, N., Pelletier, F., Hardenberg, A. V., Festa-Bianchet, M., and Côté, S. D. (2007). Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology* 88, 381–390. doi: 10.1890/06-0875

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., et al. (2011). The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Res.* 46, 15–27. doi: 10.3354/cr00936

Pierce, B. M., Bleich, V. C., Monteith, K. L., and Bowyer, R. T. (2012). Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *J. Mammal.* 93, 977–988. doi: 10.1644/12-mamm-a-014.1

Pollock, K. H., Winterstein, S. R., Bunck, C. M., and Curtis, P. D. (1989). Survival analysis in telemetry studies: the staggered entry design. *J. Wildlife Manag.* 53, 7–15. doi: 10.2307/3801296

Poole, K. G., Serrouya, R., and Stuart-Smith, K. (2007). Moose calving strategies in interior montane ecosystems. *J. Mammal.* 88, 139–150. doi: 10.1644/06-mamm-a-127r1.1

Portier, C., Festa-Bianchet, M., Gaillard, J. M., Jorgenson, J., and Yoccoz, N. (1998). Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool.* 245, 271–278. doi: 10.1111/j.1469-7998.1998.tb00101.x

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Raithel, J. D., Kauffman, M. J., and Pletscher, D. H. (2007). Impact of spatial and temporal variation in calf survival on the growth of Elk populations. *J. Wildlife Manag.* 71, 795–803. doi: 10.2193/2005-2608

Samuel, W. (2007). Factors affecting epizootics of winter ticks and mortality of moose. *Alces* 43, 39–48.

Schwartz, C. C. (1998). "Reproduction, natality and growth," in *Ecology and Management of the North American Moose*, 2nd Edn, eds A. W. Franzmann and C. C. Schwartz (Washington, DC: Smithsonian Institution Press), 141–171.

Simard, A. M., Côté, S. D., Weladji, R. B., and Huot, J. (2008). Feedback effects of chronic browsing on life-history traits of a large herbivore. *J. Anim. Ecol.* 77, 678–686. doi: 10.1111/j.1365-2656.2008.01374.x

Sinclair, A. R., and Krebs, C. J. (2002). Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 357, 1221–1231. doi: 10.1098/rstb.2002.1123

Stephenson, T. R., German, D. W., Cassirer, E. F., Walsh, D. P., Blum, M. E., Cox, M., et al. (2020). Linking population performance to nutritional condition in an alpine ungulate. *J. Mammal.* 101, 1244–1256. doi: 10.1093/jmammal/gyaa091

Stephenson, T. R., Hundertmark, K. J., Schwartz, C. C., and Van Ballenberghe, V. (1998). Predicting body fat and body mass in moose with ultrasonography. *Can. J. Zool.* 76, 717–722. doi: 10.1139/cjz-76-4-717

Stephenson, T. R., Van Ballenberghe, V., Peek, J. M., and MacCracken, J. G. (2006). Spatio-Temporal constraints on moose habitat and carrying capacity in coastal alaska: vegetation succession and climate. *Rangeland Ecol. Manag.* 59, 359–372. doi: 10.2111/04-063.1

Stewart, K. M., Bowyer, R. T., Dick, B. L., Johnson, B. K., and Kie, J. G. (2005). Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* 143, 85–93. doi: 10.1007/s00442-004-1785-y

Therneau, T. M., and Grambsch, P. M. (2000). *Modeling Survival Data: Extending the Cox Model*. Berlin: Springer Science & Business Media.

Thornton, P. E., Running, S. W., and White, M. A. (1997). Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251. doi: 10.1016/s0022-1694(96)03128-9

Tveraa, T., Fauchald, P., Gilles Yoccoz, N., Anker Ims, R., Aanes, R., and Arild Høgda, K. (2007). What regulate and limit reindeer populations in Norway? *Oikos* 116, 706–715. doi: 10.1111/j.0030-1299.2007.15257.x

van Noordwijk, A. J., and de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128, 137–142. doi: 10.1086/284547

Vartanian, J. M. (2011). *Habitat Condition and the Nutritional Quality of Seasonal Forage and Diets: Demographic Implications for a Declining Moose Population in Northwest Wyoming, USA*. MSc thesis, University of Wyoming, Laramie: Wyoming, WYthesis

Wisdom, M. J., Mills, L. S., and Doak, D. F. (2000). Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81, 628–641. doi: 10.1890/0012-9658(2000)081[0628:lssaev]2.0.co;2

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 03 February 2021
doi: 10.3389/fevo.2020.539061

Lek Territory Size and the Evolution of Leks: A Model and a Test Using an Ungulate With a Flexible Mating System

Kavita Isvaran [1,2]*

[1] Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India, [2] Department of Zoology, University of Florida, Gainesville, FL, United States

Despite many decades of research, the evolution of the rare and unusual lek-mating system continues to be debated. The key question is: why do males defend tiny territories clustered together in an aggregation when the costs of doing so are so high? Theory and empirical work on lek evolution typically focus on why males cluster their territories. Surprisingly, the other characteristic feature of classical leks, which is the unusually small size of lek-territories, has received very little attention. Here, I argue that understanding the factors favoring the reduced size of lek-territories can provide fresh insights into the evolution of leks. I used the variable mating system of an Indian antelope, the blackbuck (*Antilope cervicapra*), to investigate lek territory size. Because there are few quantitative models of mating territory size, I first constructed a spatial simulation model of territory size based on male competition costs and on mating benefits generated by a female bias for mating on central lek-territories, the processes most likely to influence lek-territory size. The model generated much systematic variation in territory size within a territory-cluster and also across territory-clusters varying in the number of territorial males. I tested predictions from the model using comparative data on territory size from six blackbuck populations, and detailed spatial and temporal data from an intensively-studied population. Empirical analyses strongly supported model predictions and assumptions. Based on these findings, I present a novel hypothesis for the small size of classical lek-territories. I suggest that much of the variation in the size of lek-territories can be explained by the competition that arises from a female bias for mating on central territories and that is intensified by the number of territorial males in an aggregation. Thus, the reduced size of classical lek-territories is likely a consequence of a central mating advantage in large aggregations. I present a framework for the evolution of leks that explicitly incorporates the evolution of reduced territory size alongside the evolution of male clustering. This framework can also help explain other forms of mating systems that are based on the defense of mating territories by males.

Keywords: lek evolution, ungulates, *Antilope cervicapra*, territory size, female mating behavior, density

Edited by:
*Vernon Bleich,
University of Nevada, Reno,
United States*

Reviewed by:
*Carl Soulsbury,
University of Lincoln, United Kingdom
David Haukos,
Kansas State University,
United States*

***Correspondence:**
*Kavita Isvaran
kavita@iisc.ac.in*

Specialty section:
*This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution*

Received: *28 February 2020*
Accepted: *17 November 2020*
Published: *03 February 2021*

Citation:
*Isvaran K (2021) Lek Territory Size and
the Evolution of Leks: A Model and a
Test Using an Ungulate With a Flexible
Mating System.
Front. Ecol. Evol. 8:539061.
doi: 10.3389/fevo.2020.539061*

INTRODUCTION

Animals display marvelously diverse behaviors in their search for mates. Among the most intriguing suites of mating behavior is lek-mating. Here, rather than adopt more conventional strategies, such as defending females from other males or defending resources that attract females, males aggregate, fiercely defend tiny territories, and perform elaborate displays toward potential competitors and mates (Bradbury, 1981; Höglund and Alatalo, 1995). Females visit these aggregations to mate and appear to be free to move between lek-territories. The potential for strong sexual selection on leks and the unusual territorial behavior of lekking males have spurred many theoretical and empirical studies. But, despite extensive efforts, the evolution of lekking is still not fully understood. Why should males cluster together and defend tiny territories when they incur enormous costs of competition associated with such dense aggregations? Hypotheses and empirical tests for the evolution of lekking have typically focused on the clustering aspect of lek territories (Bradbury, 1981; Bradbury et al., 1986; Beehler and Foster, 1988; Gosling and Petrie, 1990; Balmford et al., 1993; Clutton-Brock et al., 1993; Stillman et al., 1993; Widemo and Owens, 1995; Nefdt and Thirgood, 1997; Gibson et al., 2002; Partecke et al., 2002; Bro-Jørgensen, 2003; Jiguet and Bretagnolle, 2006; Duraes et al., 2007; Young et al., 2009; Isvaran and Ponkshe, 2013; Apollonio et al., 2014; DuVal et al., 2018). Males may cluster their territories on hotspots with high female encounter rates ("hot-spot hypothesis," Bradbury et al., 1986; Westcott, 1997; Jones and Quinnell, 2002). Alternatively, male clustering may arise because males of poorer phenotype cluster around successful "hotshots" ("hotshot hypothesis," Beehler and Foster, 1988; Partecke et al., 2002). Another hypothesis proposes that males cluster because females prefer to mate with clustered males for various reasons, such as reduced costs of mate-sampling, increased chances of obtaining high-quality mates, and reduced male harassment (Bradbury, 1981; Isvaran and Ponkshe, 2013; Apollonio et al., 2014). Yet another hypothesis is that clusters are better at retaining females than solitary territories ("black hole" model Clutton-Brock et al., 1993; Stillman et al., 1993; Jiguet and Bretagnolle, 2006).

