Research Topics

Advances in the conservation of large terrestrial mammals

Edited by
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Advances in the conservation of large terrestrial mammals

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Editorial: Advances in the conservation of large terrestrial mammals

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Editorial on the Research Topic
Advances in the conservation of large terrestrial mammals

Introduction

Large mammals are threatened worldwide (Ceballos and Ehrlich, 2002; Schipper et al., 2008; Bowyer et al., 2019; Torres-Romero et al., 2020; Greenspoon et al., 2023). These iconic animals possess life histories characterized by long life spans, delayed age at first reproduction, iteroparity, small litter sizes, and high maternal investment in large offspring, which predispose many large mammals to elevated risks of extinction (Eberhardt, 2002; Bonenfant et al., 2009; Bowyer et al., 2014). Those risks include habitat loss, habitat degradation, effects of climate change, illegal killing, disease, or inbreeding (Davidson et al., 2017; Bowyer et al., 2019), and have important implications for conservation especially for large herbivores (Atwood et al., 2020). Understanding how to counter those threats effectively is essential to conserving wild populations now and in the future. This Integrated Research Topic provides an overview of the challenges to conserving viable populations of large terrestrial mammals in modern landscapes.

Collectively, these works provide new insight into factors underlying successes and failures of historical conservation efforts for large mammals, including recommendations for the future. The roles of pernicious diseases, mismatches in adaptations of translocated animals to their new surroundings, and differences in survival between resident and translocated animals are investigated. New evidence that climate change results in interspecific competition between large mammals via a reduction in ephemeral resources is presented. Conservation efforts are linked to the critical role nutritional condition plays in shaping the dynamics of ungulate populations. Tradeoffs made by ungulates between predation risk and acquisition of forage, and the efficacy of predator control in ungulate conservation are investigated. A new method to strengthen predictions about habitat suitability is offered, and measures are developed to examine connectivity across variable land-use and species matrices to improve conservation of iconic mammals.

Conservation concerns

We offer new information relevant to the conservation of mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*), both of which have had conservation successes but remain subject to threats that warrant further attention. Whiting et al. explore the past challenges bighorn sheep have faced, and the ways in which some of those obstacles have been overcome, including intensive and successful efforts to restore those native ungulates to historical habitat (Brewer and Bleich, 2023). Whiting et al. also emphasize some short-comings associated with past efforts, while calling attention to remaining challenges, with a focus on habitat enhancements, genetic issues, selection of translocated stock, predation, and disease transmission—all of which are likely to affect future decisions regarding the restoration of bighorn sheep.

As noted by Whiting et al., diseases have played a prominent role in the conservation of bighorn sheep. Walsh et al. address this issue in greater detail and conclude that bighorn sheep in free-ranging herds are unlikely to confer immunity to novel strains of *Mycoplasma ovipneumoniae*, a pathogen that has been implicated in losses of entire populations. Separation of domestic sheep from bighorn sheep, and the implementation of management practices that prevent co-mingling of those species, likely will be the most effective approach for reducing the effects of disease and achieving bighorn sheep conservation goals (Walsh et al.).

A rapidly changing climate is predicted to modify numerous aspects of ecosystem structure and function, including community composition and distribution of many species (Walther et al., 2002). Such alterations are likely to increase risks of extinction for large mammals (Urban, 2015; Bowyer et al., 2019), especially at high elevations or extreme latitudes (Berger et al., 2018). Moreover, effects of climate change on interspecific competition are an important but often overlooked aspect of a warming climate. Berger et al., for instance, document how changes in abiotic resources (minerals, water, snow, and shade) at high elevations foster active competition between ungulates, including mountain goats (*Oreamnos americanus*) and bighorn sheep, for limited resources. Mountain goats dominated bighorn sheep in nearly all social interactions, indicating the importance of understanding effects of climate on abiotic resources and subsequent shifts of behavioral ecology of large herbivores.

Lamb et al. demonstrate that maternal nutritional condition in mule deer influences health of young from gestation through recruitment, highlighting the importance of considering direct maternal effects when examining population dynamics and reproductive success in long-lived mammals. As a result, conservationists are reminded that management plans for ungulates should include assessments of nutritional condition of adult females to maximize likelihood of effective conservation.

Cain et al. ascertain that sites at which female mule deer have been killed by mountain lion (*Puma concolor*) were associated with decreasing horizontal visibility and available forage protein of vegetation, indicating that deer may be selecting for forage quality at the cost of predation risk. Mule deer also selected for areas with higher visibility when risk of mountain lion predation was higher. This tradeoff between forage and predation risk likely holds consequences for nutritional condition and population-level vital rates of mule deer (Cain et al.).

McMillan et al. address one of the most controversial issues confronting wildlife managers—predator control. Following a detailed meta-analysis, they report that consecutive years of coyote (*Canis latrans*) removal increased survival of neonatal mule deer more than did a single year of removal, and that removals of coyotes in close proximity to birthing sites was more effective than removals farther away, the latter of which did not influence survival of young mule deer. Their results underscore the need to employ removal efforts over consecutive years, conduct targeted removal efforts within fawning habitat, and concentrate control efforts on the period when additive mortality is apt to be high.

Smedley et al. explore factors affecting success of translocation efforts for female mule deer, including techniques used to reduce 'problem' populations (Mayer et al., 1995), augment existing populations (Cronin and Bleich, 1995), or to reestablish populations in novel areas (Heffelfinger and Latch, 2023). Smedley et al. compared survival of translocated individuals with that of resident animals, and report differences during the first, but not the second, year following translocation. Younger deer also had higher survival rates than older animals. These data highlight the need to consider the age-class of individuals selected for translocation and monitor the status of translocated animals for multiple years.

Habitat connectivity contributes to biodiversity and conservation. In particular, loss and fragmentation of habitats represent substantial threats to biodiversity (Lõhmus et al., 2017), with detrimental effects on species' dispersal and gene flow (Foltête et al., 2020). Researchers previously have used network connectivity analyses to inform conservation efforts (Gil-Tena et al., 2013; Saura et al., 2018), but spatial structure of many landscape connectivity models or a species-specific approach to connectivity modeling can yield disappointing outcomes (Avon and Bergès, 2016). Camera-trap data and incorporating additional habitat features (e.g., edges) can improve model outcomes, illustrating how this novel approach can strengthen predictions of habitat suitability (Tang et al.). Additionally, selecting multiple species that have an appropriate relationship to landscape characteristics and scale can enhance model efficacy and help meet connectivity goals. This approach, termed "umbrella connectivity", as advocated by Dutta et al., encompasses areas most likely to be used by several co-occurring species and thereby enhances objectivity in selecting which, and how many, species are required for connectivity conservation. Further, this approach fosters well-informed decisions that benefit entire communities or ecosystems. To be effective, conservation measures must consider connectivity across variable land-use and species matrices, as emphasized both by Tang et al. and Dutta et al., approaches that have important implications for conserving large terrestrial mammals.

Contributions to this Research Topic provide the underpinnings necessary for successfully identifying, promoting, and implementing a number of conservation measures for large terrestrial mammals. Further, these works broadly encompass causes and consequences of conservation issues that help focus research and promote acquisition of future knowledge concerning iconic large mammals.

Author contributions

RB: Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. VB: Conceptualization, Validation, Writing – original draft, Writing – review & editing. PW: Conceptualization, Validation, Writing – original draft, Writing – review & editing. JR: Conceptualization, Validation, Writing – original draft, Writing – review & editing.

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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.

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Species conflict at Earth's edges – Contests, climate, and coveted resources

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Direct conflict between species is an infrequently witnessed biological phenomenon. Potential drivers of such contests can include climate change, especially at Earth's high elevation and latitudinal extremes where temperatures warm 2–5 times faster than elsewhere and hydro-geomorphic processes such as glacial recession and soil erosion affect species access to abiotic resources. We addressed a component of this broader issue by empirical assessments of mammalian conflict over access to four abiotic resources – minerals, water, snow, and shade – by annotation of past studies and by empirical data collection. Evidence for Nearctic and Palearctic mammals indicates that when desert waters are in short supply, contests intensify, generally favoring larger species regardless of their status as native or exotic. Our empirical data indicate that contests between two large and approximately similarly-sized mammals – mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) – along a 2,500 km gradient at three high-altitude (above tree-line) sites in the Rocky Mountains of North America, result in striking asymmetries; goats dominated > 95% of interactions. Despite far fewer observations of encounters to access shade or snow patches, an increasingly prominent dialog needs to be held about rarely explored biological phenomena where less is known than we might otherwise presume, whether induced by climate or increasing anthropological alteration because of underpinnings to understand community structure and conservation planning. Observations on the frequency and intensity by which individuals escalate behavior to access abiotic resources remains an underappreciated arena to help identify the proximate importance of scarcity in the natural environment. Notwithstanding Darwin's prediction some 165 years ago that populations in extreme environments (high-latitude, high-altitude) are more likely to be impacted by abiotic variables than biotic, conflict between species may be reflective of climate degradation coupled with the changing nature of coveted resources.

KEYWORDS

competition, climate change, extremes, species interactions, conflict, abiotic resources, mammals, ungulates

Introduction

As humans (*Homo sapiens*) continue the unabated colonization of Earth's terrestrial regions (Bradshaw and Brook, 2014), potential for conflict over access to rare resources inevitably increases. In extreme environments – such as high latitudes, the loftiest of elevations and areas of scant rainfall – abiotic forces may dictate survival more directly than species interactions. As early as 1859 this was predicted – "*When we reach the Arctic regions, or snowcapped summits, or absolute deserts, the struggle for life is almost exclusively with the elements*" (Darwin, 1859), and such limitations have been amply confirmed among mammals in Arctic, high mountain, and desert biomes (Anthony, 1976; Caughley and Gunn, 1993; Dale et al., 1994; Hansen et al., 2019). Nonetheless, persistence under exceptionally harsh conditions is about more than abiotic challenge as individuals must still meet nutrient requirements and configure interactions with other species (Krebs et al., 2003; Gauthier et al., 2004; Festa-Bianchet et al., 2011). While neither common nor frequently witnessed, overt contests between species do ensue and must be examined through the broader lens of global change where interactions may be unmasked particularly as landscapes change. Although competition may take different forms as noted long ago (Elton, 1946), conflict in extreme environments should not be discounted where warming temperatures exacerbate survival challenges (Berger, 2018; Mills et al., 2018).

Along the planet's most northern and southern edges and at the highest altitudes temperatures warm 2–5 times faster than elsewhere (Pörtner et al., 2021). Consequently, the world's mountains are experiencing mass glacial losses fomented by an accentuation in the timing and intensity of water flow (Barnett et al., 2005; Lee et al., 2021; Smith, 2021). Such physical alterations create additional cryospheric and geomorphic change through the redistribution of inorganic inert materials by leaching (Butler, 2012; Yang et al., 2021), conversions which in turn have consequence for soil development, minerals, and plants (Dixon and Thorn, 2005; Lambert et al., 2020; Zimmer et al., 2022). By example, phosphorus or other bio-metals can become concentrated at depositional sites in mineral licks, which offer essential micro-nutrients to geophagous mammals (Link et al., 2011; Pebsworth et al., 2019). Sodium, in particular, is a prominent cation in such sites and it plays a prominent role in several body functions, including lactation, though a singular universal role of sodium in ungulate salt licks may not exist (Kreulen, 1985; Robbins, 1993; Ayotte et al., 2006).

Still, the overarching importance of access to a restricted abiotic resource was noted as early as 1741. John Bartman commented on the arduous journey of white-tailed deer (*Odocoileus virginianus*): ". . . the soil, I suppose contains some saline particles agreeable to the deer who come many miles to one of these places" (Seton, 1927). Empirical documentation is now widespread from environs more extreme than the New England's temperate forests of Bartman's explorations. In the exceptionally arid Namib Desert, elephants (*Loxodonta africana*) travel up to 70 km to access water (Shoshani and Viljoen, 1992). On the comparatively dry Tibetan Plateau above 4,500 m, female wild yaks (*Bos grunniens mutus*) seek remnant snow patches to sustain milk production for nursing offspring during winter when every other source of water is frozen solid (Berger et al., 2015). Mountain goats (*Oreamnos americanus*), a species not known for broad locomotor travel efficiency (Côté and Festa-Bianchet, 2003), may cover up to 29 km in geophagous pursuits (Rice, 2010), where mineralized sites vary from caves to roadsides, outcrops and eroding mountain slopes, some because of glacial attrition, and soils below trees (Cowan and Brink, 1949). At least a dozen mammalian orders including Primates, Rodentia, Lagomorpha, Carnivora, Chiroptera, Perissodactyla and Artiodactlya go to great length seeking minerals (Kreulen, 1985; Link et al., 2011; Pebsworth et al., 2019; see also above).

Despite these abbreviated descriptors of onerous travel, we know little about how, when, or where contests resulting in interspecific competition occur between species, particularly over access to four abiotic resources – minerals, shade, water, and snow. Such deficiencies arise simply because overt interspecific interactions are rarely witnessed. Improving knowledge in this mostly uncharted arena is undermined by logistics of data acquisition in difficult-to-reach environments and, assuredly has been exacerbated by a global decline in field-oriented scientific inquiry (Ríos-Saldaña et al., 2018). Yet, understanding how species contest for access to abiotic products remains a fertile avenue for future study.

Here we report on outcomes of species conflict in mammals from extreme landscapes concentrating on priority of access to those abiotic resources most likely to be affected by climate challenge and anthropogenic modification. Specifically, we mobilize disparate evidence as to how hydrogeological and other alterations conflate to shape attainment of abiotic rewards (see schematic in **Figure 1**). We adopt two approaches: (1) contextualization of the case for conflict at a coarse scale through previously reported aggressive encounters across a range of geographies, and (2) presentation of empirical data on overt conflict at high elevation (above tree-line) sites along a 2,500 km gradient across the Rocky Mountain cordillera (North America). Our study sites were concentrated in areas of relatively recent glacial recession where two large and approximately similarly-sized mammals – mountain goats and bighorn sheep (*Ovis canadensis*) contested for access to minerals. Moreover, given the magnitude of rapid change in global ecological communities due to anthropogenic-induced impacts, many of which favor invasive species from plants to fish, and birds to mammals, we included in our assessment of conflict exotics (i.e., horse [*Equus caballus*], yak), especially because of an increasingly prominent dialog about current and future biodiversity conservation using ecological surrogates

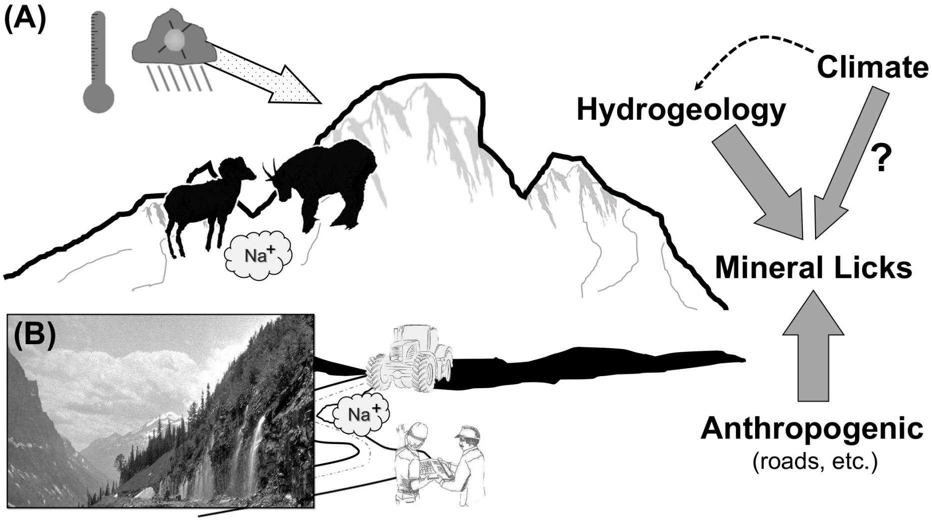

FIGURE 1
Representation of hypothesized pathways leading to high elevation conflict. **(A)** Temperature-based melting of glaciers facilitates availability of mineral licks coupled with their loss to geophagous ungulates by highways construction; (right) hydro-geomorphic changes to mineral availability, and **(B)** 1927 photograph of excessive subterranean-to-surface water flow (Glacier National Park archive photo).

(Lundgren et al., 2021). We find that when abiotic resources are in short supply, not only do interspecific contests intensify, but larger dominate species regardless of their status as native or exotic.

Assumptions, rationale, and framework

Identifying limited abiotic resources

Not all resources are of equivalent value but, by inference as judged by an animal's behavior, they may be classified as to desirability. Consider something inanimate, an abiotic resource like shade. Most of us will have witnessed a dog or cat seek thermal relief on a hot day, perhaps situating itself under a rocky overhang or a tree. Humans, other primates, and individuals of many species do this of course. In such scenarios where shade is not limited, competition for these spots will be minimal, yet the scientific literature on competition, when shade is limited for wild mammals, is scant. Not only are displacement events rarely observed – or at least not reported – but as our anthropogenic grasp tightens, a focus on its consequent impacts to species and how they interact is useful to understand components of global change.

Of fundamental interest is when a resource is scarce and different species seek to utilize it at the same time. While overt interspecific encounters may be frequently circumvented by temporal separation (Valeix et al., 2007), or by a tendency to avoid conflict through self or opponent assessment (Parker and Rubenstein, 1981; Chapin et al., 2019), the few papers that describe active displacements support the assumption that abiotic resources are at times in short supply.

Desert waters offer a case in point (**Table 1**). Nearly 300 discrete interspecies encounters involving African elephants, rhinos (*Diceros bicornis*) and other mammals at drinking points at the same time underwent a level of forced or subtle displacements (Berger and Cunningham, 1998). Aggressive assertions included rushes (or charges), head thrusts or singularly- directed walk-approaches toward interspecifics (**Figure 2**), all of which resulted in rapid displacements (**Table 1**). We operationally characterized these sorts of abiotic resources as coveted if they were sites for which species contested priority of access.

Identifying glacial loss and anthropogenic alteration of mineralized sites

Changes within our study spheres along Rocky Mountain cordillera (**Figure 1**) include those induced directly by warming temperatures (Martin-Mikle and Fagre, 2019) and by more immediate by human destruction of habitat. Higher temperatures at our three study areas (see below) are strongly associated with the phenology of snow melt and plant growth, and an upslope range shift of shrubs and trees into historical alpine tundra habitats. In northern Montana, specifically, Glacier National Park, 85% of the ice/glacial fields have been lost since the park's creation in 1916 (Hall and Fagre, 2003).

The extent to which hydrological changes caused by warming has affected mineral licks used by ungulates in the Rocky Mountains is less certain. Yet, across segments of this broad region construction, modification of highways have resulted in massive loss of previously-available habitat and mineralized sites used by elk (*Cervus elaphus*), moose (*Alces alces*), mountain goats, and, undoubtedly, other species

TABLE 1 Examples of interspecies conflict, displacement in five mammalian orders (Artiodactlya, Perissodactyla, Carnivora, Rodentia, and Primates) over access to water and minerals with notation on potential for contests for additional products (shade, snow) including (feral) horses and (domestic) yaks as exotic species.

	Dominant					
Resource	**Species***	**Native**	**Displaced species**	**Locale**	**Topography**	**References**
Water	Gemsbok	Yes	Chacma baboon	Kuiseb River	Namib Desert	Hamilton et al., 1977[1]
	Horse	No	Pronghorn, bighorn sheep, mule deer	Great Basin and Colorado deserts	Mountains and basins	Berger, 1985; Ostermann-Kelm et al., 2008; Gooch et al., 2017; Hall et al., 2018
	Elephant	Yes	Buffalo, giraffe, impala, kudu, roan and sable antelope, warthog, waterbuck, plain's zebra, wildebeest	Hwange NP	Savanna woodlands	Valeix et al., 2007
	Black rhino	Yes	Mountain and plain's zebras, gemsbok, springbok, wildebeest, giraffe, warthog, leopard, lion, brown and spotted hyena, cheetah	Etosha NP and Namib Desert	Arid savannas and desert	Berger and Cunningham, 1998
Shade	Black rhino	Yes	Gemsbok	Uniab River	Namib Desert	JB unpublished data
	Gemsbok	Yes	Springbok	Doros Crater	Namib Desert	JB unpublished data
Snow	None – see text					
Minerals	Yak	No	Takin	Jigme-Dorje NP	Bhutanese Himalayas	JB unpublished data[2]
	Mountain goat	Yes	Bighorn sheep	Glacier NP	Rocky Mts.	This paper
	Mountain goat	Yes	Hoary marmot	Glacier NP	Rocky Mts.	JB unpublished data[3]

Displacements caused actively or passively as noted in text with dominant species consuming water or minerals and supplanted individuals of other species delaying access to resource or departing area. See also Jokinen et al. (2014) for spatial overlap by northern temperate ungulates but without clear cases of aggression.

*Latin names provided in **Supplementary Table 1**.

[1] Comment in paper but no data.

[2] Three encounters in 7 days: approach by single male yak caused male takin group (size = 2) and single male ($N = 2$) to reroute.

[3] Three encounters; displacements over human urine.

(Cowan and Brink, 1949; **Table 2**). The degree that losses of these low elevation sites because of human construction promoted access to high elevation minerals is not clear but access to such mineralized sites is now possible in some areas because ice sheets no longer exist (Hall and Fagre, 2003) as we describe (**Figures 1**, **3**).

Materials and methods

We used two approaches to appraise species interactions for access to four abiotic resources – water, snow, shade and minerals: (1) a synthesis of peer-reviewed studies coupled with gray literature and opportunistic observations, and (2) field work across three high elevation sites.

Assessing conflict and access to three abiotic resources – Water, shade, and snow

We based our assessment of dominance interactions primarily on displacement or obvious cases of avoidance when members of two species approached a discrete abiotic resource. Although numerous accounts are published, we excluded those unless involvement was for an obvious coveted abiotic resource. By way of example, mule deer (*Odocoileus hemionus*) crossing an alpine meadow, which caused yellow bellied marmots (*Marmota flaviventris*) to flee (Armitage, 2003), was not included since there was no indication that resources used by the marmots were then usurped by the passing deer. Cases of conflict over resources, mostly water, are tabulated in **Table 1**.

Shade, another abiotic resource, is notably important as a thermal refuge for a variety of terrestrial vertebrates including that provided by caves, rocky overhangs, and trees (Barrett et al., 2004; Pruetz, 2007; Cain et al., 2008). We were unable to find formal reports of contests between species over access to shade but include our limited observations (**Table 1**).

Assessing conflict and access to minerals

Our empirically-based fieldwork concentrated at three sites – the Mount Evan region of Colorado (39.5882, –105.6437), the Marias Pass area of Glacier National Park, Montana

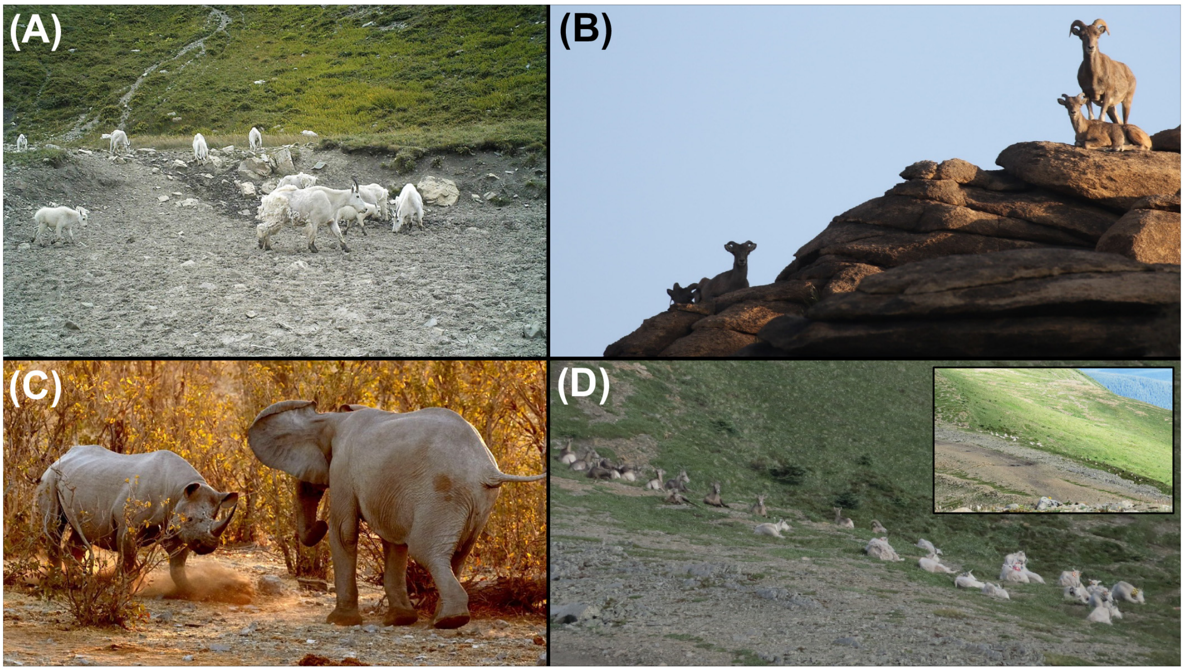

FIGURE 2
Examples of conflict and tolerance. **(A)** Mountain goats at a mineral lick in Glacier National Park, MT (W. Sarmento). **(B)** Closely related taxa of mountain goats and bighorn sheep, herein – female and young Siberian ibex (left) and argali on same rocky outcrops in the Gobi Desert of Mongolia (R. Reading). **(C)** Black rhino and elephant in Etosha National Park, Namibia (A. Forsyth). **(D)** Sizeable groups of mountain goats and bighorn sheep at rest sympatrically (and inset of them in broader landscape) on Caw Ridge, Alberta, Canada (F. Dulude-de Broin).

TABLE 2 **Examples of mineral lick usage and change in lick usage due to anthropogenic alteration or local weather conditions.**

Species*	Site	General locale	Agent	Comment	References
Elk	Selway River	Central Idaho, USA	Weather	Inverse relationship between use and soil drying	Dalke et al., 1965
Bighorn sheep	Norquay (low elevation)	Banff area, Alberta, Canada	Road construction	Post-lick destruction, sheep used salts from highway	Singer, 1975
Mountain goat	Mt. Wardle	Kootenay Park, British Columbia, Canada	Road construction	Gravel pit form construction enhanced goat use	Singer, 1975
Six ungulates[1]	29 mineral licks	Banff, Jasper, Yoho, and Kootenay, Canada	Status unclear	Needs updating[2]	Cowan and Brink, 1949

*Common and Latin names provided in **Supplementary Table 1**.
[1] Caribou, moose, elk, mule deer, mountain goats, and bighorn sheep.
[2] Site visits to these locales are necessary to understand current conditions.

(48.3166, −113.3548; **Figure 3**), and Caw Ridge in west-central Alberta (Canada, ∼ 54.8000, −119.8000). Observations were conducted at Glacier National Park (Montana) in late May–early June in 2020–2021, at Mt. Evans, Colorado June–July (2020) and June–August (2021), and at Caw Ridge in 2017–2018 (Dulude-de Broin et al., 2020).

Mountain goats are native to the Montana and Alberta sites and bighorn sheep to all three (Festa-Bianchet and Côté, 2008). In Colorado, however, mountain goats are not native. They were introduced there in 1947 and have increased greatly, as has also been the case (also as introduced species) in Wyoming, Utah, and elsewhere (Côté and Festa-Bianchet, 2003).

In Glacier, our observations concentrated at natural mineral licks. At Mt. Evans, we focused on a 3,600 m site with effluent and salt sought by both goats and sheep (Clay, 2019). At Caw Ridge conflicts were either for access to resting sites or for a few plant morsels but not abiotic products (see **Supplementary videos 1, 2**). Despite variation in elevation and latitude, the use of three high elevation sites in the Rocky Mountains offered an opportunity to gauge whether the direction of dominance and displacement between bighorn sheep and mountain goats was consistent.

Among the variables we considered to have a possible impact on the outcome of encounters were group sizes.

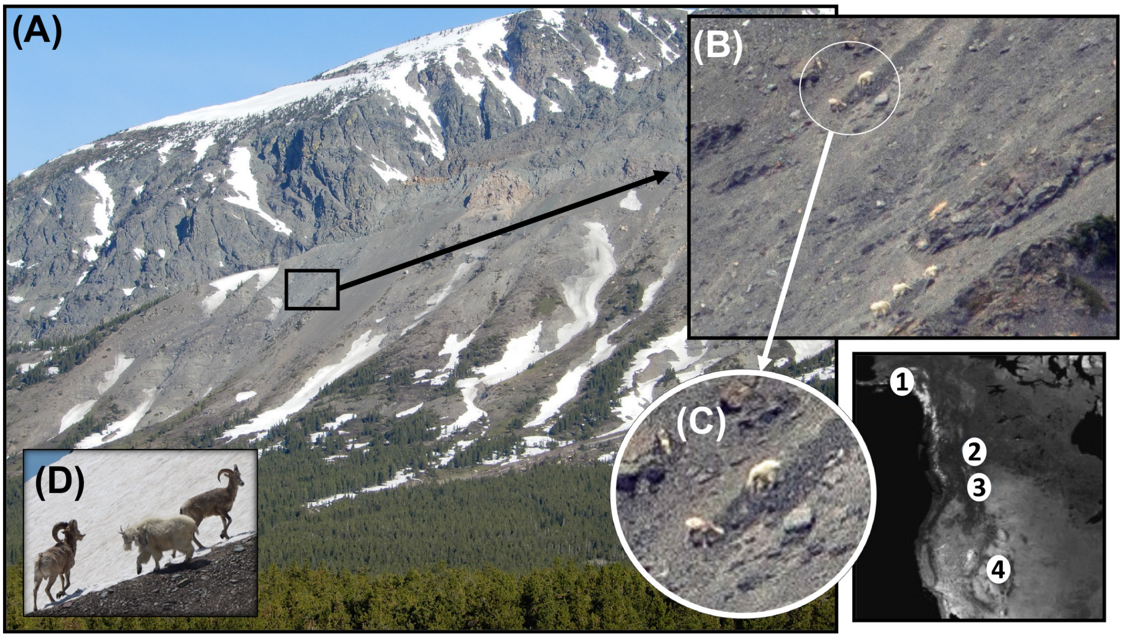

FIGURE 3
Mountain goat-bighorn sheep contests at alpine sites in Glacier National Park, MT. **(A)** Remnant snowfield and mineral lick with **(B)** three goats (lower right central) and single goat and single female bighorn top left at water-saturated mineral lick, **(C)** sympatric feeding prior to goat displacement of bighorn (enlarged), and **(D)** male goat with actionable horn threat displacing two male bighorn. Inset reflects four sites of known displacements between mountains goats and (1) Dall sheep (*Ovis dalli*) in Alaska (Klein, 2019), and bighorn sheep at (2) Caw Ridge, Alberta, Canada (3) Glacier National Park, MT, and (4) Mt. Evans, CO.

Generally, it is easy to enumerate assembly size but as individuals become more dispersed, evaluations grow more complex. For instance, a half dozen clustered moose can easily be counted as a group but if each individual is spread across several semi-distant willow patches it's less obvious if this is to be considered a group (Molvar and Bowyer, 1994). Different versions of group metrics (Bowyer, 1987) have been reported for decades; these include inter-individual distances of separation, cohesiveness, or behaviors such as coordinated feeding or resting; little consensus exists (Elgar, 1989; Treves, 2000).

We operationally defined a group as a cluster of individuals in which the behavior of one is likely to affect that of others. Our snapshot approach was obviously a judgment because at times there was certainty of response but not at other times. For example, the five pictured animals (a total of four goats and one sheep) in **Figure 3B** might be considered one group of five, or two groups, respectively of one and four. At an intraspecific level, which is typically the way groups are defined, perspective and scale matter, but as we note below, group sizes had trivial, if any effect, on outcomes over access to minerals.

Results

Most reports about species conflict at abiotic resources emanate from interactions observed at desert waters. Body size is noted as a major determinant of outcome. Elephants, for instance, are not only the typical victor, but they show little tolerance for other species (**Table 1**). Agonism, dominance, and directionality is likely to vary by site, history, and necessity. Among feral or otherwise introduced species, native mammals may be delayed or denied access (Hall et al., 2018; Ferretti and Mori, 2020; see also **Table 1**).

Other spottily distributed abiotic products like shade and snow have received much less scrutiny as resources for which species compete despite their known biological relevance (Rosvold, 2016). Beyond water, however, the only evidence for competition to access shade stems from observations in the Namib Desert or Kalahari Sands where black rhinos displaced ungulates from shade trees they subsequently used (**Table 1**). With respect to snow patches, we witnessed sympatry between mountain goats and bighorn sheep, but they remained distal without antagonism. Likewise, at about 4,900 m on the Tibetan Plateau wild yaks and chiru (*Pantholops hodgsonii*) moved to snow patches within 200 m of the other without apparent contests.

Unlike snow and shade which are strongly seasonal features of local weather, mineralized sites are less transient although their availability to animal foragers varies with insolation, local hydrology, and soil. At mineral licks, mountain goats dominated bighorn sheep in more than 95% of observed displacements (**Figure 4**).

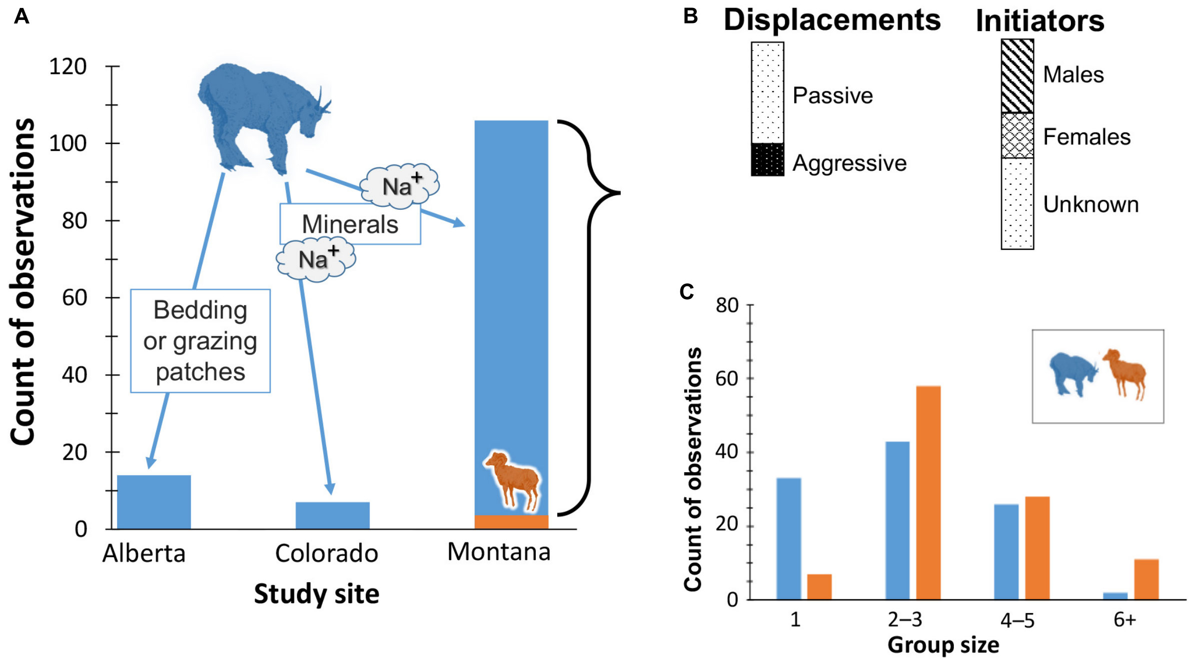

FIGURE 4
Outcomes of dominance assertion between mountain goats and bighorn sheep. **(A)** Histogram in which blue column (goats) is % of encounters won relative to orange (sheep), by study site with those in Alberta, Canada for space or food, and in Colorado for micro-nutrients. **(B)** Relative proportions of goat-initiated displacements of sheep by type (as defined in Methods), and of known sex; **(C)** distribution of goat and sheep group sizes.

Regardless of site, goats initiated every interaction, and most involved passive approaches (73% of 106) whereby subordinate sheep walked or skipped away. In 12% of the total cases neither goats nor sheep had perceptible responses. Rapid approaches or horn threats (Figure 3D) resulted in flight ($< 5\%$); the longest distance fled was $\sim 75 - 100$ m. Male goats accounted for 68% of the known encounters (Figure 4). Mean group size differed statistically between species (bighorn sheep $\bar{x} = 3.40$, $SD = 1.44$; mountain goats $\bar{x} = 2.57$, $SD = 1.43$; *t test*, $p < 0.01$) but is unlikely biologically relevant given the frequency of overwhelming dominance by goats.

Discussion

Interspecies conflict is not a commonly documented nor well-studied phenomenon, but it obviously occurs as competition for patchily scattered abiotic resources. Like other rarely observed phenomena, such as infanticide or tool use, further discovery among wild species, awaits.

Both interspecific and intraspecific competition create known strong selection pressures that sculpt morphology, behavior, and ecology via evolutionary pathways (Mayr, 1982; Bowyer, 2022). In contemporary settings, the nature of conflict to access resources may or may not be changing, an uncertainty that exists because we lack ecological baselines. Consequently, we know little about whether direct anthropogenic alterations on landscapes have facilitated animal movements into realms where the frequency of interactions has changed. While recent climate alterations are creating hydro-geological change including of soils and the loss of glacial ice that affect the distribution of abiotic resources (Barnett et al., 2005; Lee et al., 2021), due to a literal dearth of information we know little about *if* or *how* the immediacy of climate challenge affects interspecies contests.

At an intraspecific level, active competition for abiotic resources is known for reptiles, as up to 128 Aldabra giant tortoises (*Aldabrachelys gigantea*) are known to pile under a single shade tree (Swingland and Lessells, 1979). Also associated with thermal refugia, are cases involving different genera (*Egernia* and *Eulamprus*) of skinks which compete for access to high elevation crevasses (Langkilde and Shine, 2004).

Nonetheless, the extent to which mobile mammals relocate to alternative sites and encounter possible greater competition is highly uncertain because of the aforementioned issue of no ecological baseline. Just as it is often difficult to gauge patterns of trend in disease when monitoring has been insufficient, similar issues confront the immediacy of knowing whether direct interspecific interactions have changed in frequency across time.

Our data on contests for above tree line minerals is a case in point. We do not know if these mineral licks are a newly discovered resource. Perhaps they have increased in availability due recent hydro-geomorphic climate-induced high elevation alterations, as known for the Himalayas (Lee et al., 2021), or something else. Importantly and regardless of whether the mediating forces are directly human such as local habitat destruction, or broader and slower like warming temperatures, given the scarcity and patchiness of abiotic sources (e.g., mineral licks, desert waters) opportunities for interspecies conflict arise over access. Clearly, human alterations of remote desert waters heighten the accessibility challenge (Braithwaite and Muller, 1997; Simpson et al., 2011; Larsen et al., 2012), as has road construction where species have changed their behavior to access mineral licks (Kroesen et al., 2020).

Among life history variables that serve as an arbiter of dominance during interspecies conflict is body size (Berger and Cunningham, 1998). With anthropogenic change, alien-mediated displacement of native fauna occurs (Berger, 1985; Hall et al., 2018) despite scientifically-astute positions about nativity or appropriate ecological surrogates for ecological restoration (Lundgren et al., 2021). Nevertheless, conservation efforts progress in both protected areas and further afield by broadening the distribution of arid-lands water to enhance biodiversity and tourism (Simpson et al., 2011; Larsen et al., 2012).

Conflict between species remains not only of broad ecological interest but harkens to the roots of scientific curiosity about escalated aggression. In the case of high elevation mountain goats, the species occupies a basal position in the Caprini clade (Shafer and Hall, 2010) with stereotypical canalized behavior associated with primitive traits and a propensity for aggression (Geist, 1971; Festa-Bianchet and Côté, 2008). This, in turn, may explain antagonism and dominance over bighorn sheep (**Figure 4**), a situation with immediate conservation relevance given recent controversy over introduced mountain goats.

As a cold-adapted species, mountain goats symbolize climate alteration (White et al., 2018), are sought by visitors in places like Glacier National Park, and remain emblematical for the Great Northern Pacific Railway. The species was introduced to southern locales as previously noted, and public and scientific opinions are often divisive about sanctity in many areas including Grand Teton and Yellowstone national parks. Recently, nearly 60 goats were removed from the former, actions with a mix of support (National Park Service, 2018) whereas in Yellowstone no controls are in place. Knowledge about species dominance to access rare resources, such as presented in **Figure 4**, should help agencies deliberate about best conservation paths forward.

More globally, information about interspecies contests among mammals remains sparse, as does understanding whether competitive interactions have changed spatiotemporally. Anthropogenic alterations of the physical environment continue as habitats are erased and as invasive species rework food webs (Berger et al., 2020). While shade may be less apt to function as a coveted resource, snow patches at high elevation disappear with indeterminate consequence (Rosvold, 2016). By contrast, water and minerals are clearly sought where species engage for access. That we understand little of the process complexity that undermines production and change in availability of many abiotic products, other than the heighted pace of human-wreaked landscape modifications, suggests a fertile ground for future *in situ* field inquiries about species interactions.

We began this narrative pointing to Darwin's prescience that abiotic processes may be potentially more demographically limiting than biotic factors in extreme areas. We now know high latitude and high elevations sites are changing more rapidly than elsewhere due to climate, but more populated areas are losing habitats more rapidly (Caro et al., 2022). How these factors affect communities as species are more often brought together, resulting in increased competition for abiotic resources, is unclear. If conservation practitioners consider that changes in abiotic resource availability can increase competition, preemptive management decisions can be improved upon to facilitate desirable outcomes. For example, just as limited waters can be managed to benefit biodiversity, proactive recognition, and management of existing and emerging mineral licks may facilitate conservation of geophagous species. Moreover, observations of interspecific contests offer a useful method to better understand the limiting nature of important biological elements. If – which is an important caveat – under global change, contests for abiotic variables increase, this could be an additional unforeseen consequence of climate change with impacts to biodiversity. If, however, curiosity about nature coupled with field studies continue their decline, we will never know.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by IACUC, Colorado State University.

Author contributions

JB conceived the ideas of this manuscript through prolonged conversations with FPH and MB. All authors contributed to the field work, as was the writing.

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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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.991714/full#supplementary-material

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Host vs. pathogen evolutionary arms race: Effects of exposure history on individual response to a genetically diverse pathogen

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Introduction: Throughout their range, bighorn sheep (*Ovis canadensis*) populations have seen significant disease-associated declines. Unfortunately, understanding of the underlying epidemiological processes driving the disease dynamics in this species has hindered conservation efforts aimed at improving the health and long-term viability of these populations. Individual response to pathogen exposure emerges from dynamic interactions between competing evolutionary processes within the host and pathogen. The host's adaptive immune system recognizes pathogens and mounts a defensive response. Pathogens have evolved strategies to overcome adaptive immune defenses including maintaining high genetic diversity through rapid evolution. The outcomes of this evolutionary warfare determine the success of pathogen invasion of the host and ultimately the success of conservation efforts.

Methods: During an epizootic dominated by a single strain, we explore these host-pathogen dynamics by examining the variation in effects of pathogen invasion on captive bighorn sheep with differing histories of exposure to genetically diverse strains of *Mycoplasma ovipneumoniae* (Movi). We monitored clinical signs of disease and sampled animals and their environment to detect spread of Movi among 37 bighorn sheep separated into nine pens based on known exposure histories.