All hypotheses for the evolution of leks, thus, focus on the factors that favor male clustering. However, arguably an equally remarkable feature of lekking is the extraordinarily tiny size of territories. Surprisingly, there are no evolutionary hypotheses or empirical studies focusing on the small size of lek-territories. The implicit assumption in many descriptions of leks appears to be that the characteristically small size results from lek territories being primarily display territories, which females visit solely for mating (Bradbury, 1981; Clutton-Brock et al., 1993; Höglund and Alatalo, 1995). These territories typically do not involve the defense of conventional resources (such as forage and breeding sites) attractive to females. Therefore, unlike resource-based territories, they do not have to be large and territory size is not expected to be an important factor contributing to male mating success. However, comparisons across lekking species reveal an intriguing variation in territory size (Wiley, 1974; Clutton-Brock et al., 1993; Höglund and Alatalo, 1995). In some cases, this variation may even blur the distinction between leks and other territorial systems. For example, in several species, male mating territories are clustered, a lek-like feature, but are large enough so that the resources within territories appear substantial, a feature of resource-based territoriality (e.g., black lechwe *Kobus leche smithemani*, Thirgood et al., 1992; little bustard *Tetrax tetrax,* Jiguet et al., 2000; grassquit *Volatinia jacarina,* Almeida and Macedo, 2001). Within species too, territory sizes vary both among leks of different sizes and within a lek (Ranjitsinh, 1989; Gosling and Petrie, 1990). Because mating territory sizes vary so widely and do not always co-vary with male clustering, investigating the factors underlying variation in mating territory size and, specifically, favoring a reduction in size may provide important insights into lek evolution.

There are few explicit predictions in the literature about the size of lek-territories, or more broadly, the size of display or mating territories (i.e., territories that males establish to display from and that are used for mating rather than for gaining access to food, water, or any other resource). Work on territory size has typically focused on territories that animals defend for conventional resources, such as food and breeding sites (e.g., Davies, 1976; Maher and Lott, 2000; Iossa et al., 2008; Sorato et al., 2015). Therefore, to arrive at quantitative predictions of lek territory size, I first searched the literature for observations concerning lek territories to identify general factors likely to influence their size, and next constructed a formal spatial model of mating-territory size. The main factor I modeled was the movement of females on leks. A large part of male behavior at leks is thought to be in response to female behavior when visiting leks (Höglund and Alatalo, 1995). In particular, a striking pattern reported in most lekking species is that females move to and mate with males on central territories in leks (Clutton-Brock et al., 1988; Trail and Adams, 1989; Gosling and Petrie, 1990; Balmford et al., 1992; Hovi et al., 1994; Höglund and Alatalo, 1995; Isvaran and Jhala, 2000; Bro-Jørgensen and Durant, 2003). Along with higher female visits and mating success in central territories, these territories are also generally smaller than those at the periphery (Kruijt and Hogan, 1967; Fryxell, 1987; Gosling and Petrie, 1990; Hovi et al., 1994). This suggests that males on central territories receive greater competitive pressure from other males seeking to establish territories in areas attractive to females, thereby leading to a reduction in territory size toward the center of the lek. There are several possible explanations for a female bias for central territories on leks (e.g., Gosling and Petrie, 1990; Bro-Jørgensen and Durant, 2003). In this paper, I do not assess these explanations, instead, I evaluate (1) whether a female bias for central territories in a cluster of territories, however caused, can lead to systematic variation in territory size, (2) how this effect varies with the number of males in a territory cluster, and (3) what its implications are for the evolution of the reduced size of lek-territories. I also consider a simple "null" model without any female bias but with only competitive interactions among territorial males.

I then use data from the variable mating system of an Indian antelope, blackbuck (*Antilope cervicapra*), to empirically test processes that may lead to variation in mating-territory size and, specifically, that may favor small territories. Blackbuck, like many ungulates (e.g., fallow deer *Dama dama*, Thirgood et al., 1999, topi *Damaliscus lunatus*, Bro-Jørgensen and Durant, 2003) show variable mating behavior, and provide an excellent opportunity to examine processes maintaining variation in behavior and to identify conditions that favor particular behavioral forms. Male blackbuck defend mating territories that may be solitary or clustered to different degrees including classical lekking (Mungall, 1978; Ranjitsinh, 1989; Isvaran and Jhala, 2000; Isvaran, 2005). Territory size also varies (Mungall, 1978; Prasad, 1989; Ranjitsinh, 1989). Thus, territory distributions may differ dramatically among populations, from solitary, dispersed, large territories to tightly clumped classical leks. However, in all cases, these are primarily mating territories and can be analyzed in a common framework to investigate the factors influencing mating-territory size.

In this paper, I first present a spatial model of mating-territory size that evaluates the influence of a female bias for central territories on territory size. I do not evaluate processes that favor male clustering since this has been addressed extensively by previous studies (e.g., reviewed in Clutton-Brock et al., 1993; Höglund and Alatalo, 1995; Apollonio et al., 2014), but instead focus on processes that may favor a reduction in territory size. I use this model to generate predictions for how territory size should vary within a territory-cluster and across clusters with different numbers of males. I compare predictions from the female-bias model with those from a simple "null" model which does not include female bias but includes local interactions among males. I then test model predictions using data from six blackbuck populations distributed widely across the range of this species. I also use detailed spatial and temporal variation in territory size from one intensively-studied population, including variation among different territory clusters, variation within a cluster over time, and variation in the size of territories of known males over time. I also test the main assumption of the model, about a female bias for central territories, using data on female behavior.

Based on these results, I present a novel hypothesis for the small size of classical lek-territories and, more generally, for variation in the size of mating territories across populations and species. I suggest that much of the variation in the size of lek territories can be explained by the competition generated among males by a female bias for central territories and modulated by the number of territorial males in the aggregation. I compare the roles of a female bias for central territories and alternative processes in producing a central advantage in territorial aggregations. Finally, I present a framework for the evolution of leks that explicitly incorporates the evolution of reduced territory size alongside the evolution of male clustering. This framework can also help explain other forms of mating systems in ungulates that are based on the defense of mating territories by males.

METHODS

A Model of Mating-Territory Size: Modeling the Effect of a Female Bias to Mate in the Center of an Aggregation

In many lekking species, females move to and mate in the center of a cluster of territorial males (e.g., Balmford et al., 1992; Hovi et al., 1994; Bro-Jørgensen and Durant, 2003). To model the effect of this behavior on territory size, I considered a territorial arena consisting of 900 unit squares of unit size. Males sequentially entered this arena and established a territory (size = 9 units) in the part of the arena that maximized mating benefits to males devalued by the cost of male-male competition. Male mating benefits were assumed to be initially distributed uniformly across the territorial ground (i.e., benefits were drawn from a random uniform distribution). Males could establish territories in unoccupied units and could also choose to overlap their territories with those of other males, in effect, as explained below, choosing to carve out areas from previously established territories. Males did not experience any cost of competition in the unoccupied units, but in areas of overlap, males competed with others previously occupying these areas. They suffered a cost that was proportional to the number of males they were competing with: in each unit, cost = cn where c is a constant and n is the number of males occupying a unit (including the new male). In the absence of competitors, c represents a maintenance cost of territorial behavior. In addition to the costs of competition, males were assumed to share mating benefits in the areas of overlap. These areas of overlap were divided equally among males occupying them while calculating final territory sizes. This, in effect, represents new males carving out areas from previously established territories when setting up new territories. By equally dividing a unit among its occupants, males are assumed to be of equal competitive ability. Thus, the process of territory establishment involved males evaluating the territorial arena and, based on net benefits, choosing to hold territories in empty areas or carving out, to different extents, areas from previously established territories. Note that the area of the territorial arena (900 unit squares) was never limiting. The size of the arena was large enough so that all males in the largest simulated cluster (50 males) could choose to establish territories of the maximum size (9 units). This assumption, that area is never limiting, was made because the habitat available for establishing lek-territories is typically not limiting in lekking species (reviewed in Höglund and Alatalo, 1995). Rather, leks are often found to occupy a relatively small part of the habitat available for territory establishment (e.g., Balmford et al., 1993; Isvaran, 2005; Apollonio et al., 2014).

Once two territories were established, a female bias for mating in the center of an aggregation was modeled as follows. Mating benefits to males were assumed to decline exponentially from the centroid of previously established territories to the periphery (**Figure 1**). At any given unit u on the arena, the expected mating benefit was given by $M_u = p \cdot e^{-qd_u}$, where d_u is the distance of unit u from the centroid of established territories on the mating arena, p is a constant representing mating benefits in the center of the cluster, i.e., when $d = 0$; and q is a constant representing the strength of a female bias for central territories. The mating benefit surface was recalculated after every territory addition because the center of a territorial aggregation shifts with every new territory added. This process assumes (1) that females show a strong bias to mate in the center of the current territorial aggregation, and (2) the location of maximum female bias shifts to some extent as the center of the territorial aggregation shifts with the addition of each new territory.

Using these rules, each time a new male entered the territorial ground, the fitness (F_t) of each possible new territory, t, (each territory a set of 9 units) was calculated as $F_t = \sum_{u=1}^{9} \frac{M_u}{n_u}(1 - cn_u)$ where M_u is the expected mating benefit of each unit, c the cost of overlap, n_u the number of males occupying that unit (previously established males + new male), and the term $(1 - cn_u)$ represents the competition costs (see above) which act to devalue potential mating benefits over and above the maintenance cost of territorial behavior. For example, in an unoccupied unit u the net male mating success is $M_u(1 - c)$ and in a unit u with one previous occupant it is $\frac{M_u}{2}(1 - 2c)$. The term $(1 - cn_u)$ was set to 0 if it fell below 0. The territory with the maximum fitness was adopted by the new male. Thus, mating benefits were represented as the number of matings a male could expect to gain in that unit (after incorporating the matings lost to other occupants of that unit as a result of dividing matings equally among occupants, see above), and costs of competition were represented as the proportion of these matings that a male could expect to lose as a result of the energetic costs of competing with other occupants of that unit. Energetic costs could result in a loss in matings, for example, because these costs might reduce the time for which a male is able to retain his territory, and thus reduce his encounter with females visiting that unit. A reduction in territory tenure associated with an increase in fighting rates has been reported in several lekking antelope (Gosling and Petrie, 1990; Isvaran and Jhala, 2000). Note, however, that this representation of costs is meant only as an example. More specific processes generating benefits and costs were not modeled. The assumptions for costs and benefits were kept general because we know very little about patterns and processes in mating territory size. Hence, the main aim of the modeling effort was to construct a simple model of the most likely processes and generate quantitative predictions about patterns in mating territory size.

After all males sequentially established territories, I calculated final effective territory sizes. Areas of overlap were divided equally among males occupying them. I also calculated the mean size of territories in the cluster.

I ran the simulation varying the number of males in a cluster from a solitary territory ("cluster" of 1), to a cluster of 50 males. Note that this model does not investigate the causes of the clustering of territories; instead, it takes clustering as given and then explores how territory size is influenced by (1) the effect of a female central bias and (2) the number of males forming a territory-cluster. Therefore, in all simulations with more than one territorial male entering the territorial ground, clustering is assumed (i.e., territories must share a part of their boundary with at least one other territory).

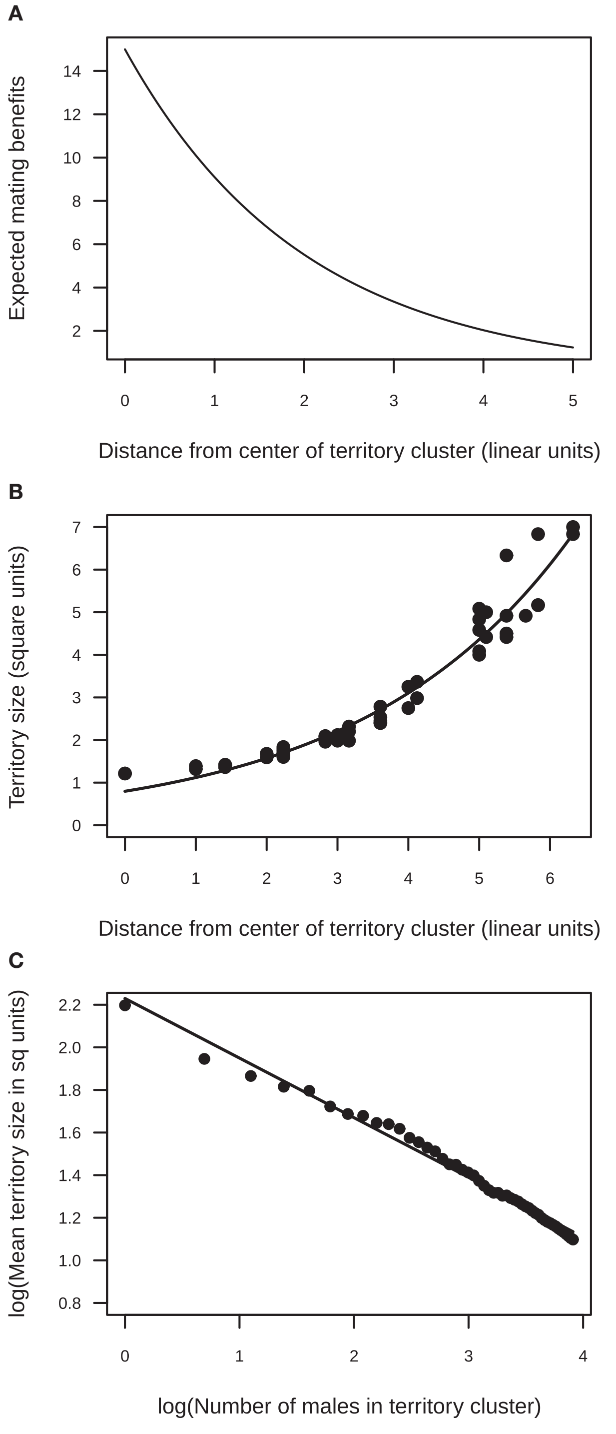

FIGURE 1 | Results from the simulation model of the effect of a female preference to mate in the center of an aggregation on territory size. **(A)** Mating benefits were assumed to decline exponentially from the center of the aggregation to the periphery (exponent = 0.5). **(B)** The model predicts that, within a cluster, territory size should increase from the center to the periphery. An example is shown for a cluster of 50 territorial males (the line shows the fit of an exponential function $Y = 0.8e^{0.34X}$). **(C)** The model predicts that, across clusters varying in size, mean territory size should decrease non-linearly with cluster size [as indicated by the slope of the log-log plot, $\log(Y) = 2.22 - 0.28\log(X)$].

To evaluate the effect on the model of the strength of female preference to mate at the center of the aggregation, I varied the exponent (q) of the function describing mating benefits from 0 to 0.9. A value of 0 for q represents a null model of no female preference and contains only competition costs. In all these model runs, the parameter p was set at 15 and c at 0.1. Each combination of parameters was run 100 times. The sensitivity of the model to the magnitude of the cost function was also evaluated (**Supplementary Figure 2**).

Model Results

Here, I present two types of predictions from the model: (1) how territory size should vary spatially within a cluster (lek) of territories, and (2) how territory size should vary across clusters with different numbers of territorial males. Under a moderate female bias for mating in the center of a cluster of territories ($q = 0.5$), the size of individual territories varied spatially within a territory cluster. Territory size was smallest in the center of the territorial aggregation and increased to the periphery (**Figure 1**). This is because more territories were established toward the center than the periphery, which, in turn, was because mating benefits were highest in the center and declined steeply toward the periphery of the cluster. This steep increase in territory size from the center to the periphery was seen in clusters with different numbers of males (**Supplementary Table 1**). Note that the area of the mating arena (900 unit squares) was never limiting. The size of the mating arena was large enough so that all males in the largest simulated cluster (50 males) could choose to establish territories of the maximum size (9 units). However, because of the pattern in mating benefits, territory sizes were usually much smaller as males tried to establish territories in areas that maximized net benefits.

A comparison across territory-clusters with different numbers of territorial males showed that mean territory size at a cluster decreased exponentially with male numbers (**Figure 1**). This is because as the number of males attending a cluster increased, many more males established territories toward the center of the aggregation. Even though males who carved out territories in central parts of the arena, in areas already occupied by other males, faced high competition costs, the large mating benefits at the center outweighed these costs. Hence, as male numbers at a cluster increased, the competitive pressure from males attempting to establish territories in areas with high mating benefits also increased. The steepness with which mean territory size declined with the number of territorial males attending a cluster depended on how steeply mating benefits fell away from the center of the cluster, that is, it depended on the strength of the female bias for central territories (**Supplementary Figure 1**).

Simulations representing a "null" model of no effect of female bias were also run. When mating benefits were assumed to be uniform throughout the territorial arena (exponent $q = 0$), territory sizes did not vary systematically from the center to the periphery within a cluster. In addition, mean territory size did not vary systematically across clusters with different numbers of territorial males (**Supplementary Figure 1**). Because mating benefits were not concentrated in a particular part of the aggregation, males gained no benefit from attempting to carve out territories in previously occupied areas to outweigh the cost of competition. Instead, new males established territories at the edge of the existing cluster. In these simulations, habitat for territories was never limiting, and such a lack of limitation has commonly been shown in lekking species (see Höglund and Alatalo, 1995). The results from this "null" model suggest that in the absence of a systematic spatial pattern in benefits across the territorial arena, costs associated with territorial interactions alone are unlikely to give rise to systematic variation in territory size, either within or between territory clusters.

Overall, the simulation model predicted that, given a female bias for central territories, (1) within a territory-cluster, territory size should increase from the center to the periphery, and (2) across clusters with different numbers of territorial males, mean territory size should decrease as the number of males in a cluster increases.

Empirical Tests of the Model

Study Organism

The blackbuck is a small antelope (31–45 kg, Ranjitsinh, 1989) native to the Indian subcontinent. It is a group-living, selective grazer. Mating typically occurs on mating territories that males defend. While males have also been observed courting females in mixed-sex groups, these seldom end in successful matings (Mungall, 1978; Prasad, 1989; Ranjitsinh, 1989; Jhala and Isvaran, 2016). Although some breeding occurs throughout the year, there are two prominent annual mating peaks, one in March and April and another from August to October (Ranjitsinh, 1989).

Study Sites

To test predictions from the model, I use data on territory size collected from six blackbuck populations in India from August to November 1998 and 1999 (Isvaran, 2003). These sites were Tal Chappar in Rajasthan state, Velavadar and Savainagar in Gujarat state, Nannaj in Maharashtra state, Rollapadu in Andhra Pradesh state, and Point Calimere in Tamil Nadu state (details of these study sites are presented in Isvaran, 2005, 2007). Territory size patterns were studied more intensively in one population, Velavadar in Gujarat, from February to May 2001.

Among Population Variation in Territory Size

I spent 2–4 weeks at each population during August-November (which covers a mating peak) in 1998 and 1999. At each site, I surveyed the area repeatedly and recorded putative territorial males. This was made possible by the relatively small size of study areas (Isvaran, 2005). Putative territorial males were observed during three to six 1-h watches performed during morning and evening hours when territorial and mating activity is high (Isvaran and Jhala, 2000). During these watches, I recorded the area used by males and interactions between males. Neighboring males engage in frequent displays (nose-up displays, parallel walks, Mungall, 1978) and fights at the boundaries of their territories (Mungall, 1978; Ranjitsinh, 1989; Isvaran and Jhala, 2000). From these data, I identified territory clusters, defined as territories that shared boundaries. Territory clusters were typically identified unambiguously because clusters were usually at least half a km apart (while the average nearest-neighbor distance between males within a cluster was 80 m). Mean territory sizes were estimated for a sample of territory clusters (mean = 4 clusters, range = 2–6) at each population. For each of these clusters, I measured territory sizes for a sample of males (mean = 5 males, range = 1–15). During 1-h focal watches, I noted the location of males every 5 min. Males were typically active and moved over the majority of the area subsequently recorded as their territories within the first half hour. At the end of these watches, I estimated territory size by pacing out the longest and shortest axes of the area used by each male during the watch. Territories varied in shape but were well-approximated by an ellipse.