Results: We documented Movi transmission within and across pens and we detected Movi DNA in air, water, and invertebrate samples. Higher levels of antibody to Movi prior to the epizootic were associated with a lower likelihood of presenting clinical signs of pneumonia. Nonetheless, higher antibody levels in symptomatic individuals were associated with more severe progressive disease, increased probability and speed of pneumonia-induced mortality, and reduced likelihood of returning to a healthy state. Bighorn sheep with previous exposure to a strain other than the predominant epizootic strain were more likely to recover.

Discussion: Our results indicate that Movi-strain variability was sufficient to overwhelm the adaptive host immunological defenses. This outcome indicates, in free-ranging herds, past exposure is likely insufficient to protect bighorn sheep from infection by new Movi strains, although it influences the progression of disease and recovery within the herd. Therefore, given Movi-strain variability and the lack of immunological protection from past exposure, focusing management efforts on minimizing the introduction of Movi into bighorn herds, through separation of domestic and bighorn sheep and avoidance of management activities that create commingling of bighorn sheep carrying differing Movi strains, will likely be the most effective approach for reducing the effects of disease and achieving bighorn sheep conservation goals.

KEYWORDS

bighorn sheep, disease state, eDNA, hazard, immune response, *Mycoplasma ovipneumoniae*, strain, transmission

Introduction

Pathogens and their hosts are involved in on-going evolutionary warfare. Many hosts have evolved defenses including the innate and adaptive immune systems, which the host uses to recognize and respond to infections with new pathogens as well as to mount rapid responses upon re-exposure to prevent re-infection with previously encountered pathogens. Successful pathogens have evolved various complex and efficient methods to tolerate, evade, circumvent, or overcome innate and adaptive host immune defenses, resulting in increased disease severity or duration of infection of the host (Finlay and McFadden, 2006). One subtle but highly successful mechanism, employed by pathogens to specifically evade adaptive immunity is rapid evolution resulting in alteration of surface exposed antigenic epitopes, which leads to multiple and genetically diverse strain types (Bloom, 1979). Pathogen genetic diversity has implications for individual host response to infection and ultimately determines the pathogen's virulence, transmissibility, and severity of epidemiological outbreaks (Coscolla and Gagneux, 2010; Chae and Shin, 2018). Extensive literature describes antigenic variation within *Mycoplasma* spp. (class *Mollicutes*), the smallest and simplest self-replicating organisms (Christiansen et al., 1997; Citti et al., 2010; Betlach et al., 2019; Qin et al., 2019). Antigenic variation is of fundamental importance in determining the underlying dynamics of host-pathogen interactions. We investigated these host-pathogen interactions by examining the impacts of pathogen genetic diversity on individual bighorn sheep (*Ovis canadensis*).

Mycoplasma ovipneumoniae (Movi) is a common pathogen of domestic sheep and goats that exhibits a high degree of genetic (strain) and phenotypic heterogeneity (Ionas et al., 1991a,b, Parham et al., 2006, Maksimović et al., 2017, Kamath et al., 2019). Spillover of Movi into bighorn sheep is often followed by epizootic transmission with high morbidity and variable mortality (Besser et al., 2012, 2013, 2014; Cassirer et al., 2018). The long-term population-level effect of exposure to Movi varies from full recovery to functional or local extinction (i.e., mortality of ≥90% of the population; Singer et al., 2000; Sells et al., 2015). Most surviving bighorn sheep clear Movi infections with immunity restricted to that strain (Plowright et al., 2013; Cassirer et al., 2017). Nonetheless, some become chronic carriers, and despite apparent immunity from clinical disease, do not clear the infection, consistently test positive for Movi carriage and pose infection risk to other individuals (Plowright et al., 2017; Garwood et al., 2020). As a result of these acute and chronic effects, respiratory disease remains one of the major factors impeding the conservation of bighorn sheep herds (Cassirer et al., 2018).

Individual host response, resulting dynamics and negative effects of disease within bighorn sheep populations is shaped by heterogeneities in Movi strain-specific virulence, exposure dosages, and prior Movi exposure histories (Cassirer et al., 2017, 2018). Describing the effects of exposure history and adaptive immune responses on disease severity and persistence, addresses an important knowledge gap regarding host-pathogen dynamics in wildlife. To address this gap, we used information collected prior to and during an unplanned Movi-associated pneumonia epizootic in a captive bighorn sheep facility containing individuals with different pathogen strain exposure histories to investigate the heterogeneity in responses to infection. We hypothesized during the epizootic that individuals with previous exposure to the dominant infecting strain would be protected whereas prior exposure to other Movi strains would provide limited protection from disease. We also predicted that disease would be less severe in individuals that mounted a greater antibody response and higher antibody levels would improve the odds of recovery. Lastly, we investigated potential environmental routes of Movi exposure that may have facilitated the epizootic. Filling these knowledge gaps cannot be easily done with free-ranging ungulates but is essential for the conservation of bighorn sheep. Therefore, this study represented a unique opportunity to increase understanding of respiratory disease processes in bighorn sheep and ultimately inform disease prevention and mitigation actions to improve the health of bighorn sheep populations and enhance conservation efforts.

Materials and methods

Study area/animals

Thirty-seven free-ranging adult bighorn sheep were tested 1 to 7 times to classify Movi infection status over a period of up to 4 years by state wildlife agencies prior to being transported to the

South Dakota State University (SDSU) Captive Wildlife Research Facility in Brookings, South Dakota (44°20′ N, 96°47′ W; Figure A in Supplementary Appendix A; Table 1). Free-ranging animals were exposed to at least 1 of 4 genetic strains (Kamath et al., 2019) of Movi. Specifically, sheep from the Hells Canyon subpopulations: Asotin (*n* = 9), Lostine (*n* = 4), and Sheep Mountain (*n* = 2) of Washington, Oregon, and Idaho, respectively, had been exposed to the HC-404 strain of Movi. Sheep transported in October 2014 from the Black Butte herd (*n* = 8) of Washington within Hells Canyon carried the HC-404 strain from 1995 until a novel Movi strain, BB-393, was detected in 2014 (Cassirer et al., 2017). We refer to this strain exposure as BB-393/HC-404. Rapid Creek (number of sheep: *n* = 1) and Badlands (*n* = 2) herds within South Dakota were exposed to the SD-398 strain, and the Snowstorm herd (*n* = 11) from Nevada entered the study with exposure to the NV-400 strain (Table 1). All strains were associated with all-age epizootics of pneumonia in the source herds (Cassirer et al., 2013, 2018; Smith et al., 2014; Kamath et al., 2019). The BB-393 strain faded out of the Black Butte herd 2 years following the epizootic and the transfer of sheep to the SDSU captive facility. The other strains persisted in the field and were associated with recurring severe pneumonia outbreaks in lambs.

Capture, transport, daily care, and animal sampling protocols were reviewed and approved by the SDSU Institutional Animal Care and Use Committee (Number 14-076A). With the exception of individuals from the Snowstorm herd (Table 1), sheep were penned together (2–4 adults per pen; Figure 1) with other bighorn sheep with similar exposure and carriage status, which were known for each individual based on prior sampling as described above. In contrast, the carrier status for sheep from the Snowstorm herd (*n* = 11) was unknown. Thus, sheep were housed together in pen 9 (Figure 1) while their carrier status was being determined; however, the epizootic occurred before their carrier status could be ascertained.

TABLE 1 Source herds for 37 bighorn sheep in the study at the South Dakota State University Captive Wildlife Facility, and *Mycoplasma ovipneumoniae* genotypes (strains) detected in those herds.

source herd	Movi strain	Strain abbreviation	*n*
Hells Canyon			
Asotin	404	HC-404	9
Lostine	404	HC-404	4
Sheep Mountain	404	HC-404	2
Black Butte	393/404 exposed	BB-393/HC-404	8
South Dakota			
Rapid Creek	398	SD-398	1
Badlands	398	SD-398	2
Nevada			
Snowstorm	400	NV-400	11
		TOTAL	37

The distance over which Movi might be transmitted was unknown, therefore, we established a minimum distance of 15 m between carrier and other pens to minimize the potential for pathogen transmission between pens under the assumption most transmission is the result of close contact between individuals. Additionally, considering the prevailing winds, chronic Movi carriers were housed in pens in the eastern\downwind edge of the research facility (Figure 1). Further, personnel strictly followed biosecurity protocols including: (1) the installation of disinfecting foot baths at each pen gate for use immediately prior to entering and exiting each pen; (2) use of pen-specific feed and water pails; (3) changing protective clothing when handling possible Movi-positive sheep; and (4) use of order-of-pen-entry from west (Movi-negatives) to east (Movi-positives; Figure 1).

Microbiological sampling

Starting the autumn after arrival at SDSU, we collected serial microbiological samples from all sheep during 1 October–15 March annually, and periodically throughout the year from sheep without lambs at heel using chemical immobilizing agents (BAM; 0.43 mg/kg butorphanol, 0.29 mg/kg azaperone, 0.17 mg/kg medetomidine, Wildlife Pharmaceuticals, CO, United States) and a CO_2 powered dart projector (Pneu-dart, Williamsport, PA, United States). Once under anesthesia, we fully inserted single polyurethane culture swabs (BD CultureSwab™ EZ System) into both nares and slowly rotated the swab shaft while gently contacting the mucosal tissue of the nasal wall and withdrawing the swab with circular motions. Duplicate swabs were collected and stored at −20°C after replacement in the sterile sheath prior to submission to the lab. We also collected 8–10 ml of blood *via* jugular venipuncture and extracted 0.5–1 ml serum for detection of antibodies to Movi *via* competitive enzyme-linked immunosorbent assay (ELISA) performed by the Washington Animal Disease Diagnostic Laboratory. We shipped all samples overnight to Washington State University (Pullman, WA, United States) for PCR analyses (Ziegler et al., 2014) and strain-typing using multi-locus sequence typing (MLST; Cassirer et al., 2017). If a mortality occurred, we collected the same samples, as well as bronchial swabs to detect and strain-type Movi from the lower respiratory tract. The ELISA values were used to assess the effect of the individual's immune response during active infection on disease transition probabilities as described below.

Clinical observations

To maintain consistency and minimize disturbance, the same observer conducted daily 20-min vehicle-based observations using binoculars at distances of ≥27 m throughout the study (1 April 2015 to 1 April 2017). We observed and ranked signs of respiratory disease from 0 to 10 to indicate severity ranging from absent to extremely severe. Signs recorded for each individual

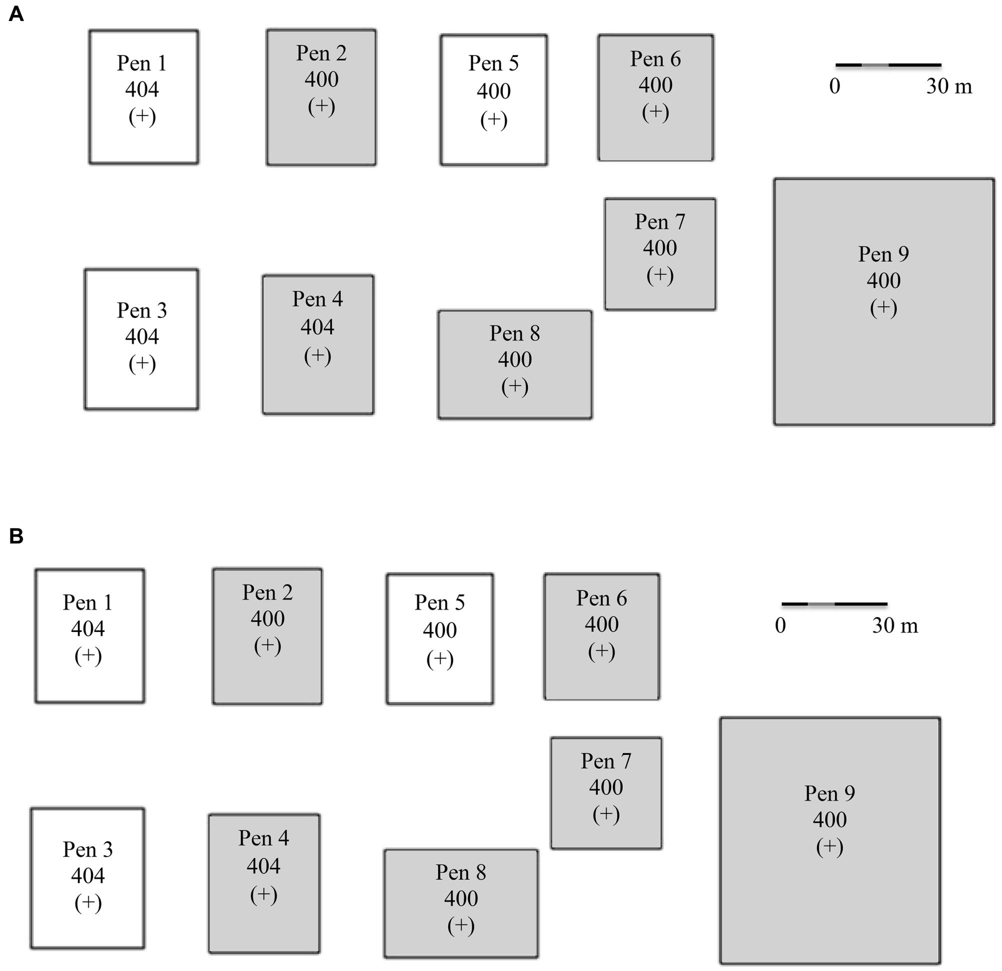

FIGURE 1
(A) Captive bighorn sheep research facility design and pen assignments based on known *Mycoplasma ovipneumoniae* history and current carriage as of 1 January 2015. **(B)** Unintentional indirect novel *Mycoplasma ovipneumoniae* strain infections as of 1 January 2016. Strain types: 404=HC-404; 400=NV-400; 398=SD-398; 393=BB-393/HC-404. A (+) indicates Movi detected in pen and (–) indicates Movi not detected in pen. Shaded pens indicate pneumonia-induced mortality occurred in that pen.

included lethargy, sternal recumbency, ear paresis, nose licking, nasal discharge, and coughing (Supplementary Appendix B). To track disease progression during the epizootic event, we used daily clinical scores for all adults from 16 July 2015 to 1 April 2017.

Environmental samples

To identify environmental factors potentially contributing to transmission of Movi across pens, we sampled air and water from August 2015 to September 2016. We conducted aerosol sampling once every other week at each of 5 pens (Sartorius MD8 Airport Portable Air Sampler, Fisher Scientific, Waltham, MA, United States) for 20-min at 3 defined locations: immediately outside and down-wind of the enclosure being tested (<1 m from pen fence), halfway between the enclosure being tested and the immediately adjacent down-wind pen (halfway from source pen fence), and immediately outside the nearest adjacent down-wind pen (15–30 m from source pen fence) of the pen being sampled. We collected weekly drinking water samples from the permanent 94.6-L trough in each pen. We collected 50-ml of surface water and then thoroughly mixed the water and collected another 50-ml sample from the center of the trough. We also opportunistically conducted sampling of flying insects, bird nests in pens, and soil. We conducted invertebrate (e.g., *Musca* spp.) contamination assessments using fly tape traps and collecting replicate swabs of the external surface of trapped flying invertebrates. Finally, twice during the sampling period, we tested observer-fomite transmission by securing gauze to the bottom of work boots and traversing the pen for 5-min focusing on areas heavily used by sheep (e.g., feed, water stations, and shelters). Immediately after collection, air sample filters were cut in half; one half was dissolved in 20 ml sterile Hayflick's broth media and the other half was placed dry in a sterile envelope. All environmental samples were overnight shipped to Dr. Tom Besser's laboratory at Washington State University for analyses.

Figure B in Supplementary Appendix A portrays the timeline for each of the major activities associated with this study.

Laboratory methods varied by sample type. We varied the volumes for resuspension and for culture in response to different amounts of debris or dirt in the sample types (i.e., air sample filters the cleanest, water samples intermediate, and boot wash samples the dirtiest). Specifically, we transferred aliquots of water samples (25–80 ml, based on 50% of the volume collected) to centrifuge tubes (Product# 3119-0050PK, Thermo-Fisher Scientific, Waltham MA) and pelleted [20 min, 4°C, 18,500 × *g* (RCF average, J-25.50 rotor)]. We resuspended pellets in 1 ml phosphate buffered saline (PBS), which was divided into two 500 μl aliquots, one of which was retained for PCR detection of Movi, and the other was cultured to detect viable Movi. For air samples, the Hayflick's broth containing the dissolved half filter cultured to detect viable Movi. The dry half air filter was dissolved in PBS, pelleted similarly, and the pellet was resuspended in a 500 μl aliquot of PBS, which was retained for PCR detection of Movi. We agitated the boot wash gauze samples in 100 ml PBS in new Ziploc bags (1 gal). We then removed 30 ml and pelleted as described above for water samples. We resuspended the pellets in 5 ml PBS and removed a 500 μl aliquot for PCR detection of Movi. Another 1 ml aliquot was then removed and cultured for detection of viable Movi. Swab samples from arthropods and other miscellaneous environmental (e.g., air) samples were processed for Movi detection by realtime PCR.

For detection of Movi by realtime PCR, we weighed pellets obtained from the 500 μl aliquots described for water and boot samples, and limited the amount retained for DNA extraction to 25 mg. For air samples, since the pellets were invariably <25 mg, we extracted the entire pellet. Swab samples were eluted directly into 500 μl aliquots of PBS. We obtained DNA extracts from these specimen and aliquots using QIAmp DNA Kit (Qiagen United States, Germantown MD) according to the manufacturer's directions. Realtime PCR was then used to analyze extracted DNA (Ziegler et al., 2014).

To culture viable Movi, if samples were not already suspended in a *Mycoplasma* broth culture media, we transferred samples to *Mycoplasma* broth tubes (Product# R102, Hardy Diagnostics, Santa Maria CA) and mixed well. One milliliter pre-incubation aliquots were removed from both Hayflick's broth (air filter samples) and *Mycoplasma* broth, and stored at −20°C. The remainder of the inoculated broths were incubated at 37°C with 5% CO_2 for 72 h, after which we removed and stored at −20°C a second 1 ml post-incubation aliquot. The pre-and post-incubation aliquots were thawed, DNA extracted (QIAmp DNA Kit), and analyzed by realtime PCR (Ziegler et al., 2014). We used relative cycle threshold (CT) values to identify samples with stronger post-incubation realtime PCR detection consistent with growth of viable Movi.

Statistical analyses

To capture the initial transmission and incubation prior to the epizootic, which was first observed 15 July 2015, we initiated our model 1 January 2015 and concluded it on 1 April 2017. Using Kermack and McKendrick's (1927) classic compartmental SIR model structure, we developed a model with three main individual disease states: susceptible (*S*; i.e., susceptible to infection), infected (*I*; i.e., those that were currently displaying clinical symptoms of respiratory disease and were presumed infectious), and recovered (*R*; i.e., those who have had the disease but were no longer symptomatic; Anderson and May, 1991). To model an individual's disease progression during the epizootic between the SIR compartments, we used a Bayesian mixture model for competing risks (Larson and Dinse, 1985; Figure 2). This approach assumed all individuals will eventually transition from their current state to a new state (i.e., probability of staying in its current state as time $\rightarrow \infty = 0)$, and this new state was determined by some stochastic mechanism when they entered their current state (Larson and Dinse, 1985). Individual host response resulted in heterogeneous transition times into each new state. We also assumed that the day when an individual entered a state was when the daily hazard of transitioning from that state began.

We modeled the overall probability an individual in state *i* transitioned to state *j*, and then, conditional on this transition, we estimated the associated daily hazard rate of making the transition. Thus, the transition probabilities acted as mixing parameters for the various hazard rates (Larson and Dinse, 1985). We initially classified all adults as *S* because no individuals were initially displaying clinical signs and a general lack of Movi cross-strain immunity (Cassirer et al., 2017). We used cough and nasal discharge scores to define disease states. We defined the start of disease state *I* as 3 weeks prior to the date of the onset of cough (score ≥ 1) or nasal discharge (score of >2; Besser et al., 2014, Supplementary Appendix B). We classified an individual as being in the *R* state if they did not present any indication of coughing or nasal discharge (score ≤ 2) during daily clinical symptom observations for a minimum of 60 days (Besser et al., 2014).

The model was structured so *I* individuals could not return to the *S* state; however, *R* individuals could return to the *I* state. We also included two absorptive states (i.e., probability of transitioning from an absorptive state = 0): (1) death unassociated with disease (mortality$_o$), and individuals could die and enter this state from any of the states; and (2) death due to pneumonia (mortality$_p$). Only *I* individuals could enter this latter state. Lastly, individuals that did not die during the study we considered right-censored in the state they occupied at the study's conclusion. The model structure is shown in Figure 2.

Transition Probabilities—We estimated most transition probabilities as a function of covariates using a logit link function as follows:

$$logit\left(p_{i,j}\right) = X\beta,$$

where $p_{i,j}$ is the probability of transitioning from state *i* to *j*, *X* is a covariate matrix, which varied between transition probabilities, and β are the parameters for the covariate effects. However, individuals transitioning from state *I* could move to 3 different potential states and therefore, we used a multinomial logit model:

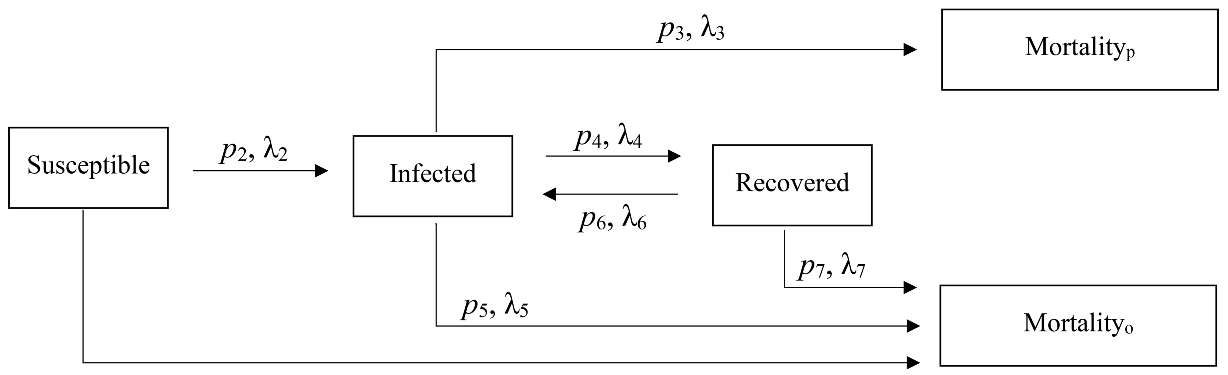

FIGURE 2
Reversible epidemiological SIR model and associated parameters used to characterize an epizootic in captive bighorn sheep.

$$p_{I,j} = \frac{\exp\left(X\beta_j\right)}{1+\sum_{j=1}^{2}\exp\left(X\beta_j\right)},$$

where β_j are the parameters for the covariates associated with transitioning to state *j* from *I*.

When estimating the probabilities of transitioning from *S*, (p_2), we included an effect for the (1) individual's immune response (Movi cELISA % inhibition value; %I_I hereafter) at the nearest sampling event (4–7 months) prior to the epizootic, and (2) the initial Movi strain detected in each individual at the study start. For the probabilities of transitioning from *I*, (p_3, p_4), for each individual we included (1) the %I_I effect, (2) the individual's immune response during active infection (i.e., averaged Movi cELISA % inhibition values for all tests conducted while an individual was alive and had an active infection based on clinical signs; %I_A hereafter), (3) the individual's initial Movi strain, and (4) an indicator of whether the NV-400 strain was detected in an individual during the epizootic (CST NV-400 hereafter). Lastly, we specified the probability of transitioning back to *I* from *R* (disease recurrence; p_6) as a function of the individual's initial Movi strain (Table 2).

Transition Hazard Rates—We used a piece-wise constant function to model each daily transition hazard as a function of covariates of interest using a proportional hazards assumption:

$$\ln\left(\lambda_{i,j,t}\right) = X\varphi + \delta_t,$$

where $\lambda_{i,j,t}$ is the daily hazard of transitioning from state *i* to *j* during interval *t*, φ are the parameters for the covariate effects and δ_t is a regularizing term for daily interval *t*, which is used to account for temporal autocorrelation and provide temporal smoothing. We used a constant model for $\lambda_{i,j,t}$ where *j* is mortality$_\text{o}$ regardless of the current state *i* because this transition hazard rate was independent of disease state.

We used a kernel convolution model (Higdon, 2002) for the δ_t parameters to regularize across days of the study when transitioning from *S* to *I* and from *I* to mortality$_\text{p}$. This modeling approach provided a flexible means of accounting for temporal autocorrelation and permitted the estimation of the level of smoothing supported by our data (Higdon, 2002). For the *S* to *I* transition hazard with knot locations set at each day of the study, the model was:

$$\delta_t = \sum_{n=1}^{N} \frac{1}{\sqrt{2\pi}\sigma_s} exp\left(\frac{dist_{t,n}^2}{2\sigma_s^2}\right) I\left[d \le 120\right] \times \alpha_n,$$

which uses a Normal density kernel truncated at 120 days (i.e., days beyond 120 days from the *t* do not influence δ_t) with a variance of σ_s^2 , $dist_{t,n}^2$ is the squared distance between *t* and the n^{th} knot location, and α_n is the latent random day effect at the n^{th} knot. Knots were created for each day. We specified a Gamma (1, 1) for $\frac{1}{\sigma_s^2}$, and a Normal ($\mu = 0, \sigma_\alpha^2$) prior for the α_n vector of effects. We used a Gamma (1, 1) prior on the precision, $\frac{1}{\sigma_a^2}$. We used the same kernel convolution model for smoothing the temporal effects, δ_t , for the hazard of transitioning from *I* to disease-associated death state and once again we used a Gamma (1, 1) prior on $\frac{1}{\sigma_s^2}$ and a Gamma (1, 1) prior on $\frac{1}{\sigma_a^2}$.

When estimating the log hazard rate for transitioning from *S* to *I*, (λ_2), we examined the effect of individual immune response and historical strain exposure. Specifically, we include aa (1) %I_I effect and (2) an effect for distance from NV-400 strain pen. To model the log hazard of transitioning from *I* to the mortality$_\text{p}$ state (λ_3), we used a (1) %I_I effect and (2) %I_A effect in the model. For the transition from *I* to the *R* state (λ_4), we modeled the log hazard using a (1) %I_I effect, a (2) %I_A effect, and the individual's initial Movi strain. Finally, we modeled the hazard of transitioning back to *I* from *R* (i.e., disease recurrence; λ_6) as a constant. Table 3 contains the covariates used in each hazard model.

Posterior Distribution—Given these probabilities and hazards, the k^{th} individual's transition from state *i* to *j* makes the following contribution to the log likelihood, $ll_{i,j,k}$:

TABLE 2 Estimated posterior distribution of disease state transition probabilities (p_n) for bighorn sheep as a function of covariates using a logit link function for state transitions from susceptible to infected (S-I) and disease recurrence (R-I) and a multinomial logit model for individuals transitioning from the infected state: infected to pneumonia-related mortality (I-Mortality$_p$) and infected to recovered (I-R).

State transition	Predictor	Median	95% LCL	95% UCL	Significant
S-I (p_2)	Intercept	9.40	2.54	24.96	
	%I$_I$†	−10.19	−21.91	−1.30	*
	Initial Strain#				
	NV-400	-	-	-	
	HC-404	7.99	−5.50	23.20	
	BB-393/HC-404	0.67	−12.84	10.68	
	SD-398	8.68	−5.16	23.68	
I-Mortality$_p$ (p_3)	Intercept	−1.17	−13.99	9.53	
	%I$_I$	−0.41	−2.96	1.52	
	%I$_A$##	3.22	0.59	7.36	*
	CST NV-400###	2.91	−7.65	15.63	
	Initial Strain				
	NV-400	-	-	-	
	HC-404	0.32	−3.71	4.62	
	BB-393/HC-404	−1.74	−6.07	2.41	
	SD-398	6.31	−3.21	22.35	
I-R (p_4)	Intercept	2.65	−6.89	14.63	
	%I$_I$	1.46	−1.33	4.70	
	%I$_A$	−2.27	−5.41	0.01	*
	CST NV-400	−7.28	−19.30	0.45	
	Initial Strain				
	NV-400	-	-	-	
	HC-404	5.21	0.28	12.58	*
	BB-393/HC-404	6.33	1.12	14.31	*
	SD-398	−1.56	−20.20	14.07	
R-I (p_6)	Intercept	5.33	−0.03	15.99	
	Initial Strain				
	NV-400	-	-	-	
	HC-404	0	0	0	
	BB-393/HC-404	−5.48	−16.15	0.32	
	SD-398	0	0	0	

Median effect of disease state transitions is presented on the logit scale, and 95% lower credible limit (LCL) and upper credible limit (UCL) are presented.

†Indicates initial percent inhibition values per individual, defined as the quantification of Movi antibody titers prior to cross-strain transmissions (disease state S (Susceptible), prior to 15 March 2015), used to evaluate immune response to enzootic pneumonia.

#Indicates the strain an individual was known to have been exposed to prior to the epizootic.

##Indicates average percent inhibition values per individual, defined as the quantification of an individual's immune response to active Movi infection, from the onset of active cross-strain infection (earliest 15 March 2015) through the end of the study.

###An indicator variable for infection by NV-400 during the epizootic as confirmed by multi-locus sequence typing to characterize strains using partial DNA sequences of the 16S-23S intergenic spacer region.

$$ll_{i,j,k} = \log\left(p_{i,j}\right) - \sum_{t=e_{i,k}}^{r_{i,k}} \lambda_{i,j,t} + \log\left(1 - \exp\left(-\sum_{t=r_{i,k}}^{e_{j,k}} \lambda_{i,j,t}\right)\right), \sqrt{2}$$

where $e_{i,k}$ is the k^{th} individual's entry time into state i and $r_{i,k}$ is the last time the k^{th} individual was known to be in state i. Note, this model allows for interval censoring of the transition time (e.g., the transition time is only known to have occurred between $r_{i,k}$ and $e_{j,k}$). Individuals who are in a state other than death at the end of the study (i.e., right censored) contribute the following:

TABLE 3 Estimated posterior distribution of daily disease state transition hazard (λ_n) for bighorn sheep as a function of antibody levels and prior exposure history.

State transition	Covariate	Mean	95% LCL	95% UCL	Significant
S-I (λ_2)	$\%I_I^{\dagger}$	−0.09	−0.46	0.32	
	Distance††	−0.32	−0.74	0.04	
I-Mortality$_p$ (λ_3)	$\%I_I$	−0.10	−0.81	0.84	
	$\%I_A^{\dagger\dagger\dagger}$	1.13	0.19	2.23	*
I-R (λ_4)	$\%I_I$	1.18	0.08	2.42	*
	$\%I_A$	−1.15	−2.31	−0.19	*
	Initial Strain				
	NV-400	-	-	-	
	HC-404	0.00	0.00	0.00	
	BB-393/HC-404	1.61	−1.00	5.00	
	SD-398	0.00	0.00	0.00	

State transitions presented are susceptible to infected (S-I), infected to pneumonia-related mortality (I-Mortality$_p$), and infected to recovered (I-R). Hazard rates are presented on the log scale, and 95% lower credible limit (LCL) and upper credible limit (UCL) are given.

†Indicates initial percent inhibition values per individual, defined as the quantification of Movi antibody titers prior to epizootic (disease state S (Susceptible), prior to 15 March 2015), used to evaluate immune response to enzootic pneumonia.

††Measure of proximity (m) of assigned pens (Pens 1–8) to the NV400 Pen, Pen 9 (Figure 2).

†††Indicates average percent inhibition values per individual, defined as the quantification of an individual's immune response to active Movi infection, from the onset of active infection (earliest 15 March 2015) until the remainder of the study.

$$ll_{i,j,k} = log\left(\sum_{j=1}^{J} p_{i,j} \times exp\left(-\sum_{t=e_{i,k}}^{T} \lambda_{i,j,t}\right)\right),$$

where the first summation is over the *J* possible states that can be transitioned to from state *i*, and *T* is the day the study ended. To complete our model, we specified diffuse Uniform (−100, 100) priors on the intercept/base-line log hazard rate, and Normal (μ=0, σ^2=100) priors for all covariate parameters used in estimating the transition probabilities and the daily hazard rates. The posterior distribution is then proportional to the sum of the log of the prior distributions and the log likelihood.

Estimation—We employed JAGS (Plummer, 2003) in Program R (R Core Team, 2018) *via* the R2JAGS package (Su and Yajima, 2015) to estimate the posterior distributions of our parameters of interest using Markov Chain Monte Carlo (MCMC) methods. Because our likelihood is in a non-standard format, we used the "zeros trick" (Lunn et al., 2013) to permit its use in JAGS. We ran 3 chains for 100,000 repetitions, and removed the first 25,000 iterations for burn-in. Each chain was started with dispersed starting values, and graphical checks were used to monitor for evidence of non-convergence.

Results

Epizootic dynamics

We first observed pneumonia in lambs, followed by adults and eventually confirmed pneumonia-induced deaths in 6 of 9 pens in the study (Figure 1). These disease events were often associated with infection by Movi strains novel to the bighorn sheep within the affected pens (Supplementary Appendix C).

Timing of Pneumonia by Age Class, Pen, and Strain Type – In 2015, parturition occurred from 24 March to 21 June and all lambs died from pneumonia or other causes by early August (Supplementary Appendix C). The onset of clinical signs of pneumonia in lambs preceded the detection of pneumonia in adults. Over the course of the epizootic, two strains of Movi spread across pens to individuals previously exposed to different strains (i.e., cross-strain transmission, Figure 1).

Clinical signs of pneumonia were first detected in the Snowstorm lambs in pen 9 (Figure 1B) on 28 April 2015. The Snowstorm lamb deaths occurred from May through June 28 at a mean age of 43 days (range = 22–87 days; *n* = 7). Comparatively, births and onset of clinical signs in lambs were observed later in the other pens. In an adjacent pen (pen 7; Figure 1B), the first observation of clinical signs was 27 May 2015 and subsequent mean age at mortality was 38 days (range = 27–49; *n* = 2). The presence of the Snowstorms NV-400 strain type detected in the mortality samples for both pen 7 lambs was not expected based on the HC-404 strain carried by ewes present in pen 7 (Figure 1A) and represented the first genetic confirmation of cross-strain transmission. The final lamb in pen 7 died 14 July 2015 from a confirmed cross-strain infection, immediately prior to clinical detection of cross-strain infection in adults (Supplementary Appendix C).

Near the end of July 2015, we witnessed the unexpected mortality of two Snowstorm ewes (pen 9; Figure 1B). Cause of death was attributed to a severe acute pneumonia associated with infection by strain NV-400. Simultaneously, we noticed adults in pen 7, which were previously asymptomatic, exhibiting severe clinical indications of pneumonia immediately after the last lamb expired in that pen (Supplementary Appendix C). Subsequent to the index case of clinical pneumonia attributed to cross-strain infections in each pen, the median number of days for all adults in the pen to display signs of clinical disease was 15 days (range = 9–47 days). Median time between onset of symptoms and mortality$_p$ was 126 days (range = 45–489 days).

Clinical observations summary—Observation of clinical symptoms of respiratory disease was the basis of the morbidity and infection calculation used in our study. We detected 21 instances of transmissions of the NV-400 strain to sheep previously exposed to HC-404, BB-393/HC-404, and SD-398 and 4 transmissions of HC-404 to the uninfected sheep previously exposed to BB-393/HC-404 and SD-398. After 1 November 2015, Movi strains NV-400 and HC-404 were the only strains detected. We documented signs of respiratory disease in 95% (*n* = 35) of study animals; however only 68% of the individuals were documented as infected with a novel Movi strain. Thus, 27% of affected individuals were symptomatic and infected with their initial strain. Most (82%, 9/11) individuals entering the study with NV-400 (the Snowstorm bighorn sheep herd) showed clinical signs when only their initial strain was detectable. Cross-strain infections were detected from July to October 2015, and time to detection varied by pen assignment but generally moved from east to west, opposite of the prevailing winds, within the research facility (Figure 1).

Health sampling

Between February 2015 and December 2016 we collected 2–10 nasal swab samples from the 37 bighorn sheep in our study. The proportion of Movi-positive individuals detected within each month increased from 0.19 to 0.83 during the epizootic. We confirmed pneumonia as the cause of death in 43% (*n* = 16) of the bighorn sheep in the study. Other sources of mortality included darting complications (*n* = 2), birthing complications (*n* = 1), West Nile Virus (*n* = 1), liver hemorrhage (*n* = 1), flystrike (*n* = 1), gastric abscess (*n* = 1), euthanasia due to emaciation (*n* = 1), and injury (*n* = 1). Survival to the end of the study was 33%, of which half (*n* = 6) remained symptomatic and in the *I* state.

Environmental samples

During the epizootic, we detected Movi DNA in air, water, and invertebrate samples (Table 4). We detected aerosolized Movi DNA *via* PCR downwind of the target pen (directly outside of target pen: *n* = 9 detected ($CT \leq 35$), *n* = 2 indeterminate (CT = 35.01–39.9); between target pen and nearest occupied pen downwind from target pen: *n* = 1 detected, *n* = 4 indeterminate; and outside nearest occupied pen downwind from target pen: *n* = 1 detected, *n* = 2 indeterminate). We detected Movi DNA in 22 water, 5 invertebrate, and 1 permanent fly trap samples. We did not detect Movi DNA on the soil surface sampled *via* the gauze on our boots or in a bird nest constructed in an occupied pen's shelter ($CT \geq 40$; Table 4). Viable Movi, based on Movi growth in broth culture, were not detected in any environmental sample.

Disease state transition analyses

Right Censored Susceptible Adults-One chronic carrier ewe with HC-404 Movi from the Lostine herd (e.g., always positive by PCR; *n* = 8) failed to display clinical symptoms of pneumonia during our study and was right censored in the *S* state. A second ewe from the Snowstorm herd was neither documented carrying Movi nor did it display clinical symptoms and therefore, was right censored in the *S* state. All other adults in our study transitioned out of the *S* state as documented by clinical signs.

Transition from the Susceptible State to the Infected State-A high probability existed that a previously exposed bighorn sheep will become clinically infected when exposed to a novel Movi strain (Table 2). The probability of cross-strain infection was not influenced by previous strain type exposure, whereas pre-infection antibody level (%I_I defined as the Movi cELISA % inhibition value) had a significant negative (protective) effect on cross-strain transmission (median effect size = −10.19; 95% credible interval [CI] = −21.91 – −1.30; effect sizes of covariates on probabilities and daily hazards are presented on the logit and log scale, respectively; Table 2), with individuals having higher pre-existing %I_I values being less likely to become infected with a novel strain (Figure 3A).

The rate at which individual bighorn sheep became infected exhibited a bimodal distribution over time. Most individuals exhibited disease onset approximately day 200 (late July 2015) or 275 [early October 2015 (λ_2; Figure 4A)]. An individual's %I_I value did not affect the rate of becoming infected (Table 3). Proximity to the NV-400 pen/pen 9 (mean effect size = −0.32; SD = 0.20; 95% CI = −0.74 – 0.04) had a marginal effect on the infection hazard, with individuals penned closer to the NV-400 pen becoming infected sooner than individuals penned farther away; however, the effect was not statistically significant.

Transition from the Infected State to the Mortality$_p$ State–There was a large degree of uncertainty when estimating the long-term probability of bighorn sheep transitioning out of the infected state (Table 2). The effects of %I_I, initial Movi strain type exposure, and CST NV-400 did not have a significant effect on the probability of an infected bighorn transitioning to mortality$_p$ (Table 2). Nonetheless, individuals that mounted a higher antibody response to active symptomatic infection (%I_A, defined as the average Movi cELISA % inhibition values for all tests conducted while an individual was alive and had an active infection based on clinical signs) were significantly more likely to transition to pneumonia-induced mortality$_p$ (median effect size = 3.22; 95% CI = 0.59–7.36; Figure 3B).

Daily hazard rate of mortality$_p$ was relatively constant with most mortality events occurring by day 300 of our study (λ3;

TABLE 4 Prevalence of *Mycoplasma ovipneumoniae* detections in environmental samples collected to identify possible modes of cross pen transmission for bighorn sheep at the South Dakota State University Captive Wildlife Facility from 2015 to 2016.

Sample	*n*	Detected[1]	Indeterminate[2]	Not detected[3]
Air	191	0.08	0.05	0.87
Water	167	0.13	0.01	0.86
Fly tape	66	0.02	0.09	0.89
Fly trap	2	0.50	0.00	0.50
Avian nest	2	0.00	0.00	1.00
Boots	2	0.00	0.00	1.00

[1] Detected – samples where Movi was detected using PCR (cycle threshold [CT] ≤ 35.0; range = 29.4–35.0).

[2] Indeterminate – Movi I – samples in which PCR for Movi was indeterminate (CT = 35.01–39.9; range = 35.4–37.3).

[3] Not detected – samples where PCR failed to detect Movi (CT = 40).

Figure 4B). Mortality$_p$ hazard was not associated with %I$_I$ (median effect size = −0.10; SD = 0.42; 95% CI = −0.81–0.84; Table 3). In contrast, there was an effect for %I$_A$ (median effect size = 1.13; SD = 0.52; 95% CI = 0.19–2.23; Table 3) on mortality$_p$ hazard, with individuals with a larger %I$_A$ experiencing mortality$_p$ faster than individuals with a lower %I$_A$ (Figure 3B).

Transition from the Infected State to the Recovered State–Our model predicts the probability that an individual remains in the infected state is relatively high (Table 2). Probability of recovery was not affected by %I$_I$ (Table 2); however, the initial strain an individual was exposed to prior to the epizootic did influence recovery. The individuals exposed to the BB-393/HC-404 or the HC-404 strain had higher recovery probabilities compared with those exposed to NV-400 or the SD-398 strains (Figure 3C; Table 2). In addition, bighorn sheep with a larger %I$_A$ were less likely to recover from novel Movi strain infection (median = −2.27; 95% CI = −5.41–0.01; Figure 3B).

The effect of immune response may drive recovery hazards (λ_4), but with varying influences. If an individual were to recover, recovery occurred faster for bighorn sheep with increased prior immunity (%I$_I$; mean effect size = 1.18; SD = 0.59; 95% CI = 0.08–2.42; Figure 3A; Table 3) but slower for bighorn sheep experiencing a higher immune response during the active cross-strain infection (%I$_A$; mean effect size = −1.15; SD = 0.53; 95% CI = −2.31 – −0.19; Figure 3B; Table 3).

Transition from the Recovered State to the Infected State–Very few individuals experienced disease recurrence in our study (*n* = 3). Although our sample size is small, our model does not indicate differences in the probability of clinical disease recurrence based on initial Movi strain exposure histories (p_6; Table 2).

Discussion

Our findings support our hypothesis and conclusions from previous work that suggest that Movi strains vary in pathogenicity and that naturally acquired immunity in the bighorn sheep host is strain-specific (Justice-Allen et al., 2016; Cassirer et al., 2017). Previous exposures may influence survival following novel strain infection although in contrast to our hypothesis, even previous exposure to the outbreak strain did not provide complete protection. Immunity from previous exposure, as indexed by serologic antibody scores prior to the outbreak, did not prevent infection but was associated with resistance to outbreak-associated disease, and a faster rate of recovery in the rare cases in which it occurred. Counter to our hypothesis, however, higher immune responses during the outbreak corresponded to both increased probability and rate of pneumonia-induced mortality, and if it occurred, a slower rate of recovery; associations likely driven by disease progression and an inability to control infection.