Within Population Variation in Territory Size

Territorial and mating behavior was studied more intensively at Velavadar in Gujarat from February 5 to May 1, 2001. I studied the principal lek (maximum of 90 males) and four relatively small clusters (with a maximum of 8, 4, 4, and 3 males). Blackbuck use dung piles, formed by repeated defecation at a site, to mark territories and a territory typically contains a principal central dung pile and several smaller dung piles at the periphery and elsewhere in the territory (Mungall, 1978; Prasad, 1989; Isvaran and Jhala, 2000). I mapped the principal dung pile of each territory in the clusters studied using a 30 m tape measure and permanent markers on the territorial ground. I identified territory boundaries by observing interactions (Nose-up displays, parallel walks and fights; Mungall, 1978; Ranjitsinh, 1989) between neighboring males. I then estimated territory sizes by measuring with a tape measure the longest and shortest axes of the area used by males and using the formula for the area of an ellipse. I also identified individual males using horn characteristics (Isvaran and Jhala, 2000), and recorded changes in the number of territories and ownership at least once in 3 days at the main lek and once a week at the smaller clusters. Furthermore, at the main lek, I intensively monitored the sizes of 20 territories (randomly chosen at the beginning of the study), at least once in 3 days, throughout the mating peak.

Female Behavior on Leks

To test the key model assumption that mating benefits decline from the center to the periphery of a cluster, I studied spatial patterns in female visits. Previous work at this study population established that female visits were closely correlated with mating success (Isvaran and Jhala, 2000). I recorded female location and behavior on the main lek at Velavadar during 1-h scan-sampling sessions. During each session, I scanned the lek every 15 min and recorded the location of all observed females and male intruders on territories. Females spend variable amounts of time at the lek (8–120 min; Isvaran K, unpublished data) and move among multiple territories during their visit. Therefore, observations across scans within a session are unlikely to be highly correlated. Scan sessions for female numbers and location on the lek were conducted in the afternoons and evenings as mating activity is concentrated during these hours (Isvaran and Jhala, 2000). I conducted these sessions at least once a week during the study period, and every 2 days during the peak in mating activity (28 February—14 March).

Analyses

I tested model predictions using four kinds of variation in territory size: (1) variation in mean territory size among territory-clusters from different populations; (2) variation in mean territory size within a territory-cluster over time; (3) spatial variation in the size of individual territories from the center to the periphery of a territory-cluster; and (4) variation in the size of the territories of known males over time. To test the first model prediction that territory size should vary spatially from the center of the territory cluster to the periphery, data from the main lek at Velavadar from the peak in mating activity (28 February—14 March) were used to build a Generalized Least Squares (GLS) model with territory size as the response, distance from the center as the predictor, and with potential spatial non-independence incorporated into the error structure by modeling correlations between territory-pairs as a linear function of the distance between them (Pinheiro and Bates, 2000). The center of a cluster was defined as the center of gravity, centroid, of all territories in the cluster in that period.

The second prediction that mean territory size should vary with the number of territories in a cluster, specifically that mean territory size should decrease with increasing number of territorial males at a cluster, was tested with data from multiple scales. I first used data from the six populations and calculated the mean territory size for each territory cluster for the six populations. A linear mixed-effects (LME) model was then fitted with mean territory size of a cluster as the response variable, the number of territorial males attending the cluster as the main predictor, and with study site as a random effect to account for non-independence among clusters from the same population. I then tested the prediction using temporal variation in territorial male numbers at the main lek at Velavader. To examine the change in mean territory size at the main lek at Velavadar as the number of territorial males attending the lek varied over time, a GLS model was built with mean territory size on a given day as the response variable, the number of territorial males on that day as the predictor variable, and with a first-order autocorrelation with a time covariate. GLS methods allow one to incorporate the possibility that mean territory size at a cluster estimated on successive days may be more correlated than values further separated in time. Finally, I also tested the prediction using data from individually identified males. An LME was fitted with the territory size of known males as the response variable, the number of territorial males attending a cluster when each territory size measurement was made as the predictor, and male identity as a random term. Territory size was $\log_e$-transformed in all analyses to normalize errors. In addition, in all analyses, two alternative shapes of the relationships between territory size and the main predictors (number of territorial males, distance from lek-center) were evaluated, namely exponential and power relationships, by comparing the fit of models using raw and $\log_e$-transformed values of the main predictors. The type of relationship that gave the better fit is reported here.

The assumption about female bias in the territory size model was tested using data on the location of female visits at the main lek at Velavadar. The relationship between female visits and distance from the lek-center was analyzed by first, dividing the

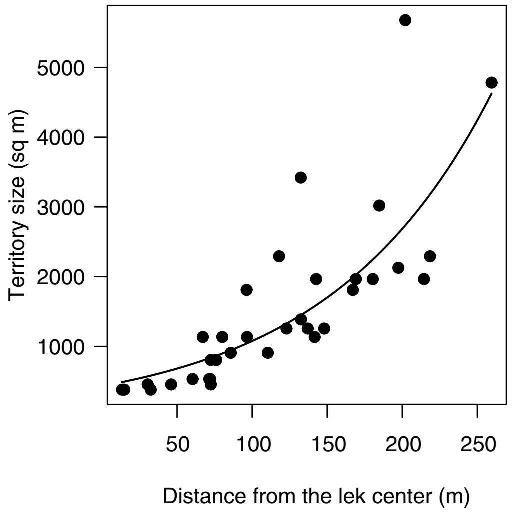

FIGURE 2 | Spatial patterns in territory size at the main lek in Velavadar during the peak in mating activity (28 February−14 March). Territories were smallest in the lek-center and increased toward the periphery. The curve is the prediction from the GLS model (see methods). Each data point is a territory.

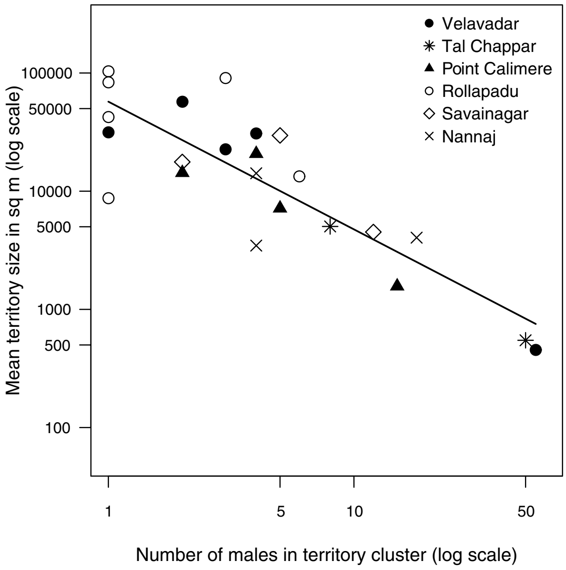

FIGURE 3 | Relationship between the number of territorial males in a cluster and mean territory size pooling together data from six blackbuck populations. Mean size of territories in a cluster decreased rapidly with the number of males in a cluster. Each data point represents a cluster and is an average of the size of a sample of territories from that cluster (range = 1–15 territories). Each set of symbols represents clusters from a particular population. The relationship is strongly non-linear and hence the data have been log-transformed to obtain a better view of the pattern. The line represents the model prediction from a linear model (see methods).

lek-area into concentric bands 40 m in diameter and centered about the lek-center; second, calculating the mean number of females (averaged across scans within a sampling session and then across the 20 sampling sessions) per unit area for each of these bands; and third, using ordinary least-squares (OLS) analyses on $\log_e$-transformed data.

In all analyses, conditional *t*- and *F*- tests were used to test fixed effects, and likelihood ratio (LR) tests to test the effects of spatial and temporal correlations in GLS models and of random terms in LME models (Pinheiro and Bates, 2000). The residuals from analyses were checked for deviations from model assumptions. If random terms were not statistically detectable in LME or GLS models, they were dropped and results from OLS models are shown. All analyses were run in R ver 3.6.2 (R Core Team, 2019). The package nlme (Pinheiro et al., 2019) was used to run GLS and LME models.

RESULTS

Model Prediction: Territory Size Should Increase From the Center to the Periphery of a Territory-Cluster

This prediction was tested using data from the main lek at Velavadar during the peak in mating (28 Feb−14 Mar). As predicted, territory sizes at the main lek increased exponentially with the distance from the lek center (**Figure 2**; GLS, $\log Y = 6.07 + 0.01X$, $N = 34$ territories, $t = 5.33$, $df = 1$, $P < 0.0001$).

Model Prediction: Mean Territory Size in a Territory-Cluster Should Decrease With an Increase in the Number of Territorial Males in the Cluster

Variation Across Clusters From Six Blackbuck Populations

Territory sizes varied widely both among and within populations from territories 350–100,000 m^2 in area. The number of territorial males attending a cluster also ranged widely from solitary males ("cluster" size = 1) to clusters of 50 territorial males. Pooling together territory-clusters from all six populations, the mean size of territories in a cluster was strongly negatively related to the number of territorial males in that cluster. Mean territory size in a cluster declined disproportionately with the number of territorial males at a cluster as indicated by the slope of the relationship between the two $\log_e$-transformed variables [**Figure 3**; OLS; $n = 23$ clusters; intercept: estimate (s.e.) = 10.95(0.27), $t = 40.58$, $df = 1$, $p < 0.0001$; slope: estimate (s.e.) = −1.08(0.15), $t = -7.35$, $df = 1$, $p < 0.0001$]. This decline was also apparent among the smaller subset of clusters within each population (**Figure 3**). The random intercept was not statistically detectable (LR test: $p > 0.5$).

Variation Within a Territory-Cluster Over Time

At Velavadar, the intensive study site, the number of territorial males varied at the main lek and at the smaller clusters throughout the study period. At the main lek, the number of territorial males increased from 35 males in the beginning of February to 90 males in the middle of March and then fell to 43 males in the end of April (**Figure 4**). Corresponding to the change in territorial male numbers, the mean size of territories at the lek also changed (GLS with $\log_e$-transformed mean territory

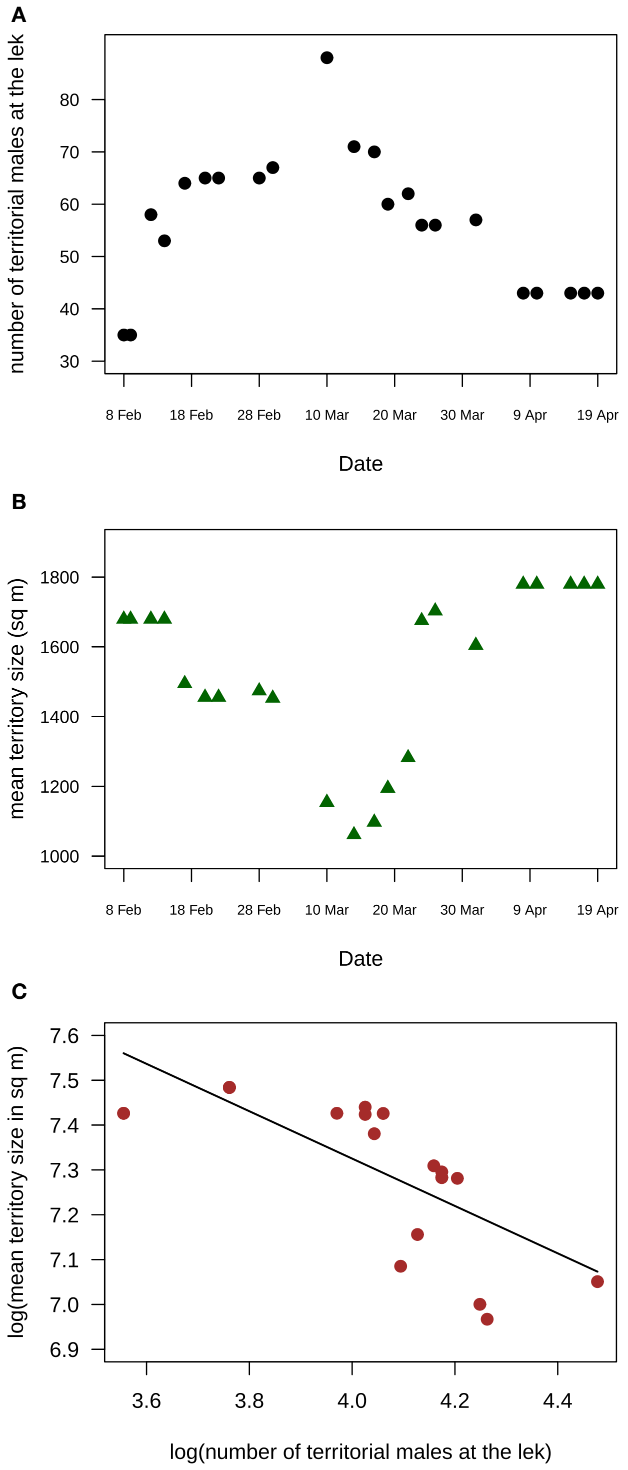

FIGURE 4 | Temporal variation in territory size and male numbers at the main lek in Velvadar indicated that mean territory size was negatively correlated with the number of males holding lek-territories **(A)** The number of males holding territories at the main lek in Velavadar increased, peaked and then decreased during the March-April mating peak, from 8 Feb to 19 April 2001. **(B)** Mean territory size at the main lek in Velvadar decreased to a minimum and then increased during the same mating season. **(C)** Mean territory size was

(Continued)

FIGURE 4 | negatively related to the number of territorial males at the main lek. The line shows the estimated relationship from a GLS model. In all three panels, each data point is a day. Territory sizes are the means of 23 territories whose sizes were monitored throughout the mating season.

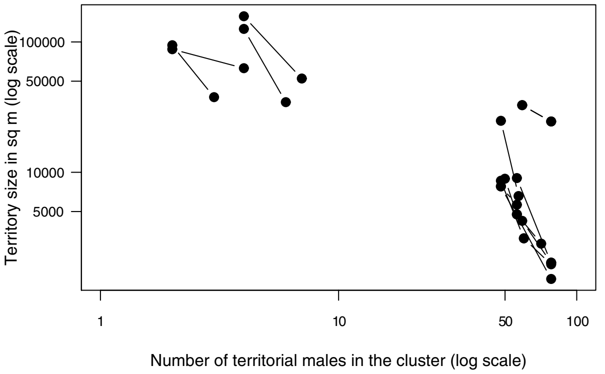

FIGURE 5 | The territory sizes of individual males changed apparently in response to the number of territorial males in the aggregation. Displayed here are examples of the change in the size of territories of known individuals in relation to the change in the number of males in the territory-cluster that the individuals belonged to. Each pair of data points connected by a line is the territory size of the same individual male measured on two different days when the number of territorial males in their territory-cluster differed. A subset of data is shown from small clusters (maximum number of territorial males ranging from 4 to 8) and from the large main lek. The relationship is strongly non-linear and hence the data have been log-transformed to obtain a better view of the pattern.

size and male numbers; intercept: estimate (s.e.) $= 8.4(0.49)$, $t = 17.22$, $p < 0.0001$; slope: estimate (s.e.) $= -0.27(0.12)$, $t = -2.17$, $p = 0.042$; $n = 22$ days). Mean territory size decreased with an increase in territorial male numbers in March and then increased again once territorial male numbers declined in April (**Figure 4**).

Variation in the Territory Size of Individual Males

Changes in territory sizes of known individual males were also negatively related to changes in the number of territorial males attending a cluster both at the main lek and at the smaller clusters [**Figure 5**; LME on $\log_e$-transformed data: intercept: estimate (s.e.) $= 12.28(0.41)$, $t = 30.07$, $p < 0.0001$; slope: estimate (s.e.) $= -0.93(0.12)$, $t = -7.62$, $p < 0.0001$; $n = 34$ measurements from 17 males]. Interestingly, the slope of the relationship indicates that the degree to which territory size changed for a given change in cluster size (e.g., an addition of one territory) was higher in small clusters than at a large one (**Figure 5**).

Testing Model Assumptions: Spatial Variation in Mating Benefits Within a Cluster

Female numbers on the lek were concentrated at the lek center (**Figure 6**). The mean number of females per scan per unit area decreased rapidly with distance from the center of the lek. Previous work at the same study site had already shown that

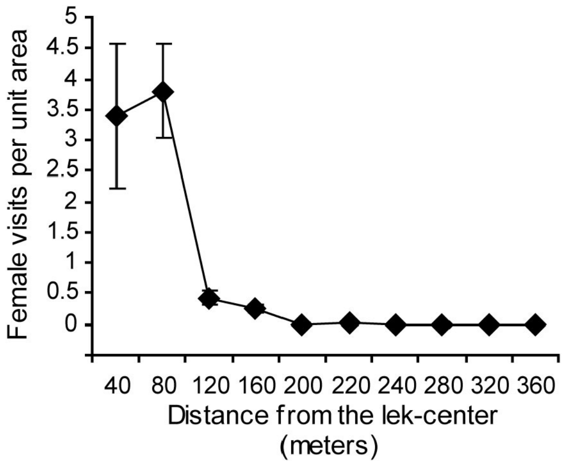

FIGURE 6 | Female visits were highest in the center of the lek and decreased toward the periphery. Means and standard errors based on 20 scan sessions are shown.

matings and courtship were similarly concentrated in the lek center (Isvaran and Jhala, 2000).

DISCUSSION

To understand the selective factors promoting the characteristically reduced size of lek territories, I modeled the effect of a female bias for central territories, a common female mating behavior on leks. This model generated much variation in territory size and made predictions about the patterns that this variation should show and the conditions favoring small territories. Empirical analyses from blackbuck strongly supported model predictions and key assumptions. These findings outline a clear evolutionary process for the evolution of reduced size of lek territories. I argue that lek territory size results from competition generated by a female bias for central territories and modulated by the number of territorial males attending an aggregation. Furthermore, both in the model and in the data from blackbuck, there was a range of conditions under which males clearly clustered their territories, but reduced territory sizes and classical leks did not occur. Therefore, I also argue that alongside formulating hypotheses for male clustering, understanding the processes underlying the classically small territory sizes in leks is key to understanding the evolution of leks.

A Novel Hypothesis for the Evolution of Reduced Territory Sizes on Classical Leks

The female bias model and data from blackbuck suggest that the characteristically small size of lek-territories, a key feature of lekking, is explained well by competition that arises from a female bias for mating on central territories and that is intensified by the number of territorial males in an aggregation. First, the model predicted that within a territorial aggregation, territory size should decrease from the periphery to the center, as a consequence of increased competition for the areas preferred by females. This prediction was closely matched by data from blackbuck. This pattern has also been reported from many lekking species (e.g., White-eared kob, *Kobus kob leucotis,* Fryxell, 1987; topi, *Damaliscus lunatus*, Gosling and Petrie, 1990, black grouse, *Tetrao tetrix*, Hovi et al., 1994, sage grouse, *Centrocercus urophasianus*, Wiley, 1991).