Surprisingly, we observed that the most pathogenic, predominant strain in the study, which was detected in 81% of deaths, was associated with high mortality (45%) of sheep with previous exposure to and current infection with this strain. This result contrasts with observations of relatively low levels of sporadic pneumonia deaths of adults in chronically infected, free-ranging, bighorn sheep populations attributed to protective immunity (Cassirer et al., 2013; Plowright et al., 2013; Smith et al., 2015). Generally, immunity is developed during infection of a host, and acts to reduce pathogen establishment, survival, reproduction, or maturation (Wilson et al., 2002). Nevertheless, immune responses may also be non-protective, ranging from benign non-neutralizing responses that simply serve as a marker of antigenic exposures associated with infection to immunopathological responses associated with adverse reactions and increased disease severity (Hornef et al., 2002; Monack et al., 2004; Quinton and Mizgerd, 2015). An incomplete immunity in the host observed in this study might have been aggravated by simultaneous exposure to more than one strain, infectious dose, and undetected genetic variation in the pathogen.

Host immune response

Our findings indicate that adaptive immunity is an important factor driving individual heterogeneity in the response of bighorn sheep to disease. It is generally accepted that immune responses are genotype-specific, with previously unseen genotypes providing those pathogens with a growth advantage in semi-immune hosts (Simenka, 2005). Our finding reflects the complex notion that individual bighorn sheep with stronger immune responses following previous Movi exposure were less likely to exhibit disease symptoms and experienced shorter recovery times (Table 3; Figure 3). Only their initial strain or a strain that they

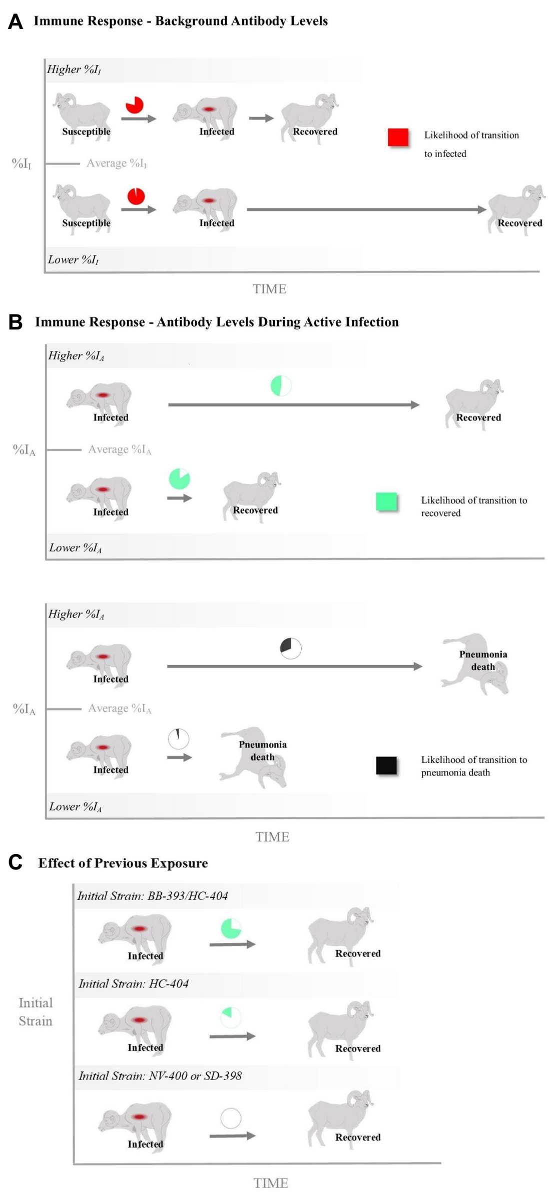

FIGURE 3
The relationship of bighorn sheep immune responses with infection and death as represented by the probability and rate of transitioning between disease states (i.e., susceptible, infected, recovered and disease-induced mortality). Shown are effects of antibody levels measured **(A)** prior to and **(B)** during a *Mycoplasma ovipneumoniae* (Movi) epizootic and **(C)** as a function of past exposure history. The $\%I_I$ effect is an individual's Movi cELISA percent inhibition (%I) value at the nearest sampling event prior to the epizootic. The $\%I_A$ effect is the averaged Movi cELISA % inhibition values for all tests conducted while an individual was alive and had an active infection based on clinical signs. The initial strain is the strain the individual was known to have been exposed to prior to the epizootic. Pie charts for $\%I_I$ and $\%I_A$ depict the mean probabilities above (*Higher*) or below (*Lower*) the mean covariate values. Times to transition are depicted as the relative difference in rates between 1 standard deviation above and below the mean covariate values.

had previously been exposed to in the wild (NV-400 or BB-393/HC-404, respectively) was detected in most (67%; $n=6$) of bighorn sheep that recovered. In contrast, only 13% ($n=3$) of bighorn sheep that experienced a novel cross-strain transmission event recovered in our study.

Pathogen strain type and competition

Some investigators have reported that simultaneous Movi infections with multiple strains in domestic hosts can result in more severe pneumonia (Parham et al., 2006; Rifatbegović et al., 2011). Our strain typing method was unable to detect more than one strain unless both strains were at similar concentrations in the sample and were amplified for sequencing at similar efficiency. We did not detect a cross-strain infection in any of the sheep in pens with current infection and with prior exposure to the predominant strain, although they were in close proximity to and downwind of the prevailing wind direction to the pens with other strain types. This outcome indicates that the predominant strain was more prolific and outcompeted other strains making it unlikely that we would detect co-infection with MLST. The question as to whether co-infection with a subdominant strain contributed to disease and mortality in this study is unclear.

While most mortality in this study was attributed to a single strain of Movi, any intrinsic reasons for this virulence could not be determined. The MLST strain-typing method used in our study has been widely applied in epidemiologic and evolutionary studies. Kamath et al. (2019) validated the strengths of employing this method to describe Movi strain diversity and bighorn sheep spillover events from 1984 to 2017 throughout the western United States. The MLST, however, characterizes approximately 0.15% of the genome (Cassirer et al., 2017) and provides no information about variation in presence or expression of specific virulence genes. Therefore, our strain-typing method fails to distinguish within-strain variants that may differ in virulence or neutralizing surface epitopes. Consequently, another possible explanation for unexpected lack of protection of prior exposure to a strain is that a new, undetected, variant developed during the outbreak. The likelihood and effect of multiple simultaneous Movi strain infections and antigenic or other variation within strains in this host is unknown and warrants investigation.

Modes of transmission

We detected instances of Movi transmission based on invasion of new strain types across distances of up to 30 m from infected bighorn sheep. In spite of careful planning and consideration of prevailing winds, we hypothesize that spread occurred through aerosolized droplets produced by symptomatic bighorn sheep in adjacent pens. Closely related *Mycoplasma* spp. infectious agents have been recognized as viable and transmissible through aerosolization. *Mycoplasma hyopneumoniae*, which causes atypical pneumoniae in swine (Stärk et al., 1998; Desrosiers, 2011), has been documented to be transmissible *via* aerosol droplets 9.2 km from the infected source pen (Otake et al., 2010). In addition, *M. bovis*, the primary agent in cattle pneumonia epizootics, and *M. synoviae* and *M. gallisepticum*, which cause acute or chronic respiratory disease in poultry, respectively, can infect livestock by

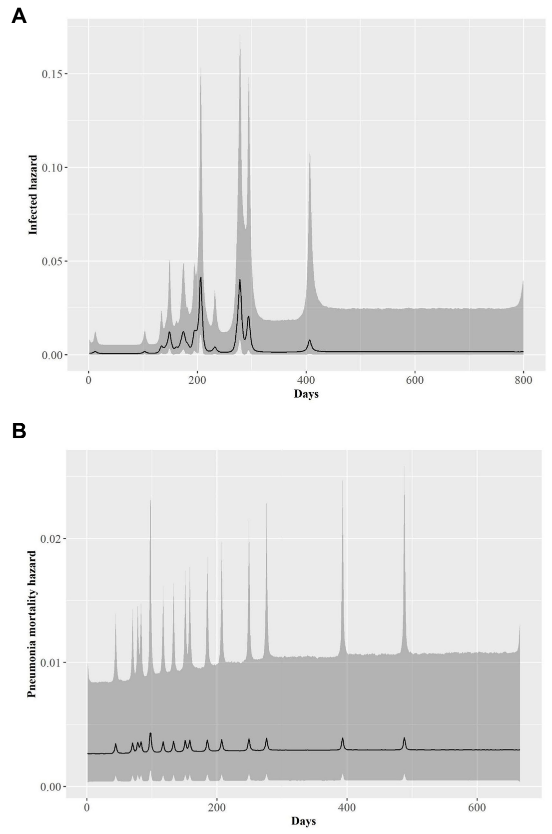

FIGURE 4
Time series of the estimated posterior distributions on the log scale of daily hazard rates (black line) for bighorn sheep **(A)** transitioning from being healthy to infected by pneumonia and **(B)** dying of pneumonia-related causes from 1 January 2015 to 1 April 2017. Gray shading is associated the 95% credible envelopes.

airborne pathogen transmissions (Landman et al., 2010; Kanci et al., 2017). Furthermore, secondary *Pasteurellaceae* agents are transmissible through aersolization up to 18 m (Dixon et al., 2002) as well as by fomite contamination (Burriel, 1997; Clifford et al., 2009).

We detected Movi DNA in aerosol, fly, and water samples although we were unable to culture viable organisms from any samples that were cultured. This is likely due, at least in part, to the fastidious nature and rapid death of Movi outside the host and we might have been more successful if we had immediately inoculated aerosolized droplets into culture broth. Besser et al. (2014) reported Movi transmission within and between pens up to 12 m distant. Although average wind direction was generally opposite to pen-to-pen transmissions (Supplementary Appendix C), wind direction frequently varied and wind speeds of >60 km/h were common; wind gusts >100 km/h that occurred in late June and early August may have facilitated rapid movement of droplets containing viable bacteria across the facility (Figure 1). We detected aerosolized Movi DNA at the boundary of the nearest downwind pen at the maximum range tested (30 m) from infected bighorn sheep.

Our study is the first to document flies (*Musca* spp.) as a possible vector of transmission for Movi in bighorn sheep infections. Some fly species feed on nasal and oral discharge and have been implicated in the rapid spread of similar agents, including *M. conjunctivae*, which causes infectious keratoconjunctivitis in wild and domestic Caprinae (Degiorgis et al., 1999; Giacometti et al., 2002; Fernández Aguilar et al., 2019). Permanent fly traps were secured to the roof of shelters where symptomatic bighorn sheep spent a considerable amount of time, particularly as disease progressed. The positive Movi detection of the permanent fly trap could be the result of airborne particles expelled during coughing. Nonetheless, the Movi-positive fly tape was a direct sample of flies and offers strong evidence as a possible route of transmission in captive studies. Nonetheless, the strain-type that was identified directly from flies (SD-398) was never detected in bighorn sheep carriage in that pen (i.e., pen 1). Pens 4 and 6, which were approximately 35 m and 115 m away, were the pens containing bighorn sheep with the previously detected SD-398 strain. Additional investigations aimed at detecting transmissible and viable Movi from flies that feed on oronasal secretions are necessary to better understand the effect of vector-borne Movi transmission in bighorn sheep epizootics.

Study limitations

We did not intend to evaluate bighorn sheep responses to novel Movi strain invasions, and we purposefully designed the pens to prevent this from happening. Because we were not prepared for the outbreak, our data are largely limited to observation of clinical signs. Close observation of clinical signs in habituated animals or animals in captive facilities, however, has been used to classify health status and pathogen transmission in previous studies (Lonsdorf et al., 2018; Sandel et al., 2021), and when capture and testing were feasible our disease state classifications based on observations concurred with 94% of all PCR and serological analyses. Another weakness of the opportunistic nature of the study is that the first adult infections may have pre-dated the start of our intensive monitoring of clinical signs on 15 July. Therefore, duration of infection may have been longer than we assumed in the model.

Secondly, we could not directly measure dose effects. Pen 9 contained the most adults (11) of which 7 gave birth to lambs that subsequently became infected and developed respiratory disease, whereas other pens contained from 2 to 4 adults and 0–3 infected lambs. Therefore, pen 9 had the highest disease burden and adults in pen 9 were likely exposed to the highest cumulative doses of Movi from each other and from their offspring. We attempted to account for dose effects using an index, the distance to pen 9 (Figure 1), the index pen. We did not document a significant effect of this index on the rate at which individuals became infected (Table 3); however, we were not able to completely disentangle the effect of distance and strain exposure histories. Thus, a better understanding is needed of how dose might overcome immunity obtained from prior exposure and influence response to infection and conversely, whether reducing dose could decrease virulence.

Lastly, our measure of immune response to Movi is a cELISA test, which detects antibodies based on their ability to inhibit binding of a Movi-specific monoclonal antibody to Movi antigen *in vitro*. The monoclonal antibody used in the assay was selected on the basis of immunodominance of its epitope across multiple bighorn sheep populations infected by diverse Movi strains, but this epitope has not been shown to be involved in protective immunity. As a result, immune responses as measured by percent inhibition (%I) should be considered to primarily reflect the intensity of current or past Movi exposure but not the effectiveness of the immune response. Both beneficial and adverse effects of immune responses to Movi infection are plausible: while immune responses may be associated with decreased pathogen carriage (Niang et al., 1998; Plowright et al., 2013), strong humoral immune responses may induce autoimmune responses in domestic sheep and have been hypothesized in wild sheep (Niang et al., 1998; Cassirer et al., 2018). Lacking a better understanding of the interactions between the host's immune system and Movi virulence factors, the cELISA may fail to distinguish protective from ineffective or harmful immune responses, complicating interpretation of immunity in the study.

Conclusion

Despite limitations associated with an unplanned outbreak, this study provided the rare opportunity to examine the effect of exposure history on individual response of animals from multiple free-ranging populations to a pathogen with high genetic diversity. The results offer insight into patterns of repeated respiratory disease outbreaks observed in various bighorn sheep populations, demonstrating cross-strain infections may produce similar morbidity and mortality patterns as initial exposure of naïve bighorn sheep populations to Movi. Additionally, some Movi strains appear to cause more disease and outcompete others. Therefore, in free-ranging herds past exposure is likely insufficient to protect bighorn sheep from infection by new Movi strains, although it may influence the progression of disease and recovery within the herd.

This study illustrates the complexity of interactions and outcomes arising from the host-pathogen evolutionary arms race and underscores the need for ecologists, when investigating wildlife systems where pathogens are directly affecting conservation efforts, to account for dynamic evolutionary processes that give rise to heterogeneity in individual responses because they ultimately determine the negative effects of disease on a population. Finally, our findings emphasize that although exposure history might influence the progression of disease and recovery, bighorn sheep conservation would benefit from focusing on preventing pathogen introduction; reliance on past exposure and bighorn sheep adaptive immunological defenses to protect populations from pathogen invasion is unlikely to protect the health of the herd. Therefore, maintaining separation of domestic and bighorn sheep and avoiding management efforts that commingle bighorn sheep with differing Movi strains (e.g., translocations) will likely be the most effective management strategy for minimizing respiratory disease effects to bighorn sheep herds and achieving conservation goals.

Data availability statement

Data and code collected and used in this study is available at: https://doi.org/10.5066/P9Q69IAL.

Ethics statement

The animal study was reviewed and approved by South Dakota State University Institutional Animal Care and Use Committee. Written informed consent was obtained from the owners for the participation of their animals in this study.

Author contributions

DW provided funding, statistical support, and contributed to manuscript development. FC provided experimental animals and contributed to manuscript development. TB provided laboratory support and contributed to manuscript development. JJ provided funding, support for animal care and handling, and contributed to manuscript development. BF led animal care and handling, led data collection, assisted with analysis and contributed to manuscript development. All authors contributed to the article and approved the submitted version.

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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.

Publisher's note

Supplementary material

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Both temporal and spatial aspects of predator management influence survival of a temperate ungulate through early life

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Recent meta-analyses indicate that predator removal experiments result in marginal increases in prey abundance at best. However, most predator removal studies take place for less than the target prey's generation time and lack a targeted spatial approach. Our objective was to determine how temporal and spatial aspects of predator control influenced neonate survival of a temperate ungulate. We conducted multiyear coyote (*Canis latrans*) removals using a crossover experimental design. We found that consecutive years of predator removal increased survival of neonate mule deer (*Odocoileus hemionus*) more than a single year of removal. We also found that removing coyotes from areas near fawn birth sites increased fawn survival, whereas removing coyotes from areas farther from birth sites did not influence fawn survival. Our results underscore the need for coyote removal programs to (1) employ removal efforts over consecutive years to maximize effectiveness, (2) conduct spatially explicit removal efforts targeting fawning habitat, and (3) occur when the likelihood of additive mortality is high and prey populations have the resources available to grow.

KEYWORDS

mule deer, *Odocoileus hemionus*, predation, predator control, neonate survival, coyote, *Canis latrans*

Introduction

Intentionally removing predators from an ecosystem for the purpose of increasing prey populations is a common wildlife management strategy (Connolly, 1978; Salo et al., 2010; Peek et al., 2012). However, a growing number of studies question whether such predator removals are effective (Bergstrom, 2017). Given that predator removal efforts continue in many regions throughout the world, it is important to capitalize on ongoing removal programs by experimentally testing their efficacy and providing stakeholders with data needed to make informed management decisions (Bergstrom, 2017). A recent meta-analysis, for example, found that experimental predator removals only resulted in modest increases in prey abundance and/or survival at best, but that most studies lacked rigor in experimental design (Clark and Hebblewhite, 2021). Importantly, just six of the 52 experiments were conducted over a period of time that exceeded the target prey's generation time (Clark and Hebblewhite, 2021). This mismatch is problematic because such removal schedules may not be long enough or in the locations needed to generate observable effects on prey survival (Connell and Sousa, 1983).

It is likely that both temporal and spatial aspects of predator removal influence response of prey. Temporal aspects can include both time of year and single vs. multiple years of predator control. An observed increase in survival over multiple years could result from (1) an absolute decrease in the total number of predation events in a given year or (2) a decrease in the proportion of animals taken due to increases in population size in subsequent years of predator removal. Both of these scenarios result in the desired outcome of increasing survival in prey populations. In either case, it is likely that time of year when predators are removed will affect likelihood of success. For example, predator removal during late winter may increase likelihood of increased prey survival because that timing disrupts social structure of predators during the time of pair bonding or reproduction and occurs just prior to birthing of prey species (Blejwas et al., 2002). Nonetheless, some predator species refill home ranges vacated by removed predators quickly. For example, under intense coyote (*Canis latrans*) removal programs, coyotes have been reported to repopulate areas within months to a short number of years (Beasom, 1974; Connolly and Longhurst, 1975; Connolly, 1995), although there are examples where coyotes do not rapidly recolonize (Mahoney, 2017). Because predators can exhibit compensatory natality and increased survival following reductions in density (Knowlton, 1972; Knowlton et al., 1999), it is likely that removal at the most important time of year and across multiple consecutive years has the greatest likelihood of a resulting increase in survival of prey.

Predation rates on domestic livestock have been correlated with density of coyotes on the landscape (Stoddart et al., 2001) leading to predator control programs that are often non-selective and broad in spatial scale (Mitchell et al., 2004). However, wild ungulates do not live and reproduce evenly or randomly across the landscape. Therefore, predator control programs focused on habitat where prey are most vulnerable have the greatest likelihood of success. Further, survival of prey should increase even if predators backfill the vacated space over several months to a few years since individuals that disperse or backfill tend to be young individuals that are less likely to take large prey items compared to resident adults (Harrison, 1992; Watine and Giuliano, 2017). Coyotes have the greatest effect on mule deer (*Odocoileus hemionus*) during the first few months of life when mule deer are small and unable to escape or during late winter when some individuals have exhausted energy reserves (Bowyer, 1987; Lingle, 2000). Mule deer susceptible to coyotes in late winter are likely individuals with severely depleted energy reserves (often associated with old age). Therefore, this source of mortality is more likely to be compensatory or have little effect on population growth. Consequently, coyote control programs focused on birthing and early-life rearing habitat have the greatest likelihood of benefiting mule deer by decreasing mortality that is more likely to be additive. Indeed, numerous studies indicate that coyote predation is a common source of mortality for mule deer fawns (Bartmann et al., 1992; Whittaker and Lindzey, 1999; Pojar and Bowden, 2004; Bishop et al., 2009). However, in perhaps the largest coyote removal experiment, mule deer fawn survival increased when coyotes were removed, but increases were modest and only evident when alternate prey (i.e., lagomorph) populations were low (Hurley et al., 2011). While the study by Hurley et al. (2011) employed a robust experimental design over six consecutive years, the number of coyotes removed varied drastically from year to year, ranging from a mean of 31.15–79.96 coyotes per 1,000 km^2 and occurred in a traditional manner over a broad spatial scale. This high variability in the number of coyotes removed combined with the broad spatial scale (i.e., non-targeted) leaves questions about the effectiveness of coyote removal during this early life stage of mule deer.

Mule deer have high cultural and economic value as a primary big game ungulate in western North America but have recently experienced fluctuations in population size (Bleich and Taylor, 1998; Unsworth et al., 1999; Peek et al., 2002; Bergman et al., 2015). As in other ungulate species (Gaillard et al., 1998), low fawn survival and subsequent low recruitment may drive fluctuations in mule deer populations (Peek et al., 2002; Lomas and Bender, 2007). In this study, we explicitly tested the effect of two consecutive years vs. a single year of coyote removal on survival of mule deer fawns in Utah, United States. Further, we attempted to examine the effectiveness of spatially explicit removal (i.e., removal from birthing and rearing habitat). Therefore, the objective of our study was to determine the effect of coyote removal on fawn survival using (1) a crossover experimental design in two comparably sized locales, (2) two consecutive years of control and treatment conditions in both locales, and (3) relatively consistent numbers of coyotes removed across years. Further, we examined the relationship between location of removal relative to birthing habitat and the likelihood of fawn survival. We hypothesized that both spatial and temporal aspects of predator removal would influence survival of neonate mule deer. We predicted that multiple years of predator removal would increase survival of mule deer fawns because reproduction by coyotes would be disrupted, densities would be further reduced, and the recovery of coyotes to pre-control levels would be prolonged. In addition, we predicted that control efforts in birthing habitat would be more effective at reducing fawn mortality than control efforts at a broad spatial scale. Importantly, our research site experienced normal climatic patterns (no extremely harsh winters or dry summers) during the years of the study, which enabled the examination of predation effects that were not confounded by severe weather.

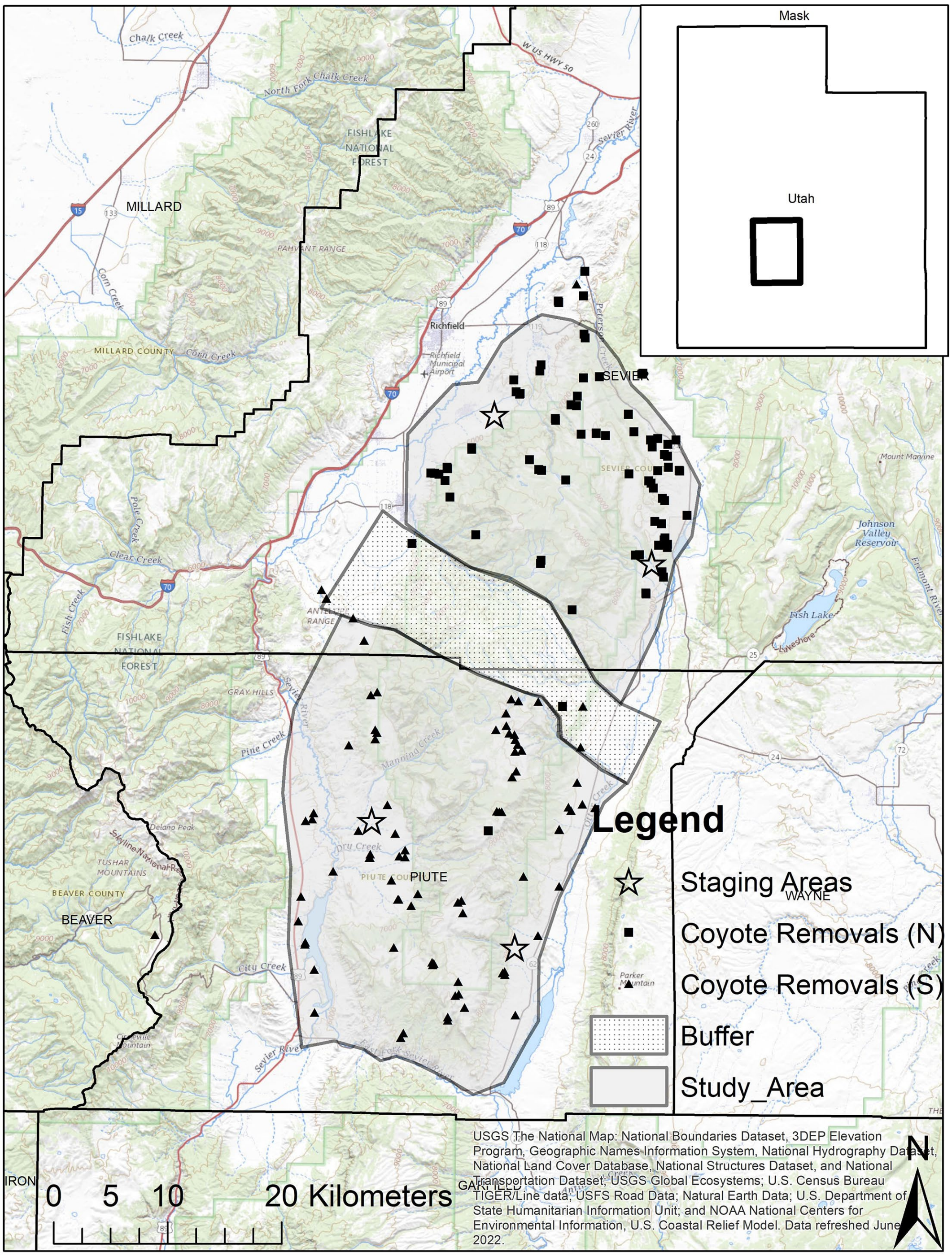
Materials and methods

Study area

Our study areas were located on Monroe Mountain in south-central Utah. Monroe Mountain is approximately 70 km long (north to south) and 20 km across. Several thousand mule deer inhabit the mountain and surrounding winter range. Land ownership is split between federal agencies (Forest Service and Bureau of Land Management), state lands, and private lands. The mountain was divided into two study areas and a buffer zone (south study area, north study area, and a central buffer; Figure 1). The buffer area was an east to west corridor that separated the north study area from the south study area. This buffer was 5 to 10 km wide and was delineated by large canyons on the north and south where it bordered the study areas (an effort to ensure independence of the treatments). Habitat types on the mountain include areas dominated by big sagebrush (*Artemesia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), Gambel oak (*Quercus gambelii*), aspen (*Populus tremuloides*), pinion pine (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*). Potential predators of mule deer inhabiting this area were coyotes (*Canis latrans*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*), although black bears are uncommon.

Experimental design

We determined the effects of predator removal on survival of neonate mule deer (birth to 4 months of age) during 2012–2015. To evaluate the effects of predator removal, we implemented an experimental crossover design. During 2012–2013 (first 2 years of the



USGS The National Map: National Boundaries Dataset, 3DEP Elevation Program, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; USGS Global Ecosystems; U.S. Census Bureau TIGER/Line data; USFS Road Data; Natural Earth Data; U.S. Department of State Humanitarian Information Unit; and NOAA National Centers for Environmental Information, U.S. Coastal Relief Model. Data refreshed June, 2022.

FIGURE 1
Map of Monroe Mountain, Utah, United States with polygons delineating north (coyote removal area 2012–2013) and south (coyote removal area 2014–2015) study areas where we evaluated survival of neonate mule deer. The stippled area indicates the buffer zone between the two study areas and was bordered on the north and south by deep canyons that traversed the mountain. Squares and triangles indicate the location of coyotes that were removed from the mountain during 2012–2013 and 2014–2015, respectively. Stars represent the centroid of areas on winter range where adult females were captured each March of the study.

study), USDA Wildlife Services used standard techniques, including aerial gunning, to remove coyotes from the north study area, but not from the south study area. In 2014, treatments were switched; coyote removal occurred on the south study area, but not the north study area for the final 2 years. Similar numbers of coyotes were removed from both the north and south study areas during the first 2 years and last 2 years of the study (Mahoney, 2017).

For coyote removals, Wildlife Services focused on high elevation habitat where birthing was more likely to occur. However, removals were influenced by snow and other weather conditions (e.g., wind and cloud cover) and, therefore, there was spatial variation in the locations of removals. All removal flights were performed within 3 days of a snow event. Wildlife Services would systematically fly the entire study area. Once a coyote track was located, they would follow that track to locate the animal and attempt to remove that animal. Once removed, they would record a GPS location of the removal and return to the original path to continue the search effort. With the GPS location of each removed animal, we were able to examine the spatial effects of coyote removal on the survival of neonate mule deer as describe below.

To determine survival of neonate mule deer, we captured neonates on each study area during each year. To aid in the capture of neonate mule deer, we captured adult female mule deer (*via* helicopter net-gunning) in March of each year from four locations on winter range of the study areas (Angle, Burrville, Thompson Basin, and Elbow Ranch; Figure 1). We assessed body size (weight, hind foot length, chest and neck girth), condition (body condition score method; Cook et al., 2007), and age (estimated based on tooth wear and eruption pattern) of each captured individual (Severinghaus, 1949; Robinette et al., 1957). Additionally, we determined body condition and pregnancy *via* ultrasonography (E.I. Medical Imaging portable ultrasound; Smith and Lindzey, 1982). We fitted pregnant females with VHF collars [Telonics Inc., Advanced Telemetry Systems (ATS)] and vaginal implant transmitters (VIT; ATS). We used a vaginoscope to insert VITs until the antennae did not protrude from the opening of the vagina (Bishop et al., 2009).

Between the original capture of adult females and parturition, we located collared females using radio telemetry. During March and April, individuals were located sporadically from the ground and a fixed-wing aircraft. Beginning in May, we attempted to locate every female twice a week. Beginning the last week of May, we located each female at least every other day until all VITs had been expelled. When an expelled VIT was detected (pulse rate doubled after a reduction in temperature), we located the VIT and conducted an extensive search for the neonate(s). In addition, we opportunistically captured neonate mule deer while searching for those associated with a VIT or while observing female mule deer not previously captured.

To determine survival of neonate mule deer, we attached VHF radio collars to captured individuals. We handled neonates with latex gloves while we fitted collars, and we recorded morphological measurements. Additionally, we estimated the age of individuals using hoof condition/length, pelage, and behavior (Lomas and Bender, 2007). Radio collars placed on neonates were designed to expand with the growing animal and drop off after approximately 8 months.

We monitored collared neonate mule deer on a schedule designed to ensure that mortalities were located promptly. Early detection of mortalities minimized the likelihood of confusion between the true cause of mortality and scavenging. Specifically, we relocated neonates at least 3 times weekly between the time of initial capture and the end of August. We decreased monitoring frequency to once a week beginning in September because most mortality of neonate mule deer occurs in the first few months of life (Pojar and Bowden, 2004; Lomas and Bender, 2007).

We attempted to locate deceased animals whenever a transmitter was in mortality mode, which was reflected by a doubling of the pulse rate of the collar after 8 h of no movement. After locating a collar, we searched for the deceased neonate mule deer and determined a probable cause of death based on evidence found at that location. If the probable cause of death was attributed to predation, we used a suite of indicators that are predator specific to determine what species of predator was most likely responsible for the mortality (Gese and Grothe, 1995). In a few cases, assignment of the predator responsible for death was ambiguous (e.g., most of the carcass was consumed and there was sign from multiple species of predators) and, therefore, we classified these mortalities as unknown predation. Other cause-of-death categories included starvation, accidents (e.g., vehicle strikes, fences, etc.), disease, and unknown.

Statistical analyses

We used multi-model inference within Program MARK and a known-fate model (White and Burnham, 1999) to estimate survival of neonate mule deer in both treatments (removal and non-removal), and to investigate factors potentially influencing survival. Preliminary analysis revealed that coyotes have the greatest impact on survival of neonate mule deer during the first 16 weeks of life and, therefore, we modeled survival during the first 16 weeks of life in our subsequent analyses. Rather than use a staggered entry into the model when an animal was born, we set week one for each mule deer neonate to begin at birth, regardless of calendar date (Bishop et al., 2008). We used a hierarchical approach to draw inferences regarding *a priori* hypotheses about potential influences on survival rates (Burnham and Anderson, 1998). We first tested for temporal effects by comparing models where survival varied linearly through time (T), quadratically through time (T^2), by week (Week), and by year (Year); we also tested models that used interactions of these time components. We advanced models to the next step based on Akaike's Information Criterion adjusted for small sample sizes (AICc) if they had at least 5% AICc weight ω_i.

In our second step, we tested the influence of removal of coyotes by adding variables to models that advanced from our first step. Covariates related to removal of coyotes included study area (north or south; StdArea), treatment (Treatment), year of treatment (YrofTrtmt), number of coyotes removed within 2,250 meters (the average summer home range diameter of mule deer; Webb et al., 2013) surrounding the capture location of each neonate (HRCKills), and lagomorph abundance [LagAbund (a measure of alternate prey for coyotes)]. We obtained estimates of lagomorph abundance from a concurrent study of predators on the study site (Mahoney, 2017).

In our final step, we added various individual characteristics of neonate mule deer as covariates. These characteristics included sex of each individual (Sex), new hoof growth (NewGrowth), whether or not the neonate was a twin (Twin), and weight (Weight). We included neonate mule deer age at capture in all our models that included weight to account for the effects of age-related weight gain.

Fate of siblings is not completely independent and, therefore, using siblings as independent observations can lead to over-dispersion in known-fate models. To account for potential dependence among the fate of siblings, we estimated $\hat{c}$ (degree of overdispersion) by bootstrapping our data using methods described by Bishop et al. (2008). We then ranked final models based on Quasi-AICc values (QAICc) adjusted for $\hat{c}$. We checked models in our final list for uninformative parameters and then produced model-averaged estimates of β coefficients and survival (Arnold, 2010). We judged the importance of variables in top models based on overlap in 85% confidence intervals around these β estimates (Arnold, 2010).

To further visualize the relationship between survival of neonates and years of predator removal, we used a Kaplan–Meier function to produce survival curves for neonates (Kaplan and Meier, 1958; Jager et al., 2008). We grouped individual neonates into the following three groups: no coyote removal (0), 1 year of removal (1), and 2 years of removal (2). We then plotted these survival curves with time on the x-axis and survival on the y-axis.

Results

During 2012–2015 we captured 287 adult female mule deer from winter-range locations surrounding Monroe Mountain (Table 1). Range of percent ingesta-free body fat (IFBF) was 2.9%–12.1% and was normally distributed around the mean. Of the 287 females captured, 95% ($n = 273$) were pregnant. Vaginal Implant Transmitters were inserted into 260 of these 273 pregnant females; 13 females were not used because they were recaptured and known to summer outside the two study areas ($n = 5$), their vaginas were too small for VIT insertion ($n = 5$), or they experienced capture-related injury ($n = 3$). Of the 260 animals that received VITs, 146 moved onto one of our study areas on Monroe Mountain. The remaining females either died before parturition or transitioned onto summer range outside the study areas and could not be included in the study (Table 1).

During late winter and early spring 2012–2015, Wildlife Services removed a total of 166 coyotes. These removals included 47, 34, 38, and 47 in 2012, 2013, 2014, and 2015, respectively. In 2012 and 2013, coyote removal efforts were on the north study area whereas removal efforts focused on the south study area in 2014 and 2015 (Figure 1). Ten coyotes were removed from the buffer area or from outside the study area. Each of these animals had at least part of their home range within the study area as all tracking events to locate a coyote were initiated within the removal study area.

Searches for neonate mule deer associated with expulsion of VITs began on 29 May, when the first VIT was expelled, and continued through early July. Based on expulsion of VITs, we obtained dates of parturition for 140 of the 146 females that remained in the study area during parturition. Five females died prior to parturition, and one female that received a VIT never gave birth. Mean dates of parturition were June 13th, 16th, 15th, and 14th for 2012–2015, respectively. Using VITs and opportunistic searching, we captured 266 neonate mule deer, including 71 sets of twins, between the two study areas. We excluded six neonates from our sample because they were stillborn ($n = 2$) or their deaths were human-caused (poaching, vehicle strike; $n = 4$); consequently, 260 neonates were used in final analyses.

TABLE 1 The distribution of female mule deer captured from four regions of wintering range around Monroe Mountain, Utah during 2012–2015, including the number of captured animals that migrated to a different summer range and those with VITs that moved onto Monroe Mountain.

	Capture location			
	Thompson	Burrville	Angle	Elbow
Females inserted w/ VITs	62	53	101	44
Females migrating	29	16	53	10
Females in Buffer	0	2	0	2
VIT females remaining*	32	30(+5)*	47(−5)	32
Fawns Captured from VITs	29	25(+2)	52(−2)	26

Numbers in parentheses are deer that migrated from Angle to Burrville (between study areas) during winter. *This number includes only those females that moved onto one of the Monroe Mountain study areas. One female captured at Burrville never gave birth.

We attributed mortality of neonate mule deer to predation, starvation, disease, stillbirth, roadkill, and unknown (Table 2). Predation was the leading cause of mortality accounting for approximately 68% of all mortalities. Coyotes killed 16% of all collared neonates on the north study area and 13% of all neonates monitored on the south study area. Approximately 90% of coyote-related mortality occurred during the first 16 weeks of life for neonates.

Survival of neonate mule deer to 16 weeks averaged 65% across all years. Sex and weight were influential variables in our models (Table 3). Females had a higher likelihood of survival than males. Additionally, survival of neonate mule deer increased as weight increased. None of our models contained uninformative parameters (Arnold, 2010).

Number of consecutive years of treatment (YrofTrtmt) was a prominent variable in our known-fate analyses, appearing in 8 of the top 10 models (Table 3). Likelihood of survival to 16 weeks of age for fawns in a treatment area with no coyote removal was 57.6% ± 5.1% (±SE). In contrast, likelihood of survival to 16 weeks of age increased to 65.4% ± 7.9% and 72.8% ± 5.1% with one and two consecutive years of coyote removal, respectively. Survival curves from a Kaplan–Meier function illustrated the pattern of survival relative to year of treatment (Figure 2).

The location of coyote removal relative to birth sites (HRCKills) appeared in 6 of the top 10 models which accounted for 40% QAICc weight. The support for HRCKills in our models indicated that proximity of coyote removal to fawning locations positively influenced the likelihood of survival of neonate mule deer (Table 3). The probability of a neonate mule deer surviving to 16 weeks increased with increasing numbers of coyotes removed in a deer home range surrounding birth locations (Figure 3).

Discussion

Removing coyotes had a positive effect on survival of neonate mule deer to 16 weeks of age regardless of the density of alternate prey. Importantly, subsequent years of coyote control in the same area had a greater effect than a single year of control (Figure 2). This result is consistent with a study on pronghorn (*Antilocapra americana*) that highlighted the need for multi-year coyote removal to increase fawn survival (Smith et al., 1986). Even under intense coyote removal programs, coyotes have been reported to repopulate areas within months or a short number of years (Beasom, 1974; Connolly and Longhurst, 1975; Connolly, 1995). Additionally, some coyote populations have returned to pre-treatment levels through recolonization, compensatory breeding, and increased survival rates following coyote removal (Knowlton, 1972; Knowlton et al., 1999). Our findings underscore the need for consecutive annual removal efforts, with consistent removal among years, to have positive effects on survival of mule deer fawns.

Removing coyotes near birth sites of fawns increased fawn survival, whereas removing coyotes from areas distant from birth sites did not influence survival of neonates. Coyote removal is often conducted during winter months because coyotes leave tracks in the snow that managers can use to locate and remove them. Since coyotes generally use the same areas in winter as they do in summer on Monroe Mountain (Mahoney, 2017), removing coyotes from potential fawning habitat in winter would likely benefit neonate mule deer the following summer. Our results support this prediction. This finding is notable because many coyote removal studies do not consider proximity to prey birth

TABLE 2 The distribution and probable causes of mortality of neonate mule deer that were captured on Monroe Mountain, Utah during 2012–2015.

	2012 fawns per study area		2013 fawns per study area		2014 fawns per study area		2015 fawns per study area	
	Removal	Non-removal	Removal	Non-removal	Removal	Non-removal	Removal	Non-removal
Total captured	34	27	35	32	39	33	36	32
Still births	0	2	0	0	0	0	0	0
Predation mortalities	5	9	4	13	16	7	11	4
Coyote	5	6	0	4	7	4	5	2
Cougar	0	2	2	3	8	3	6	2
Unknown	0	1	2	6	1	0	0	0
Road kill mortalities	1	0	0	0	0	1	0	0
Disease/ deformity	2	0	0	1	1	0	1	0
Starvation	3	2	0	2	0	0	1	0
Unknown mortality	3	2	2	3	5	6	4	4

During 2012 and 2013, coyotes were removed from the north study area and no removal occurred on the south study area. During 2014 and 2015, removal occurred on the south study area and no removal occurred on the north study area.

TABLE 3 Model selections results for survival of neonate mule deer through 16 weeks of age on Monroe Mountain, Utah during 2012–2015.

Model	QAICc	Δ QAICc	AICc ω_i	K	QDeviance
{S(T + StdArea + YrofTrtmt + Sex + Weight + Age)}	679.6116	0	0.1512	7	665.5771
{S(T + StdArea + HRCKills + StdArea × HRCKills + YrofTrtmt + Sex + Weight + Age)}	679.9357	0.3241	0.12858	9	661.8803
{S(T + StdArea + YrofTrtmt + Weight + Age)}	680.9298	1.3182	0.07822	6	668.904
{S(T + StdArea + HRCKills + StdArea × HRCKills + YrofTrtmt + Weight + Age)}	681.2247	1.6131	0.0675	8	665.1804
{S(T + Side + HRCKills + StdArea × HRCKills + Sex + Weight + Age)}	681.2311	1.6195	0.06728	8	665.1869
{S(T + StdArea + YrofTrtmt + Sex)}	681.6154	2.0038	0.05552	5	671.597
{S(T + StdArea + YrofTrtmt)}	681.8101	2.1985	0.05037	4	673.7978
{S(T + StdArea + HRCKills + StdArea × HRCKills + Weight + Age)}	681.8181	2.2065	0.05017	7	667.7837
{S(T + StdArea + HRCKills + StdArea × HRCKills + YrofTrtmt + Sex)}	682.0013	2.3897	0.04578	7	667.9669
{S(T + StdArea + HRCKills + StdArea × HRCKills + YrofTrtmt)}	682.0491	2.4375	0.0447	6	670.0233

Variables in our top models include linear time trend (T), study area (north or south; StdArea), year of coyote removal treatment (YrofTrtmt), number of coyotes removed within a deer home range relative to fawn birth sites (HRCKills), sex (Sex), weight at capture (Weight), and age at capture (Age).

sites when removing coyotes, which may explain the equivocal impacts on fawn survival that have been reported, if some studies removed coyotes far away from prey birth sites. Our results underscore the need for coyote removal programs to target coyotes near fawning habitat in order to be effective, whereas removal programs targeting coyotes distant from fawning habitat likely have no effect on prey populations.