Second, across territory clusters varying in the number of attending territorial males, the female bias model predicted that mean territory size should decrease as male attendance increases, because the competition for more central territories intensifies with an increase in the number of males attempting to defend territories. As predicted, mean territory size in blackbuck was strongly negatively associated with the number of territorial males in a cluster. This pattern was seen across multiple blackbuck populations, in comparisons of mean territory size in clusters with different numbers of territorial males. Even at individual clusters, mean territory size was strongly associated with territorial male numbers, as territorial males numbers changed over time. For example, mean territory size at the main lek in Velavadar decreased as the number of lekking males increased and then increased again as territorial males left the lek toward the end of the mating season. A third line of support was provided by changes in the territory sizes of known males. Again, individual territories expanded when the number of males at a territory cluster decreased and shrank when more males joined the cluster. Interestingly, the female bias model predicted that since territory size is expected to decrease disproportionately with territorial male numbers, the incremental change in territory size should be greater at small than at large clusters. This prediction was also supported by data from blackbuck. Apart from reflecting the influence of the number of territorial males in an aggregation, these results also suggest that territory size is dynamic and changes flexibly in response to immediate changes in costs and benefits.

Taken together, the model and the lines of evidence presented above suggest that variation in mating territory size, and specifically the reduced territory size in classical leks, in species such as blackbuck can be explained by two interacting factors: a female bias for mating on central territories and territorial male numbers at a cluster. A female bias for mating in the center of a territorial aggregation can lead to a reduction in the size of territories toward the center as a result of males competing to establish territories as close as possible to areas preferred by females. Central territories receive more competitive pressure from males and are smaller than peripheral ones. This pressure on central territories can escalate with the number of males attending a territory-cluster. Thus, female bias and the number of males in an aggregation may interact so that the effect of a female preference is greatest when territorial male numbers are high and the smallest territories are found in the largest aggregations. *The reduced size of lek territories may, therefore, be explained by a central mating advantage in large aggregations.*

The importance of a central advantage was also highlighted by a simple "null" model which did not include female bias but included the other rules concerning the costs of competition and local interactions between males. This did not produce systematic variation in territory size suggesting that in the absence of systematic spatial variation in benefits, the presence of competitive male interactions alone is not sufficient to explain the small size of lek territories. Note that in all simulations habitat for territories was unlimited, as has been typically reported for lekking species (reviewed in Höglund and Alatalo, 1995), including blackbuck (Isvaran, 2005). If habitat is limited, then competition for available habitat could result in mean territory size decreasing as territorial male attendance increases.

The main assumption of the female bias model, that mating benefits decline exponentially from the center of the aggregation to the periphery, was supported by data from blackbuck. Both female numbers (this study) and mating activity (Isvaran and Jhala, 2000) declined exponentially from the lek center. Furthermore, studies of many lekking species report similar spatial patterns in female visits and mating success (reviewed in Höglund and Alatalo, 1995) suggesting that territory size variation may be related to a central territory advantage in a wide range of lekking species. Note, however, that a decrease in female visits and mating benefits from the lek-center to the periphery could arise for multiple reasons. Females may use territory centrality as a cue in mate choice (e.g., Isvaran and Jhala, 2000; Bro-Jørgensen and Durant, 2003). Alternatively, females may preferentially visit males of a particular phenotype (e.g., Rintamäki et al., 1995; Vitousek et al., 2008) who are then surrounded by less-preferred males attempting to intercept females traveling to mate with attractive males. Both these processes are expected to generate competition among males for more central territories, but the nature of competition is likely to be different.

The second important factor in the model, the number of territorial males forming a cluster, is likely to be influenced by local female distribution in blackbuck. At Velavadar, variation in local numbers of territorial males at a spatial scale of a square kilometer was closely related to local variation in female group size (Isvaran, 2005) and local female abundances. Local female abundances were, in turn, closely related to ecological conditions, specifically openness of the habitat and forage availability (Isvaran, 2007). Thus, apart from evolutionary factors, such as selection for a female mating bias for central males and selection for male clustering, ecological factors affecting local densities likely affect whether leks form in a population.

Factors Potentially Promoting a Central Advantage in Territorial Aggregations

Although the main mechanism in the model is a female bias for mating in the center, the model can be interpreted more generally as one in which benefits to territorial males are highest in the lek center, thereby generating increased competition for central territories. Therefore, any process that results in a strong central advantage to males could lead to the kind of variation in territory size predicted by the model. Three factors (apart from female bias) that are thought to be important in lekking species and therefore, should be assessed are the harassment of estrous females by non-territorial intruders, predation risk, and female copying.

In many lekking species, courtship is often disrupted by intruding non-territorial males harassing the female and such harassment is thought to play an important role in the maintenance of leks by favoring male territory clustering (Clutton-Brock et al., 1993; Nefdt and Thirgood, 1997). This factor has not been previously discussed in relation to territory size. Male intrusions might explain variation in territory size if patterns in intrusion rates lead to greater benefits to males on central territories than to those on peripheral ones. For example, this might occur if it becomes progressively more difficult for intruders to penetrate into the center of leks because of the resistance from territorial males that they encounter during their progress into a cluster. However, in blackbuck, intrusion rates were highest in the lek-center and decreased toward the periphery, suggesting that intrusions by non-territorial males are unlikely to influence lek territory size in this species (K Isvaran, unpublished data). Another lekking antelope, *D. lunatus*, shows a similar pattern of high intrusion rates on central lek-territories (Bro-Jørgensen, 2002). There are few data on spatial variation in predation risk within a lek. One study of lekking kob (*Kobus kob thomasi*) reported that the distribution of carcasses on a lek did not support a reduction in predation rates from the periphery of the lek to the center although peripheral males did show greater vigilance than central males (Balmford and Turyaho, 1992). It remains to be investigated whether patterns in predation risk within clusters may provide a central territory advantage leading to territory size variation.

Female copying, while difficult to assess in the field, is thought to be an important source of variation in male mating success in several lekking species (Gibson et al., 1990; Clutton-Brock et al., 1993; Höglund and Alatalo, 1995). Female copying could also influence territory sizes by leading to a strong decline in mating benefits from the center of a cluster to the periphery. Suppose the first few females entering a lek mate on a particular territory on the lek (chosen either at random or based on mating preferences). If their locations are copied by females subsequently visiting the lek, this would give rise to a pattern of mating benefits that decline sharply from the site of initial female preferences. Such a female copying model is likely to make predictions similar to the model of female bias for mating in the center. Data from several lekking species suggest that the initial females visiting a lek and females visiting a lek alone do not randomly visit territories but preferentially visit central territories (Höglund and Alatalo, 1995). Thus, there seems to be a preference to visit central territories that is independent of copying. To summarize, intrusion rates are unlikely to influence lek-territory size and there is, at present, little evidence for the influence of predation risk and female copying. A female bias for central territories is currently the most likely factor to generate a strong central advantage and thereby influence territory size in a wide range of lekking species.

Since this is the first systematic study of lek-territory size, I aimed to present a simple, general model that incorporates factors most likely to influence territory size and makes quantitative predictions about patterns in lek-territory size. An empirical test revealed that this simple model can explain much of the variation in territory size seen at different scales in

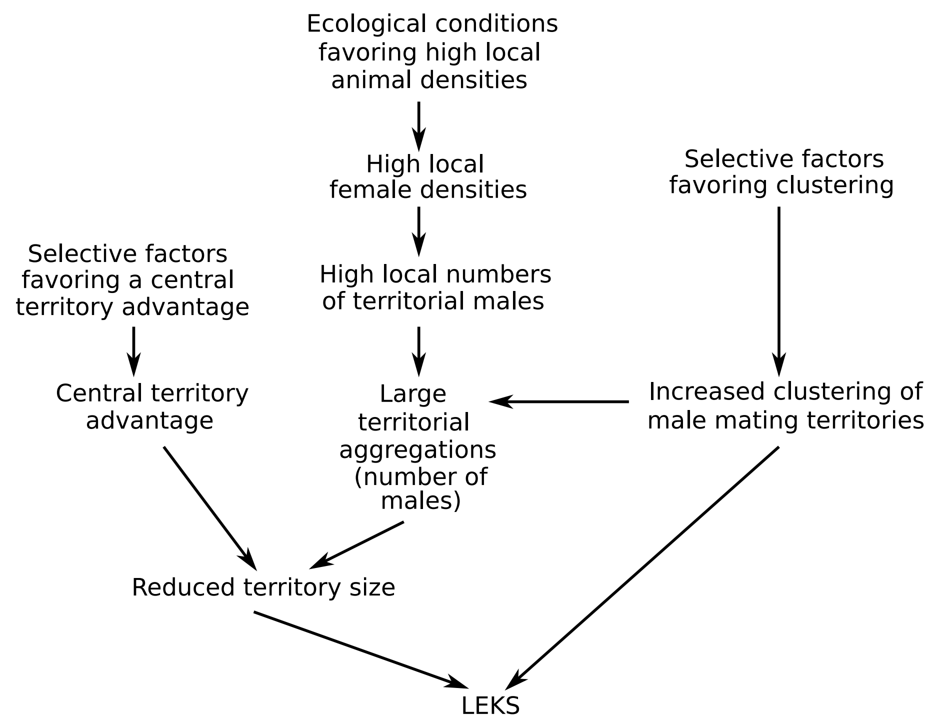

FIGURE 7 | A hypothesis for the evolution of leks that proposes that leks are the outcome of selection acting on two male traits: clustering of territories and the size of mating territory. Leks form when conditions favoring both *male clustering* and *reduced territory size* are met. This study, focusing on reduced territory size, proposes that both evolutionary and ecological factors interact to produce the tiny territories characteristic of classical leks. A central territory advantage (e.g., provided by a female bias for central territories) in large territorial aggregations likely results in reduced territory sizes. Large territorial aggregations (many males in an aggregation) are likely to be an outcome of the male decision to cluster interacting with ecological conditions that favor high local numbers of territorial males.

blackbuck leks. Apart from the processes considered in this study (a central territory advantage and number of competitors), several other factors could potentially influence lek-territory size. For example, together with paying attention to immediate costs and benefits, males returning to the lek in successive mating seasons may show fidelity to locations where they have previously held territories (Rintamäki et al., 1995; Kokko et al., 1998). Males typically vary in their competitive ability (Alatalo et al., 1991; Bro-Jørgensen and Durant, 2003; Ciuti and Apollonio, 2011) and this could influence the location and size of their territories. The relatedness between males on a lek (Lebigre et al., 2014) may also influence the nature of their competition and territory size. In future work, as data on lek territory sizes become available, more detailed and complex models could be constructed that examine the impact of these additional factors on lek territory size.

Implications for Lek Evolution: Leks an Emergent Phenomenon Appearing When Female and Male Mating Decisions Play Out Under High Densities

The model and empirical tests of lek territory size have two major implications for the evolution of leks. First, the hypothesis for lek territory size presented here strongly suggests that understanding lek evolution requires examining the causes of variation in both male clustering and territory size (**Figure 7**). Even if male clustering (the factor that is typically explored by studies of lek evolution) is favored, classical leks may not form if the conditions for a reduction in territory size are not met. For example, consider a small population in which clustering is strongly selected for. Even if all territorial males in that population cluster together, the number of males attending a cluster will remain small. When the number of territorial males in an aggregation is low, the model predicts that territory sizes will be relatively large, unlike classical lek territories. The territorial system is then likely to resemble the clustered resource-based mating territories seen in some antelope (e.g., low density populations of *D. lunatus*) or the exploded leks seen in some bird species, rather than classical leks. Thus, the two main characteristics of lekking—male clustering and reduced territory size—may not always co-vary and may be affected by different sets of factors. This may explain why leks are so rare, even though mating systems based on the defense of mating/display territories by males are fairly common (Clutton-Brock, 1989). That is, if leks form only when multiple conditions that favor male clustering and reduced territory size are met, we would expect that a change in any of these conditions will result in the disappearance of leks and the appearance of a different form of spatial distribution of mating territories.

A second implication of this study is that there is a strong role for ecology in the formation of classical leks in an area (**Figure 7**).

The female bias model and data from blackbuck indicate that the tiny size of classical lek territories is seen only when the number of territorial males in an aggregation is relatively high. That is, even when a population shows male clustering and a female bias for central territories (both evolved traits), if territorial male numbers are low, territory sizes are likely to remain large and classical leks are unlikely to form. Previous work on blackbuck suggests that territorial male numbers in an area are strongly correlated with local female densities, which, in turn, are affected by ecological conditions related to predation risk and food. *Thus, to understand the maintenance of the lek mating system, we need to evaluate both evolutionary processes favoring key male and female mating decisions (such as clustering and a central bias) and ecological processes favoring high local densities.* This link between local animal densities and lekking has previously been reported (Leuthold, 1966; Clutton-Brock et al., 1993; Deutsch, 1994). For example, Clutton-Brock et al. (1993) report that with a decrease in local animal densities as a result of hunting, lekking disappeared and was replaced by the defense of larger resource-based mating territories. However, while these studies call lekking a "default" mating tactic when female densities are high, they have not been able to find a mechanism connecting the two. The findings from this study on the impact of the number of territorial males in an aggregation provide a potential mechanism for the influence of high local densities on lek formation.

An extension of the argument presented above is that the female bias model of territory size can suggest novel explanations for the occurrence of territorial systems intermediate between lekking and resource-based territories. Specifically, it shows that by varying the central territory advantage and/or territorial male numbers at a cluster we can get territorial distributions ranging from large dispersed territories to classical leks. Evidence for such processes is provided by findings from a non-lekking *K. kob thomasi* population with clustered, resource-based territories. Fischer and Linsenmair (1999) report that a reduction in the number of territorial males at clusters over several years was associated with an increase in mean territory size. These results suggest that the factors captured by the female bias model: (1) decline in benefits from the center of an aggregation to the periphery (leading to male-male competition for central locations); and (2) size of the aggregation (influencing the magnitude of the competition for more central locations), may be more widely applicable to a range of territorial systems.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by Institute Animal Care and Use Committee, University of Florida.

AUTHOR CONTRIBUTIONS

KI designed the study, collected the data, performed statistical analyses, and wrote the manuscript.

ACKNOWLEDGMENTS

I am grateful to the Forest Departments of Rajasthan, Gujarat, Maharashtra, Andhra Pradesh, and Tamil Nadu for permission to work in protected areas and for support in the field; the Indian Institute of Science, the Animal Behavior Society, the American Society for Mammalogists, Sigma Xi and University of Florida for funds; Ben Bolker, Jane Brockmann, Suhel Quader, YV Jhala, and Colette St. Mary for discussions and comments on the manuscript; and two reviewers for constructive comments on the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.539061/full#supplementary-material

REFERENCES

Alatalo, R. V., Höglund, J., and Lundberg, A. (1991). Lekking in the black grouse—a test of male viability. *Nature* 352, 155–156. doi: 10.1038/352155a0

Almeida, J. B., and Macedo, R. H. (2001). Lek-like mating system of the monogamous blue-black grassquit. *Auk* 118, 404–411. doi: 10.1093/auk/118.2.404

Apollonio, M., De Cena, F., Bongi, P., and Ciuti, S. (2014). Female preference and predation risk models can explain the maintenance of a fallow deer (*Dama dama*) lek and its 'handy'location. *PLoS ONE* 9:e89852. doi: 10.1371/journal.pone.0089852

Balmford, A., Albon, S., and Blakeman, S. (1992). Correlates of male mating success and female choice in a lek-breeding antelope. *Behav. Ecol.* 3, 112–123. doi: 10.1093/beheco/3.2.112

Balmford, A., Deutsch, J. C., Nefdt, R. J., and Clutton-Brock, T. (1993). Testing hotspot models of lek evolution: data from three species of ungulates. *Behav. Ecol. Sociobiol.* 33, 57–65. doi: 10.1007/BF00164347

Balmford, A., and Turyaho, M. (1992). Predation risk and lek-breeding in Uganda kob. *Anim. Behav.* 44, 117–127. doi: 10.1016/S0003-3472(05)80761-4

Beehler, B. M., and Foster, M. S. (1988). Hotshots, hotspots and female preferences in the organization of lek mating systems. *Am. Nat.* 131, 203–219. doi: 10.1086/284786

Bradbury, J. (1981). "The evolution of leks," in *Natural Selection and Social Behavior*, eds R. D. Alexander and T. W. Tinkle (New York, NY: Carron Press), 138–169.

Bradbury, J. W., Gibson, R. M., and Tsai, I. M. (1986). "Leks and the unanimity of female choice," in *Evolution: Essays in Honour of John Maynard Smith*, eds P. J. Greenwood, P. H. Harvey, and M. Slatkin (Cambridge: Cambridge University Press), 301–314.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proc. Natl. Acad. Sci. U.S.A.* 99, 9290–9293. doi: 10.1073/pnas.142125899

Bro-Jørgensen, J. (2003). The significance of hotspots to lekking topi antelopes (*Damaliscus lunatus*). *Behav. Ecol. Sociobiol.* 53, 324–331. doi: 10.1007/s00265-002-0573-0

Bro-Jørgensen, J., and Durant, S. M. (2003). Mating strategies of topi bulls: getting in the center of attention. *Anim. Behav.* 65, 585–594. doi: 10.1006/anbe.2003.2077

Ciuti, S., and Apollonio, M. (2011). Do antlers honestly advertise the phenotypic quality of fallow buck (*Dama dama*) in a lekking population? *Ethology* 117, 133–144. doi: 10.1111/j.1439-0310.2010.01862.x

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. R. Soc. Lond. B* 235, 339–372.

Clutton-Brock, T. H., Deutsch, J. C., and Nefdt, R. J. C. (1993). The evolution of ungulate leks. *Anim. Behav.* 46, 1121–1138. doi: 10.1006/anbe.1993.1302

Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M., and Albon, S. D. (1988). Passing the buck: resource defense, lek breeding and mate choice in fallow deer. *Behav. Ecol. Sociobiol.* 23, 281–296. doi: 10.1007/BF00300575

Davies, N. B. (1976). Food, flocking and territorial behaviour of the pied wagtail *Motacilla alba yarrellii* gould in winter. *J. Anim. Ecol.* 45, 235–253. doi: 10.2307/3777

Deutsch, J. C. (1994). Lekking by default: female habitat preferences and male strategies in Uganda kob. *J. Anim. Ecol.* 63, 101–115. doi: 10.2307/5587

Duraes, R., Loiselle, B. A., and Blake, J. G. (2007). Intersexual spatial relationships in a lekking species: blue-crowned manakins and female hot spots. *Behav. Ecol.* 18, 1029–1039. doi: 10.1093/beheco/arm072

DuVal, E. H., Vanderbilt, C. C., and M'Gonigle, L. K. (2018). The spatial dynamics of female choice in an exploded lek generate benefits of aggregation for experienced males. *Anim. Behav.* 143, 215–225. doi: 10.1016/j.anbehav.2018.01.009

Fischer, F., and Linsenmair, K. E. (1999). The territorial system of the kob antelope (*Kobus kob kob*) in the comoé national park, côte d'ivoire. *Afr. J. Ecol.* 37, 386–399. doi: 10.1046/j.1365-2028.1999.00194.x

Fryxell, J. M. (1987). Lek breeding and territorial aggression in white-eared kob. *Ethology* 75, 211–220. doi: 10.1111/j.1439-0310.1987.tb00654.x

Gibson, R. M., Aspbury, A. S., and McDaniel, L. L. (2002). Active formation of mixed-species grouse leks: a role for predation in lek evolution? *Proc. R. Soc. Lond. B* 269, 2503–2507. doi: 10.1098/rspb.2002.2187

Gibson, R. M., Taylor, C. E., and Jefferson, D. R. (1990). Lek formation by female choice: a simulation study. *Behav. Ecol.* 1, 36–42. doi: 10.1093/beheco/1.1.36

Gosling, L. M., and Petrie, M. (1990). Lekking in topi: a consequence of satellite behaviour by small males at hotspots. *Anim. Behav.* 40, 272–287. doi: 10.1016/S0003-3472(05)80922-4

Höglund, J., and Alatalo, R. V. (1995). *Leks*. Princeton, NJ: Princeton University Press.