Predation was the leading cause of mortality of neonate mule deer accounting for at least 68% of all mortalities. It is likely this estimate, however, is low and underestimates the actual effects of predators. For example, it is probable that at least some of the cases we assigned to starvation were due to the mother being killed by a predator resulting in the subsequent starvation of the neonate. In fact, we had multiple instances where we were able to determine this was the case by locating the deceased collared mother of the neonate mule deer that had starved. However, we do not know the full extent of this type of mortality because many of our collared neonates were opportunistically captured from unmarked adults. If populations are not limited by resources or there is capacity for the landscape to support a larger population, it is likely that reducing predation, the leading cause of mortality, will lead to an increase in population size.

The availability of alternative prey did not appear in any of our top models suggesting that alternative food was not a driving factor in the patterns of predation on mule deer that we observed. This finding is inconsistent with previous research demonstrating that alternative prey can influence the rate of predation on neonate mule deer (Hamlin et al., 1984). However, Sacks and Neale (2002) demonstrated that small prey

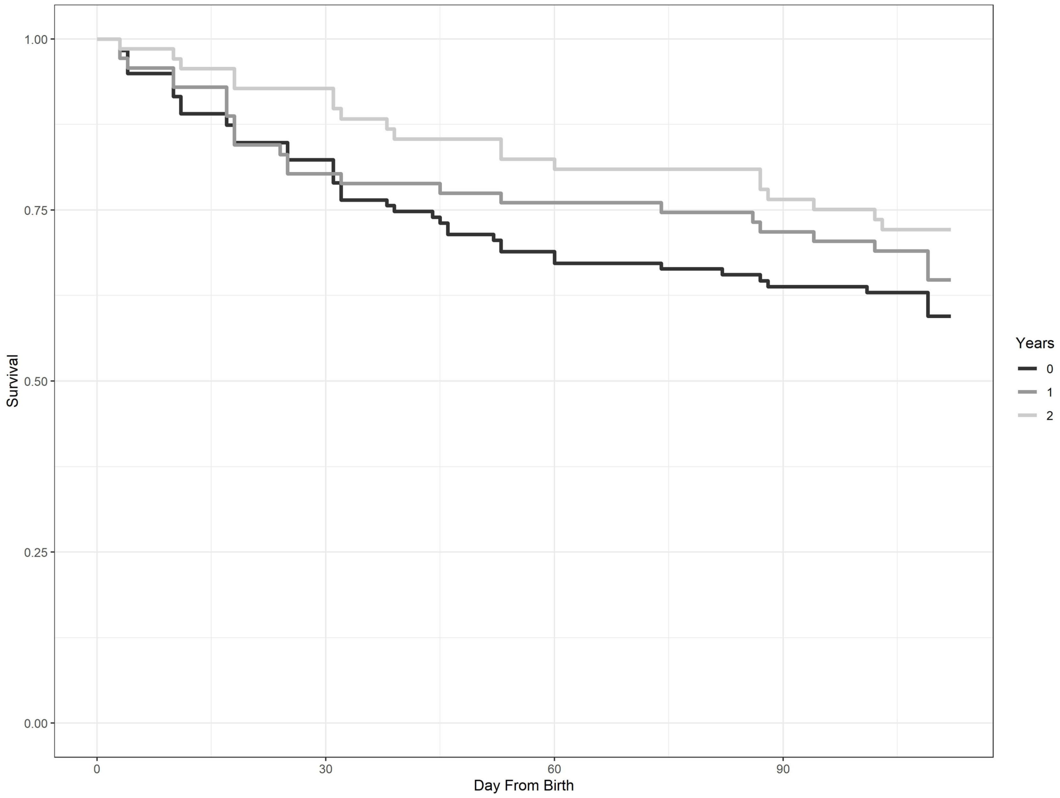


FIGURE 2
Survival curves for neonate mule deer produced using a Kaplan–Meier function. The three curves illustrate survival of fawns with no removal of coyotes (0), 1 year of removal of coyotes (1), and 2 years of removal of coyotes (2). This study was conducted on Monroe Mountain, Utah, United States during 2012–2015.

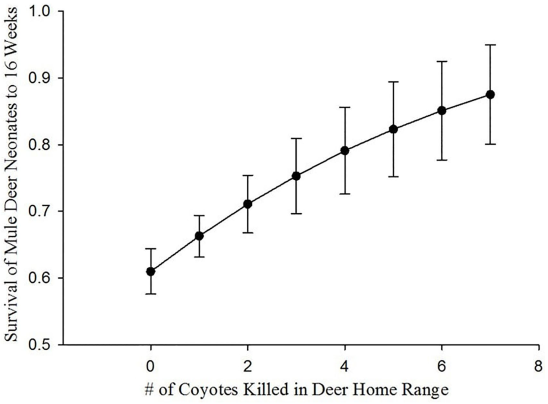


FIGURE 3
Probability of neonate mule deer surviving to 16weeks of age on Monroe Mountain, Utah, United States during 2012–2015 based on the number of coyotes removed within 2.25km (average diameter of a mule deer home range) of the birth site.

comprise only a minor portion of coyote diet when neonate sheep are present on the landscape. We suggest that neonate mule deer are an optimal food source for coyotes due to their large size and relative ease of capture. Therefore, coyotes potentially take neonate mule deer selectively when available. Coyotes did not start killing neonate mule deer until approximately the mean date of parturition each year (Hall, 2018), suggesting that the predators were unaware of the presence of the new food source on the landscape initially. Once coyotes started killing neonates, loss to coyotes became common suggesting that the predators shifted their behavior to target neonate mule deer. Indeed, some generalist predators switch to being a specialist when a potentially preferred prey becomes available (Roughgarden, 1974). A possible alternative explanation for the pattern we observed is that lagomorphs (i.e., alternative prey) were not randomly distributed with greater distribution at low elevations, whereas fawning habitat was at relatively high elevations. If coyotes do not transition up and down the mountain as suggested by Mahoney (2017), coyotes living in areas with mule deer neonates did not have access to lagomorphs, and therefore, shifts in abundance of lagomorphs should not influence taking of neonate mule deer.

Our study focused on spatial aspects of predator control and the effect of two consecutive years vs. a single year of coyote removal on fawn survival. Our results indicate that predator control efforts focused on fawning habitat have the greatest likelihood of leading to increased population growth. This finding is especially meaningful because there were significant sources of error (e.g., variation in the spatial density of predators and prey) that our study could not control. In addition to the spatial effects of predator control efforts, we found that two consecutive years of predator control are better than a single year. While it would be ideal to test the effect of additional consecutive years, it is difficult to maintain optimal experimental conditions for extended durations. As we described in the Introduction, the study by Hurley et al. (2011) took place over 6 years, but coyote removal numbers varied drastically from year to year in that study (we maintain that their study was a feat despite this limitation). Focusing on only 2 years of removal using a crossover design allowed us to maintain consistent removal efforts and carry out our desired goal of experimentally evaluating the effect of removal years, but it also precluded our ability to thoroughly examine population growth in response to our removal efforts given the short timeframe. Although increasing the survival rates of neonate ungulates can increase recruitment and the rate of population growth, it is possible that predator-related mortality is compensatory and not additive—especially for populations that are limited by the availability of nutritional resources. Therefore, it is crucial for future studies to determine the parameters of a prey population where increased fawn survival resulting from multiple consecutive years of consistent coyote removal translates to positive population growth. Further, future studies should determine how long the effect of predator removal lasts after removal efforts cease. Nevertheless, our results are valuable given that we were able to experimentally demonstrate the effect of multiple years vs. a single year of removal on fawn survival in a controlled naturalistic setting.

Managing for robust deer populations is often a high priority for agencies charged with managing wildlife. Our results indicate that coyote control can increase survival of neonate mule deer. Coyote control increased survival when (1) control efforts occurred for multiple consecutive years, and (2) when control efforts occurred in or near fawning habitat. Therefore, efforts to control predators should occur at relatively high elevation with shrubby understory consistent with the location of fawning habitat (Long et al., 2009; Freeman, 2014). Likewise, efforts should occur when populations have room to grow (size is below carrying capacity) to decrease the likelihood of compensatory mortality.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Brigham Young University Institutional Animal Care and Use Committee.

Author contributions

BM, KH, and RL conceived the ideas and designed the study and its methods. JH and EF conducted much of the fieldwork and data collection. JH and RL conducted the statistical analyses and produced the figures. BM and JH drafted the initial version of the manuscript. All authors contributed to the article and approved the submitted version.

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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.

Publisher's note

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Restoration of bighorn sheep: History, successes, and remaining conservation issues

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Mammals are imperiled worldwide, primarily from habitat loss or modification, and exhibit downward trends in their populations and distributions. Likewise, large-bodied herbivores have undergone a collapse in numbers and are at the highest extinction risk of all mammals. Bighorn sheep (*Ovis canadensis*) are among those large-bodied herbivores that possess a slow-paced life history, suffer from debilitating diseases, and have experienced range contractions across their historical distribution since the late 1800s. Translocations and reintroductions of these mountain ungulates are key aspects of restoration and often are used to re-establish populations in historical habitat or to supplement declining herds. Millions of US dollars and much effort by state and federal natural resource agencies, as well as public and private organizations, have been expended to restore bighorn sheep. Despite those efforts, translocated populations of bighorn sheep have not always been successful. We assessed restoration of bighorn sheep to provide insights in the context of conservation of populations of bighorn sheep, because this management tool is a frequently used to re-establish populations. We focused briefly on past efforts to restore bighorn sheep populations and followed with updates on the value of habitat enhancements, genetic issues, the importance of ecotypic or phenotypic adaptations when restoring populations, predation, and disease transmission. We also raised issues and posed questions that have potential to affect future decisions regarding the restoration of bighorn sheep. This information will help conservationists improve the success of conserving these iconic large mammals.

KEYWORDS
bighorn sheep, mountain sheep, *Ovis canadensis*, reintroduction, translocation

1. Introduction

Mammals are imperiled worldwide (Bowyer et al., 2019). Rates of recent extinctions far exceed previous levels, constituting a conservation crisis for many species (Ceballos and Ehrlich, 2002; Ceballos et al., 2017). Indeed, numerous mammals exhibit downward trends in their populations and distributions (Schipper et al., 2008; Ceballos et al., 2017), which necessitate efforts to ensure their continued survival (Goble et al., 2012). Threat of extinction and body size are positively correlated (Purvis et al., 2000; Cardillo et al., 2005), and large mammals are especially vulnerable to threats to their existence. Loss, modification, and fragmentation of habitat pose the greatest threats to mammals worldwide (Wilcox and Murphy, 1985; Schipper

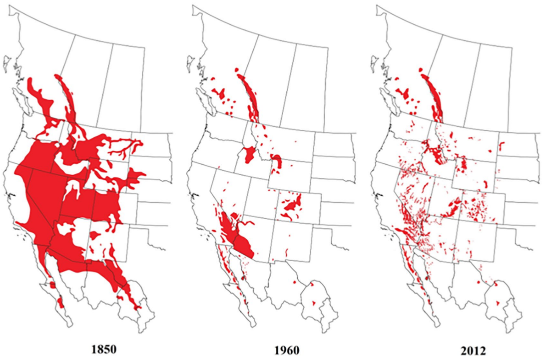

FIGURE 1
Historical (1850), at ostensibly the lowest extent of distribution (1960), and more recent distribution of bighorn sheep based on restoration of these ungulates in North America (Wild Sheep Foundation and WAFWA Wild Sheep Working Group, 2012).

FIGURE 2
Examples of capturing bighorn sheep using a helicopter and a net gunner (top left) and a drop net (top right), as well as methods of releasing bighorn sheep after captures (bottom; Jessup et al., 2015).

et al., 2008), and such threats typically are driven by human population density or climate change, which present increasingly greater dangers to the continued existence of mammals (Vitousek et al., 1997; McKee et al., 2013; Bowyer et al., 2019).

Large herbivores have undergone a collapse in numbers worldwide (Figure 1 in Ripple et al., 2015), and are at the highest extinction risk of all mammals (Atwood et al., 2020). High risks of extinction among large herbivores also are related to intrinsic characteristics, including susceptibility to disease, limited geographic distributions, and a slow-paced life history typified by low adult mortality, iteroparity, small litter size, high maternal investment in large young, long generation times, and low intrinsic rates of increase (Caughley and Krebs, 1983; Davidson et al., 2017; Bowyer et al., 2019). Those life-history characteristics are linked with strong density-dependent processes in the dynamics of ungulate populations, and such populations are connected intrinsically with the habitats they occupy (Bowyer et al., 2014).

Ungulates have experienced massive contractions in their distributions across North America (Laliberte and Ripple, 2004), and are undergoing elevated threats of extinction (Bowyer et al., 2019; Berger et al., 2020). Bighorn sheep (*Ovis canadensis*) are endemic to North America, are among the large-bodied ungulates that have experienced range contractions, and populations have declined considerably since the late 1800s (Buechner, 1960; Geist, 1971; Krausman, 2000; Figure 1). These ungulates are listed as least concern under The IUCN Red List of Threatened Species although some subspecies are endangered.[1] Krausman (2000), and more recently Donovan et al. (2020), analyzed the status of many bighorn sheep populations in western North America. Restoration of populations has been an important tool for the conservation of bighorn sheep (Seddon, 2010; Taylor et al., 2017), but there is much to be learned from an examination of the overall circumstances leading to success or failure of efforts to conserve populations of these iconic large mammals.

Translocations and reintroductions (herein referred to as restoration), both key aspects of restoration, often are used to re-establish bighorn sheep in historical habitat or to supplement declining populations (Risenhoover et al., 1988; Roy and Irby, 1994; Singer et al., 2000a; Figure 2). Despite those efforts, translocations have not always been successful (Roy and Irby, 1994; Krausman, 2000; Singer et al., 2000b). Translocations and reintroductions, however, can be critically important to the restoration of bighorn sheep, particularly for endangered taxa or distinct population segments of those specialized mountain ungulates (Rubin et al., 1998; Ostermann et al., 2001; Cahn et al., 2011).

Translocation has three forms: introduction, reintroduction, and restocking (IUCN, 1987). Hale and Koprowski (2018) refer to these as: (1) intended or unintended movement of an organism out of its native range; (2) intentional movement of an organism into native range from which it has been extirpated, and (3) movement of members of a species to augment the number of individuals in an original habitat. Whether in the context of introduction, reintroduction, or restocking, translocation has been, and remains, an essential component of wildlife management and conservation biology (Armstrong and Seddon, 2008; Seddon, 2010; Polak and Saltz, 2011), and is a positive step in restoring function to ecosystems of western North America, whether with bighorn sheep or other species (Kie et al., 2003; Bleich, 2020). Millions of US dollars and much effort by state and federal natural-resource agencies, as well as public and private organizations, have been expended to restore bighorn sheep to historical ranges (Krausman, 2000; Krausman et al., 2001; Hurley et al., 2015; Donovan et al., 2020).

Twenty-three years ago, Singer et al. (2000b) assessed factors associated with translocation success and provided recommendations for future translocations of bighorn sheep (Singer et al., 2000a). Herein, we conducted a review of translocation as a management tool for bighorn sheep with emphasis on new insights stemming from subsequent research, particularly regarding disease, evolutionary history, local adaptation, genetics, and climate change, as well as habitat considerations and the role of hunting.

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[1] https://www.iucnredlist.org/species/15735/22146699

2. Past success and habitat considerations

Bighorn sheep are endemic to North America. Suitable habitat extends from the northern Rocky Mountains in western Canada south through the western United States to northern Mexico (Buechner, 1960; Geist, 1971; Trefethen and Corbin, 1975; Valdez and Krausman, 1999; Figure 1). Bighorn sheep populations declined as human settlement expanded through much of their range; that downward trend in numbers began with the human settlement of vast, uninhabited areas (Grinnell, 1928; Buechner, 1960). Much attention has been accorded to unregulated market hunting and habitat loss, or modification, as causes of population declines (Grinnell, 1928; Buechner, 1960). Another, more onerous, factor that exacerbated declines was the introduction of livestock, primarily domestic sheep (*O. aries*), across much of the range of bighorn sheep (Buechner, 1960). As a result, naïve bighorn sheep populations were exposed to novel bacterial pathogens, resulting in epizootics of respiratory disease and depressed population performance (Grinnell, 1928; Skinner, 1928; Marsh, 1938), which may have begun during the late 1700s in some locations. Indeed, an ancient Kaliwa legend makes reference to a pestilence that destroyed many of the bighorn sheep in northern Baja California within a few years after Spanish padres arrived with their livestock (Tinker, 1978).

Cary (1911) provided additional evidence that disease was a factor in the early decline of bighorn sheep. Such declines were thought to have coincided with the advent of domestic livestock grazing on ranges occupied by bighorn sheep (Warren, 1910; Grinnell, 1928; Shillinger, 1937; Honess and Frost, 1942). Epizootics among native bighorn herds were reported in various locations following European settlement and establishment of domestic livestock grazing throughout the central and southern Rocky Mountains. Diseases, therefore, likely were the primary cause of decline among bighorn sheep populations across much of western North America (Beecham et al., 2007). Many native populations fell to <10% of historical numbers (Wild Sheep Working Group, 2012); as a result, bighorn sheep currently occur in far fewer locations and in fewer numbers than in the past (Figure 1). Despite an estimate of at least 1.5 million bighorn sheep occupying North America in 1850 (Seton, 1929), a number that was popularized by Buechner (1960), Valdez (1988) suggested that the number of wild sheep (*O. canadensis* and *O. dalli* combined) inhabiting North America probably never exceeded 500,000. Similarly, others have noted the absence of reliable historical population estimates and acknowledged that the number of wild sheep inhabiting North America in pristine times likely was in the hundreds of thousands (Wild Sheep Working Group, 2015). A combined total (Larkins, 2010; Sandoval et al., 2019) of about 81,000 bighorn sheep currently exist across the range of the species in Canada (~12,000), Mexico (~12,000), and the United States (~57,000).

Bighorn sheep occur largely in a metapopulation structure (Schwartz et al., 1986; Bleich et al., 1990a, 1996; Epps et al., 2006) and, as habitat specialists, are slow to colonize vacant habitat (Geist, 1971), although such events may occur more frequently than previously recognized (Bleich et al., 2021). The use of translocations to restore wild sheep to historical ranges began in 1922 with the capture of 20 Rocky Mountain bighorn sheep (*O. c. canadensis*) in Alberta, Canada, and release of 12 animals in Montana and eight animals in South Dakota. As of 2015 at least 1,460 additional projects have resulted in the translocation of ≥21,500 bighorn sheep in the United States and Canada (Wild Sheep Working Group, 2015; Figures 2–5). In the United States, states from which bighorn sheep had been extirpated—Nebraska, North Dakota, Oregon, South Dakota, Texas, and Washington—were completely dependent on the availability of translocation stock originating from outside of their jurisdictions.

Bighorn sheep formerly occurred in at least six Mexican states, but native populations remain only in Baja California, Baja California Sur, and Sonora (Valdez, 2011). Bighorn sheep occur in only 40% of their historical range in Baja California and Baja California Sur (DeForge et al., 1997). Elsewhere in Mexico, bighorn sheep have been re-established in historically occupied habitat in Sonora, Chihuahua, and Coahuila, and bighorn sheep in Mexico now number nearly 13,000 individuals (Sandoval et al., 2019; Brewer and McEnroe, 2020).

Bighorn sheep used to restore formerly occupied habitat in Mexico have originated largely from insular populations, captive populations, or from free-ranging populations on privately owned land (Sandoval et al., 2019). Mexico has a successful captive-breeding program, and current laws allow individual landowners to maintain facilities for the captive propagation of wildlife (Gonzalez-Rebeles Islas et al., 2019; Valdez, 2019). Economic considerations have been an important force driving those efforts, and they have occurred largely in the context of a demand for hunting opportunities for this iconic species (Lee, 2011; Gonzalez-Rebeles Islas et al., 2019). These efforts have resulted in establishment of ≥40 management areas in Sonora alone, with similar programs existing elsewhere in Mexico where the benefits to conservation are becoming widely recognized (Sandoval et al., 2019; Brewer and McEnroe, 2020).

Recovery of bighorn sheep throughout North America largely has been a function of successful programs, carried out by state or provincial wildlife agencies, to return those mountain ungulates to their historical ranges wherever possible. Most restoration efforts have involved the translocation of animals from existing, free-ranging populations to areas from which the species had been extirpated. Although uncommon, some successful restorations or augmentations have depended on captive populations to produce stock for translocation in Nebraska (Fairbanks et al., 1987), Texas (Hailey, 1971; Kilpatrick, 1980), New Mexico (Snyder, 1980), California (Ostermann et al., 2001), and perhaps other jurisdictions. There are, however, no commercial enterprises that breed bighorn sheep to be released in the wild. Regardless of the origin of translocation stock, recovery has restored an important biological component of many desert and alpine ecosystems. For example, in the most arid portions of the Mojave Desert in California, United States, bighorn sheep are the only large native herbivore present and serve as prey for native predators, including mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*; Ober, 1931; Wehausen, 1996; Bleich et al., 1997).

Among habitat characteristics shared throughout the distribution of bighorn sheep is their association with steep, rugged terrain, which plays a vital role in predator-evasion strategies and in survival of lambs (Berger, 1991; Bleich et al., 1997; Bleich, 1999; Schroeder et al., 2010). Additionally, openness of terrain and vegetation enhances the ability of bighorn sheep to detect predators (Berger, 1991; Bleich et al., 1997) and spend less time vigilant while foraging (Berger, 1978; Risenhoover and Bailey, 1985), with probable energetic benefits to individuals. Additionally, surface water (as well as condensation and as preformed water in forage) is a critically important resource for bighorn sheep occupying desert ecosystems in which those large mammals are unable to meet their physiological needs *via* metabolic water during the hot summer (Turner, 1973; Leslie and Douglas, 1979; Epps et al., 2004). The availability of water and vegetation, however, in historical range may not be suitable for reintroduction because the landscape and land use may have changed. There are four attributes of critical habitat for bighorn sheep: availability of surface water in desert ranges, vegetation composition or structure, isolation from diseases carried by domestic sheep, and rugged terrain. All of these attributes can be considered in selecting a translocation site but water, vegetation, and diseases are much more dynamic than terrain if the animals remain in the selected area. Despite this limitation, the potential for success of translocations can be enhanced by selecting areas with appropriately rugged terrain for translocations (Smith et al., 1991; Zeigenfuss et al., 2000), or by manipulating and emphasizing the importance of several other habitat features that are important to bighorn sheep (Smith et al., 1999; Bleich, 2009; Whiting et al., 2011a).

Seasonal differences in habitat selection between males and females are a consequence of differential distributions between sexes of bighorn across the landscape, resulting principally from modifications in digestive morphology and physiology (Barboza and Bowyer, 2000, 2001) and varying susceptibility to predation (Bleich et al., 1997) by the sexes—those differences have important implications for the conservation of bighorn sheep (Bowyer, 2022). Males and females exhibit disparate life-history patterns (Bleich et al., 1997; Schroeder et al., 2010; Whiting et al., 2010a,b), and the restoration of bighorn sheep to previously occupied ranges is complicated by these behavioral differences in their habitat requirements (Bleich et al., 1997; Villepique et al., 2015). Unfortunately, the differential selection of habitat by males and females during much of the year has not often been considered in translocation efforts but is necessary for successful restoration of these large mammals (Bowyer, 2022).

2.1. Benefits of water development

In the Chihuahuan, Sonoran, and Mojave deserts, and to a lesser extent in the Great Basin Desert, water development has been a prominent and widespread habitat-enhancement technique (Rosenstock et al., 1999; Bleich, 2009; Larsen et al., 2012) albeit, in some instances, a contentious activity, as bighorn sheep may not always rely on these features (Cain et al., 2008). That aside, water-development projects have played a critical role in managing habitat for extant populations and have been implemented widely to ensure the availability of that important resource prior to restoration efforts in desert ecosystems (Bleich, 2009; Whiting et al., 2011a).

Numerous techniques for providing surface water have been developed, ranging from enhancing storage of water flowing from natural springs, the use of horizontal wells to create surface water where it previously was unavailable, modification of natural water sources that previously were unavailable because bighorn sheep could not negotiate the near-vertical walls of tenajas (natural features that retain run-off water for long periods of time), the use of sand dams for underground storage, and construction of artificial catchments that trap and store rainfall in areas where no surface water previously existed (Bleich et al., 2020). Water developments can accomplish several objectives simultaneously, among which is provision of a resource without which bighorn sheep cannot persist. This is particularly important where water has become unavailable in desert environments because of anthropogenic activities that have resulted in shifts in the water table, or loss of free water resulting from a changing climate (Epps et al., 2004; Whiting et al., 2011a; Larsen et al., 2012).

Given the metapopulation structure of bighorn sheep in desert regions (Schwartz et al., 1986; Bleich et al., 1990a, 1996; Epps et al., 2007), enhancement of water availability also facilitates metapopulation processes, encourages colonization events, increases population size (albeit not necessarily population density), enhances gene flow among subpopulations, and increases the probability of individual survival during periods of drought (Bleich, 2009). As such, water provision has played a major role in translocation of desert bighorn sheep (*O. c. nelsoni*) to areas from which they had been extirpated and helps to ensure their persistence in currently occupied areas.

Early habitat-assessment models (Smith et al., 1991; Zeigenfuss et al., 2000) identified the need to consider availability of reliable water sources to existing populations, and prior to re-establishing bighorn sheep, particularly in deserts. Recent work has highlighted the need to consider water sources that will benefit males and females separately, because sexual segregation is a life-history characteristic of these ungulates (Bleich et al., 1997; Bowyer, 2004; Rubin and Bleich, 2005; Bleich, 2009; Schroeder et al., 2010). For example, in one re-established population, although female and male bighorn sheep used small, adjacent areas during segregation, the sexes still visited different sources of water (Whiting et al., 2010a). This information highlights the value of water sources in areas used by sexes regardless of the size of the area occupied by these animals. Whiting et al. (2010a) also reported that all water sources were within 3.2 km of 50% core areas used by either sex of re-established bighorn sheep. Use of that resource differed, however, according to the proximity of water to habitats used by males or females. Indeed, some sources of water were used rarely by either males or females during particular seasons (Whiting et al., 2010a; Larsen et al., 2012).

2.2. Vegetation management

In addition to maintaining or providing reliable sources of surface water, manipulation of vegetation often is desirable, and in some situations is necessary to enhance success of translocation efforts or ensure the persistence of populations. Numerous methods that are mechanical or biological in nature, as well as the application of prescribed fire, offer viable approaches (Green, 1977a,b; Bleich and Holl, 1982; Bleich et al., 2020). Prescribed burning is a tool for reducing fuels and restoring a process to landscapes that historically experienced fire, but that have been altered by decades of fire exclusion or fire suppression. Results from prescribed ignitions are dependent, however, on numerous variables, each of which can affect the final outcome (Stephens et al., 2009). Nevertheless, vegetation manipulation in the form of prescribed fire is widely recognized as an important method of enhancing forage quality or availability for bighorn sheep (Peek et al., 1979; Hobbs and Spowart, 1984; Seip and

Bunnell, 1985;Smith et al., 1999; Clapp and Beck, 2016) and other large herbivores, or enhancing habitat quality indirectly by decreasing barriers to visibility (Risenhoover and Bailey, 1980; Smith et al., 1999). Vegetation management to enhance habitat quality is likely to be successful in those areas of the southwestern United States occupied by bighorn sheep and dominated by coastal chaparral, or by Madrean evergreen woodland, vegetation types in which shrub density increases, and forage quality declines with time elapsed since previous fire or other types of perturbation (Green, 1977a; Cain et al., 2005; Bleich et al., 2008; Holl et al., 2012). Vegetation types differ, but similar positive results have been obtained in areas occupied by Rocky Mountain bighorn sheep (Peek et al., 1979; Smith et al., 1999; Clapp and Beck, 2016).

Although the U.S. Forest Service has changed its policy from fire suppression to fire management (DeBruin, 1974), use of prescribed fire to enhance or maintain conditions suitable for restoring bighorn sheep is infrequent and, even when implemented, is limited in scope (Smith et al., 1999; Clapp and Beck, 2016). Further, the phenomenon of sexual segregation dictates that habitat requirements of male and female bighorn sheep be considered when implementing prescribed fire for habitat enhancement, and physical characteristics of the landscape have important implications for success (Bowyer, 2022). Regardless of the amount of 'high-quality' habitat created as a result of prescribed ignition, the relative increase in habitat possessing suitable physical or geological characteristics (e.g., steepness or ruggedness) will dictate the degree of benefit independently of any increase in forage availability, quality, or visibility (Holl, 1982). Further, many areas identified for reintroductions, even though occupied historically by bighorn sheep, likely have changed considerably since bighorn sheep were extirpated (Risenhoover et al., 1988), and decreases in suitability of habitat may have been subtle and likely not evaluated prior to translocations (Wakelyn, 1984; Wakelyn, 1987). Moreover, management of vegetation specifically to enhance bighorn sheep habitat has been severely constrained within legislated wilderness areas in the United States since the Wilderness Act was passed in 1964, and existing policy will continue to complicate such efforts (Bleich, 2005, 2016; Bleich et al., 2019).

2.3. Managing disease susceptibility

In addition to the physical or vegetational characteristics of sites to be considered, the potential for exposure to pathogens remains a key consideration. Disease, in addition to habitat quality, has primary consequences for conservation of wild sheep in North America (Bleich, 2009). Thus, the third aspect of bighorn sheep habitat that can be manipulated or managed prior to a restoration is the proximity of translocation sites to domestic sheep, whether on private or public lands. Bighorn sheep are especially vulnerable to *Mycoplasma ovipneumoniae* as an agent predisposing them to respiratory disease; *Pasteurella multocida, Mannheimia haemolytica,* and *Bibersteinia trehalosi* also occur widely among domestic sheep (Besser et al., 2013; Cassirer et al., 2013, 2018). As a result, even areas that are geologically or topographically suitable, provide vegetation characteristics that are adequate to meet predator-evasion strategies and nutritional requirements, and meet the physiological needs of bighorn sheep through the availability of reliable surface water, may be excluded from consideration because of the potential for pathogen transmission from domestic sheep.

Prudent and responsible stewardship dictates that the potential for pathogen transfer to bighorn sheep be a primary factor when considering restoration locations. Current guidelines caution strongly against implementing such actions where the probability of translocated animals coming into contact with domestic sheep does not approach zero, or where there is substantial uncertainty of the disease status of either source or recipient populations (Brewer et al., 2014; Jex et al., 2016). Efforts to restore native bighorn sheep to historical ranges that otherwise were suitable have been postponed, and even canceled, because of risks associated with the presence of, or proximity to, grazing of domestic sheep (Shannon et al., 2014). Until such risks are eliminated, proposed restoration efforts should be halted. While survival of desert bighorn sheep infected by *M. ovipneumoniae* has been observed to be higher when forage conditions are good (Dekelaita et al., 2020), the risks of allowing novel pathogen strains to enter a restored system likely outweigh the quality of the habitat.

2.4. Climate change and future habitat conditions

Climate change provides challenges for managing wildlife populations, and the need for climate-informed management of species, particularly in restoration of alpine specialists such as bighorn sheep, is now well-recognized (Gude et al., 2022). Studies have attempted to estimate effects of past and future climate variation on bighorn sheep, including both native and restored populations (Epps et al., 2004; Colchero et al., 2009). Nonetheless, a study investigating temporal mismatch between vegetation green-up and parturition date in Rocky Mountain bighorn sheep, an expected consequence of climate change, concluded that mismatch did not have major consequences for fitness (Renaud et al., 2022).

Changes in precipitation regimes across western North America may be more dramatic and less predictable than current conditions and could have major implications for management of both natural and artificial water sources (Dolan, 2006; Terry et al., 2022), snowpack and avalanche risk (Conner et al., 2018), forage quantity and quality (Epps et al., 2004), or metapopulation dynamics in desert systems (Epps et al., 2004, 2006). For instance, in Colorado, increased precipitation increased deposition of inorganic nitrogen, acidifying surface waters and potentially affecting the bottom of the food chain with consequences for bighorn sheep foraging (Williams et al., 2002). Increased variation in rainfall in Baja California Sur, Mexico, is expected to disrupt conservation of bighorn sheep and the associated hunting-based economy (Zamora-Maldonado et al., 2021); indeed, translocation of individuals might be necessary to sustain huntable populations under some climate conditions, although the long-term success of such an approach is questionable if nutrition limitations are the cause of the decline. Alternatively, Creech et al. (2020) considered vulnerability of desert bighorn sheep across a portion of their range with respect to climate change as a function of adaptive capacity (genetic diversity and connectivity) and predicted rates of environmental change. Some reintroduced populations ranked poorly in that assessment because of low genetic diversity caused by founder effects from translocations (Creech et al., 2020).

Across the range of bighorn sheep, managers of restored systems or those contemplating restoration would be well advised to consider habitat resources in a changing climate, and whether historically occupied but now unoccupied habitats would still support populations if restored (Wehausen and Epps, 2021). Likewise, climate change is a primary reason to maintain the ability of restored bighorn sheep to adapt by preserving genetic diversity and connectivity where not precluded by other considerations.

3. Genetic considerations

Efforts to restore bighorn sheep in North America during the 20th and 21st centuries exemplify the challenges posed by an incomplete understanding of their evolutionary histories. Two primary problems exist: first, when both local and regional extirpation of species have occurred, which potential source stocks are most evolutionarily and ecologically appropriate for restoration? Second, how can genetic diversity in translocated populations be maximized and maintained without precipitating outbreeding depression? Both questions warrant serious consideration and require a spatially detailed and correct assessment of the evolutionary history of extirpated and remaining populations. The second question also requires careful assessment of population history or genetic variation in remaining populations (Bleich et al., 2021).

Wild sheep colonized North America from Asia approximately 2 million years ago (Bunch et al., 2006; Rezaei et al., 2010), diverging subsequently into two species, bighorn sheep and Dall's sheep. Subspecies designations remain unresolved, but specific divergence likely resulted from isolation of bighorn sheep in different refugia during the glacial cycles of the Pleistocene (Buchalski et al., 2016). Cowan (1940) recognized up to seven subspecies on the basis of morphology, but subsequent morphometric and genetic analyses indicated that all four desert subspecies (*O. c. nelsoni, O. c. mexicana, O. c. cremnobates,* and likely *O. c. weemsi*; although *O. c. weemsi* was not formally included in the analyses) should be synonymized and referred to taxonomically as *O. c. nelsoni* (Wehausen and Ramey, 1993). Specifically, PCA and discriminant function analyses of 17 skull and horn measurements from 198 rams and 145 ewes did not support clear distinction among those taxa, nor did RFLP analyses of mitochondrial DNA haplotypes (Ramey, 1993a,b). More recent genetic analyses, however, show some evidence for distinction of populations previously described as *O. c. cremnobates* (in part, although the lines of distinction differ somewhat from the estimation of Cowan, 1940) and *O. c. mexicana* from *O. c. nelsoni* (Buchalski et al., 2016). Sierra Nevada bighorn sheep represent a deeply divergent evolutionary lineage (Buchalski et al., 2016) and are now recognized as a distinct subspecies (*O. c. sierrae*; Wehausen and Ramey, 2000; Wehausen et al., 2005). Based on morphological analysis of horn and skull characters, Wehausen and Ramey (2000) proposed synonymizing Rocky Mountain and California (*O. c. californiana*), as well as the extinct *O. c. auduboni*, as *O. c. canadensis*. Wildlife agencies in North America, however, mostly continue to manage bighorn sheep from those lineages separately, and microsatellite analysis of populations in British Columbia, Washington, Oregon, and Idaho showed clear distinction by lineage (Barbosa et al., 2021).

Bighorn sheep in the northwestern U.S. and southwestern Canada pose a particular management challenge. Bighorn sheep were extirpated from Oregon, Washington, southeastern Idaho, and northwestern Nevada by the first one-half of the 20th century (Buechner, 1960). At that time, Cowan (1940) considered the range of California bighorn to extend from British Columbia southward to the Sierra Nevada of California (Figure 3). Subsequent restoration efforts relied largely on bighorn sheep translocated from British Columbia. Since then, Wehausen and Ramey (2000) assigned extinct and extant populations in Washington and British Columbia to the Rocky Mountain subspecies, but argued that extirpated native populations in Oregon, southeastern Idaho, northeastern California, and

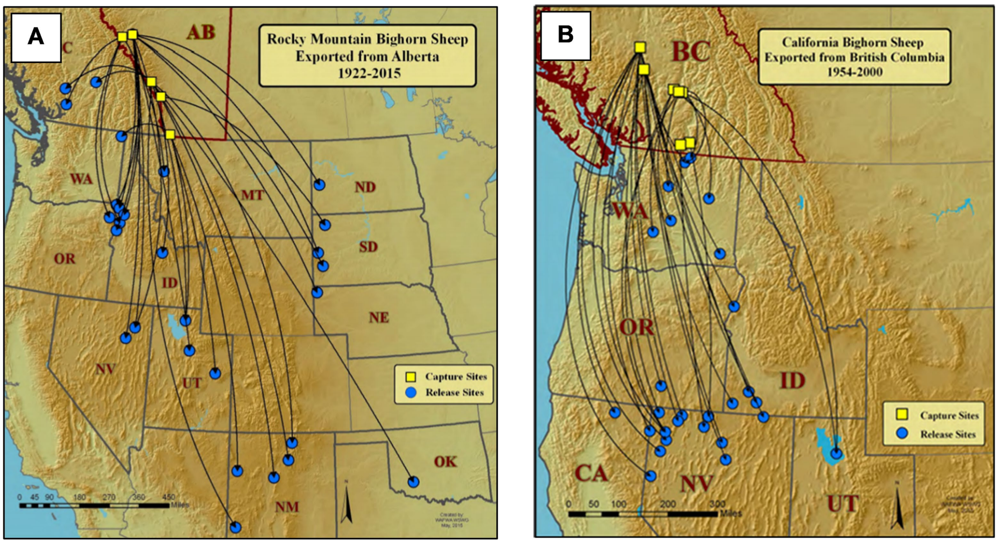

FIGURE 3
Examples of historical restoration of Rocky Mountain **(A)** and California bighorn sheep **(B)** from Canadian provinces to states of the western United States (Wild Sheep Working Group, 2015).

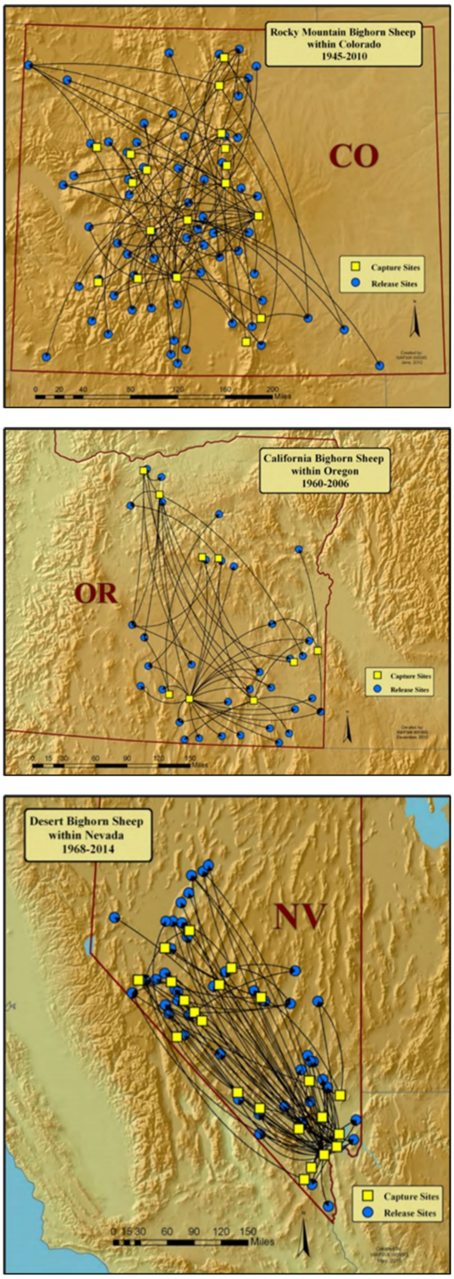

FIGURE 4
Examples of historical interstate restoration of Rocky Mountain bighorn sheep in Colorado, United States (top), California bighorn sheep in Oregon, United States (middle), and desert bighorn sheep in Nevada, United States (bottom; Wild Sheep Working Group, 2015).

northwestern Nevada represented a Great Basin form of desert bighorn sheep. Managers now question what the most appropriate source for future translocations should be—whether translocation stock representing California and Rocky Mountain bighorn sheep can or should be mixed, or even whether poorly performing populations in the Great Basin region should be augmented with desert bighorn sheep (Epps et al., 2019). Across much of the range of bighorn sheep, resolving questions of evolutionary history thus remains relevant to future management.

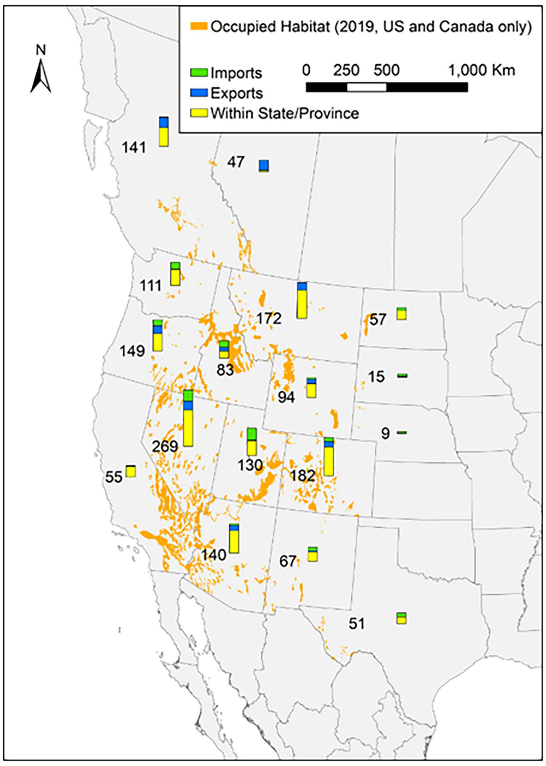

FIGURE 5
Currently occupied habitat of bighorn sheep populations in western North America with the number of restoration events (imported, exported, and moved within states and provinces).

Determining appropriate strategies to manage genetic diversity of translocated bighorn sheep populations continues to generate keen interest and debate (Epps et al., 2019; Flesch et al., 2020), but will require distinctive approaches in different systems. In largely intact native systems of bighorn sheep, such as the metapopulations of desert bighorn occurring in the Mojave and Sonoran deserts of California (Schwartz et al., 1986; Bleich et al., 1990a, 2021), genetic diversity is strongly shaped by connectivity among populations (Epps et al., 2005; Flesch et al., 2020), habitat quality (Epps et al., 2006; Creech et al., 2016), and extinction and colonization dynamics (Epps et al., 2010, 2018). Connectivity, in turn, is influenced by both natural and anthropogenic fragmentation (Bleich et al., 1996; Epps et al., 2007).