Hovi, M., Alatalo, R. V., Hoglund, J., Lundberg, A., and Rintamaki, P. T. (1994). Lek center attracts black grouse females. *Proc. R. Soc. Lond. B* 258, 303–305. doi: 10.1098/rspb.1994.0177

Iossa, G., Soulsbury, C. D., Baker, P. J., and Harris, S. (2008). Body mass, territory size, and life-history tactics in a socially monogamous canid, the red fox Vulpes vulpes. *J. Mamm.* 89, 1481–1490. doi: 10.1644/07-MAMM-A-405.1

Isvaran, K. (2003). *The evolution of lekking: insights from a species with a flexible mating system* (Doctoral dissertation). University of Florida, Gainesville, FL.

Isvaran, K. (2005). Female grouping best predicts lekking in blackbuck (*Antilope cervicapra*). *Behav. Ecol. Sociobiol.* 57, 283–294. doi: 10.1007/s00265-004-0844-z

Isvaran, K. (2007). Intraspecific variation in group size in the blackbuck antelope: the roles of habitat structure and forage at different spatial scales. *Oecologia* 154, 435–444. doi: 10.1007/s00442-007-0840-x

Isvaran, K., and Jhala, Y. (2000). Variation in lekking costs in blackbuck (*Antilope cervicapra*): relationship to lek-territory location and female mating patterns. *Behaviour* 137, 547–563. doi: 10.1163/156853900502204

Isvaran, K., and Ponkshe, A. (2013). How general is a female mating preference for clustered males in lekking species? A meta-analysis. *Anim. Behav.* 86, 417–425. doi: 10.1016/j.anbehav.2013.05.036

Jhala, Y. V., and Isvaran, K. (2016). "Behavioural ecology of a grassland antelope, the blackbuck *Antilope cervicapra*: linking habitat, ecology and behaviour," in *The Ecology of Large Herbivores in South and Southeast Asia* (Dordrecht: Springer), 151–176.

Jiguet, F., Arroyo, B., and Bretagnolle, V. (2000). Lek mating systems: a case study in the little bustard *Tetrax tetrax*. *Behav. Process.* 51, 63–82. doi: 10.1016/S0376-6357(00)00119-4

Jiguet, F., and Bretagnolle, V. (2006). Manipulating lek size and composition using decoys: an experimental investigation of lek evolution models. *Am. Nat.* 168, 758–768. doi: 10.1086/508808

Jones, T. M., and Quinnell, R. J. (2002). Testing predictions for the evolution of lekking in the sandfly, *Lutzomyia longipalpis*. *Anim. Behav.* 63, 605–612. doi: 10.1006/anbe.2001.1946

Kokko, H., Lindström, J., Alatalo, R. V., and Rintamäki, P. T. (1998). Queuing for territory positions in the lekking black grouse (*Tetrao tetrix*). *Behav. Ecol.* 9, 376–383. doi: 10.1093/beheco/9.4.376

Kruijt, J. P., and Hogan, J. A. (1967). Social behavior on the lek in black grouse, *Lyrurus tetrix tetrix* (L.). *Ardea* 55, 204–240. doi: 10.5253/arde.v55.p203

Lebigre, C., Alatalo, R. V., Soulsbury, C. D., Höglund, J., and Siitari, H. (2014). Limited indirect fitness benefits of male group membership in a lekking species. *Mol. Ecol.* 23, 5356–5365. doi: 10.1111/mec.12941

Leuthold, W. (1966). Variations in territorial behavior of Uganda kob *Adenota kob thomasi* (Neumann 1896). *Behaviour* 27, 215–258. doi: 10.1163/156853966X00164

Maher, C. R., and Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *Am. Mid. Nat.* 143, 1–29. doi: 10.1674/0003-0031(2000)143[0001:AROEDO]2.0.CO;2

Mungall, E. C. (1978). *The Indian Blackbuck Antelope: A Texas View*. *Kleberg Studies in Natural Resources*. College Station, TX: Caesar Kleberg Research Program in Wildlife Ecology.

Nefdt, R. J. C., and Thirgood, S. J. (1997). Lekking, resource defense, and harassment in two subspecies of lechwe antelope. *Behav. Ecol.* 8, 1–9. doi: 10.1093/beheco/8.1.1

Partecke, J., von Haeseler, A., and Wikelski, M. (2002). Territory establishment in lekking marine iguanas, *Amblyrhynchus cristatus*: support for the hotshot mechanism. *Behav. Ecol. Sociobiol.* 51, 579–587. doi: 10.1007/s00265-002-0469-z

Pinheiro, J., and Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS*. New York, NY: Springer Science & Business Media.

Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D., R., Core Team. (2019). *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-143.* Available online at: https://CRAN.R-project.org/package=nlme

Prasad, N. L. N. S. (1989). Territoriality in the Indian blackbuck, *Antilope cervicapra* (Linnaeus). *J. Bombay Nat. Hist. Soc.* 86, 187–193.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available online at: https://www.R-project.org/

Ranjitsinh, M. K. (1989). *The Indian Blackbuck*. Dehradun: Natraj Publishers.

Rintamäki, P. T., Alatalo, R. V., Höglund, J., and Lundberg, A. (1995). Male territoriality and female choice on black grouse leks. *Anim. Behav.* 49, 759–767. doi: 10.1016/0003-3472(95)90050-0

Sorato, E., Gullett, P. R., Creasey, M. J., Griffith, S. C., and Russell, A. F. (2015). Plastic territoriality in group-living chestnut-crowned babblers: roles of resource value, holding potential and predation risk. *Anim. Behav.* 101, 155–168. doi: 10.1016/j.anbehav.2014.12.012

Stillman, R., Clutton-Brock, T. H., and Sutherland, W. J. (1993). Black holes, mate retention and the evolution of ungulate leks. *Behav. Ecol.* 4, 1–6. doi: 10.1093/beheco/4.1.1

Thirgood, S., Langbein, J., and Putman, R. J. (1999). Intraspecific variation in ungulate mating strategies: the case of the flexible fallow deer. *Adv. Stud. Behav.* 28, 333–361. doi: 10.1016/S0065-3454(08)60220-X

Thirgood, S. J., Robertson, A., Jarvis, A. M., Belbin, S. V., Robertson, D., and Nefdt, R. J. (1992). Mating system and ecology of black lechwe (Kobus: Bovidae) in Zambia. *J. Zool.* 228, 155–172. doi: 10.1111/j.1469-7998.1992.tb04439.x

Trail, P. W., and Adams, E. S. (1989). Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. *Behav. Ecol. Sociobiol.* 25, 283–292. doi: 10.1007/BF00300055

Vitousek, M. N., Rubenstein, D. R., Nelson, K. N., and Wikelski, M. (2008). Are hotshots always hot? *A longitudinal study of hormones, behavior, and reproductive success in male marine iguanas. Gen. Comp. Endocrinol.* 157, 227–232. doi: 10.1016/j.ygcen.2008.04.015

Westcott, D. A. (1997). Lek locations and patterns of female movement and distribution in a neotropical frugivorous bird. *Anim. Behav.* 53, 235–247. doi: 10.1006/anbe.1996.0294

Widemo, F., and Owens, I. P. F. (1995). Lek size, male mating skew and the evolution of lekking. *Nature* 373, 148–151. doi: 10.1038/373148a0

Wiley, R. H. (1974). Evolution of social organization and life-history patterns among grouse. *Q Rev. Biol.* 49, 201–227. doi: 10.1086/408083

Wiley, R. H. (1991). Lekking in birds and mammals: behavioral and evolutionary issues. *Adv. Study Behav.* 20, 201–291. doi: 10.1016/S0065-3454(08)60322-8

Young, K. A., Genner, M. J., Joyce, D. A., and Haesler, M. P. (2009). Hotshots, hot spots and female preference: exploring lek formation models with a bower building cichlid fish. *Behav. Ecol.* 20, 609–615. doi: 10.1093/beheco/arp038

Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Advantages of publishing in Frontiers

OPEN ACCESS
Articles are free to read
for greatest visibility
and readership

FAST PUBLICATION
Around 90 days
from submission
to decision

HIGH QUALITY PEER-REVIEW
Rigorous, collaborative,
and constructive
peer-review

TRANSPARENT PEER-REVIEW
Editors and reviewers
acknowledged by name
on published articles

Frontiers
Avenue du Tribunal-Fédéral 34
1005 Lausanne | Switzerland

Visit us: www.frontiersin.org
Contact us: frontiersin.org/about/contact

REPRODUCIBILITY OF RESEARCH
Support open data
and methods to enhance
research reproducibility

DIGITAL PUBLISHING
Articles designed
for optimal readership
across devices

FOLLOW US
@frontiersin

IMPACT METRICS
Advanced article metrics
track visibility across
digital media

EXTENSIVE PROMOTION
Marketing
and promotion
of impactful research

LOOP RESEARCH NETWORK
Our network
increases your
article's readership