Translocations of desert bighorn sheep in that region largely have addressed localized extirpations. As a result, and in most instances, potential for those translocated populations to be integrated into the existing metapopulation by dispersal is high. Indeed, for most translocated populations in that region, dispersal has been documented to or from nearby native populations (e.g., Epps et al., 2010, 2018; Bleich et al., 2021) except in instances of extreme isolation (e.g., the Sespe population near San Rafael Peak in Ventura County, California, United States; Bleich et al., 2019). Similarly, integration of translocated populations into current, native population structure has been observed elsewhere, as on the north rim of the Grand Canyon in Arizona (Gille et al., 2019). Nonetheless, relationships between genetic diversity and geographic and genetic measures of isolation largely were decoupled for translocated populations in that region, indicating that genetic equilibrium has not yet been reached (Creech et al., 2020). Over time, genetic diversity of translocated populations can be expected to benefit from connections to nearby native populations, thereby potentially increasing genetic diversity of nearby native populations, as has occurred in the Coxcomb Mountains in southern California, United States (Epps et al., 2010).

As the proportion of translocated populations increases within a particular system, effects of genetic bottlenecks and founder effects can become more apparent. Founder effects are well-documented among translocated and subsequently isolated populations of bighorn sheep (Gutiérrez-Espeleta et al., 2000; Hedrick et al., 2001; Hogg et al., 2006; Johnson et al., 2011; Barbosa et al., 2021). In the Sierra Nevada of California, where bighorn sheep likely declined to fewer than 100 individuals, restoration efforts have relied on translocation as a primary tool, and much consideration has been given to conserving what genetic diversity survived bottlenecks by this subspecies (Few et al., 2013; Bleich et al., 2021). In other systems with significant numbers of translocations but greater connectivity and more source populations, bottlenecks are less apparent, but translocation histories still leave readily detectable genetic footprints of source populations, sometimes admixed with other source populations or native individuals (Jahner et al., 2019; Flesch et al., 2022).

In some parts of the range of bighorn sheep, restoration at the regional scale was necessary, leading to more serious challenges from a genetic standpoint. Restoration of bighorn sheep to historically occupied areas in Washington, Oregon, southern Idaho, northwestern Nevada, and northeastern California, United States, was conducted using animals from British Columbia, Canada (subspecies *californiana*), or Rocky Mountain bighorn (subspecies *canadensis*), which likely were of a different evolutionary lineage than animals that were present before extirpation (Wehausen and Ramey, 2000). Using translocated populations as sources for later translocations led to a complicated history of bottlenecks and severe, repeated founder effects, resulting in very low genetic diversity in many contemporary populations in those regions (Whittaker et al., 2004; Barbosa et al., 2021). Recognition of the potential negative consequences of that history led to efforts in Oregon to restore genetic diversity in several populations through additional translocations from other sources (Olson et al., 2012). Maintaining or improving genetic diversity in those regions remains a concern, and further questions, including how well adapted those animals may be to Great Basin environments, and whether bighorn sheep from California or Rocky Mountain sources represent evolutionarily divergent lineages, also have been raised or are now being evaluated (Olson et al., 2013; Epps et al., 2019; Bleich et al., 2021).

Moving forward, low genetic diversity and inbreeding depression remain a common concern for management of small, isolated populations of bighorn sheep, particularly because of growing evidence for links between genetic diversity and fitness. Genetic diversity has been linked to nematode resistance in Soay sheep (Hayward et al., 2014). In the Mojave Desert of California, desert bighorn sheep populations with higher genetic diversity had lower prevalence of exposure to and infection by *M. ovipneumoniae*, and more genetically diverse individuals had stronger adaptive immune responses (Dugovich et al., 2023). Genetic rescue of an isolated population of bighorn sheep exhibiting inbreeding depression has been reported (Hogg et al., 2006; Miller et al., 2012), but outbreeding depression (Dobzhansky, 1948) is also a concern when selecting source stock for translocations or augmentations. Outbreeding depression can result from inappropriate mixing of individuals from different environments because of disruption of co-adapted gene complexes (Waits and Epps, 2015). Further, individuals from different environments may fare poorly when compared with locally adapted individuals (e.g., Whiting et al., 2012; Wiedmann and Sargeant, 2014; Bleich et al., 2018). Finally, any movement of individuals to actively manage genetic diversity increases the risk of introducing or spreading disease (see Disease section). In areas such as the northwestern United Sates, where extirpations were especially widespread, better understanding of evolutionary history, inbreeding, and adaptive genetic variation in bighorn sheep are urgently needed.

4. Ecotypic and phenotypic considerations

Bighorn sheep are habitat specialists (i.e., dependence on steep, rugged terrain of variable elevations), and the successful restoration of these iconic animals to historical ranges is conditioned on a number of critically important factors that are shared among the various clades (Buchalski et al., 2016), subspecies (Wehausen and Ramey, 2000), or ecotypes (i.e., those possessing physiological, reproductive, or behavioral adaptations to localized environmental conditions or habitats; Bleich et al., 2018). In the past, translocation of bighorn sheep to historically occupied ranges was based largely on selection of a source population thought to represent the appropriate taxon according to subspecies boundaries recognized at the time (Cowan, 1940), the availability of translocation stock (Leslie, 1980), or in an effort to maintain subspecific purity (Ramey, 1993a,b). Although emphasized strongly by Leslie (1980), the importance of similarities between habitat occupied by a source population and the location to which bighorn sheep are translocated has become widely recognized within recent decades (Whiting et al., 2012; Wiedmann and Sargeant, 2014; Bleich et al., 2018, 2021), just as have the genetic consequences of translocations (Whittaker et al., 2004; Jahner et al., 2019; Barbosa et al., 2021). In some instances, hybridization of subspecies or putative subspecies has occurred because of underestimation of the ability of bighorn sheep to make long distance dispersal movements (e.g., Jahner et al., 2019), and managers have stated the need to prevent hybridization between strongly divergent subspecies—e.g., Rocky Mountain and desert bighorn, (Latch et al., 2006), because of concerns about outbreeding depression.

Indeed, because of the variation in success of translocations (Singer et al., 2000b), the importance of local adaptations or ecological similarities between habitat occupied by source populations and that at proposed translocation sites now receives greater emphasis (Whiting et al., 2012; Brewer et al., 2014; Wiedmann and Sargeant, 2014; Bleich et al., 2018). Timing of birthing seasons, diet, composition of predator communities, climate, and vegetative structure all have implications for the success or failure of a restoration effort. Although some traits such as birthing season and migration appear to be plastic and do adjust over time (Whiting et al., 2011b, 2012; Jesmer et al., 2018), others may be less malleable because of a genetic basis, such as body size, or size and rates of horn growth (Ramey, 1993a,b).

The potential for adjustment of life-history characteristics and behaviors, thus, is an essential consideration when translocating bighorn sheep that may be adapted to environments different than those that occur, or historically occurred, at a particular release site. For example, female bighorn sheep captured in Canada and released in Utah, United States, did not adjust maternal care to compensate for late-born young within the first 3 years following release, which possibly influenced survivorship of young (Whiting et al., 2010b). Young males and a low male-to-female ratio of bighorn sheep captured in Canada and Montana, United States, and released in Utah did not affect the number of young born per female or timing and synchrony of births (Whiting et al., 2008). Moreover, some of those populations adjusted timing and synchrony of parturition to environmental conditions of their release site within 5 years after release (Whiting et al., 2011b). Slow adjustment of those life-history characteristics by females, however, possibly contributed to lower survival of young to their first winter, which could slow successful establishment of bighorn sheep populations (Whiting et al., 2011b).

In another example, bighorn sheep from British Columbia performed poorly in terms of population dynamics and survival rates when compared with those from Montana, an area much more similar to the Badlands of western North Dakota, United States, where animals had been released (Wiedmann and Sargeant, 2014; Bleich et al., 2018). Thus, consideration should be given to the adjustment of timing and synchrony of births when restoring populations of bighorn sheep, and biologists should select source populations occupying areas that are ecologically similar to proposed release sites (Whiting et al., 2012). Further, ecotypic differences among source stocks may have long-term implications for recruitment and demographic performance of reintroduced populations, and use of appropriate source stock may greatly improve prospects for successful reintroductions of bighorn sheep (Wiedmann and Sargeant, 2014).

5. Predation and its implications for restoration

Mountain lions, coyotes, bobcats, and golden eagles are important predators of adult bighorn sheep (Bleich, 1996, 1999; Bleich et al., 1997, 2004). Relative abundance of coyotes was up to 12× greater on ranges occupied by male bighorn sheep when compared to areas occupied primarily by females and young during sexual segregation, but relative abundance of bobcats was similar between male and female ranges (Bleich et al., 1997). Mountain lions generally occur at exceedingly low densities (0.4–7.0/100 km^2; Pierce and Bleich, 2003, 2014). Nevertheless, predation by mountain lions is a common source of mortality for bighorn sheep (Ross et al., 1997; Hayes et al., 2000; Rominger, 2018) and can impede restoration of populations of this ungulate (Wehausen, 1996; Rominger et al., 2004; McKinney et al., 2006). An additional aspect of predation involves apparent competition (Holt, 1977; Holt and Lawton, 1994; Sinclair et al., 1998). Predation can affect a rare competitor negatively if the population dynamics of a shared predator are associated primarily with a more numerous species of sympatric prey (Keddy, 2001). Consequently, the two species of prey appear to be in competition with each other, and the rare competitor may be threatened by increased predation (DeCesare et al., 2010; Wielgus, 2017). The endangered Sierra Nevada bighorn sheep is preyed upon by mountain lions, but the dynamics of the mountain lion population are dependent upon more numerous mule deer (*Odocoileus hemionus*), and results in the bighorn sheep population being threatened by higher rates of predation from mountain lions than if mule deer occurred at lower densities or were not present (Johnson et al., 2013).

In western North America, mountain lions, mule deer, and bighorn sheep often share ranges, seasonally or year-round (Wehausen, 1996; Holl et al., 2004). In some areas, mule deer have been implicated in negatively affecting bighorn sheep by potentially impeding population growth or contributed to declining populations of bighorn sheep (Wehausen, 1996; Holl et al., 2004; Rominger et al., 2004; Holl and Bleich, 2009, 2010). Such outcomes ostensibly have occurred because mountain lions have switched prey from mule deer to bighorn sheep following declines in numbers of mule deer (Holl et al., 2004; Holl and Bleich, 2009, 2010; Rominger, 2018), although prey switching may not always occur (Villepique et al., 2011). Risk of predation also may have caused bighorn sheep to abandon useable habitat (Wehausen, 1996; Rominger, 2018), although other environmental explanations are plausible (Villepique et al., 2015). Thus, the abundance and distribution of predators are essential considerations when re-establishing populations of bighorn sheep, and likely will receive increasing emphasis in the future.

6. Disease and restoration

Disease long has been recognized as a primary hindrance to the persistence of bighorn sheep populations (Gross et al., 2000; Zeigenfuss et al., 2000; Singer et al., 2000b). Nonetheless, new discoveries, particularly with respect to ovine pneumonia as subsequently described, have greatly clarified the scope and significance of the problem. Indeed, the issue of pathogen transmission has become one of the central challenges to bighorn sheep restoration. Since attempts to restore bighorn sheep to historic range began, disease likely has played a primary role in failures noted in some reviews of translocations (Singer et al., 2000c, 2001). For instance, in 1971, bighorn sheep were translocated to an enclosure within the Lava Beds National Monument in northeastern California (Blaisdell, 1972). In 1980, after contact with domestic sheep, all individuals within the enclosure died from respiratory pneumonia (Foreyt and Jessup, 1982). Subsequently, as agencies struggled to manage new outbreaks, elimination of entire populations—whether native or restored—at times has been deemed necessary to contain outbreaks, albeit with unclear success (Cassirer et al., 2018).

Evidence obtained over nearly 40 years underscores the risk of disease transmission to wild sheep from domestic sheep or goats (*Capra hircus*; Wild Sheep Working Group, 2012). Managers and researchers consistently have recommended temporal or spatial separation of domestic sheep or goats from wild sheep to reduce the potential for disease in the latter—evidence supporting this recommendation is overwhelming. The risks associated with contact between bighorn sheep and domestic sheep or domestic goats have been clearly identified by recent risk assessments and reviews (Beecham et al., 2007; Schommer and Woolever, 2008; Baumer et al., 2009;Wehausen et al., 2011; Cassirer et al., 2018), conservation management strategies or plans (George, 2009), modeling exercises or locally specific risk assessments (Clifford et al., 2009; Cahn et al., 2011; Carpenter et al., 2014; Anderson et al., 2022), and many wildlife biologists or veterinarians (Dubay et al., 2004; Garde et al., 2005; Jansen et al., 2006; Foreyt et al., 2009).

Although bighorn sheep suffer from a variety of diseases—including scabies (Boyce and Weisenberger, 2005), sinusitis (Paul and Bunch, 1978), contagious echthyma (Jansen et al., 2007), lungworm (Luikart et al., 2008), bluetongue (Singer et al., 2000a,b,c), and others—ovine respiratory pneumonia remains the primary concern for conservation of this unique large mammal (Wehausen et al., 2011; Cassirer et al., 2018). Despite clear evidence that contact between domestic sheep and bighorn sheep often resulted in fatal pneumonia among bighorn sheep, the primary pathogens had, until recently, remained unclear. Bacteria, including *Pasteurella multocida, Mannheimia haemolytica,* and *Bibersteinia trehalosi* were implicated, but presence of those species was not always consistent with a disease outbreak (Cassirer et al., 2018). The role of *Mycoplasma ovipneumoniae* as an agent predisposing bighorn sheep to other pathogens that result in respiratory disease has become increasingly apparent (Besser et al., 2008, 2012, 2013; Dassanayake et al., 2010). This pathogen is spread from domestic sheep or domestic goats to bighorn sheep by incidental contact, but then can spread readily among bighorn sheep populations following conspecific contact with infected individuals.

At first contact with a novel strain of *M. ovipneumoniae*, all-age die-offs of bighorn sheep frequently are observed (Cassirer et al., 2018). Although animals that survive an initial outbreak appear to maintain immunity for some years, juveniles are naïve, and mortality within the first 4–6 months after birth frequently is high for several years following exposure (Cassirer and Sinclair, 2007; Smith et al., 2014), leading to consistent suppression of recruitment (Butler et al., 2018). Moreover, adult immunity is strain-specific (Cassirer et al., 2017). Thus, continued contact with domestic sheep, or with other bighorn sheep infected with differing strains of *M. ovipneumoniae*, can result in a new cycle of all-age mortality, followed by suppression of juvenile recruitment that slows, or even prevents, population growth (Manlove et al., 2016; Cassirer et al., 2017), as well as reduction in size and growth rate of sexually selected traits (e.g., horn length; Martin et al., 2022). Virulence appears to differ among strains of *M. ovipneumoniae* (Johnson et al., 2022), and other factors (host-related or environmental) likewise also cause epidemics to have widely varying effects on adult and juvenile survival (Manlove et al., 2022).

Recent research has demonstrated that removal of chronically infected adult females from wild populations can increase juvenile recruitment (Garwood et al., 2020), but that strategy may be logistically challenging to implement in some systems; when prevalence is low, natural mortality may also remove carriers and allow recovery at least temporarily (Besser et al., 2021). Modeling of *M. ovipneumoniae* disease dynamics indicates that depopulation and restoration can assist recovery following an epidemic (Almberg et al., 2022). Indeed, following rapid depopulation of bighorn sheep in the Montana Mountains of northwestern Nevada, United States, in 2015 after detection of a new outbreak of *M. ovipneumoniae* with high mortality, that strain was not detected in subsequent monitoring of the nearby Trout Creek metapopulation of bighorn in southeastern Oregon (Spaan, 2022). Depopulation is likely considered more readily in systems of restored rather than native populations.

Earlier cautions that translocations pose a risk of establishing new lines of transmission of pathogens (Bleich et al., 1990a) have been verified. Newly translocated individuals often range widely and explore new habitats (Robinson et al., 2019), during which contact with livestock becomes more likely, and translocated animals may return to their native area even if moved far from their initial point of capture (Torres et al., 2000). Translocated individuals also may be linked to other nearby populations through natural movements (Epps et al., 2007, 2010). Thus, establishing a new population in an area with a high risk of contracting pathogens, either from wild conspecifics or domestic sheep, could result in inadvertent spread of the pathogen to previously unexposed populations within the region. Consequently, some otherwise suitable habitats may not be available for restoration under existing conditions (Shannon et al., 2014).

The lingering debate over which pathogens play a primary role in outbreaks of respiratory pneumonia clarifies one of the greatest problems with translocation: how can surveillance be conducted for pathogens for which their pathogenicity is unknown? Although managers were well-aware of the risks of disease from contact with domestic livestock, translocations prior to *ca.* 2012 may have spread *M. ovipneumoniae* to other herds or metapopulations of bighorn sheep. For instance, archived serum samples demonstrated that populations within California's Mojave Desert showed evidence of previously unrecognized exposure to *M. ovipneumoniae* as early as 1986 (Shirkey et al., 2021), including some bighorn sheep used as source stock for within-state translocations (Bleich et al., 1990b).

Recently, a transmissible sinus tumor has been identified (Fox et al., 2011, 2016) that is associated with co-infection by *M. ovipneumoniae*, and may contribute to chronic shedding of that pathogen (Fox et al., 2015). Adult females that persistently carry and chronically shed *M. ovipneumoniae* appear to be an important mechanism causing persistent juvenile mortality (Plowright et al., 2017; Garwood et al., 2020). Thus, sinus tumors may have played a role in facilitating chronic shedding of *M. ovipneumoniae* and furthered the spread of the pathogen through translocation. Therefore, any movement of animals must be acknowledged as having some risk of spreading previously unrecognized pathogens.

Management guidelines developed in the recent past advocate health assessments for source and recipient populations prior to and following translocations. If the presence of pathogens is confirmed, or if substantial uncertainty regarding health status of either the source or recipient (or nearby) populations exists, translocations should be avoided (Brewer et al., 2014). Even when such guidelines are followed, however, the potential for spillover or pathogen transmission between wild populations remains a reality (Werdel et al., 2020).

Finally, tradeoffs between the benefits and costs of inter-population connectivity are of concern, especially for landscapes where large-scale restoration of bighorn sheep was, or is, required. In most ecosystems, bighorn sheep exist in naturally or anthropogenically fragmented populations or groups. As described previously, movement among such populations is critically important to maintain genetic diversity, facilitate demographic rescue, or allow for recolonization of vacant habitat following a local extirpation (Bleich et al., 1990a; Epps et al., 2006). Therefore, when re-establishing bighorn sheep across landscapes, a metapopulation is the ideal distribution to enable these processes to approximate demographics observed in largely intact systems by creating local populations that could be linked by natural dispersal. Yet, that same inter-connectedness likewise provides simultaneous opportunities for the spread of pathogens by contact, as observed in Rocky Mountain bighorn sheep in the Hells Canyon system (Cassirer et al., 2017). One strategy to ameliorate this tradeoff would be to establish systems of populations potentially linked by dispersal but separated from other such systems either by distance or by potential barriers.

7. Conservation, restoration, and the role of hunting

The genesis of current efforts to restore bighorn sheep began with total protection in many jurisdictions during the late 1800s. At that time, total protection was a good-faith effort to halt the decline of bighorn sheep, and it occurred at a time when it was desperately needed; nevertheless, that status ultimately hindered or confounded efforts to conserve or restore bighorn sheep to their historical ranges. For example, in California, such protection was completely insufficient, and indirectly hindered conservation by discouraging allocation of resources to non-game species; the results were inadequate inventory data, absence of awareness that populations were disappearing—with the result that there were no efforts to stop those losses—and, subsequently, a lack of incentive for active management (Wehausen et al., 1987; Bleich, 2006; Bleich and Weaver, 2007).

Continuing losses indicated that legislative protection did not affect factors that led to extirpations; the notion that total protection would stop any declines likely revolved around the mistaken assumptions that: (1) over-hunting was a cause of extirpations, and (2) that protected populations would increase in size and expand into unoccupied habitat. Both of those assumptions were faulty (Wehausen et al., 1987). The first failed to consider the potential role of diseases and habitat destruction, and the second was erroneous, because some mountain sheep may be slow to disperse from occupied ranges (Geist, 1971).

Many may view with irony the essential role that hunting has played in the restoration of bighorn sheep and other large mammals in North America. Thus far, funds from hunting that have helped with restoration have been a remarkable conservation success, as a result of efforts by wildlife and land management agencies, conservation organizations, concerned members of the academic community, private landowners, and other stakeholders (Heffelfinger et al., 2013; Krausman and Bleich, 2013; Hurley et al., 2015; Bleich, 2018). Among those stakeholders have been individuals that hunt "big game," and numerous conservation organizations that support the scientific management and legal harvest of bighorn sheep (Hurley et al., 2015). Indeed, regulated hunting has played an extremely important role in the restoration of bighorn sheep, both directly and especially indirectly, through provision of funds to implement restoration efforts (Williamson, 1987; Regan, 2010).

Bighorn sheep likely experience the most conservative management of hunted species in North America (LaSharr et al., 2019). As a result, both government and non-governmental organizations have seized opportunities to generate funds specifically for restoration, and millions of US dollars are raised for that purpose through the sale of special permits on an annual basis (Hurley et al., 2015). In the United States and Canada, where most hunting opportunities occur on federal or crown lands, sale of those permits are largely cooperative efforts between state or provincial wildlife agencies and nongovernmental organizations having a special interest in the conservation of bighorn sheep (DiGrazia, 1999). In Mexico, however, most efforts to re-establish bighorn sheep populations have occurred on private land. Financial incentives through the sale of permits by private landowners have resulted in widespread and incredibly successful efforts to restore bighorn sheep to historically occupied mountain ranges in that country (Brewer and McEnroe, 2020). Regardless of the source, available funds will be stretched further as the human population continues to increase, and subsequent demands on the environment create new challenges to conservation (Krausman and Bleich, 2013; Bowyer et al., 2019).

The restoration of bighorn sheep populations through translocation is extremely costly, and costs continue to escalate; for example, from 1983 to 1989 the average cost of translocating a bighorn sheep ($n = 336$) was $ 2,257 (Bleich, 1990). Corrected for inflation, the average cost was $6,025/animal translocated during 2022. Although agencies provide the bulk of funds associated with translocation efforts, monies generated through the sale of hunting permits, whether through special opportunity permits (i.e., fund-raising tags) made available by conservation agencies, First Nations or Tribes, or enterprising landowners that have realized the financial benefits of bighorn sheep on their property, have played important roles in the conservation of these iconic ungulates. For example, one organization that is comprised largely of hunter-conservationists has raised approximately $136 M since 1977, and from 2011 to 2021 alone, that organization contributed $49.75 M toward bighorn sheep conservation (Wild Sheep Foundation, 2022). Dozens of similar organizations have contributed millions of dollars more specifically to conserve or restore bighorn sheep on an annual basis (Hurley et al., 2015). Fortunately, an increasing proportion of the public is gaining an appreciation of the importance of a broad funding base for wildlife conservation, and "… it is appropriate [and essential] that all citizens contribute to the cost of wildlife conservation" (Regan, 2010), nonetheless, it is essential that even more people understand and practice a conservation ethic. Funds raised through the sale of special opportunity tags are but one example of that conservation ethic and continue to play an important role in efforts to conserve bighorn sheep across North America. We anticipate that source of stakeholder funding will become even more important in the future.

8. Future considerations

While translocation has been the primary tool used to re-establish bighorn sheep in alpine, desert, and other ecosystems across western North America, future use of that method may be more limited (Bleich et al., 2021). Reducing risk of spillover of disease from domestic livestock is critically important to the effective restoration of this species, and future translocation efforts must squarely confront ways to minimize contact with domestic sheep or goats. In many regions, particularly those with large numbers of small private landowners with livestock, the risk of pathogen spillover simply may be too great to overcome. Thus, managers may need to shift from a paradigm where "excess" individuals from successful populations were used primarily as translocation stock to a new paradigm where both males and females are subject to hunter harvest.

Harvest of female bighorn sheep remains uncommon, but it is practiced in several states and provinces (Monteith et al., 2013, 2018;

LaSharr et al., 2019). A male-biased harvest, however, has a limited effect on population dynamics of ungulates, because abundance of males has little influence on nutrition of females and, consequently, recruitment of young into the population (McCullough, 1979, 2001; Bowyer et al., 2014, 2020; Monteith et al., 2018). Thus, female harvest offers a beneficial, but underused, management option for regulating density-dependent processes for many ungulate populations by holding populations below *K* (ecological carrying capacity; Monteith et al., 2018). Consequently, females occupy the principal role in the dynamics of most ungulate populations, and female harvest can allow managers to manipulate population size to decrease nutritional limitations and competition for resources (McCullough, 1979, 2001; Solberg et al., 2002), or to decrease the potential for pathogen transmission by reducing population density. Moreover, body mass and fat reserves of females are strongly related to horn size in mature male bighorn sheep—a management objective for many populations of these ungulates (LaSharr et al., 2019). The decision to implement such harvests, however, rests on several biological and sociological considerations.

Translocation is subject to other constraints as well—the growing recognition that moving animals always includes risk of moving diseases. In some instances, lack of public support for efforts that may increase risk of death of translocated individuals may require removal of apex predators, or otherwise raise concerns about animal welfare. Managers also face continued uncertainty about the appropriateness of allowing mixing of bighorn sheep from different evolutionary lineages, or continued questions about the most appropriate source of bighorn sheep to be used in restoration efforts (Epps et al., 2019). Finally, because of the lingering legacies of founder effects and genetic bottlenecks, managers face questions about how best to manage for genetic diversity while limiting disease transmission risk among bighorn sheep—both from natural movement and translocation. Little is yet known about how variation in genetic diversity contributes to success of restored populations, beyond examples of extreme isolation and inbreeding (e.g., Hogg et al., 2006), and this remains an active and important area of consideration for ensuring the long-term success of extensive restoration efforts in the 21st century.

Author contributions

JW, VB, RB, and CE designed the study and wrote an initial draft of the manuscript and finalized it. All authors contributed to the article and approved the submitted version.

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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.

Publisher's note

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From conception to recruitment: Nutritional condition of the dam dictates the likelihood of success in a temperate ungulate

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Maternal effects are the influence of maternal phenotype and the maternally-provided environment on the phenotype (i.e., expression of traits) of offspring. Frequently, maternal effects are manifest both before and after parturition. Pre-parturition effects are primarily direct allocation of energy to the offspring that is *in utero*. Post-parturition effects can include direct (e.g., nursing and defending offspring) and indirect (e.g., selection of habitat that is relatively safe or has high nutritional value) influences. While both direct and indirect effects are often discussed, there is a paucity of information on the relative importance of each type on offspring due to the difficulty in monitoring mothers prior to parturition and mother-offspring relationships after parturition in free-ranging animals. Our objective was to determine the importance of direct maternal effects on birth weight, growth rates, and survival of mule deer (*Odocoileus hemionus*) fawns from birth through the first 18months of life. We determined the effect of nutritional condition of the dam (mother) on birth weight (pre-parturition direct effect). We also examined the post-parturition direct effect of dam nutritional condition on growth rates and survival of fawns. Direct maternal effects were evident both before and after parturition; dams in better nutritional condition produced offspring with greater mass at birth, higher rates of growth, and increased survival. Our findings demonstrate that maternal nutritional condition influences fawn health from gestation through recruitment. These links highlight the importance of considering direct maternal effects when examining population dynamics and reproductive success in long-lived mammals. Management plans for ungulates should include assessment of nutritional condition of adult females to maximize likelihood of effective conservation.

KEYWORDS

maternal condition, mule deer, *Odocoileus hemionus*, recruitment, neonate survival, birthweight

1. Introduction

Maternal effects are the influence of maternal phenotype and "the maternally provided environment" on the phenotype (i.e., expression of traits) of offspring (Bernardo, 1996; Wolf and Wade, 2009). Life history theory posits that females must balance their own needs and probability of survival with current and future reproductive events (Festa-Bianchet et al., 1998;

Marshall and Uller, 2007). When resources are abundant, females often produce larger or more offspring by allocating more energy toward current reproduction (Haywood and Perrins, 1992; Bardsen et al., 2008). However, when resources are scarce, females often allocate less energy to current reproduction (e.g., produce smaller and fewer offspring) to maximize lifetime fitness (Smith and Fretwell, 1974; Einum and Fleming, 2000). Producing smaller offspring potentially decreases current maternal reproductive success in exchange for enhancing survival to a future reproductive bout. Therefore, maternal effects may have a positive or negative influence on the fitness potential of offspring (Kirkpatrick and Lande, 1989; Marshall and Uller, 2007; Freeman et al., 2013). Because of this maternal influence on fitness and production, effective conservation can only be achieved with an understanding maternal effects.

Identifying the life-history traits of offspring that are influenced by maternal effects can be difficult, as there are numerous mechanisms driving both life-history traits and maternal effects (Kirkpatrick and Lande, 1989; Benton et al., 2001). Maternal nutritional condition and subsequent energy allocation have been shown to influence offspring traits, including size at birth (Feiner et al., 2016), growth rate (Haywood and Perrins, 1992), survival (Duquette et al., 2014), age at first reproduction, and fecundity. Nonetheless, maternal effects may disappear after the period of maternal care (Gendreau et al., 2005) or be masked by the influence of environmental conditions in long-lived species (Hewison and Gaillard, 1999). Further, relatively little is known about the importance of maternal effects in large, long-lived species due to the difficulty of studying maternal-offspring relationships in free-ranging mammals. Therefore, determining the duration of maternal effects can be challenging but is critically important for understanding life-history, and can have important implications for conservation.

Ungulates provide a model system to study the duration of maternal effects because they are iteroparous and long-lived (Freeman et al., 2013). Short-term maternal effects, from birth to weaning and during early-life growth, exist in some ungulate species (Kojola, 1993; Wauters et al., 1995; Festa-Bianchet and Jorgenson, 1998). Long-lasting maternal effects may also be present. An intergenerational maternal effect exists on growth and size at maturity in white-tailed deer (*Odocoileus virginianus*; Monteith et al., 2009). Additionally, maternal effects last into adulthood for antler growth in elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*), a sexually selected trait that influences fitness potential (Freeman et al., 2013). Despite some evidence for both short- and long-term maternal effects, maternal effects among offspring of ungulate species from early life through recruitment are not well understood.

Maternal effects can manifest both before and after parturition (Bernardo, 1996). However, there has been little differentiation between effects *in utero* or during rearing of offspring. Pre-parturition effects are primarily direct allocation of energy to the offspring that is *in utero* (Robbins and Robbins, 1979). Nevertheless, both direct and indirect maternal effects can influence offspring post-parturition. For example, direct effects include energy and nutrient allocation such as milk to nursing young and indirect effects include protection of young (Wolf and Wade, 2009), habitat selection, and maternal care other than nursing (Bernardo, 1996).

Here we focus on direct maternal effects in mule deer fawns. Our objective was to determine the importance of direct maternal effects on birth weight, growth rates, and survival of neonates through 18 months of life. More specifically, we examined the influence of nutritional condition of dams on birth weight, growth rates, and survival of offspring. We hypothesized that maternal nutritional condition would influence offspring both while *in utero* (birth weight) and throughout the lactation period (growth rate and survival). We predicted that greater maternal condition would be correlated with increased birth weight, growth, and survival of fawns. We predicted that greater maternal condition would lead to larger body sizes for fawns at 6 months of age and that larger fawns would have a greater likelihood of survival through their first winter to recruitment at 18 months of age.

2. Materials and methods

2.1. Study area

We conducted this study on the Cache Management Area in northern Utah, United States. This area comprised a portion of the Bear River Range and consisted of federal, state and private lands. Land uses in this area included crop cultivation, agricultural grazing, forest recreational use, and private residences. The topography included steep mountains, deep canyons and high mountain valleys with elevation that ranged from 1,300 to 3,000 meters. The area was comprised of high elevation coniferous forest and lower elevation shrub steppe habitats. High elevation forests were predominantly comprised of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea englemannii*), and white fir (*Abies concolor*). Low elevation shrub steppe was dominated by sagebrush (*Artemisia tridentate*), bitterbrush (*Purshia tridentate*), snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), and aspen (*Populus tremuloides*). Mule deer in this system typically migrated from relatively high elevations to low elevation each fall (e.g., November) and returned to high elevations each spring (e.g., April–May). Potential competitors of mule deer included elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), domestic cattle (*Bos taurus*), and domestic sheep (*Ovis aries*). Primary predators of mule deer included coyote (*Canis latrans*) and mountain lion (*Puma concolor*). Average annual temperature ranged from 7 to 27° C during the summer and from −10 to 2° C during the winter, with average annual precipitation of 80 cm per year, the majority of which occurred during winter (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, accessed 15 Jan 2021).

2.2. Capture of adult female mule deer

During March of 2018–2020, we captured adult female deer *via* helicopter net-gunning (Barrett et al., 1982; Krausman et al., 1985; White and Bartmann, 1994). Individuals were hobbled, blindfolded, and transported to one of four processing stations in the study area. We recorded weight, body size (hind foot length, chest and neck girth), nutritional condition, and age (estimation based on tooth wear; Severinghaus, 1949; Robinette et al., 1957) of each captured female prior to release. We estimated nutritional condition by estimating ingesta-free body fat using ultrasonography measures of rump fat and loin muscle thickness, body weight, and a palpation score (Cook et al., 2004, 2010). We determined pregnancy *via* transabdominal ultrasonography (E.I. Medical Imaging portable ulstrasound; Smith and Lindzey, 1982). Pregnant females were fitted with GPS collars equipped with Neolink technology and a vaginal implant transmitter (VIT; Model M3930U, Advanced Telemetry Systems Inc., Isanti, MN, United States) with a temperature and light sensitive switch (Bishop et al., 2007). Neolink radio-pairing technology in the GPS collar monitors the status of the VIT and allows remote monitoring of both VITs and neonate collars *via* the mother's collar. When VITs were expelled from deer during parturition and the VIT detected light or a temperature below 32°C, the VIT broadcast a birth message to the GPS collar. The birth message sent to the GPS collar triggered an email alerting us of the birthing event. In addition, the very high frequency (VHF) beep pattern of the VIT also changed from a 30 ppm pattern to a 60 ppm pattern. Because we were interested in maternal effects through early life, only those females that lived through December were incorporated in the study.

2.3. Neonate capture and monitoring

When an email alert of a birthing event was received, we waited at least 6 h to allow time for bonding between adult and offspring before beginning our search for neonates (Heffelfinger et al., 2018). We used a combination of the GPS location, from the adult collar at the time the VIT was expelled, and radio-telemetry to locate the VIT and parturition site. Once the VIT was located, we performed a systematic search to locate neonatal fawn(s). Upon discovery of neonates, we fitted them with a Neolink series VHF, mortality-sensing, drop-off radio collar (Model M4230BU, Advanced Telemetry Systems, Isanti, MN, United States). We recorded several measurements including weight, chest girth, hind foot length, and new hoof growth. We measured new hoof growth as a secondary measure of neonate age because the birth of some fawns was delayed from the time the VIT was expelled (to estimate the age of the neonate(s); Haugen and Speake, 1958; Robinette et al., 1973; Sams et al., 1996; Lomas and Bender, 2007). We handled neonates with nitrile gloves, kept handling time to a minimum, and replaced them at site of capture in order to reduce the transfer of human scent and the likelihood of maternal abandonment.

If the neonate collar remained motionless for 8 h, a mortality warning was also sent and the VHF beep-pattern increased from 30 to 60 ppm. We attempted to locate neonates within 24 h of a mortality notification in order to determine cause of mortality. After locating a mortality, we searched for the fawn carcass and examined evidence found at the mortality site. We used field or lab necropsies to determine cause of death and classified mortalities into the following causes using criteria from the literature: bobcat predation, cougar predation, coyote predation, unknown predation, malnutrition/disease, accident, capture related, and unknown (White, 1973; Gese and Grothe, 1995; Stonehouse et al., 2016). We did not analyze cause of death relative to nutritional condition of the dam because sample size was too small to determine relationships between nutritional condition and the many causes of death. All handling of animals was approved by the Institutional Animal Care and Use Committee at Brigham Young University, and was in accordance with guidelines of the American Society of Mammologists (Sikes, 2016).

Growth rate was determined by subtracting birth weight from weight at 6 months of age and dividing by the number of days between captures. To bolster our sample size of fawns monitored from 6 months of age to 18 months of age, we captured uncollared fawns each December. These new animals were captured at the same time we captured collared fawns to determine body weight and growth rate of neonates when they had reached 6 months of age. The data collected on new fawns that were captured for the first time during December each year included sex and body weight. These new animals were only included in our analysis of the relationship between body weight and the likelihood of survival from 6 months to 18 months of age.

2.4. Statistical analyzes

We used generalized linear models and model selection in program R (version 4.0.2) to determine the influence of maternal effects on birth weight and growth rate of neonates, and body size at 6 months. In addition to the base program, we used the MuMIn package to rank models and the ggplot2 package to produce figures (Wickham, 2016; Barton, 2020). We used the explanatory variables maternal age and condition, neonate birth weight, sex, presence of twin, hoof growth, capture date, year of birth, and fawn growth. We formulated a list of *a priori* models for each of the response variables including birth weight, growth rate, and body size at 6 months of age. Prior to construction of models, we evaluated variables for multicollinearity and excluded explanatory variables that were correlated ($r > |0.50|$) in the same model. We evaluated and ranked *a priori* models using Akaike's Information Criteria adjusted for small sample sizes (AICc) and AICc weights (Akaike, 1973; Anderson and Burnham, 2002). We considered strongly competing models to be those with ΔAICc <2. In the event of competing models, we averaged β coefficients from models that carried >5% AICc weight.

We evaluated survival from birth to 6 months of age, and from 6 months of age to 18 months of age using Cox Proportional Hazard (CPH) models using the s package in program R (Therneau, 2015). CPH models allow for estimates of survival for each individual, based on sampled variables and varying time components (Cox, 1972; Fox and Weisberg, 2002). Time components for survival to 6 months included monthly survival from zero to 6 months of age, and a comparison of survival between the first month of life and months two through six following parturition. Potential explanatory variables included maternal nutritional condition, neonate sex, birth weight, presence of a twin, and day relative to mean date of parturition. We modeled survival to 18 months of age as a daily time step. Because some of the additional juveniles sampled had unknown parentage, we limited variables included in this model to sex, year, and capture weight. We determined the most influential factors associated with neonate survival to 6 months and juvenile survival to 18 months. Similar to the generalized linear models, we first formulated *a priori* models and then ranked them based on minimization of Akaike's Information Criteria adjusted for small sample sizes (AICc) and AICc weights (Akaike, 1973; Anderson and Burnham, 2002).

3. Results

Between March of 2018 and March of 2020 we captured and marked 89 female mule deer with GPS collars. Of these adults, 22 individuals were captured in two consecutive years and one individual was captured all 3 years for a total of 112 capture events. Average ingesta-free body fat (IFBF) for adult females was 6.06% in 2018, 4.34% in 2019, and 6.26% in 2020. Ultrasonography revealed that 106 of 112 (95%) captured animals were pregnant. We captured neonates from 61 collared adult females. In three fawning seasons we located 104 neonates and captured and collared all 98 individuals (6 were stillborn). Over the course of the study we observed 39 sets of twins, and 20 singletons. Of neonates captured, 49 were male and 49 were female. Parturition dates ranged from 28 May to 29 June. Mean date of parturition was June 8th, 14th, and 9th during 2018–2020, respectively. Between December of 2018 and December of 2020, we captured and collared 59 mule deer fawns at approximately 6 months of age. Of the 59 juveniles captured, 27 were individuals originally captured as neonates. Average weight was 30.5 kg in 2018 (SE = 1.2), 31.0 kg in 2019 (SE = 0.8), and 33.6 kg in 2020 (SE = 1.0).

We examined the influence of maternal IFBF on birth weight for 98 neonates. Explanatory variables associated with timing of parturition (mean, median, onset) were highly correlated ($r > |0.50|$) along with onset and hoof growth. Thus, we did not include these variables together in the same model, but did allow them to occur across models for evaluation. Out of 23 candidate models, the top model examining neonate birth weight accounted for 78.4% of the AICc weight compared to 15.4% for the second-ranked model (no competing models, ΔAICc<2; Table 1). The most supported model included influence of twin, sex, hoof growth, IFBF, and maternal age. As predicted, birth weight of neonates was positively related to IFBF. On average for females with the lowest IFBF, neonates weighed 3.0 kg at birth (SE = 0.1). For females with higher IFBF, neonates averaged 3.5 kg at birth (SE = 0.1; Figure 1). Presence of a twin was associated with lower birth weight. On average, neonates associated with a twin weighed 0.2 kg less than those that were singletons. Age was in the top model but confidence intervals around the estimate overlapped zero. Hoof growth was positively associated with birth weight, but of limited relevance. Measurement of hoof growth is used to determine age of neonate at capture, and older neonates would be heavier than those captured closer to parturition. Males were also associated with greater birth weight (Table 1).

Growth rate of neonates from birth to 6 months of age was related to nutritional condition of the dam. We had four competing models (ΔAICc<2) and averaged all models that carried >5% AICc weight. The averaged models had a cumulative weight of 65.3% (Table 1). Variables in supported models included maternal IFBF, birth weight, sex, and presence of a twin. Maternal IFBF during gestation was positively related to growth through the first 6 months of life. On average neonates from females with higher IFBF grew at a rate of 5.2 kg per month (SE = 0.2), while those from females with low IFBF grew at a rate of 4.4 kg per month (SE = 0.2; Figure 2).

Our top CPH model for neonate survival to 6 months accounted for 50% of the AICc weight (no competing models, ΔAICc<2.0) and included the influence of maternal IFBF, a variable time component of month one versus months 2–6, and whether the neonate was born before or after the peak of parturition (Table 1). Neonate survival to 6 months was positively influenced by maternal IFBF. Neonates born to females with higher IFBF had a higher likelihood of survival than neonates from females with lower IFBF (Figure 3). There was a lower likelihood of survival in month one compared to months two through six, especially for fawns born after peak parturition.

We also examined the influence of maternal IFBF on body size at 6 months for 59 individuals. The top model, with 43% of the AICc weight included maternal age and birth weight (Table 2). After

TABLE 1 Model selection results for response variables of birthweight, growth, and survival to 6 months of age for mule deer (*Odocoileus hemionus*) in northern Utah, United States, 2018–2020.

	K	LogLik	AICc	ΔAICc	Weight
Birthweight					
Twin+Sex+IFBF+Hoof+AdAge	7	−100.4	215.9	0.00	0.78
Year+Twin+Sex+IFBF+Hoof+AdAge+Date	10	−98.4	219.2	3.25	0.15
Year+Twin	5	−106.9	224.4	8.47	0.01
Year+IFBF	5	−107.3	225.2	9.27	0.01
Twin+IFBF	4	−108.4	225.2	9.31	0.01
Growth: IFBF+Birthweight	4	−25.1	60.0	0.00	0.39
IFBF+Sex+Birthweight	5	−24.9	62.6	2.56	0.11
IFBF+Twin+Birthweight	5	−25.1	63.1	3.04	0.09
Birthweight	3	−28.5	64.0	3.92	0.06
IFBF	3	−28.6	64.3	4.24	0.05
Survival: Mo1 + EvL + IFBF	3	−282.4	570.9	0.00	0.50
Month+EvL + IFBF+Month^2	4	−282.8	573.7	2.87	0.12
Month+EvL + IFBF	3	−284.0	574.2	3.29	0.10
Halves+EvL + IFBF	3	−284.1	574.3	3.46	0.09
Halves+EvL	2	285.7	575.4	4.53	0.05

IFBF is ingesta free body fat of the dam; AdAge represents age of the dam; Hoof represents hoofgrowth of the neonate (i.e., an estimate age); Date represents Julian date of neonate capture; Mo1 represents the first month of life; EvL represents birth timing relative to mean date of parturition; Month^2 represents month squared to account for non-linear growth of the neonate; Halves represents dividing the first 6 months of life into equal halves. We report model structure including variables in top model (see footnote), number of parameters (K), log likelihood (LogLik), Akaike's Information Criterion adjusted for small sample sizes (AICc), delta AICc, and model weight.

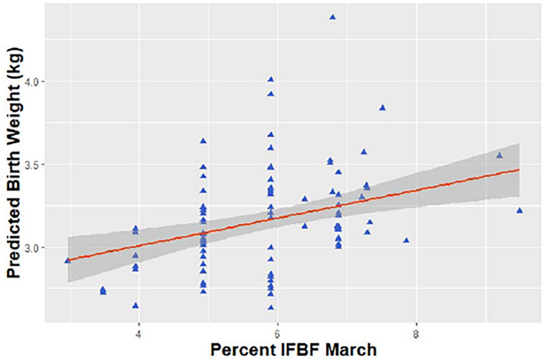

FIGURE 1
Predicted relationship between birth weight of neonatal mule deer (*Odocoileus hemionus*) and maternal condition (measured in March) in northern Utah, United States, 2018–2020.

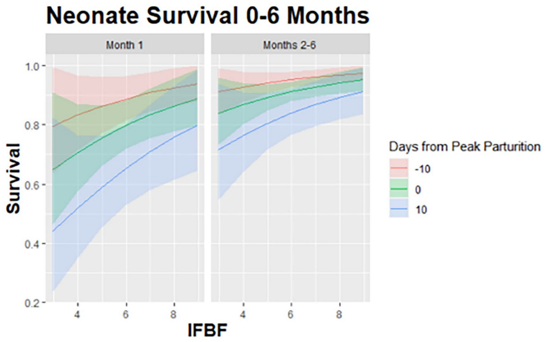

FIGURE 3
Predicted relationship for survival of neonatal mule deer (*Odocoileus hemionus*) to 6 months of age based on maternal condition and birth timing (EVL) in northern Utah, United States, 2018–2020.

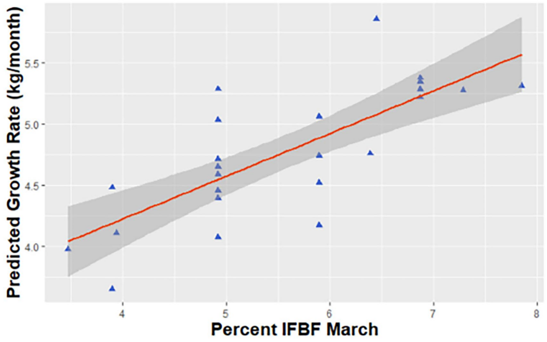

FIGURE 2
Predicted relationship between growth of neonatal mule deer (*Odocoileus hemionus*) to 6 months of age and maternal condition in March for animals from northern Utah, United States, 2018–2020.

accounting for the effect of maternal age and birth weight, the next ranked model, with 24% of the AICc weight, included maternal IFBF. While the effect was not as strong as at birth, juveniles from females with higher IFBF weighed an average of 4.1 kg more than juveniles from females with lower IFBF (SE = 1.3; Figure 4).

Our top CPH model for survival from six to 18 months accounted for 87% AICc weight. Our most supported model of survival included the influence of weight and year (Table 2). As predicted, larger fawns had a greater likelihood of survival. Deer fawns weighing 35 kg at 6 months of age had at least a 50% probability of survival (Figure 5). Year of birth was a random effect in our models that also influenced survival likely due to the variation in summer precipitation (i.e., food availability) and winter severity among years.

4. Discussion

The study of maternal effects to determine phenotypic quality of offspring has become foundational for understanding life-history characteristics (Kirkpatrick and Lande, 1989; Bernardo, 1996). Until recently, technological constraints have limited the ability to monitor free-ranging ungulates and their offspring. Recent technological advancements, however, allow insight into the relationship between maternal nutritional condition and outcomes for offspring (Johnson et al., 2019). These advances have enabled the more precise study of mother-offspring relationships and the natural history of mule deer during early life. Nutritional condition of the dam has been linked to increased survival of neonatal mule deer to 140 days (Monteith et al., 2014). Here, for the first time, however, we connect the influence of maternal nutritional condition to indicators of health (including survival) in mule deer from birth to recruitment at 18 months of age. Consistent with other ungulates, nutritional condition influenced neonatal mule deer both before (e.g., birth weight of neonate mule deer) and after (e.g., growth rate and survival of neonate mule deer) parturition (Duquette et al., 2014; Feiner et al., 2016). Consistent with our prediction, increased nutritional condition of the dam was correlated with increased birth weight, growth rate, and survival of fawns to 6 months of age. Additionally, the effects of maternal nutritional condition lasted through early life and influenced juvenile body weight at 6 months of age and survival through recruitment at 18 months of life.

Mule deer experienced a pre-parturition direct effect of allocation of energy to offspring *in utero*, manifest as birth weight. Our findings indicate that nutritional condition of females (measured as IFBF) during gestation had a significant impact on birthweight of offspring. Fawns born to females in relatively good nutritional condition were approximately 40% heavier at birth, which could lead to greater potential fitness (Monteith et al., 2009). This finding is consistent with previous research (Hudson and Browman, 1959; Short, 1970; Heffelfinger et al., 2018). Moreover, birth weight is a strong predictor of growth and survival (Monteith et al., 2014).

Post-parturition direct effects were also present through the lactation period, as demonstrated by the influence of maternal nutritional condition on growth rates. There is likely a correlation between quality or quantity of milk and maternal nutritional condition during gestation. The amount and quality of milk produced by the mother is important for growth and development of young (Cook et al., 2004; Tollefson et al., 2010, 2011). Adult females in better condition likely produce more or higher quality milk, which in turn provides greater energy to nursing fawns and subsequent increased growth and survival rates. While there are many environmental factors that may also influence growth to 6 months, few investigators

TABLE 2 Model selection results (Akaike's Information Criterion) from analyzes examining the effect of covariates on weight of mule deer fawns at 6 months of age and survival of mule deer fawns from 6 months of age to 18 months of age.

	K.	LogLik	AICc	ΔAICc	Weight
Weight at 6 months:					
AdAge+Birthweight	4	−71.6	153.1	0.00	0.43
IFBF+AdAge+Birthweight	5	−70.7	154.3	1.16	0.24
AdAge+Birthweight+EvL	5	−71.4	155.7	2.61	0.12
IFBF+Birthweight	4	−73.5	156.8	3.67	0.07
IFBF+Birthweight+EvL	5	−72.5	157.9	4.77	0.04
Survival from 6 to 18 months of age:					
Year+6MonthWeight	3	−109.9	226.2	0.00	0.87
Sex+Year+6MonthWeight	5	−109.4	230.0	3.89	0.12
Year	2	−119.2	242.6	16.4	0.00
6MonthWeight	1	−121.9	245.8	19.7	0.00
Sex+Year	4	−118.7	246.1	20.0	0.00

AdAge represents age of the dam; Birthweight represents the weight of the neonate at first capture; IFBF is ingesta free body fat of the dam; EvL represents birth timing relative to mean date of parturition; 6MonthWeight represents weight of the mule deer fawn when captured at 6 months of age. This study was done during 2018–2020 in northern Utah, United States.

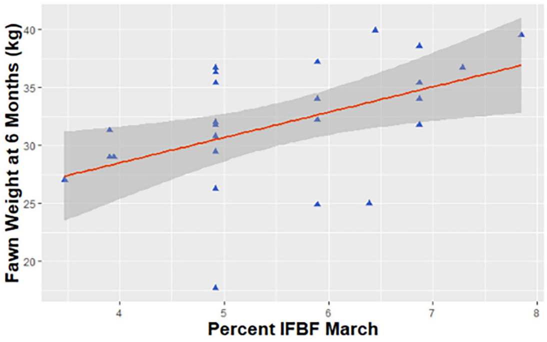

FIGURE 4
Predicted relationship between weight of mule deer (*Odocoileus hemionus*) fawns at 6 months of age and maternal condition in northern Utah, United States, 2018–2020.

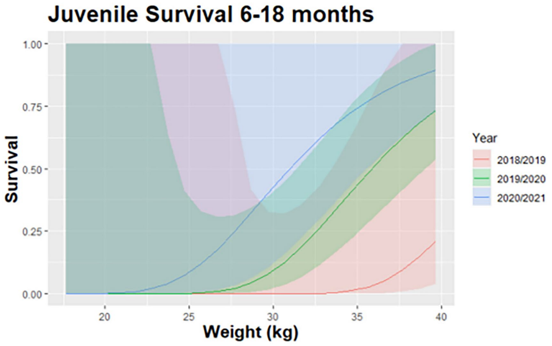

FIGURE 5
Predicted relationship between survival of mule deer (*Odocoileus hemionus*) fawns from 6 months of age to 18 months of age and juvenile weight in northern Utah, United States, 2018–2020.

have been able to recapture free-ranging juveniles to monitor growth during the initial months of life.

We were able to clearly link maternal nutritional condition to survival of juvenile mule deer after parturition consistent with current understanding in this species (Monteith et al., 2014). This effect was present even after accounting for the influence of parturition timing or Julian date that the neonate was born. Fawns have a higher likelihood of survival if their mother is in good nutritional condition and if they are born at or before the mean date of parturition. Specifically, fawns from females in the best nutritional condition, born before peak parturition had a roughly 50% greater chance of survival than fawns from females in poor nutritional condition, born after peak parturition (Figure 3). There are likely two advantages associated with being born early—the animal becomes mobile before predators have developed a search image for neonates and the neonates have extra time to grow before the onset of winter. The effects of maternal nutritional condition on survival are consistent with evidence in other ungulate species that heavier females give birth earlier (Cameron et al., 1993; Keech et al., 2000).

Our results do not support the assertion that maternal effects weaken after maternal care ends (Gendreau et al., 2005). Maternal care lessens after weaning, which occurs during late summer and early fall for mule deer (Bowyer, 1991; Tollefson et al., 2011). Here, however, we found that maternal nutritional condition influenced offspring even after weaning, as fawns from mothers in better nutritional condition were heavier when recaptured in early winter at approximately 6 months of age (Figure 4). Further, the influence of maternal nutritional condition persists through the first 18 months of life because capture weight at 6 months of age strongly predicted survival to recruitment age at 18 months. Small sample sizes of recaptured individuals with known parentage prevented us from directly examining the influence of maternal nutritional condition on survival to 18 months. Nonetheless, our data demonstrate that weight at 6 months of age influenced survival to 18 months. Therefore, we infer a connection between maternal nutritional condition, mass of fawns at 6 months of age, and survival of fawns to 18 months of age.

Understanding the link between maternal effects and population dynamics is critical for the conservation and management of mule deer and other long-lived ungulates. For example, the reproductive potential of a population is not only influenced by pregnancy rate and litter size (Noyes et al., 2002; Souza et al., 2022), but also nutritional condition of the dams that influences the survival and expression of phenotypic traits in offspring. The phenotypic traits of young ungulates likely influence all aspects of life history, beyond just survival as we have demonstrated here, including susceptibility to predation (Murray, 2002) and disease (Beldomenico and Begon, 2010), and potential size and reproductive success (Keech et al., 2000; Freeman et al., 2013) as an adult. Therefore, monitoring and managing nutritional condition is fundamental to management and conservation of mule deer, and likely other ungulate populations.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SL, BM, PF, KH, and RL conceived and designed the study. SL, BM, KH, and RL collected the field data. SL, MK, and RL conducted the statistical analysis. SL and BM wrote the manuscript with input from all authors. All authors contributed to the article and approved the submitted version.

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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.

Publisher's note

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Outcomes associated with translocation of mule deer (*Odocoileus hemionus*): Influence of age, release timing, and year on survival

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Translocation of large mammals has become common practice for wildlife managers charged with conservation of animals and their genetic integrity on increasingly modified landscapes. Translocations of ungulates have occurred around the world with varying outcomes. Although translocations have been used to manage mule deer (*Odocoileus hemionus*) in western North America, only recently have the outcomes associated with this management practice been documented. Our objective was to evaluate survival of translocated mule deer in comparison to resident mule deer over multiple years following release and provide information useful in judging the relative value of translocation as a conservation strategy for this species. In January and March 2013, the Utah Division of Wildlife Resources (UDWR) captured and translocated 102 mule deer from winter range near Parowan, Utah to winter range near Holden, Utah (approximately 145 kilometers north of capture location). We fitted each deer with a radio transmitter (n=102 total: 21 GPS collars, 81 VHF collars) prior to release. We also captured and marked a total of 70 resident deer (9 GPS collars, 61 VHF collars) to serve as a reference group. Survival of translocated deer in the first year was similar among release dates in January (0.51; 95% CI=0.40–0.63) and March (0.53; 95% CI=0.40–0.66). Annual survival of translocated deer, however, was lower than survival of resident deer (0.83; 95% CI=0.72–0.90) in the first year after release. During the second year following release, however, survival of translocated animals (0.85; 95% CI=0.71–0.93) was not different from that of resident deer (0.80; 95% CI=0.69–0.88). Additionally, age strongly influenced the survival of translocated deer; young deer (e.g., 1.5 year olds) were more than twice as likely as old deer (e.g., 7.5 year olds) to survive the initial year following translocation. These data highlight the need to monitor translocated animals for multiple years following release and suggest that wildlife managers should expect to see higher survival rates during the second year following translocation and higher survival rates in younger deer compared to older deer.

KEYWORDS

ungulate, conservation, wildlife management, movement, deer

1. Introduction

Translocation is an increasingly common strategy for managing large mammals and this approach has been applied to a variety of species in many parts of the world. Typical goals of translocation include reducing population density in the source area, supplementing existing populations in the release area, reestablishing extirpated populations, introducing new populations, and increasing genetic diversity (Griffith et al., 1989; Baxter et al., 2008). Although there have been successes, translocation efforts do not always produce positive outcomes. In a review of translocations from around the world, it was estimated that more than 25% of those involving mammals ended in failure (Wolf et al., 1996).

Reasons for failure included movement of translocated individuals out of release areas, limited reproduction by translocated individuals, and low genetic diversity due to founder effects (Mock et al., 2004; Dickens et al., 2009a). Recent evidence further suggests that translocation can alter stress physiology, thereby creating survival challenges for released individuals (Dickens et al., 2009b). For some species, a positive relationship with the number of released individuals and translocation success has been observed (Griffith et al., 1989; Wolf et al., 1996; Singer et al., 2000). For others, the details associated with the release itself (e.g., hard versus soft release or time of year) are important predictors of success (Bright and Morris, 1994). Results of translocation for large mammals often vary across species creating a need for species-specific information.

Despite decades of intensive management in western North America, outcomes associated with translocation of mule deer (*Odocoileus hemionus*) have only recently been documented. Typical results show increased movements and reduced survival for translocated animals in the initial year following release (Wakeling, 2003; Cain et al., 2018; Howard, 2018; Smedley et al., 2019; Wright et al., 2020). Annual survival of translocated mule deer during the initial year following release, for example, ranged from 15 to 79 percent which is low for this species (Wakeling, 2003; Cain et al., 2018; Wright et al., 2020). Most of these efforts, however, did not involve monitoring of translocated mule deer during their second year following release or comparison with resident deer in the release area.

Our objective was to document the outcomes associated with translocation of mule deer. More specifically, we evaluated the survival of translocated mule deer in relation to timing of release (early versus late winter) and individual covariates such as age and body condition. Mule deer released in early winter would have more time to integrate with resident deer prior to spring migration and be in relatively good condition compared to deer released in March that were expected to be in relatively poor body condition and would have less time to integrate with resident deer prior to spring migration, but perhaps more likely to stay near release areas due to their relatively poor condition. We predicted that translocated mule deer would experience lower survival rates than resident deer during the first year following release. During the second year following release, however, we predicted survival rates for translocated deer would be higher than those observed in year one, similar to what has been documented for white-tailed deer (*Odocoileus viginianus*) and elk (*Cervus canadensis*) (*sensu* Frair et al., 2007; Foley et al., 2008). We further expected covariates such as age and body condition to influence survival rates (Hawkins and Montgomery, 1969; Jones and Witham, 1990; Haydon et al., 2008).

2. Materials and methods

2.1. Study area

Translocated deer were captured from the Parowan front in southern Utah, United States which is winter range for mule deer in the Panguitch management unit (Figure 1). The predominant geographic feature in the Panguitch management unit is the Markagaunt Plateau which is approximately 91 km long (north to south) and 34 km wide (at its widest point). Mean high air temperatures during the summer and winter months over the past century were 29.4° C and 6.6° C respectively, with average annual precipitation of 31.0 cm at 1862 m (Western Regional Climate Center). Elevations across this mountain range varied from 1762 to 3,446 m. Mule deer in this area were thought to migrate seasonally using high-elevation areas in summer and low-elevation areas during winter. Habitat types at high-elevation included areas dominated by aspen (*Populus tremuloides*), bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), and Gambel's oak (*Quercus gambelli*). The winter range along the Parowan front was dominated by juniper (*Juniperus* sp.), pinion (*Pinus edulis*), and sagebrush (*Artemisia* sp.). Over the last decade, population estimates for this deer herd have exceeded management objectives and the quality of the

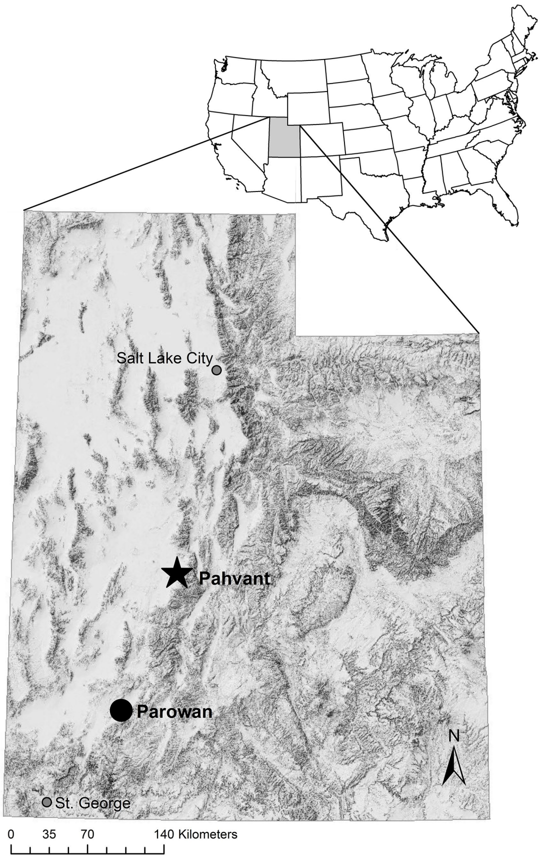

FIGURE 1
Map of Utah, United States showing our study area where the Utah Division of Wildlife Resources (UDWR) captured (circle) and released (star) mule deer (*Odocoileus hemionus*) in January and March of 2013.

winter range was rated in only poor to fair condition (UDWR, 2013, 2014).

Translocated deer were released by the Utah Division of Wildlife Resources (UDWR) onto the Pahvant mountain range (approximately 144 km north of capture areas) in central Utah (Figure 1). The Pahvant study area was chosen for release due to similarities with the Parowan capture area. These similarities included north to south mountain ranges, migratory deer herds with west to east migration, similar climates, and winter ranges bordered by Interstate 15 on the west and high-elevation mountains on the east. The Pahvant Mountain Range is approximately 54 km long (north to south) and 22 km wide at its widest point. Elevations across this mountain range varied from 1,520–3,117 m. Mean high temperatures during the summer and winter months over the past century were 31.4° C and 5.7° C, respectively, with average annual precipitation of 38.1 cm at 1,552 m (Western Regional Climate Center). The winter range along the foothills of the Pahvant mountain range was dominated by bitterbrush, cliffrose (*Purshia stansburiana*), Gambel's oak, juniper, mountain mahogany, and sagebrush. Higher elevation areas were composed of mixed brush communities, aspen, and a variety of conifers (e.g., genus *Abies* and *Pinus*) and juniper. Unlike the Parowan front, the deer population on the Pahvant range has consistently been below management objectives and the release area was considered by UDWR to consist of high-quality winter range (UDWR, 2012). Potential predators of mule deer inhabiting both the area where deer were captured from and the release area included black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*).

2.2. Capture, translocation, and monitoring

In January and March 2013, UDWR contracted with a private helicopter company to capture female mule deer *via* helicopter net-gunning (Krausman et al., 1985; Van de Kerk et al., 2020) and sling them to 3 different staging areas along the Parowan front in southern Utah (Figure 1). During handling, we weighed deer and then estimated age (*via* tooth wear and eruption pattern; Severinghaus, 1949; Robinette et al., 1957), body size (chest, hind foot length, neck girth), condition (body condition score method; Cook et al., 2007), and pregnancy (*via* transabdominal ultrasound; E.I. Medical Imaging portable ultrasound; Smith and Lindzey, 1982). Preliminary results suggest >80% accuracy within 2 years when aging mule deer in Utah from tooth wear (Hinton et al., 2023). UDWR administered 3 cc banimine and 1.5 cc ivermectin to each individual deer and fitted them with a radio collar (VHF or GPS) and unique ear tag. UDWR also conducted rectal biopsies to test for chronic wasting disease (Thomsen et al., 2012) and collected blood samples to verify pregnancy. Following the handling process, UDWR loaded mule deer in stock trailers and drove them to the Pahvant range (Figure 1) where the majority were immediately released (hard release; average of 6.9 h between capture and release; range 1.5 to 17.9 h). To serve as a reference group, resident deer in the Pahvant study area were also captured and radio-marked (VHF or GPS). Resident deer were fitted with a radio collar by the capture company and released immediately at point of capture. For additional detail on capture and release protocols see Smedley (2016) or Smedley et al. (2019).

Following release, we used radio telemetry from the ground (weekly) and fixed-wing aircraft (approximately monthly, $n = 19$ different flights over 2 years) to locate and assess the status (alive or dead) of each radio-marked deer throughout the year. When mortality signals were detected (triggered after 8 h of inactivity), we located the carcass as soon as possible to determine cause of death by postmortem examination and evidence (tracks, cached carcass, feces, etc.) from the surrounding area (Rominger et al., 2004; Kilgo et al., 2012). When we found carcasses that showed no signs of predation or vehicle impact, we collected them for necropsy by the Utah State University, Veterinary Diagnostics Laboratory. We classified mortalities as predation, undetermined, capture-related (capture myopathy and capture-related injuries), roadkill, poached, or other which included diseases not directly associated with capture.

2.3. Data analysis

We used model selection and known-fate models within Program MARK (White and Burnham, 1999) to estimate seasonal and annual survival for each group of mule deer (resident, January release, and March release) and evaluate support for covariates that included age, body mass, body condition, and pregnancy. We formatted our encounter history by month and year beginning 1 January and ending 31 December for both 2013 and 2014. Structuring our encounter history by year (i.e., year as a group) allowed us to graduate deer (in age) and easily obtain unique estimates of annual survival for resident and translocated deer in year 1 and year 2 following release. We evaluated relative model support using Akaike's Information Criterion (Akaike, 1973) adjusted for small sample sizes (AIC_c) and then used model averaging based on AIC_c weights to produce estimates of annual survival (Burnham and Anderson, 2002). To evaluate differences across groups (e.g., resident versus translocated deer), we looked for overlap in 95 percent confidence intervals associated with estimates of annual survival. To assess the influence of individual covariates, we examined confidence intervals (95%) surrounding β estimates.

We used a 3-stage, hierarchical approach to model selection to provide structure to our analysis and allow us to identify the most-supported seasonal (time), group (translocated or resident), and individual covariates (e.g., age). First, we identified the best model of time (seasonal and annual structure) while keeping survival for all groups equal. Our time models were based on month, season, year, and migration dates as well as time trends (linear and quadratic) following release. Our seasonal models included 2, 3, and 4-season models based on spring, summer, fall, and winter as well as average migration dates. Our 4-season model, for example, allowed for differential survival during the spring, summer, fall, and winter whereas the 2 and 3-season models collapsed those seasons into different combinations (e.g., spring/summer and fall/winter). We defined spring as March–May, summer as June–August, fall as September–November, and winter as December–February. We determined migration dates based on when deer left either winter or summer range and did not return (*sensu* Northrup et al., 2014). Second, we added the grouping structure to supported models (i.e., ≥ 0.05 AIC_c weight) of time from step 1. Our groups included the following: resident (2013), January translocations (2013), March translocations (2013), resident (2014), and surviving January and

TABLE 1 Akaike's Information Criterion selected models of survival (s) for resident and translocated mule deer (*Odocoileus hemionus*) on the Pahvant Range in central, Utah, USA for 2013 and 2014.

Model	AIC_c	ΔAIC_c	w_i	*K*	Dev
Time models					
{S(2 seasons [spring/summer vs. fall/winter])}	620.78	0.00	0.57	2	616.77
{S(3 seasons [spring/summer migration + year])}	624.33	3.55	0.10	3	618.32
{S(4 seasons [winter, spring, summer, fall])}	624.58	3.80	0.09	4	616.56
{S(4 seasons [winter, spring migration, summer, fall migration])}	625.34	4.57	0.06	4	617.32
{S(2 seasons [spring/summer/fall vs. winter])}	625.37	4.60	0.06	2	621.36
Time models with groups					
{S(2 seasons [spring/summer vs. fall/winter] + 3 groups[a])}	603.60	0.00	0.19	6	591.57
{S(2 seasons [spring/summer vs. fall/winter] + 4 groups[b])}	603.63	0.03	0.19	8	587.57
{S(4 seasons [winter/spring, spring migration, summer, fall migration] + 4 groups[c])}	604.03	0.43	0.15	16	571.80
{S(4 seasons [winter/spring, spring migration, summer, fall migration] + 3 groups[a])}	604.19	0.58	0.14	12	580.06
{S(2 seasons [spring/summer/fall vs. winter] + 3 groups[a])}	606.04	2.44	0.06	6	594.01
{S(3 seasons [winter/spring/summer/fall, spring migration, fall migration] + 3 groups[a])}	606.11	2.50	0.05	9	588.03

We report AIC_c, change in AIC_c (ΔAIC_c), AIC_c weight (w_i), number of parameters (K), and deviance (Dev, defined as −2 x log likelihood) for all time models (stage 1, top half of table) and time plus grouping structure (stage 2, bottom half of table) with $w_i \geq 0.05$.

[a] Grouping structure: (1) 2013 and 2014 resident deer, (2) 2013 translocated deer, and (3) all surviving translocated deer (from 2013 translocation) in 2014.

[b] Grouping structure: (1) 2013 and 2014 resident deer, (2) 2013 January translocation, (3) 2013 March translocation, and (4) all surviving translocated deer (from 2013 translocation) in 2014.

[c] Grouping structure: (1) 2013 resident deer, (2) 2014 resident deer, (3) 2013 translocated deer, and (4) all surviving translocated deer (from 2013 translocation) in 2014.

March translocations from 2013 that were combined in 2014 to maintain adequate precision around estimates of survival. In our final step, we evaluated the influence of individual covariates (age, age^2, percent body fat, body mass, and pregnancy when available for the specific year evaluated) to models with ≥0.05 AIC_c weight from step 2. Inclusion of age^2 allowed us to represent a potential asymptotic relationship with age. We evaluated the final list of supported models for evidence of uninformative parameters and used model averaging to avoid any potential bias (Arnold, 2010). In addition, we used a logistic regression to estimate odds ratios for annual survival in relation to group and age.

3. Results

In January and March 2013, UDWR translocated 102 female mule deer (51 in January; 51 in March) from winter range near Parowan, Utah to winter range near Holden, Utah on the Pahvant mountain range (Figure 1). We marked 81 deer with VHF radio collars (41 in January, 40 in March) and 21 deer with GPS collars (10 in January, 11 in March). Estimated age of captured deer ranged from 1 to 9 ($\bar{x}$ = 3.9 years for January and 4.1 years for March, SE = 0.03 for both January and March). Percent ingesta free body fat ranged from 3.9–16.3% and was higher in January 2013 compared to March 2013 as expected (Barboza et al., 2009, 2020). Of the 102 females captured for translocation, 91% (N = 93) were pregnant and none tested positive for chronic wasting disease. Prior to capturing deer for translocation, we marked 50 resident deer in the Pahvant study area (41 VHF, 9 GPS). An additional 20 resident deer (20 VHF) were captured during January 2014 in the Pahvant study area to assess body condition and bolster sample sizes for this reference group.

Our first stage of model selection resulted in 5 supported models of time with at least 5% AIC_c weight that we advanced to step 2. These models divided the year into 2, 3, and 4 seasons and accounted for 88% of the total AIC_c weight (Table 1). In stage 2, we added group structure to supported models of time and identified 6 models with at least 5% AIC_c weight (Table 1). These models included three 2-season models (based on season, year, and group), two 4-season models, and one 3-season model. The two 4-season models were defined by year and migration dates (winter, spring migration, summer, and fall migration). The 3-season model was also defined by year and migration dates with survival rates modeled as equal during winter and summer, but different during the spring and summer migrations. Four of the 6 models included a 3-group structure (residents [2013 and 2014 combined], 2013 translocations combined with January and March releases, and translocations in year 2 [2014]). The other 2 models each had 4 groups (residents [2013 and 2014 combined], 2013 January translocations, 2013 March translocations, and translocations in year 2 [2014] or 2013 residents, 2013 translocations, 2014 residents, and 2014 translocations).

In stage 3, we added covariates to our best models from stage 2. This stage resulted in 6 models (2, 3, and 4 seasons) with an AIC_c

TABLE 2 Akaike's Information Criterion selected models of survival (s) for resident and translocated mule deer (*Odocoileus hemionus*) on the Pahvant Range in central, Utah, United States during 2013 and 2014.

Model	AIC$_c$	ΔAIC$_c$	w$_i$	K	Dev
{S(2seasons [spring/summer vs. fall/winter] + group^a + age + age^2)}	592.34	0.00	0.17	12	568.21
{S(2seasons [spring/summer vs. fall/winter] + group^b + age + age^2)}	592.40	0.05	0.16	10	572.30
{S(4seasons [winter/spring, spring migration, summer, fall migration] + group^c + age + age^2)}	592.72	0.38	0.14	20	552.37
{S(4seasons [winter/spring, spring migration, summer, fall migration] + group^b + age + age^2)}	592.85	0.51	0.13	16	560.62
{S(2seasons [spring/summer/fall vs. winter] + group^b + age + age^2)}	594.35	2.01	0.06	10	574.26
{S(3seasons [winter, spring, summer, fall, spring migration, fall migration] + group^b + age + age^2)}	594.51	2.16	0.06	13	568.36

We report AIC$_c$, change in AIC$_c$ (ΔAIC$_c$), AIC$_c$ weight (w_i), number of parameters (K), and deviance (Dev, defined as −2 x log likelihood) for all stage 3 models with $w_i \geq 0.05$.

[a] Grouping structure: (1) 2013 and 2014 resident deer, (2) 2013 January translocation, (3) 2013 March translocation, and (4) all surviving translocated deer (from 2013 translocation) in 2014.

[b] Grouping structure: (1) 2013 and 2014 resident deer, (2) 2013 translocated deer, and (3) all surviving translocated deer (from 2013 translocation) in 2014.

[c] Grouping structure: (1) 2013 resident deer, (2) 2014 resident deer, (3) 2013 translocated deer, and (4) all surviving translocated deer (from 2013 translocation) in 2014.

weight ≥ 5% that accounted for 73% of the total AIC$_c$ weight. The top model was a 2-season model that combined spring with summer and fall with winter periods. This model had 4 separate groups (residents [2013 and 2014 combined], 2013 January translocations, 2013 March translocations, and surviving translocations in 2014) and included age and age^2 as individual covariates (Table 2). Age or age^2 occurred in all models with $w_i > 0.05$ (Table 2). We found little support for body condition, pregnancy, or body mass as influencing survival as models with these covariates received <5% of AIC$_c$ weight.

We experienced low rates of capture myopathy and capture-related deaths. Four of 102 (3.9%) deer captured and translocated during 2013 died of capture-related causes. All of these deer died within 3 days of release and 2 of the 4 deaths were attributed to injuries (e.g., broken bones) sustained during capture. Two of 70 (3%) resident deer died of capture-related causes. Predation accounted for the majority of mortalities ($n = 54$) for translocated deer (50%) followed by undetermined (28%), other including disease (8%), poached (8%), and roadkill (6%). Predation was also the highest cause of mortality ($n = 21$ deaths) for resident deer (63%) followed by undetermined (32%) and other (5%).

Overall annual survival of resident deer during 2013 was estimated at 0.83 (95% CI = 0.72–0.90). Annual survival of mule deer translocated in January during 2013 (year one following release) was 0.51 (95% CI = 0.40–0.63) compared to 0.53 (95% CI = 0.40–0.66) for mule deer translocated in March. During their second year following release, translocated deer maintained much higher survival rates with annual rates estimated at 0.85 (95% CI = 0.71–0.93). This rate was not different from that of residents in 2014 (0.80; 95% CI = 0.69–0.88; Figure 2). Resident and translocated deer experienced similar monthly survival rates during their initial year following release in winter and spring months (January through April). Beginning in May, however, and lasting through September of 2013, number of mortalities for translocated deer increased compared to those of resident deer. In October of 2013, survival rates of translocated deer stabilized and were again similar to resident deer.

We found support for age influencing survival of translocated deer. The β estimate for age was negative in the top model ($\beta = -0.73$), although the 95% CI slightly overlapped zero (−1.61–0.14). The β estimate for age^2 in the top model was positive with the 95% CI slightly overlapping zero ($\beta = 0.06$, 95% CI = −0.03-0.14). A plot of odds ratios for annual survival showed reduced likelihood of survival during the initial year for animals translocated in January and March compared to resident deer, but not during the second year following release (Figure 3). This plot also showed reduced odds of survival as age of animals increased. Estimates of annual survival for 2-year old mule deer during year 1 following release were more than double (0.71; 95% CI = 0.52–0.84) those of 7 year olds (0.35; 95% CI = 0.17–0.58) (Figure 4).

4. Discussion

We observed very few capture-related deaths and documented low mortality rates immediately following release for translocated mule deer. Our observed 3.9% rate of mortalities associated with capture was similar to that observed with resident deer released at point of capture (3%) as well as rates common in traditional capture, radio-marking, and release projects that do not involve translocation (general range 3–5%; Quinn et al., 2012; Lendrum et al., 2014; Van de Kerk et al., 2020). The majority of mortalities we observed for translocated deer occurred during the spring and summer (May–September) months and were similar to causes reported in other areas (primarily predation, but also poaching and vehicle strikes) for mule deer (Beringer et al., 2002; Rominger et al., 2004; Frair et al., 2007; McIntosh et al., 2014).

Survival rates for translocated mule deer, during the first year post release, were lower than rates commonly observed for animals not translocated. We observed annual survival for resident deer of 0.83, which was similar to data from Colorado, Idaho, and Montana (annual survival estimated at 0.85) for mule deer (Unsworth et al., 1999). Survival rates for translocated mule deer in year one (0.51 and 0.53) were lower than those of resident deer (0.83). These lower rates during the initial year following release, however, are similar to those reported for black-tailed or mule deer translocated in other areas using a variety of methods (O'Bryan and McCullough, 1985; Martinez-Garcia, 2009; Cain et al., 2018; Wright et al., 2020). During the second year, survival rates for translocated mule deer were higher and not different from resident deer (Figure 2) suggesting that survival challenges related to translocation were transitory and dissipated by the end of the initial year. This finding supports our prediction that translocated deer would experience lower survival rates than resident deer during the first year after release, but higher rates of survival (when compared to survival for translocated deer in year 1) during the second year once acclimated to release areas. While low survival of ungulates is a common observance following translocation (Beringer et al., 2002; Frair et al., 2007), there are few translocation studies that have

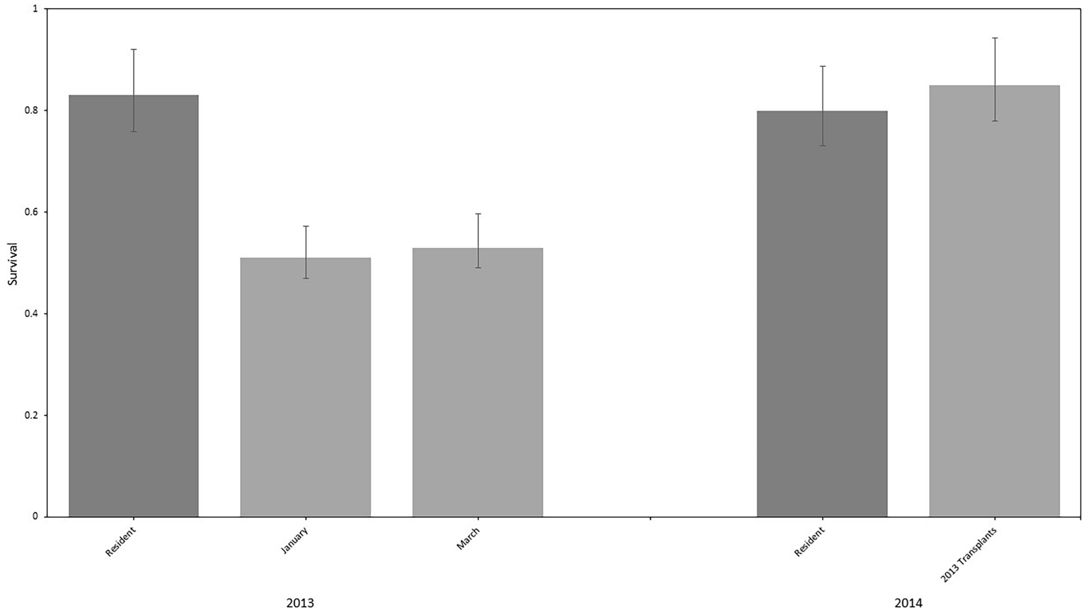

FIGURE 2
Annual survival rates (± 95% CI) of resident (reference group) and translocated mule deer (*Odocoileus hemionus*) released in January of 2013 and March of 2013 on the Pahvant Range in southern Utah, United States during 2013 (year one following release) and 2014 (year two following release).

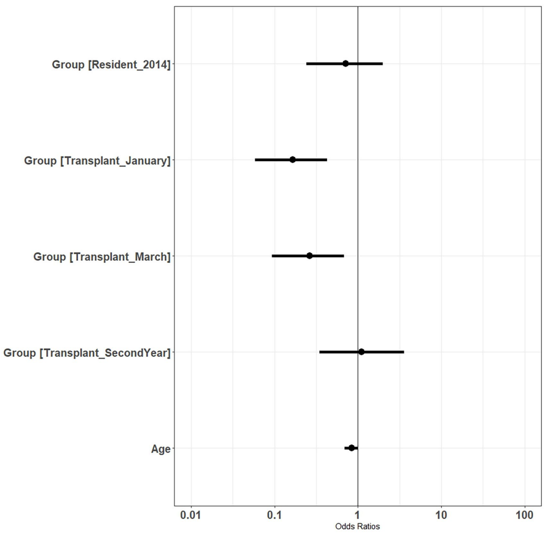

FIGURE 3
Odds ratios for annual survival of resident (reference group) and translocated mule deer (*Odocoileus hemionus*) released in January of 2013 and March of 2013 on the Pahvant Range in southern Utah, United States during 2013 (year one following release) and 2014 (year two following release). Intercept is set to resident deer during 2013.

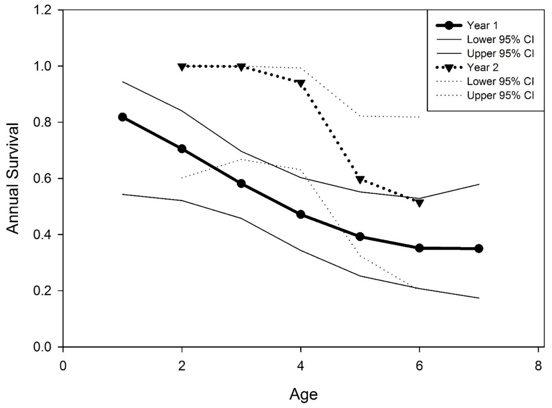

FIGURE 4
Annual survival of translocated mule deer (*Odocoileus hemionus*) in relation to estimated age (tooth eruption and tooth wear; Severinghaus, 1949; Robinette et al., 1957) during the first 2years (2013, year 1; 2014, year 2) following release on the Pahvant Range in central Utah, United States.

documented survival for multiple years following release (Haydon et al., 2008; McIntosh et al., 2014; Wright et al., 2020). These data reinforce the need to monitor translocated animals for multiple years following release.

We found no difference in annual survival rates for deer translocated in early versus late winter. Deer released in early winter (January) were in better condition at time of release than deer released later in winter, but these differences did not influence survival rates and we only observed limited mortality during winter and spring months. Moreover, we did not detect a relationship between survival and body condition. However, winter conditions during our study years were mild as temperatures were above the long-term mean and precipitation below the long-term average (Western Regional Climate Center). Translocating mule deer during a severe winter may yield different results. The results of our study did not support our hypothesis of differences in survival between early and late winter as survival rates were not different for deer released at either time. These results suggest managers could translocate mule deer throughout the winter period as survival rates were not related to the timing of release (early or late winter) when winter conditions are not severe.

We found strong support for age as a predictor of survival, with younger animals more likely to survive the initial year following translocation than older animals (Figure 4). Two year old deer, for example, were approximately 2 times more likely to survive the initial year post release than 7 year old animals. Jones and Witham (1990) found that translocated white-tailed deer fawns had higher survival that translocated adults while Hawkins and Montgomery (1969) and Parker et al. (2008) found no difference in survival based on age of translocated white-tailed deer. Moreover, higher survival for young mule deer from urban environments translocated to non-urban areas was observed in British Columbia (Wright et al., 2020). Younger animals may have more plasticity in their behavior and may have responded to novel environments better than older animals in our study. The specific mechanisms explaining this result, however, are unclear.

5. Conclusion

Our results suggest that translocation is a strategy that could be used to address conservation and management objectives for mule deer populations. We experienced low rates of capture myopathy. We observed survival rates for translocated mule deer that were lower than resident deer during the first year following translocation. During the second year after translocation, however, translocated mule deer had much higher survival rates that were not different from resident deer suggesting challenges to survival were transitory. Moreover, we found a strong relationship with age as young deer survived the initial year following translocation much better than older deer. Given the difference we observed between survival in year one compared to year two, we recommend that translocated animals be monitored for at least 2 years following release. Results from multiple years provide critical data when considering the relative value of translocation as a conservation and management strategy. In our study, there was no difference in survival rates for deer translocated in January or March. Although winters during our study period were mild, this result suggests managers can use translocation throughout winter months to address management concerns.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Brigham Young University's IACUC Committee.

Author contributions

DS collected these data as part of his MS thesis. BM and RL provided oversight as graduate advisors. KH and JS helped design the study and collect the data as part of their roles as biologists for the Utah Division of Wildlife Resources. All authors contributed to the article and approved the submitted version.

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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.

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An objective approach to select surrogate species for connectivity conservation

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Introduction: Connected landscapes can increase the effectiveness of protected areas by facilitating individual movement and gene flow between populations, thereby increasing the persistence of species even in fragmented habitats. Connectivity planning is often based on modeling connectivity for a limited number of species, i.e., "connectivity umbrellas", which serve as surrogates for co-occurring species. Connectivity umbrellas are usually selected *a priori*, based on a few life history traits and often without evaluating other species.

Methods: We developed a quantitative method to identify connectivity umbrellas at multiple scales. We demonstrate the approach on the terrestrial large mammal community (24 species) in continental Europe at two scales: 13 geographic biomes and 36 ecoregions, and evaluate the interaction of landscape characteristics on the selection of connectivity umbrellas.

Results: We show that the number, identity, and attributes of connectivity umbrellas are sensitive to spatial scale and human influence on the landscape. Multiple species were selected as connectivity umbrellas in 92% of the geographic biomes (average of 4.15 species) and 83% of the ecoregions (average of 3.16 species). None of the 24 species evaluated is by itself an effective connectivity umbrella across its entire range. We identified significant interactions between species and landscape attributes. Species selected as connectivity umbrellas in regions with low human influence have higher mean body mass, larger home ranges, longer dispersal distances, smaller geographic ranges, occur at lower population densities, and are of higher conservation concern than connectivity umbrellas in more human-influenced regions. More species are required to meet connectivity targets in regions with high human influence (average of three species) in comparison to regions with low human influence (average of 1.67 species).

Discussion: We conclude that multiple species selected in relation to landscape scale and characteristics are essential to meet connectivity goals. Our approach enhances objectivity in selecting which and how many species are required for connectivity conservation and fosters well-informed decisions, that in turn benefit entire communities and ecosystems.

KEYWORDS

connectivity, umbrella species, Europe, objectivity, surrogate species, landscape, human influence

1 Introduction

Biodiversity is highly threatened due to increasing human influence on the planet. We are currently witnessing the so-called sixth mass extinction, primarily due to rapid habitat loss and fragmentation, which is further exacerbated by climate change (Ceballos et al., 2017). Habitat alteration restricts species to small populations in isolated patches with a high rate of ecosystem decay (Chase et al., 2020). This reduces movement and gene flow between populations (Crooks et al., 2017), and ultimately elevates the risk of species extinction (Gilpin and Soulé, 1986). Halting biodiversity loss therefore requires urgent, concerted and sustained efforts to protect high-quality sites capable of sustaining viable populations, while simultaneously supporting connectivity among populations and movement of individuals across the landscape (Boyd et al., 2008).

Landscape connectivity buffers the effects of local extinction processes by facilitating the movement and effective dispersal of individuals, thus maintaining gene flow between populations, and supporting species range-shifts in response to changing climate and land-use regimes (Robillard et al., 2015). By increasing the potential for species dispersal into climatically suitable areas (Belote et al., 2017), ecological connectivity fosters resilient ecosystems that are effective in delivering ecosystem services (Mitchell et al., 2013). Consequently, connectivity has been recognized as an integral component of biodiversity conservation in international agreements, e.g. Aichi Target 11 of the United Nations Convention on Biological Diversity (CBD, 2010), the current draft of the post-2020 CBD framework (CBD, 2020), and in the European Union's Habitats Directive and Biodiversity Strategy for 2030 (European Commission, 2020).

Surrogate approaches are frequently used in conservation planning to compensate for incomplete ecological knowledge on all species in any ecosystem (Wiens et al., 2008). Two types of surrogates used in connectivity planning are species-based (or fine-filter) approaches where one or few species are used as surrogates for several co-occurring species (Caro and O'Doherty, 1999), and habitat-based (or coarse-filter) approaches wherein landscape naturalness (Theobald et al., 2012) or land-facets (Brost and Beier, 2012) are used as surrogates for the species that inhabit them. Evaluations of coarse vs fine-filter approaches suggest significant trade-offs (Krosby et al., 2015), but overall the fine-filter approach has been found to be more effective (Meurant et al., 2018).

The species-based surrogate approach should aim to identify a suite of surrogate species, which we refer to as a "connectivity umbrella" in this paper, that encompass areas most likely to be used by several co-occurring species. Connectivity umbrellas are often chosen based on a few traits such as body mass or home range size, their charisma, conservation status (Beier et al., 2009; Wang et al., 2018), or because they have previously been identified for other purposes such as flagships for fund-raising, indicators of ecosystem health, or umbrellas for habitat management (Caro and Girling, 2010). Pre-selected connectivity umbrellas based on few criteria such as charismatic large species, have been shown to be ineffective at representing other species in multiple studies (Beier et al., 2009; Cushman and Landguth, 2012; Wang et al., 2018).

In addition to species-based surrogates being better performing than habitat based surrogates, research suggests that multiple species are better than any single surrogate species (Meurant et al., 2018; Wang et al., 2018), surrogate species are effective within their own taxonomic group (Brodie et al., 2015), and a diverse set of species reflects the needs of other co-occurring species (Cushman and Landguth, 2012). Despite the emphasis on multi-species connectivity models (Wood et al., 2022), there are only a few methods that use data-driven approaches to identify which and how many species could represent the connectivity needs of all species in any given region.

In this study, we address this research gap in connectivity science. Our goal is to develop an approach that increases the objectivity in selecting connectivity umbrella species from a pool of candidate species. We demonstrate the approach at multiple scales and evaluate the interaction of landscape characteristics and connectivity umbrella selection using the terrestrial large-mammal community in continental Europe as a case study.

2 Methods

For the large mammal community in Europe, we modelled potential connectivity between protected areas (PAs) and created a connectivity target representing high-probability connectivity areas for multiple species present in the region. We then ranked each species in the region using a cumulative measure that indicates how well a species represents the target and connectivity network of co-occurring species. Starting with the highest-ranked species, we sequentially added the connectivity network of all species, and plotted the contribution, i.e., percent increase of the connectivity target for each addition (Figure 1). The final connectivity umbrella comprises the combination of species that are required to reach a certain coverage of the target (set at 95% in this study), as adding more species contributed only marginally towards reaching the connectivity target. All steps of the analyses are presented in greater detail in Figure S1. All quantitative analysis was performed using R statistical software (https://www.r-project.org/) and all maps were created in ArcGIS 10.3.

The four main steps involved in this approach are: (1) Modelling connectivity for each species, (2) Generating connectivity targets per region, (3) Ranking species in each region, and finally (4) Determining the suite of umbrella species.

2.1 Step 1. Modelling connectivity for each species

We modelled connectivity between Protected Areas (PAs) within the suitable habitat for all large terrestrial mammals in Europe. We first selected species for the analysis, identified PAs

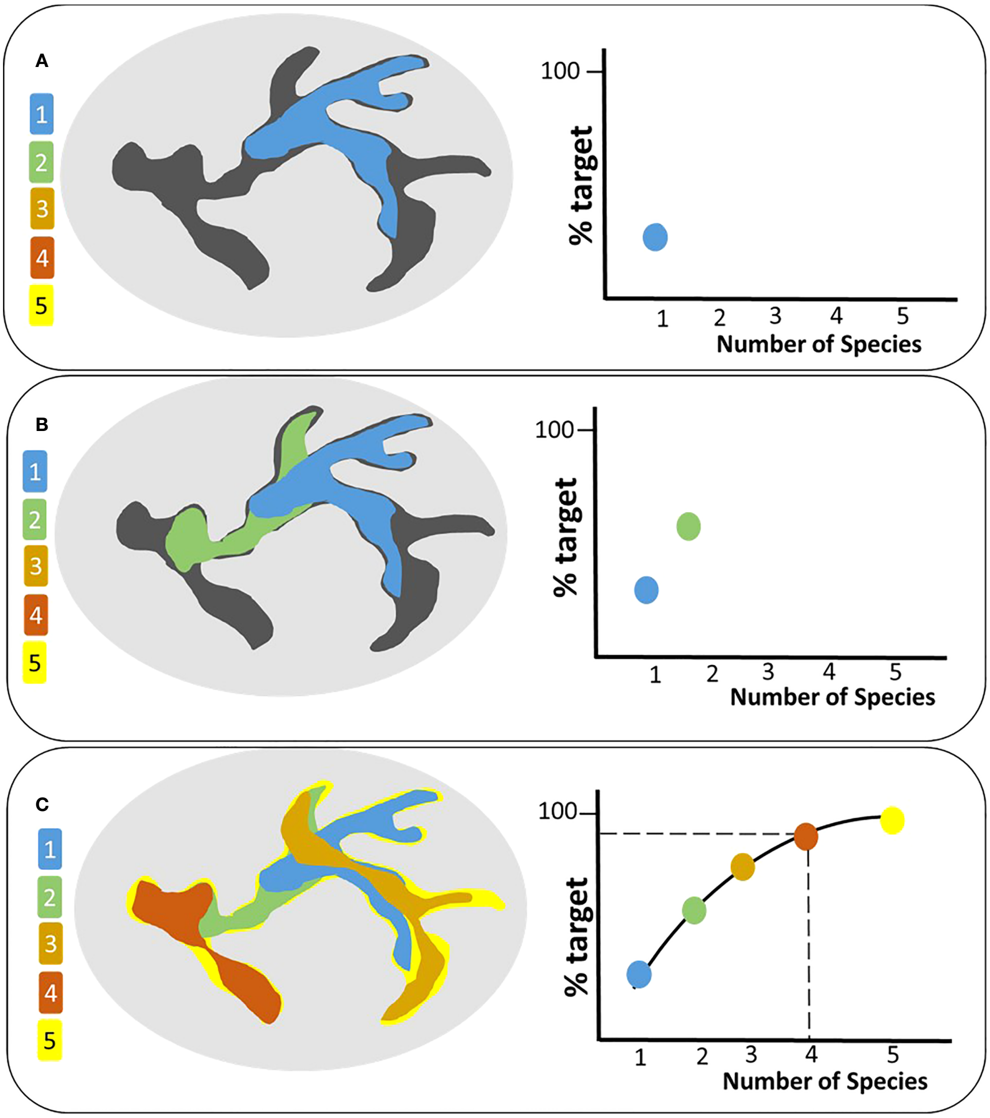


FIGURE 1
Conceptual figure of the selection process for connectivity umbrellas. The oval represents the region of analysis; the dark gray polygon represents the connectivity target. Five hypothetical species are shown in different colors and arranged according to their overall rank. Species are then added sequentially while quantifying their contribution towards the connectivity target **(A–C)** until an asymptote is reached. In this example, four species (blue, green, orange, maroon) are required to cover 95% of the target [dashed line in **(C)**].

to be used as nodes for connectivity analysis for each species, generated species-specific resistance surfaces that represented the potential difficulty of movement between nodes, and estimated potential connectivity for each species (Figure S1, Step 1).

2.1.1 Step 1a. Selecting species and traits for the study

We selected large terrestrial mammals, species with a mean body mass larger than 3 kg (Cardillo et al., 2005), that are native to Europe. We used the PanTHERIA database to obtain data on species traits (Jones et al., 2009) and putative maximum dispersal distances based on allometric scaling equations from previous studies (Santini et al., 2013; Whitmee and Orme, 2013). Details of the species used in this study are presented in Table S1.

2.1.2 Step 1b. Selecting nodes

Within the extent of occurrence and suitable habitat of each species (Maiorano et al., 2013), we selected PAs (IUCN Level I–IV) and Natura 2000 sites that reported presence of the species (European Environment Agency, 2020). We calculated the Euclidean distance between each pair of nodes and only retained pairs that were equal to or less than the putative maximum dispersal distance presented in Table S1. As a result, each species had a unique set of pairwise nodes.

2.1.3 Step 1c. Generating the resistance surface

We used previously published habitat suitability maps of mammals in Europe (Maiorano et al., 2013), which were generated from three environmental variables – land cover, elevation, and distance to water. The habitat suitability models contained pixel values of 0, 1, 2 corresponding to non-habitat, marginal habitat, suitable habitat, respectively, for each species. Because animals are more tolerant of suboptimal habitat during dispersal (Mateo-Sánchez et al., 2015), we coded the suitability values as 0 (unsuitable) and 1 (suitable, where we pooled suitable and marginal habitats) and resampled each raster using a 3×3 moving window. For each of the 24 species, this step produced a continuous habitat suitability raster at 1 km resolution. We then converted this suitability surface to a landscape resistance raster, which represents the ability of an organism to cross a particular environment (Zeller et al., 2012).

Previous studies have found that resistance is often a non-linear negative exponential function of habitat suitability (Dudaniec et al., 2013; Mateo-Sánchez et al., 2015). Therefore, we converted habitat suitability surfaces using a negative exponential function (Balkenhol et al., 2020) derived from the following formula:

$$R = CS \times 100^{(1-HS)}$$

where R is the resistance assigned to a specific cell, CS is the cell size in meters (here 1000 m) and HS is the habitat suitability associated with that cell. This conversion assumes that animals are more tolerant of suboptimal habitat and respond less strongly to low habitat suitability during dispersal. The final resistance values ranged from 1000–10,000 resistance units.

2.1.4 Step 1d: Corridor simulation

We mapped potential connectivity for each species using the stochastic modelling program LSCorridors (Ribeiro et al., 2017). LSCorridors uses the resistance surface to produce potential corridors between each pair of nodes by simulating multiple dispersal events. It then adds all pairwise maps to produce the overall connectivity map for the species, quantified as the Route Selection Frequency Index (RSFI), a measure of the probability that a particular pixel will be used by any dispersing individual. We conducted 50 simulations between each pair of nodes, without landscape influence (Measures by Pixel, MP method, scale = 1000m, variability = 2). With these settings, stochasticity between simulations is introduced by different starting and ending points within the nodes for each simulation and by the variability factor in the resistance map, which represents uncertainty in the values used to produce the resistance surface. We estimated potential connectivity between a total of 53023 pairs of nodes, which amounts to a total of 2,651,150 pairwise simulations.

At the end of all simulations for each species, we further pruned the pairwise simulations to retain only those PA-pairs that had a mean corridor length equal to or less than the maximum putative dispersal distance. Since the maximum RSFI values were different for each of the species, we normalized the final connectivity maps of the 24 mammals for further analyses. We conducted further analyses at two spatial scales as described below.

2.2 Step 2: Generating connectivity targets per region

Defining regions: We conducted analyses at two hierarchical levels based on ecoregion classifications within broad geographical regions in continental Europe. We combined the six biomes present in Europe (Olson et al., 2001) with the six broad geographic regions (excluding islands) which produced 13 geographic biomes, henceforth referred simply as biomes in this study. Nested within these 13 biomes there are a total of 36 ecoregions (eight biomes have 31 nested ecoregions while five biomes do not have ecoregions) (Figure S2).

Connectivity target: Our approach requires users to pre-define a spatially explicit connectivity target. We tested the impact of different connectivity targets based on three different conservation goals. The three targets are aimed at protecting connectivity networks for all species in the region (Target EQ), only high-quality connectivity networks (Target Q), or connectivity networks of conservation-concern species only (Target T) (Figure S1, Step 2). Details of how these targets were derived are explained here:

- Target EQ: This target represents the best quality corridor cells for all species equally. It is produced by first extracting high-quality corridor cells (top 25 percentile values for each species), and then summing the high-quality corridor cells for all species.
- Target Q: This target represents only the best quality corridor cells irrespective of which species are represented in the target. It is produced by first adding all the

normalized species corridor maps into one composite raster, and then extracting the cells that contain the top 25 percentile values.

- Target T: This target represents all corridor cells used by species of conservation concern, which we defined as species endemic to Europe or with an IUCN red list status of Near Threatened or higher (Table S1). In Europe, these species are *Lynx pardinus, Bison bonasus, Gulo gulo, Marmota marmota, Rupicapra pyrenaica, Capra ibex*, and *Capra pyrenaica*. This target is produced by adding corridor cells of all conservation-concern species in any given region. Because nine of the 13 biomes contain species of conservation concern, this target existed only in nine biomes.

We chose target EQ to demonstrate our data-driven approach to select connectivity umbrella species as we believe most conservation actions would be concerned about several species in the region, rather than just high-quality regions (target Q) or only species of conservation concern (target T). We compared connectivity umbrellas selected for target EQ with target Q and T to test the sensitivity of our approach and results are presented in Figure S3.

2.3 Step 3: Ranking species

To rank the species in each region, we calculated an umbrella score "*Uir*", which quantifies the suitability of each species as a connectivity umbrella. For each region, we used the connectivity maps of each species, wherein the normalized RSFI value represents the probability of connectivity of each cell for that species and a set of five criteria using the calculation:

$$Uir \sim N, A, F, S, P$$

U is the overall umbrella score for species *i* in region *r*, calculated as the product of five criteria listed below:

N is the total number of species present in the region *r* whose corridors overlap with that of species *i*, calculated as the total number of overlapping species (Figure S1, Step 3a).

A is the mean area of overlapping corridors of species *i* with all species corridors present in region *r*, calculated as the mean area (km^2) of pairwise overlap of species *i* with all other species (Figure S1, Step 3b).

F is the fraction of the connectivity target in region *r* covered by species *i*, calculated as the percent area of intersection between the connectivity target and the corridor network of species *i* (Figure S1, Step 3c).

S is the mean strength of pairwise overlapping corridors, calculated as the mean of Bhattacharyya's affinity index (Bhattacharya, 1943) that measures volumetric intersection of each pair of species (Fieberg and Kochanny, 2005). Bhattacharyya's affinity index is a statistical measure of affinity between two populations that assumes they use space independently of one another. Values range from zero (no overlap) to 1 (complete overlap) (Figures S1, Step 3d).

P is the proportion of the total connectivity network of species *i* that lies within the connectivity target of region r, calculated as the sum of all pixel values within region *r* (Figure S1, Step 3e).

Criteria *N* (number of overlapping species), *A* (overlapping area with other species), *F* (fraction of target covered by the species) characterize the numerical suitability of a species at representing other species and the target. Criteria *S* (strength of overlapping corridors) and *P* (proportion of the species corridors within target) characterize the quality of a species at representing co-occurring species corridors and the target. Combining these criteria effectively select species that are representative of co-occurring species and the region under consideration (Figure S1, Step 3e).

2.4 Step 4: Determining the suite of umbrella species

Within each region, we ranked each species by its *Uir* value so that the species with the highest value received the highest rank. Effectively, this means that species with the highest ranks are those that overlapped with many other species, and did so over a larger area, with the highest strength of overlap, represented a large part of the connectivity network, and had a large part of their connectivity network within the region of interest. We plotted the species by their rank vs the additional contribution they made to the connectivity target. We first plotted the proportion of the connectivity target achieved by adding the corridors of the highest ranked species. We continued adding species according to their ranks, calculating the additional coverage of the connectivity target (that was not already covered by the previous species) for each species addition. We defined the suite of umbrella species as the number and combination of species required to cover at least 95% area of the connectivity target as adding more species beyond this asymptote did not make much improvement towards achieving the connectivity target (Figure S1, Step 4).

2.5 Evaluating the role of underlying landscape

Finally, to evaluate the role of landscape characteristics on the selection of connectivity umbrellas, we conducted a cluster analysis of all 36 ecoregions based on their mean human footprint, mean landscape fragmentation and the mean latitude. The human footprint index (Wildlife Conservation Society – WCS and Center for International Earth Science Information Network – CIESIN, Columbia University, 2005), generated from human population pressure, land use and infrastructure, and access, represents the cumulative anthropogenic impact on the environment, whereas the landscape fragmentation index (European Environment Agency, 2016) measured as the effective mesh density, i.e. landscape patches per 1000 km^2, represents a measure of the degree to which the landscape is fragmented. We performed agglomerative hierarchical cluster analysis on ecoregions to identify distinct clusters in our dataset. We used Ward's method of agglomeration, which produces clusters of more equal size by keeping distances within the clusters as small as possible (Ward, 1963). We identified five unique groups using a dendrogram on the cluster solutions that we had obtained using the hclust function available with R library fastcluster (Müllner, 2013).

Within the clusters, we evaluated six attributes of connectivity umbrella species (mean body mass, home range size, population density, putative maximum dispersal distance, geographic range in Europe and conservation status (Table S1). We conducted Kruskal-Wallis tests to identify significant differences of attributes of connectivity umbrella species in the different clusters and used a *post-hoc* Dunns test to identify which clusters were significantly different using Holms-adjusted p-values to account for multiple comparisons.

3 Results

Using the approach presented in Figure 1, we demonstrate that a systematic and objective assessment of which and how many species are required to meet connectivity needs of multiple co-occurring species is indeed possible. In this process, we discovered some important patterns.

Multiple species are required to meet connectivity goals at both scales considered. Ninety-two percent of the biomes (Figure 2) and 83% of the ecoregions (Figure 3) had more than one connectivity umbrella species. Both the number and identity of species are scale dependent. More species are selected at the biome level (average 4.15, range 1–9 species; Figure 2) than at the ecoregion level (average 3.16, range 1–9 species; Figures 3A, S4). The identity of the species selected also varies across scales. For example, six species are selected in the temperate broadleaf mixed forest biome

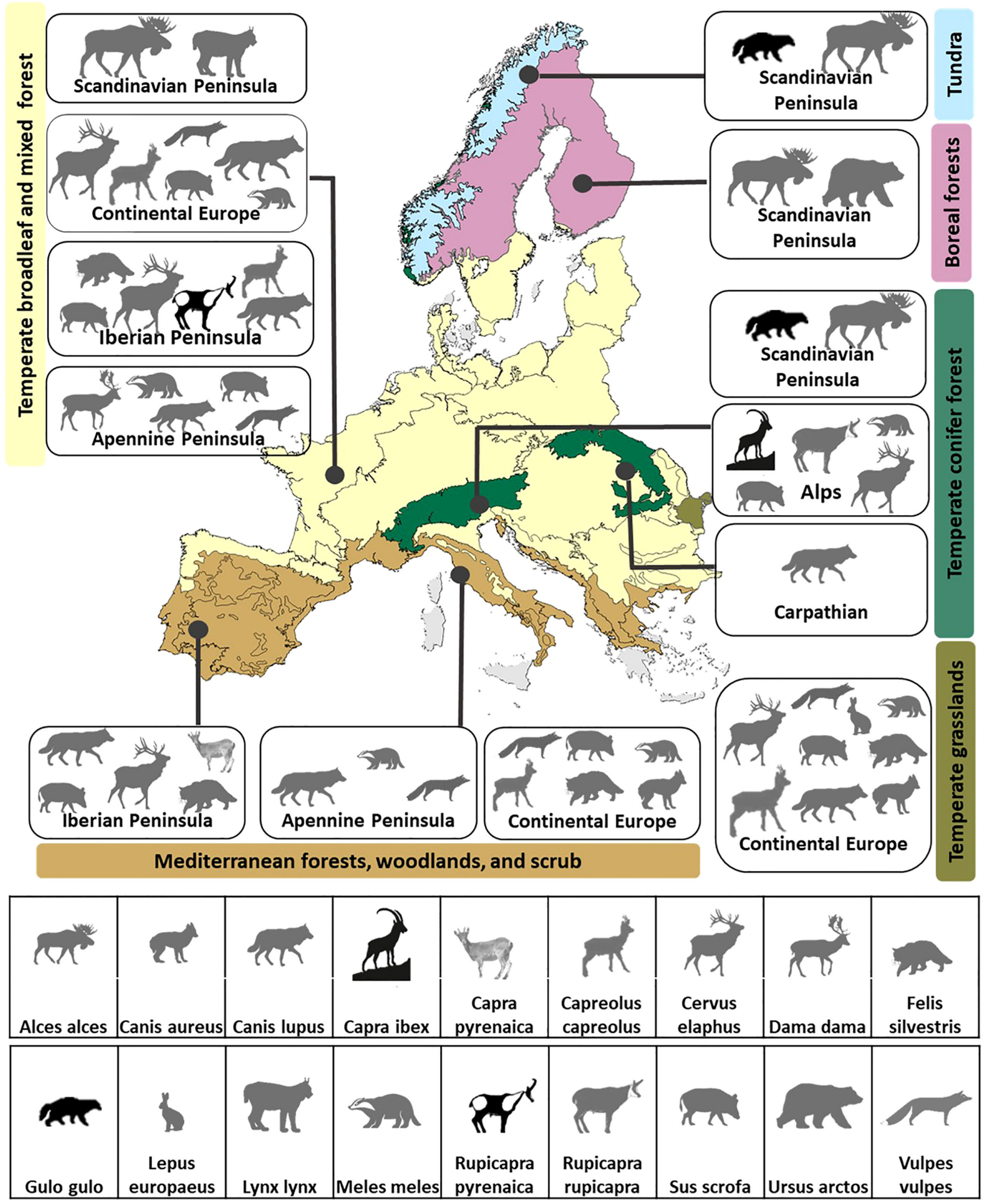


FIGURE 2
Connectivity umbrella species selected to reach 95% of the connectivity target in the thirteen biomes within major geographic regions in Europe. Species of conservation concern in Europe-wide assessments are represented by black silhouettes, all other species are represented by gray silhouettes.

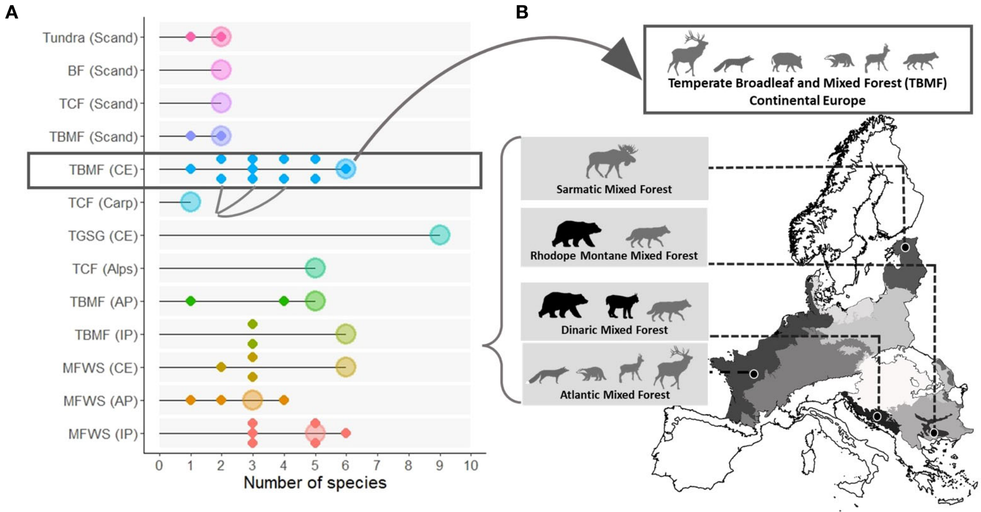
(Figure 3A), whereas several of the species selected in the eleven nested ecoregions (ranging from 1 to 6) are exclusive to the ecoregions, i.e., not selected in the biome-level analysis (Figure 3B).

Connectivity coverage achieved using single species is highly variable (Figure S5). For example, if only the highest-ranking species were to be selected, an average of 75% of the regional targets would be covered, ranging from ~14% by the Iberian lynx (*Lynx pardinus*) in Southwest Iberian Mediterranean sclerophyllous and mixed forests to ~97% by the wolf (*Canis lupus*) in South Apennine mixed montane forests. If only the highest-ranking species of conservation concern is selected, an average of 25% of the individual regional targets would be covered, ranging from ca. 1% by the bison in the Carpathian Mountains to 95% by the wolverine in the Scandinavian Tundra. Some ecoregions in the Scandinavian and Apennine peninsulas are exceptions to this general pattern.

Our results indicate that even when species of conservation concern are present in a region, they may not necessarily be the most suitable connectivity umbrellas. A total of seven conservation-concern species are present in 17 ecoregions (47% of ecoregions, average 1.3 conservation-concern species/region), but are selected as connectivity umbrellas in only 9 ecoregions (~53% where they are present). The number or proportion of conservation-concern species present in any region is not significantly correlated to the number or proportion of conservation-concern species in the suite of connectivity umbrella species (Pearson's r = 0.04 and 0.26, respectively; p > 0.05 in both cases). We used Red List status at the European level because it was consistent with the European extent of our study, but threat assessments at regional scales may also be relevant. For example, none of the species selected as connectivity umbrellas in the temperate broadleaf mixed forest biome are of conservation concern at the European scale (Figure 3B), but the brown bear (*Ursus arctos*) and Eurasian lynx (*Lynx lynx*), selected at the ecoregion scale are categorized as vulnerable and endangered in the Rhodope and Dinaric Mountain ecoregions (Temple and Terry, 2007).

Of the 24 species evaluated, not even one species is an effective connectivity umbrella across its entire range (Figure 4). Even the species selected most often, the wolverine (*Gulo gulo*) and moose (*Alces alces*), were only selected as connectivity umbrellas in 60% of the regions in which they occur. While there is a significantly higher chance of being selected as an umbrella species for wider ranging species, i.e., species that occur in many regions (Pearson's r = 0.73, p<.05), this effect is lost when comparing the occurrence of species across multiple ecoregions with the proportion of the times that it is selected as a connectivity umbrella (Pearson's r = 0.13, p = 0.66).

We identified five unique clusters of ecoregions that ranged from very low to very high human influence (Figure S6). Mountain ranges and regions at higher latitudes are generally less fragmented and impacted by humans than regions in the plains or at lower latitudes. The maximum dispersal distance (Kruskal-Wallis chi-squared = 10.942, df = 4, p-value = 0.027), home range (chi-squared = 12.401, df = 4, p-value = 0.014), proportion of range in Europe (chi-squared = 21.014, df = 4, p-value = 0.0003), and conservation status (chi-squared = 9.9392, df = 4, p-value = 0.041) of connectivity umbrella species are significantly different between the clusters. On average, species selected as connectivity umbrellas in regions with low human influence have higher mean body mass, larger home ranges, longer dispersal distances, smaller geographic ranges, occur at lower population densities, and are of higher conservation concern than connectivity umbrellas in more



Biomes – Tundra, BF: Boreal forest, TCF: Temperate Coniferous forest, TBMF: Temperate Broadleaf and Mixed Forest, TCF: Temperate Coniferous forest , TGSG: Temperate grasslands, savannas and grassland, MFWS: Mediterranean forest, woodland and scrub.

Geographic regions in Europe - Alps, AP: Apennine Peninsula, IP: Iberian Peninsula, Scand: Scandinavia, CE: Continental Europe, Carp: Carpathian

FIGURE 3
The number **(A)** and identity **(B)** of connectivity umbrella species vary across spatial scales. More species are selected at the broad biome level [represented by large dots in **(A)**] than at the finer ecoregion level [represented by smaller dots in **(A)**]. Biomes are represented by different colors. Connectivity umbrellas selected at finer scale often include unique and conservation-concern species [grey boxes in **(B)**], not selected at the coarse scale white box in **(B)**. Species identified to be of conservation concern in ecoregional assessments are represented by black silhouettes.

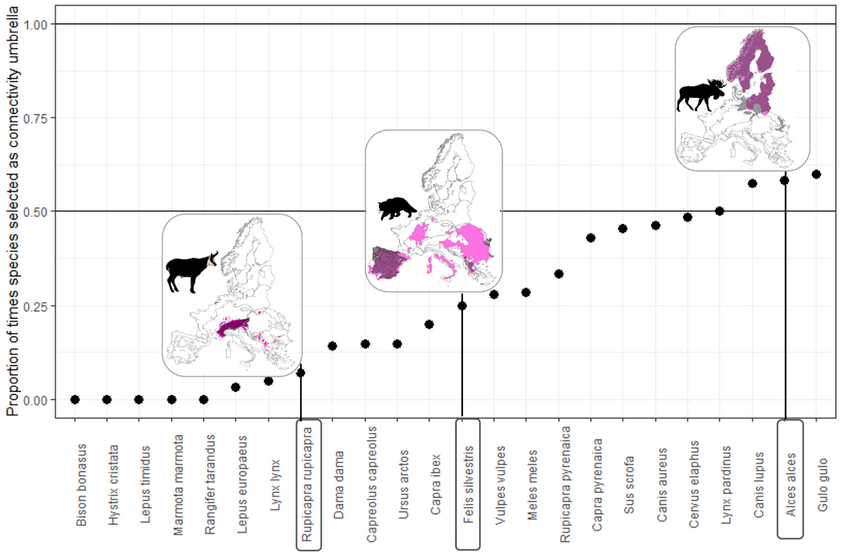


FIGURE 4
No species is selected as a connectivity umbrella everywhere it occurs. For each species in the x-axis, the y-axis represents the number of times it was selected as a connectivity umbrella everywhere it is present. For example, the distribution ranges of the moose (*Alces alces*), wildcat (*Felis silvestris*), and chamois (*Rupicapra rupicapra*) are shown in pink, and the ecoregions where they are selected as connectivity umbrellas are shown in hashed lines.

human-influenced regions (Figures 5A–F). Proportionally more species are required to meet connectivity targets in regions with high human influence (Figure 5G).

4 Discussion

Our approach increases objectivity when selecting umbrella species for connectivity conservation. It can be applied to multiple-taxonomic groups and to varying spatial scales. Unlike static target-setting in conservation prioritization exercises, our approach is flexible and can be adapted to test which species would suit different conservation goals and scenarios.

Two methods have been developed to specifically select species-based surrogates for connectivity planning. Lechner et al. (2017) use a cluster analysis on habitat requirements, connectivity elements, and gap-crossing distance thresholds to group twelve candidate mammal species into five distinct dispersal guilds. Connectivity for each guild is then modelled separately to identify which guild of species are more sensitive to habitat fragmentation. Meurant et al. (2018) present an approach to select multi-taxa surrogates from a pool of candidate species that represent a diversity of habitat needs and movement abilities. From a set of fourteen candidate species, the authors create a reference spatial prioritization map and run multiple permutations and combinations of the fourteen candidate species to identify the species subset that best retains different thresholds of the reference spatial priority map. Our approach is different from both methods. First, we include the entire terrestrial large mammal community in Europe without going through a pre-selection process as in Meurant et al. (2018), where they selected fourteen candidate species from a pool of 48 mammals, 216 birds, and 32 amphibians and reptiles based on a previous study (Albert et al., 2017). Second, we do not group species into dispersal guilds, diversity of habitat, or movement requirements. We treat each species independently. Further, instead of using a conservation concern filter in selecting the species to include in the candidate pool, we use the results to guide and test how frequently species of conservation concern are suitable connectivity umbrellas. Finally, in addition to addressing which and how many species are required for connectivity planning, we also evaluate the species-surrogates approach across two different geographic scales and assess the characteristics of connectivity umbrellas in landscapes with varying levels of human influence.

Our results re-confirm previous findings on the fine-filter surrogate approach that multiple species are better than any single surrogate species (Meurant et al., 2018; Wang et al., 2018) and *a priori* selection of certain groups, e.g., carnivores, may not be suitable connectivity umbrellas (Beier et al., 2009). Most suites of species selected in our analyses consist of a combination of herbivores and carnivores. Such mixed suites of species have diverse ecological attributes and dispersal abilities and are therefore more likely to accommodate the ecological requirements of diverse terrestrial mammal communities and their differing sensitivities to environmental conditions. In addition to corroborating previous findings, we show that both the number and the identity of species differ by the scale of analysis, and that species selected at finer scales are not subsets of those selected at broader scales (Figure 3).

Our approach is flexible in two ways. First, the result is a suite of species that are needed to cover 95% of the connectivity target. Depending on the regional context, it is possible to sub-select from within this suite of species, especially when species provide very little percent improvement towards the overall target. Second, the evaluation of sensitivity to different connectivity targets (Figure S3)

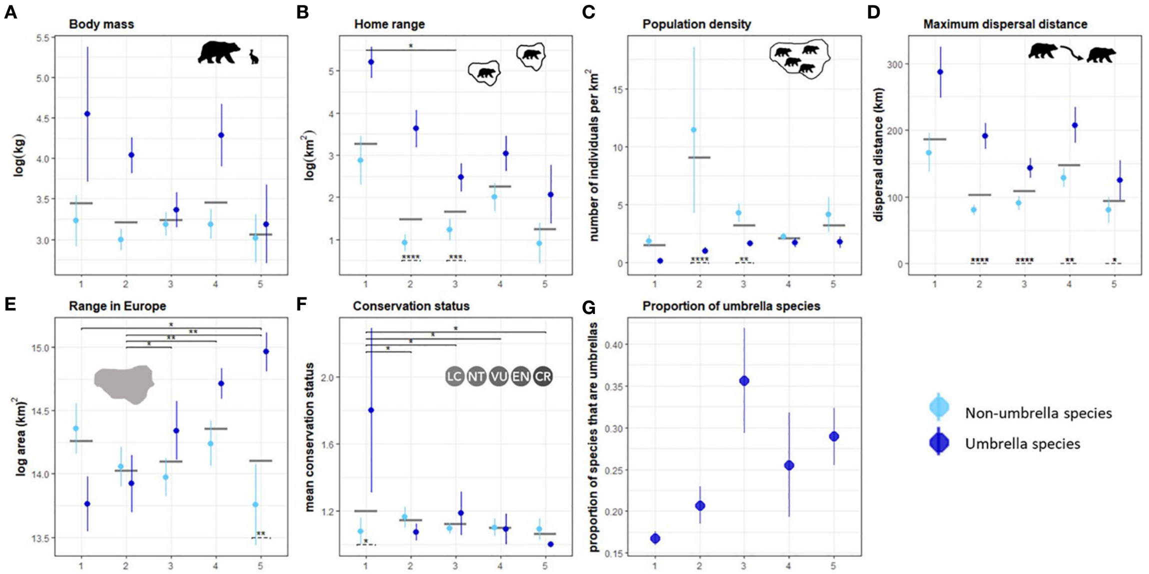


FIGURE 5
Attributes of species across clusters arranged from lowest (1) to highest (5) human impact. The means and standard errors of attributes of connectivity umbrellas (dark blue) and non-umbrellas (light blue) are shown in **(A–F)**, along with the mean attribute value in the cluster as a grey bar. The proportion of species selected as connectivity umbrellas in each cluster is shown in **(G)**. Significant difference of mean values between clusters are shown on the top in solid lines and between umbrella and non-umbrella species within clusters are shown at the bottom in panels **(A–F)**. * indicates a p-value ≤ 0.05, ** a p-value ≤ 0.01, and *** a p-value ≤ 0.001.

provides a way to select species that are suitable for a diversity of conservation goals. For example, moose and wolverine in the northern regions, red deer (*Cervus elaphus*) and Iberian Ibex (*Capra pyrenaica*) in the Mediterranean forests, woodland and scrub of the Iberian Peninsula and wolf in the Apennine peninsula, red deer and red fox (*Vulpes vulpes*) in temperate broadleaf and mixed forest in central Europe, and the Alpine ibex in the Alps, are species selected in all three connectivity targets which were created with very different conservation goals. In general, target EQ required more species than target Q or T. This is intuitive because target EQ represents all species, target Q represents only high-quality corridors irrespective of species, and target T only represents species of conservation concern. The identity of species selected across the targets changed in their rank, but in general the top-ranking species were consistent across the different targets, and the pool of species that was most highly ranked remained similar. This redundancy in the selection of species across disparate conservation goals can be a valuable tool to incorporate more certainty about including a particular species to be an umbrella for connectivity conservation.

An important finding is the interaction between the attributes of landscape and species selected as connectivity umbrellas. The interaction between species and landscape indicates that species selected to be surrogates for connectivity conservation need to be tailored to the level of human influence in the landscape under consideration. To be effective in highly humanized landscapes, numerically more species with a certain set of attributes (widely distributed but smaller-bodied species that occur at higher population densities and disperse over shorter distances) may be required. These attributes are generally not associated with umbrella species but may be the key to developing region-specific effective connectivity plans.

The aim of our study is not to prescribe which species should be used for connectivity conservation in Europe. Rather, we use continental Europe as an example to demonstrate an approach that is quite flexible and can accommodate many different conservation and modelling choices. Due to the continental scale of analyses, we use several simplifications in our modelling to optimize computational time. We used coarse-scale (1 km) existing habitat suitability maps to generate resistance surfaces and model connectivity between PAs, but it is noteworthy that source populations may also be present in habitat patches outside of the PA network, and individual species are likely to be impacted by more and different sets of variables. Therefore, we caution the use of the species presented here to be effective and "correct" connectivity umbrellas. The species presented here can be starting points, but we recommend users to create resistance surfaces using variables and resolutions that are relevant to their region of interest. It will most likely be computationally plausible to run regional models using non-protected habitat patches as source populations at a finer resolution and include more variables to develop more realistic resistance surfaces.

Our approach can easily be extended to other systems not presented here. For example, we analyze only terrestrial mammals, but other taxonomic groups of interest can easily be used to conduct similar analyses. We define three different connectivity targets based on different conservation goals, but connectivity targets may be defined in many other ways. Finally, we use a threshold of 95% of the target as our goal (guided by our observation that an asymptote is reached around 95%), but users may decide to use a different threshold. Our approach should be applicable in any focal landscape where it is possible to generate a connectivity network for multiple species.

Overall, we demonstrate that an objective selection of surrogate species for connectivity planning is possible. Considering multiple species, not just in relation to species attributes but in relation to landscape scale and characteristics may be the key towards identifying connectivity umbrellas that better represent the needs of entire species communities. In practice, decision-making in conservation is a complex process, involving many stakeholders, and is highly contextual. When species are tied in rank and contribution to the connectivity target, managers or conservationists could select species with a higher social acceptance or other issues that are relevant locally or regionally. Rather than advocating for one species over another, we present an approach to remove the guesswork over which species should be selected as connectivity umbrellas and increase objectivity in the selection of multispecies conservation strategies.

Conservation targets, whether modest at 30% of terrestrial land (CBD, 2023), or ambitious at 50% (Dinerstein et al., 2017), are unachievable without integrating connectivity conservation, especially in rapidly changing ecosystems in the Anthropocene. The key to selecting umbrella species for connectivity conservation is to move beyond arbitrary selection of species, for the selection process to be objective, and in relation to the scale and attributes of the landscape. Only then can the overall goal of connectivity conservation be realized and be effective in restoring ecosystems and decreasing biodiversity loss.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: https://figshare.com/s/23831fdc52a9dcc60a36.

Author contributions

TD, NB, and MDB contributed to conception and design of the study. JS contributed towards the analyses and SF's contributions helped improve the figures. TD wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Author MDB is a founder of DivjaLabs Ltd.

The remaining 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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1078649/full#supplementary-material

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Determination of forest priority levels for wild boar by analysis of habitat suitability and landscape connectivity

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The reduction and fragmentation of forests due to human activities are two primary factors that have led to forest biodiversity losses. The lack of forest continuation may prevent organisms from escaping areas that are no longer habitable due to altered environmental conditions and the reduction in size of habitat regions. Therefore, protecting and promoting forest connectivity has become one of the important objectives of forest management. The forests were regarded as independent elements, and the connectivity of the forest itself was directly evaluated in previous studies. However, this approach ignores the maintenance of forest connectivity, while requiring the participation of other landscape elements. In this study, we indirectly determine the forest priority by evaluating the landscape priority by integrating analysis with the habitat suitability (HS) model, MSPA and and BC_k^{PC} and dPC_k index. We studied the wild boar (*Sus scrofa*) habitats in and around Hupingshan and Houhe National Nature Reserves to illustrate the indirect evaluation method of forest priority. The results showed that forests with high priority, medium priority, low priority, and non-priority comprised 596, 64, 58 and 105 km^2, respectively, accounting for the 41.2, 2.7, 3.0, and 11.9% of the total forest area. Our research revealed that evaluating the forest priority by analysing the landscape priority was an effective method for forest priority identification, and this strategy can be used to other regions or species for the goal of identifying the forest priority for biodiversity conservation.

KEYWORDS

forest, priority level, habitat suitability, network analysis, *Sus scrofa*

1 Introduction

The forest is the dominant component of the terrestrial ecosystem and plays a crucial role in the conservation and management of biodiversity. Reduced and fragmented forest habitats (caused by urban sprawl, forest logging, intensified agriculture, etc.) are widely regarded as the greatest hazards to biodiversity (Lõhmus et al., 2017). The lack of forest continuity may impede the ability of organisms to leave areas that are no longer habitable due to altered environmental conditions and the reduction in size of habitat regions (Campbell Grant et al., 2007; Baranyi et al., 2011). Connectivity enables dispersal and gene flow, both of which are crucial for preventing population reduction and extinction (Foltête et al., 2020). In this context, preserving and promoting forest connectivity has become one of the most important objectives of forest management, as suitable forest landscape connectivity facilitates the movement of individual animals between forest regions and ensures genetic exchange between populations (Martin et al., 2017; Velázquez et al., 2017).

Landscape connectivity is defined as "the extent to which the landscape facilitates or impedes species movement across habitat patches and for a particular organism" and is influenced by both the landscape and the species in question (Baranyi et al., 2011). The network method combined with landscape connectivity index is an effective way to identify the key elements (patches, corridors, and stepping stones) of landscape (Gil-Tena et al., 2013; Saura et al., 2018). The network technique proposes that landscapes can be represented by a graph with nodes representing habitat patches and connections reflecting the dispersal probabilities of a species to travel between patches. Numerous indicators have been devised to reflect the landscape connectivity with a focus on either the elements or the entire landscape, but probability of connectivity (PC) is the most widely used. The importance of each patch or link determined by how much the PC metric decreased when it was removed (Baranyi et al., 2011; Cabarga-Varona et al., 2016; Hernando et al., 2017). This approach implies that organisms that formerly moved through a specific element are able to find alternative dispersal pathways and that there is no competition among dispersers for the use of the fewer remnant pathways in the disturbed landscape. To overcome the limitations of remove experiments, the BC_{k}^{PC} metric integrated the benefits of remove experiments and centrality, which gives greater weight to the paths that are anticipated to transport larger flows of organisms and that connect bigger and thus likely more ecologically significant patches (Bodin and Saura, 2010).

Land cover and vegetation type, patch area, and crown closure are three popular markers for designating nodes in a forest landscape network, and the connectivity between forest patches has been explicitly investigated in prior studies (Saura et al., 2011; Velázquez et al., 2019; Foltête et al., 2020). However, this network approach regards forests as independent elements and ignores the maintenance of forest connectivity, while requiring the participation of other landscape elements. This method only makes sense if the only location where the species lives is in a forest. However, species often affect the suitability of a habitat is, and it is a lot more complicated than just describing it in terms of plants or land cover (Avon and Bergès, 2016). For instance, not all forests identified on a land cover map may be suitable for certain animals (Avon and Bergès, 2016; Duflot et al., 2018). The network findings are only useful if the node and link properties are biologically important for the species under consideration (Urban et al., 2009).

In this study, we indirectly determine the priority of the forest through determining the priority levels of the landscape. To accomplish this, we initially evaluated the suitable area based on the habitat demand of the specific species by the habitat suitability (HS) model. The prediction accuracy of HS outputs was evaluated by the infrared monitoring data of the species. Furthermore, we developed the habitat networks and applied the landscape connectivity index (BC_{k}^{PC} and dPC_k) to assess the priority patches and corridors, respectively, and the priority of forest is consistent with the priority of the landscape area where it belongs to.

We studied the wild boar (*Sus scrofa*) habitats in Hupingshan–Houhe National Nature Reserves (Hupingshan–Houhe NNR) and three adjacent counties around them to illustrate the indirect evaluation method of forest priority. Hupingshan–Houhe NNR reconsidered as the most appropriate places to harbor a small population of the South China tiger (*Panthera tigris amoyensis*) individuals (Qin et al., 2015; Shurong et al., 2022). It has been claimed that population density, ungulate prey size and biomass are typically crucial to the survival and reproduction of wild tiger populations (Sunquist, 1981; Karanth and Sunquist, 1995; Miquelle et al., 1996; Burge, 1999; Karanth and Sunquist, 2000; Karanth et al., 2004; Hebblewhite et al., 2011; Hebblewhite et al., 2014; Qin et al., 2015; Kafley et al., 2016). Main tiger prey includes forest and grassland ungulates, ranging in size from tiny deer such as barking deer (*Muntiacus muntjak*) and wild boar to huge animals such as water buffalo (*Bubalus bubalis*) (Karanth et al., 2004; Smith et al., 2008; Karanth and Nichols, 2010; Xie and Smith, 2013; Froese et al., 2017). The infrared camera monitoring survey in Hupingshan NNR reveals that wild boars are one of the main prey that satisfy the demands of South China tigers (Shurong et al., 2020). As the major habitat of the tiger prey, the forest, which comprises more than 50 percent of the total area of the study area, plays a critical role in maintaining its population (Tang et al., 2023). Therefore, identifying the priority of forests at different locations in the study area for wild boar is of significance for maintaining the number of wild boar populations, which have a positive promoting effect to the survival and reproduction of South China tigers.

2 Materials and methods

2.1 Study area

Hupingshan–Houhe NNR (110° 29′–110° 59′ E, 29° 50′–30°09′ N; Figure 1) consists of two adjacent regions, Hupingshan NNR is located on the northern border of the Hunan Province and Houhe

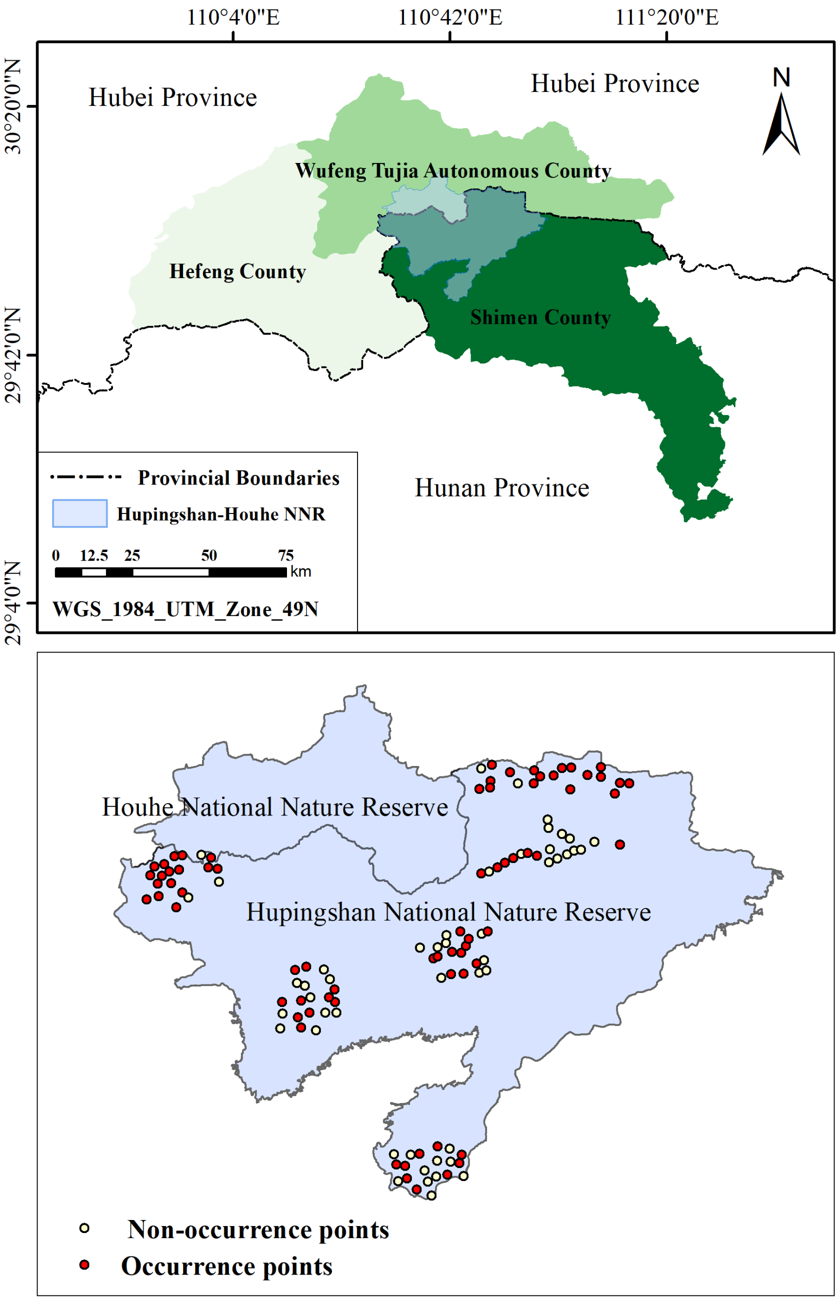

FIGURE 1
Location of the study area.

NNR on the southern border of the Hubei Province. Located in the transition region between the Guizhou Plateau and hilly zones in southeast China, Hupingshan–Houhe NNR is topographically heterogeneous, including steep and deep ravines, narrow valleys, and high mountains. The terrain includes deep ravines, narrow valleys, and high altitudes, with the highest altitude at 2,299 m (Shu-Rong et al., 2019). The region has a subtropical mountain climate that is significantly impacted by the North Pacific warm current, resulting in hot and rainy summers and cold and snowy winters. The annual mean temperature is 9.2°C, and the annual mean precipitation is 1900 mm (Shurong et al., 2020). The study area consists of two NNRs and three adjacent counties: Shimen County in Hunan Province, Hefeng County, and the Wufeng Tujia Autonomous County in the Hubei Province. The overall area of these regions is approximately 12300 km^2, and forests with canopy > 30% and shrubs with canopy > 40% account for approximately 54% of the total area. The area includes six typical soil types, among which yellow brown soil is the most widely distributed (Wei et al., 2020).

One hundred and twenty infrared cameras were set up in Hupingshan NNR to obtain the distribution data of wild boars (Figure 1). Infrared cameras are located in each 1km × 1km grid generated by ArcGIS, and a total of 120 infrared cameras are deployed (Yu et al., 2018). From October 2020 to October 2021,

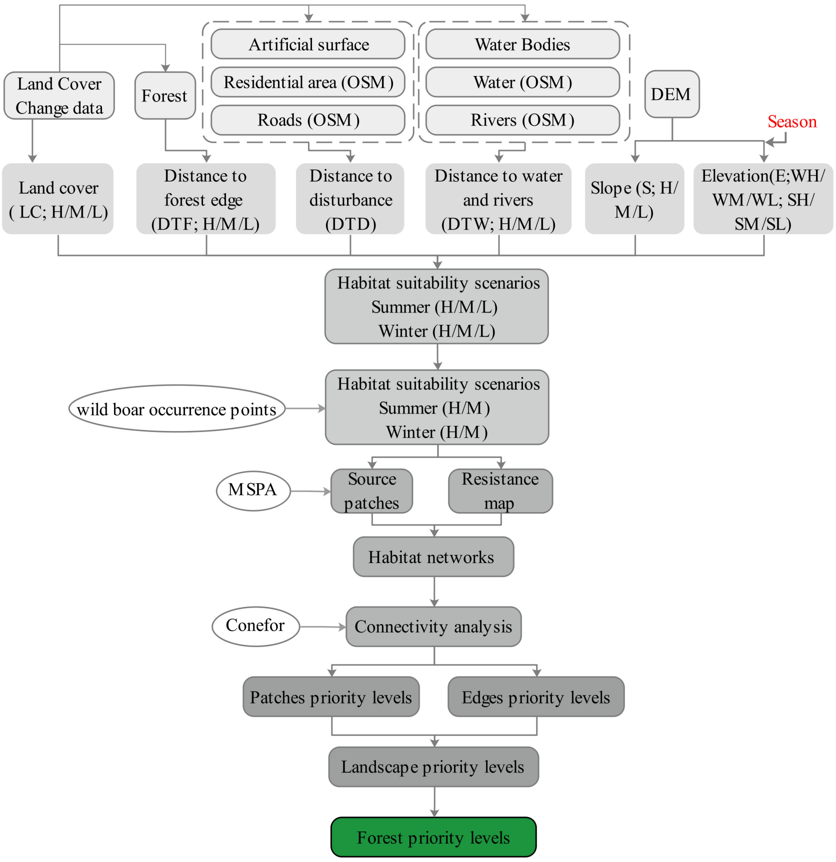

FIGURE 2
Schematic overview of the analytical procedure.

there were 579 independent and effective wild boar photos distributed in seventy-two infrared camera points were captured (Yu et al., 2018).

2.2 Habitat suitability assessment

A diagrammatic summary of the analytical method is shown in Figure 2. Based on the work of Qin et al. (2015) and Tang et al. (2021), a habitat suitability (HS) model has been developed to identify the suitability of the study area. The HS model was computed using the geometric mean of six suitability indices (SIs) as described:

$$HS = (LC \times S \times E \times DTF \times DTW \times DTD)^{1/6} \tag{1}$$

where LC, S, E, DTF, DTW, and DTD refer to landscape cover, slope, elevation, distance to the forest edge, distance to water bodies, and distance to disturbance, respectively. To account for uncertainty in parameterizations of habitat requirements (Bennett et al., 2009; Battisti et al., 2016), the SI habitat suitability was parameterized under three different scenarios (high: H, medium: M, and low: L) for the LC, S, E, DTF, and DTW indices. Only one scenario was established to parameterize the DTD. Habitat selection by wild boar seasonally varies, and particularly with elevation changes. Thus, summer (S) and winter (W) scenarios were constructed with different elevation parameterizations to accommodate such potential variability across seasons. Six HS scenarios were developed, including summer high SH, summer medium SM, summer low SL, winter high WH, winter medium WM, and winter low WL conditions. Then, the seventy-two infrared camera positions where wild boars appeared were utilized to evaluate the prediction accuracy of the six HS outputs. This scenario will be kept if the forecast accuracy is greater than 85%; otherwise, it will be removed. The patches with an HS > 6 and area >1 km^2 were initially considered to be suitable habitats patches for wild boar, while others were considered unsuitable.

2.3 Developing networks

Then, morphological spatial pattern analysis (MSPA) (Soille and Vogt, 2009; https://forest.jrc.ec.europa.eu/en/activities/lpa/gtb/) was used to select the source patches from the suitable habitats. MSPA can divide the binary map, yielding seven classes including core, islet, edge, bridge, perforation, loop, and branch areas. In this study, the patch containing the core is considered as the source patch, which have more robust biological structures than sections lacking core regions (Tang et al., 2023). Using edge width (EW) parameters, the MSPA segmentation method can be fine-tuned. The EW was set to nineteen pixels, which corresponded to a Euclidean distance of 570 meters. The EW was equivalent to a 1 km^2 circle with an optimal radius for wild boar habitat.

The effective distances were calculated using the cumulative costs along the path with the lowest cost, disregarding the distances between sections. To convert the suitability of habitats into resistance value, the HS results were classified into seven classes, with class 1: $0 \leq HS \leq 1$; class 2: $1< HS \leq 2$; class 3: $2< HS \leq 3$; class 4: $3< HS \leq 4$; class 5: $4< HS \leq 5$; class 6: $5< HS \leq 6$; and class 7: $6< HS \leq 10$. The HS values were inverted such that appropriate sites for wild boar (i.e., areas with higher HSs) had lower mobility resistance, and vice a versa (Duflot et al., 2018). Using a negative exponential calculation (Préau et al., 2020; Tang et al., 2023), the resistance values for classes 1, 2, 3, 4, 5, 6, and 7 were calculated to be 373, 139, 52, 19, 7, 3, and 1, respectively. A decreasing exponential function was used to incorporate LCPs into the PC index (Saura and Pascual-Hortal, 2007). The cost distance-decay coefficient was also set at 0.05 for the maximum connectivity distance between patches (Urban et al., 2001). The habitat networks were developed in the Graphab v2.4 software (Foltête et al., 2012; http://thema.univ-fcomte.fr/productions/Graphab/).

To avoid the excessive connectivity between patches (Liu et al., 2017), the connectivity distance threshold was identified by exploring the correlation between the overall probability connectivity (PC) and the dispersal distance, in addition to using community analysis (Tang et al., 2021). Patches belonging to the same community are connected by edges, whereas different communities are not connected. In the community analysis, the area accounting for 85% of the total study area was used as the predetermined threshold for the largest community area (Tang et al., 2021).

2.4 Evaluating of forest priority

In this study, we used the BC_k^{PC} to evaluate the importance of nodes, which takes into account patch areas and maximum product probabilities between patches instead of only the number of shortest paths. This metric could assign more weight to the paths that carry larger flows of organisms and that connect bigger and therefore more ecologically important patches for wild boar populations (Bodin and Saura, 2010). As suggested by Saura and Rubio (2010), dPC_k was derived from the overall PC index to evaluate the connectivity importance of edges. According to Saura and Torné (2009), the connectivity index was analyzed using the Conefor Sensinode v2.6 program (http://www.conefor.org/).

Patches and corridors were classified by connectivity index from the largest to the smallest, and then divided into three categories including 0–50%, 50.1–90%, and 90.1–100%, that corresponded to three connectivity importance levels (CIL; high H, medium M, and low L) that were assigned coded values of 3, 2, and 1 respectively (Tang et al., 2021). Buffer analysis for corridors was conducted using a Euclidean distance of 570 m that was equal to the edge width used in the MSPA. Since the corridors spatially intersect with patches in each scenario, the maximum CIL value between patches and corridors was taken as the value of overlapped pixels. Then, calculate the arithmetic mean of the landscape priority under the four assessment scenarios as the CIL of landscape, which were separated into four priority levels including high: $2 \leq CIL \leq 3$, medium: $1 \leq CIL \leq 2$, low: $0 \leq CIL \leq 1$, and non: CIL=0. The forest priority was consistent with the priority of the landscape that it belongs to.

3 Results

3.1 The distribution of suitable habitats

The evaluation of six different HS scenarios revealed priority, non-priority habitat ranges and prediction accuracy of the appearance positions of wild boars (Figure 3). Specifically, priority habitat ($HS > 6$) in summer ranged from 6,911 (SL) to 10,211 km^2 (SH) in area, the non-priority habitat ($HS \leq 6$) ranged from 2,095 (SH) to 5,395 km^2 (SL) in area (Table 1). The priority habitat ($HS > 6$) in winter ranged from 6,044 (WL) to 10,117 km^2 (WH) in area, the non-priority habitat ($HS \leq 6$) ranged from 2,189 (SH) to 6,262 km^2 (SL) in area (Table 1). The prediction accuracy of the appearance position ranged from 56.9 to 97.2%. Four habitat suitability assessment scenarios with prediction accuracy greater than 85% are shown in Figure 3.

3.2 Graph-based networks

In conjunction with a community analysis, a connectivity distance threshold of 530–550 cumulative resistance value (CRV) was established based on the correlation between the overall PC index and the dispersal distance. In this study, connectivity distances of 550 CRV were used to establish habitat networks.

Statistical characteristics for the six networks with connectivity distances threshold of a 550 CRV are shown in Table 2. In summer, the number of patches was 92 (M) and 94 (H), the average patch area was 99 km^2 (M) and 108 km^2 (H), the total patch area was 9,061 km^2 (M) and 10,117 km^2 (H), and the number of edges was 144 (M) and 152 (H). In winter, the number of patches was 95 (M) and 94 (H), the average patch area was 90 km^2 (M) and 107 km^2 (H), the total patch area was 8,524 km^2 (M) and 10,013 km^2 (H), and the number of edges was 149 (M) and 151 (H). Patches and corridors and their corresponding networks were shown in Figure 4.

3.3 Forest priority levels

The area of landscape and forest priority are shown in Figure 5, The area of landscape and forest priority are shown in Table 3. The

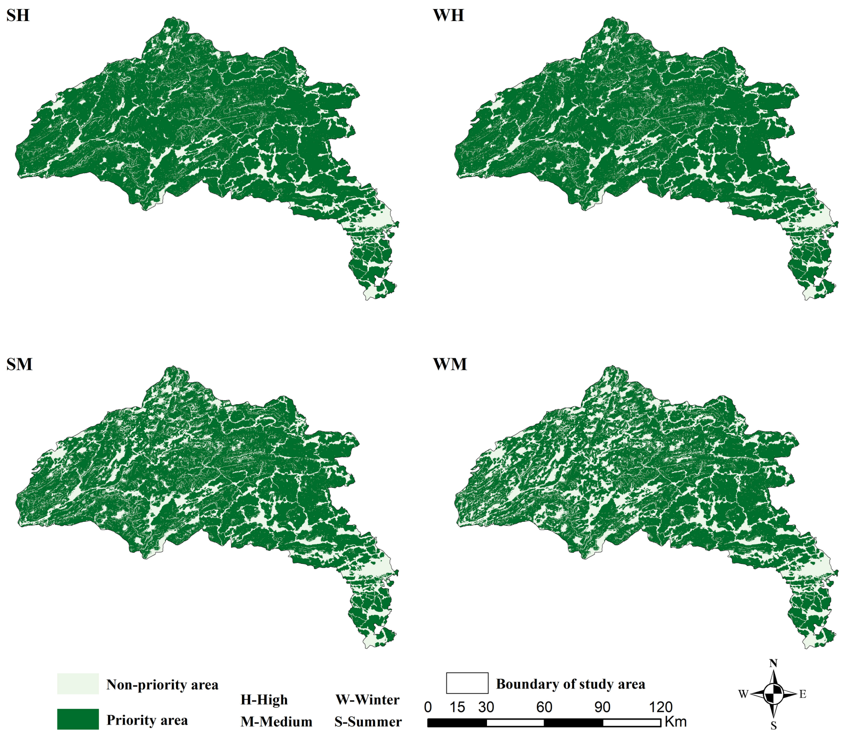

FIGURE 3
Priority area and non-priority area in the four suitability assessment scenarios with prediction accuracy greater than eighty-five percent.

landscape with high priority, medium priority, low priority, and non-priority comprised 2,027, 3,825, 3,828, and 2,627 km^2, respectively. The forests with high priority, medium priority, low priority, and non-priority comprised 1,448, 2,396, 1,929, and 886 km^2, respectively. The forests in Hupingshan–Houhe NNR with high priority, medium priority, low priority, and non-priority comprised 596, 64, 58 and 105 km^2, respectively, accounting for the 41.2, 2.7, 3.0, and 11.9% of the total forest area.

4 Discussion

The priority of forest is indirectly identified by determining the priority areas of the landscape, that is, the priority of the forest is consistent with the priority of the landscape where it is located in. As far as we know, this is a new perspective for assessing forest priorities. In previous study, forest patches with area larger than the predefined threshold were usually regarded as nodes, and then the connectivity between forest patches is directly evaluated. For example, Velázquez et al. (2017) defined areas labelled with the "forest" and "shrub and/or herbaceous vegetation associations" areas as nodes. Saura et al. (2011) selected broadleaved forest, coniferous forest and mixed forest for the connectivity analyses. Jie et al. (2012) selected forest and agricultural dryland patches with an area > 30 km^2 as source patches to analyse the importance of agricultural landscape for forest restoration. Ruppert et al. (2016) defined the mature jack pine stands, rocky outcrops, and shallow soil sites as the most preferred habitat type for woodland caribou.

In this study, we built a HS model based on literature reviews, preliminary field work, and expert opinion to assess the suitability of the habitat. Furthermore, we utilized the field data of wild boar to evaluate the outputs of HS model, and only four scenarios (SH, SM, WH, WM) were retained for forest connectivity analysis. The review shows that landscape graphs can benefit from field data of different types at varying scales (Foltête et al., 2020). But biological data are usually gathered from a limited set of locations, as collecting species data on a large scale requires a significant amount of financial and time resources. Thus, we do not discard the results of HS model as they indirectly benefit from methodological improvements and ecological knowledge acquired in studies based on field data. Dutta et al. (2018) showed that HS assessment based on information derived from the literature and field data were a better proxy of empirical models than those designed exclusively from expert opinion.

In our investigation, we kept all patches that contained the core class as source patches. However, only the core class of MSPA analysis was regarded as a source patch in previous study, following the seminal paper of Saura et al. (2011). The patches containing cores and edges can better represent a more natural ecological

TABLE 1 Characteristics of suitable and non-priority areas and prediction accuracy the appearance position of wild boar under six different HSI scenarios.

	Priority areas (km^2)	Non-priority areas (km^2)	Prediction accuracy (%)
Summer			
High	10,211	2,588	97.2
Medium	9,242	6,281	90.3
Low	6,911	11,545	72.2
Winter			
High	10,117	2,839	97.2
Medium	8,734	7,600	88.9
Low	6,044	16,433	56.9

interference system and provide more interior and edge environmental sources than islets, which then buffers species extinction events due to environmental changes. This novel application of MSPA results may theoretically improve the reliability of source patches analyses.

In this study, the habitat connectivity for wild boar was quantified by indices of BC_k^{PC} and dPC_k. The forests in Hupingshan–Houhe NNR with high priority comprised 596 km^2, accounting for the 41.2% of the total forest area. The results showed that almost all forests in the Hupingshan–Houhe NNR were classified as high priority, which is consistent with the ecological important protection level of Hupingshan–Houhe NNR (Figure 5). But the more important discovery is that 59.8% of the high priority forests are located outside the reserve, which indicates that in order to maintain the connectivity of the wild boar population, the high-priority forests outside the reserve also need to be protected. Strengthening the connectivity between the high priority forests inside and outside the NNR is crucial for the continuation of the wild boar population.

The connectivity distance threshold of links in our study was evaluated by exploring the correlation between the overall probability connectivity (PC) and the dispersal distance, in addition to using community analysis. This method can effectively avoid the adverse effects of excessive connectivity. Since the field data of wild boar dispersal was not recorded, the connectivity distance threshold of edges can be evaluated by using information sourced from like published literature and naturalist association records, but which may produce an excessive connectivity, promoting the spread of pests, diseases or wildfire among populations (Saura et al., 2018; Tang et al., 2021).

4.1 Alternatives and limitations of the methodological framework

As presence–absence data of wild boar are available, which can be directly embedded in the definition of patches from an species distribution model SDM or another output of suitability modeling, following procedures synthesized in Duflot et al. (2018). For instance, the MaxEnt model can provided a reliable predictive map of species habitat and the environmental predictor effects fitted well with the known ecology of the species (Brown et al., 2018).

The habitat suitability data were inverted to provide a resistance map, however habitat suitability does not represent species movement per se. Inferring resistance maps from HS presumes that mobility behavior follows the same criteria as habitat selection, which is not necessarily the case (Zeller et al., 2012). HSI derived from presence points may be a decent surrogate for these processes, and employing inverted HSI as resistance is likely a solid choice in this regard (Blazquez-Cabrera et al., 2016). A further possibility is to combine expert opinion with HSM-derived resistance maps.

The priority of the forest is determined indirectly by determining the priority area in the landscape. This may theoretically improve the reliability of forest priority analyses and the way they are carried out. To be reliable, this approach should preferably be supplemented by a validation process with genetic and telemetry data (Zeller et al., 2018).

5 Conclusions

In this study, the suitable area was evaluated by the habitat suitability (HS) model, and the prediction accuracy of HS outputs was evaluated by the infrared monitoring data of wild boar. The networks combined with the connectivity index of B

TABLE 2 Characteristics of nodes and edges of networks at a connectivity distance threshold of 550.

	Number of nodes	Total area	Mean area (km^2)	Number of edges
Summer				
High	94	10,117	108	152
Medium	92	9,061	99	144
Winter				
High	94	10,013	107	151
Medium	95	8,524	90	149

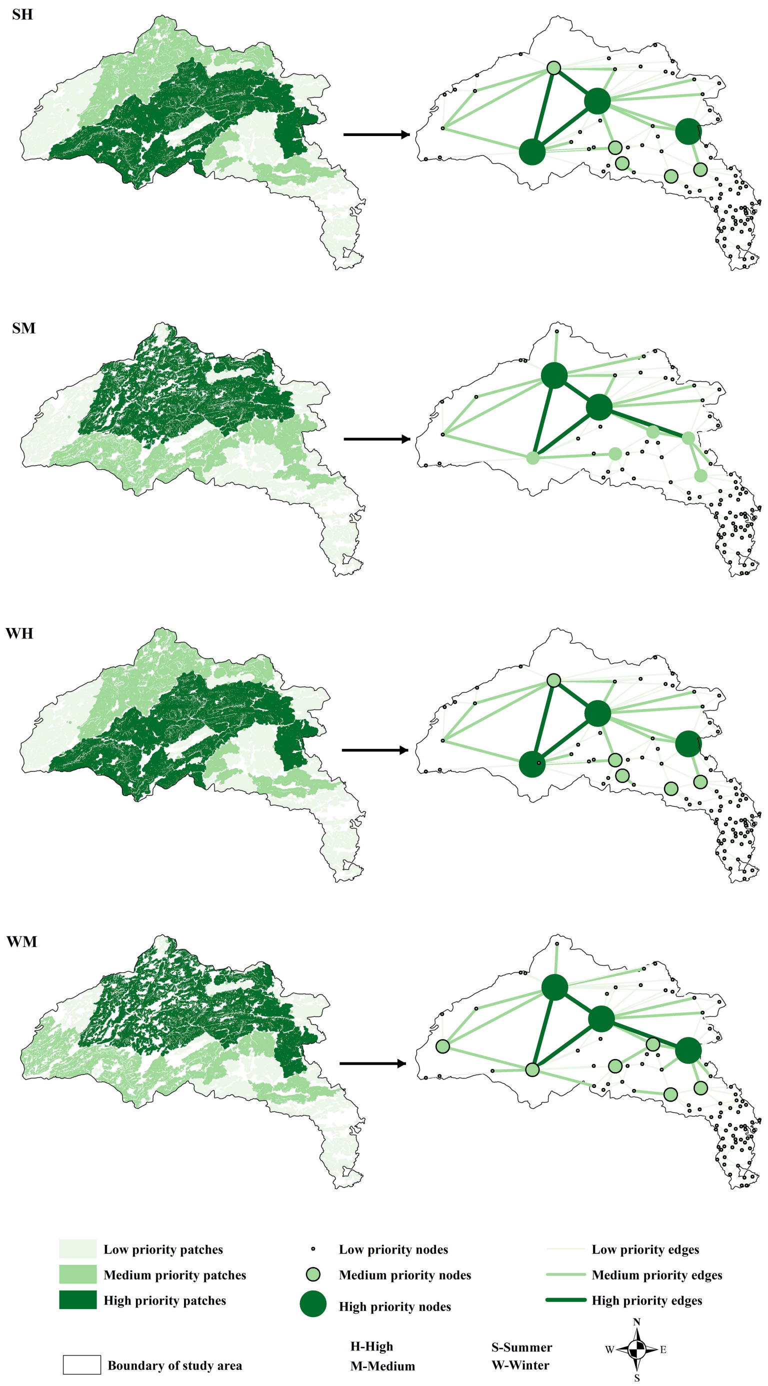

FIGURE 4
Patches and corridors and their corresponding networks.

C_k^{PC} and dPC_k were utilized to assess the priority patches and corridors, respectively, and the forest priority is consistent with the priority of the landscape area it belongs to. The results show that not only the forests in the NNR, but also a part of the forests around the NNR are of great significance to maintain the habitat connectivity of wild boar in and around Hupingshan–Houhe NNR. Results of our study are informative for wild boar habitat conservation, corridor establishment, and land use planning of study area in the future. Our study indicated that determining the forest priority through evaluating

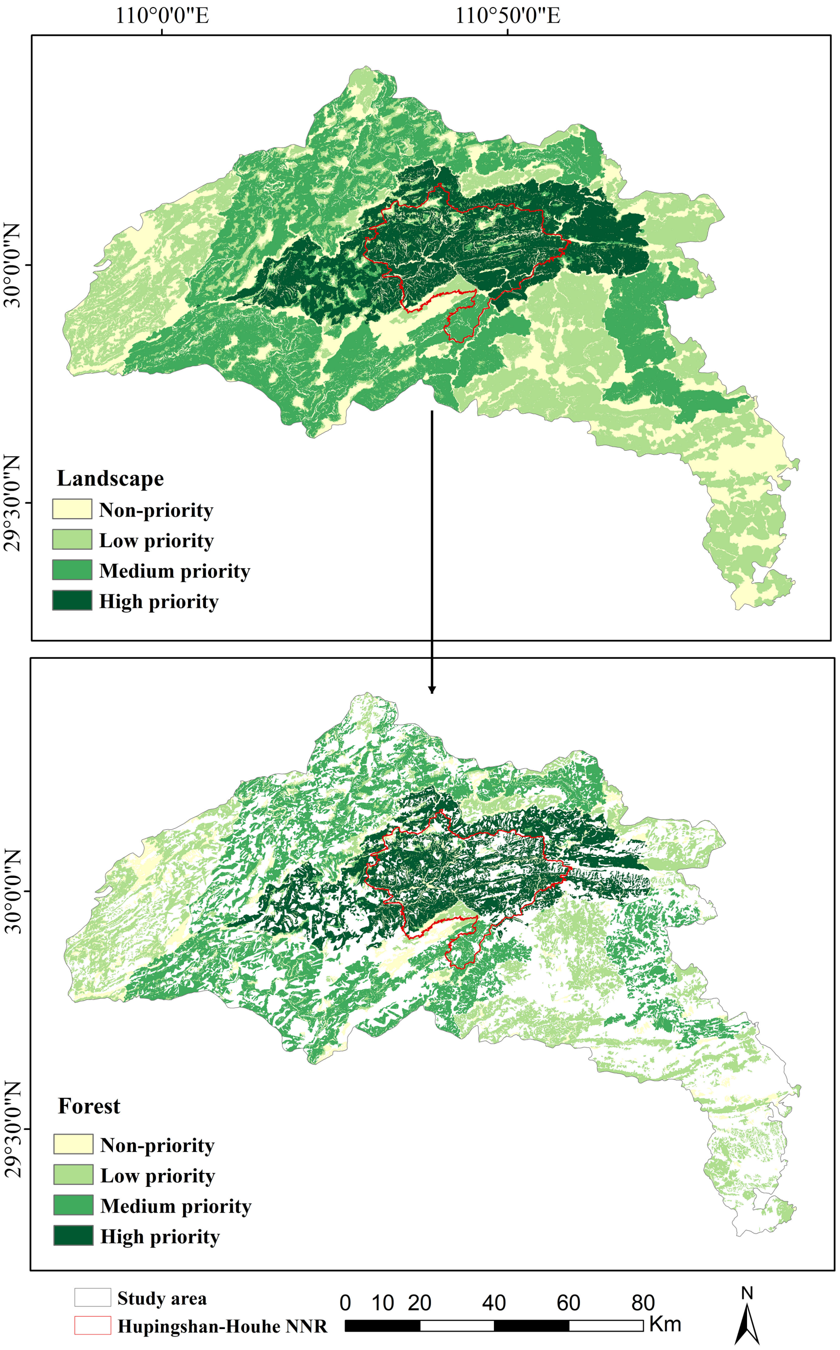

FIGURE 5
Priority of landscape and forest.

TABLE 3 Area of landscape and forest priority.

Priority level	Area of landscape (km^2)	Area of forest (km^2)	Area of forest in Hupingshan–Houhe NNR (km^2)	Proportion in total forest area (%)
High	2,027	1,448	596	41.2
Medium	3,825	2,396	64	2.7
Low	3,828	1,929	58	3.0
Non	2,627	886	105	11.9

the landscapepriority was an effective approach for forest hotspot selection, and this method can be applied for other areas or animals to identify the priority of forests in the purpose of biodiversity conservation.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

TT completed the draft. JL obtained projects and provided financial support. JV reviewed and edited the paper. All authors contributed to the article and approved the submitted version.

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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.

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Supplementary material

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Mule deer (*Odocoileus hemionus*) resource selection: trade-offs between forage and predation risk

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Ungulates commonly select habitat with higher forage biomass and or nutritional quality to improve body condition and fitness. However, predation risk can alter ungulate habitat selection and foraging behavior and may affect their nutritional condition. Ungulates often choose areas with lower predation risk, sometimes sacrificing higher quality forage. This forage–predation risk trade-off can be important for life history strategies and influences individual nutritional condition and population vital rates. We used GPS collar data from adult female mule deer (*Odocoileus hemionus*) and mountain lions (*Puma concolor*) to model mule deer habitat selection in relation to forage conditions, stalking cover and predation risk from mountain lions to determine if a forage-predation risk trade-off existed for mule deer in central New Mexico. We also examined mountain lion kill sites and mule deer foraging locations to assess trade-offs at a finer scale. Forage biomass and protein content were inversely correlated with horizontal visibility, hence associated with higher stalking cover for mountain lions, suggesting a forage-predation risk trade-off for mule deer. Mule deer habitat selection was influenced by forage biomass and protein content at the landscape and within home range spatial scales, with forage protein being related to habitat selection during spring and summer and forage biomass during winter. However, mule deer selection for areas with better foraging conditions was constrained by landscape-scale encounter risk for mountain lions, such that increasing encounter risk was associated with diminished selection for areas with better foraging conditions. Mule deer also selected for areas with higher visibility when mountain lion predation risk was higher. Mountain lion kill sites were best explained by decreasing horizontal visibility and available forage protein, suggesting that deer may be selecting for forage quality at the cost of predation risk. A site was 1.5 times more likely to be a kill site with each 1-meter decrease in visibility (i.e., increased stalking cover). Mule deer selection of foraging sites was related to increased forage biomass, further supporting the potential for a trade-off scenario. Mule deer utilized spatio-temporal strategies and risk-conditional behavior to reduce predation risk, and at times selected suboptimal foraging areas with lower predation risk.

KEYWORDS

forage, mountain lion predation, mule deer, *Odocoileus hemionus*, *Puma concolor*, predation, resource selection, trade-off

Introduction

When forage abundance or nutritional quality is limiting, ungulate resource selection should be focused towards areas with forage conditions that allow individuals to maximize nutritional condition. However, accessibility of forage can be moderated by environmental constraints, physiological tolerances, and interspecific interactions (Kie, 1999; Johnson et al., 2000; Dupke et al., 2016; Gedir et al., 2020). Predation risk can alter habitat selection and foraging behavior of prey species, and consequently affect their nutritional condition (Barten et al., 2001; Creel et al., 2005; Panzacchi et al., 2010; Dellinger et al., 2019). The effects of predation risk on prey behavior have been demonstrated in numerous species (e.g., Bleich et al., 1997; Altendorf et al., 2001; Creel and Christianson, 2008; Hay et al., 2008).

The effectiveness of proactive responses (e.g., habitat selection, shifting activity periods, and vigilance) used by prey to reduce risk of predation depends on the predictability of risk (Creel, 2018). If risk is predictable, prey can select habitat to avoid risky areas or adjust activity patterns so that use of riskier areas occurs at times when their primary predators are less active (Gehr et al., 2018; Kohl et al., 2018, 2019; Smith et al., 2019a). Coursing predators may be less predictable than stalking or ambush predators because they tend to be wide-ranging, and do not depend strongly on concealment cover or other habitat features to enhance hunting success (Peterson et al., 2021). In contrast, hunting by stalking predators is often associated with fine scale landscape features which may contribute to susceptibility of prey and predictability of risk (Laundré and Hernández, 2003; Schmidt and Kuijper, 2015). Predation risk for ungulates can be influenced by topographic features, vegetative characteristics and horizontal cover, distance to edge, season, time of day, and anthropogenic features (Atwood et al., 2009; DeCesare, 2012; Knopff et al., 2014). For stalking predators, these elements can influence where and when to search for prey, and alter hunting efficiency (Coon et al., 2020).

Under ideal conditions, ungulates would have access to high quality foraging areas with low risk of predation. For example, Pierce et al. (2004) reported that the highest quality forage for mule deer (*Odocoileus hemionus*) was in areas with lower predation risk from mountain lions (*Puma concolor*), thus mule deer were able to select higher quality foraging areas without an increased risk of predation. However, ungulates often choose areas with lower predation risk, sacrificing access to higher quality forage (Lima and Dill, 1990; Basille et al., 2015; Chitwood et al., 2022). For example, a mule deer population in Colorado selected better foraging areas but with higher risk of mountain lion predation, resulting in increased vigilance and less efficient foraging, thus there was a trade-off between efficient foraging and predation risk (Altendorf et al., 2001). Similar trade-offs between predation risk and forage have been documented in other ungulate species (Bleich et al., 1997; Hamel and Côté, 2007; Fortin and Fortin, 2009; Rignos, 2015). When forage-predation risk trade-offs occur, animals in better nutritional condition are more likely to avoid riskier areas than those in poor body condition (McNamara and Houston, 1986; Sinclair and Arcese, 1995; Rignos, 2015). Thus, ungulate nutritional condition, often related to proximity of the population to nutritional carrying capacity, can moderate ungulate responses to variable forage conditions and predation risk. At times and places where ungulates are forced to make a trade-off between higher quality foraging conditions and predation risk, it can have important implications for life history strategies with major effects on body condition of individuals, and subsequently population vital rates (Laundré et al., 2001; Hernández and Laundré, 2005; Christianson and Creel, 2010; Creel, 2018). For example, Monteith et al. (2014) reported that mule deer that migrated to summer ranges with superior forage conditions incurred significantly higher neonatal mortality from black bear (*Ursus americanus*) predation, resulting in lower overall productivity.

The influence of nutritional resources, environmental constraints, and interspecific interactions on habitat selection can vary with the behavioral state of animals. Habitat selection of foraging ungulates should be directed toward finding high quality forage, while simultaneously mitigating predation risk or thermoregulatory constraints. Conversely, habitat selection by satiated ungulates should be primarily driven by the need to find safe areas for resting and ruminating. The forage–rest/rumination cycle of many ungulate species typically has a distinct diel pattern with foraging bouts concentrated during crepuscular periods and resting–ruminating during midday (Sargeant et al., 1994; Roberts et al., 2016; Morano et al., 2019; Patten et al., 2019; Khan et al., 2023). Similarly, predators often have regular diel activity rhythms, with active hunting periods generally related to the time of day most favorable to their hunting style (e.g., stalking vs. coursing; Kohl et al., 2019). Thus, drivers of and constraints on resource selection of ungulates can vary across the diel cycle with selection patterns focused towards meeting behavior-specific resource needs and mitigating constraints imposed by the environment or interspecific interactions.

Heterogeneity in habitat conditions is linked to spatial and temporal variation in forage resources and predation risk (Brown and Litvaitis, 1995; Lowrey et al., 2019; Davidson et al., 2012; Gulsby et al., 2017; Smith et al., 2019b). Natural and anthropogenic disturbances contribute to habitat heterogeneity, influencing forage availability and nutritional quality for herbivores as well as habitat use by predators. Wildfire is one such disturbance, with the magnitude of the changes to habitat and forage conditions for herbivores varying with fire severity and post-fire recovery time (Proffitt et al., 2019; Roerick et al., 2019; Bristow et al., 2020; Hayes et al., 2022; Lewis et al., 2022). Predators also respond to fire-induced changes in habitat heterogeneity, particularly those that increase availability of prey that are attracted to increased forage in burned areas or accessibility of prey due to increased stalking cover resulting from post-fire recovery of woody shrubs (Smith et al., 2019b; Doherty et al., 2022; Gigliotti et al., 2022; Lewis et al., 2022; Suraci et al., 2022). Thus, wildfires or other landscape disturbances resulting in resource heterogeneity can cause favorable changes in forage conditions for herbivores, while simultaneously creating habitat conditions that increase hunting success of predators, which can contribute to the forage–predation risk trade-off for herbivores (Ganz et al., 2022; Lewis et al., 2022).

In this study, we collected field data on forage availability and nutritional quality, predation risk, risk-sensitive foraging site selection, and predation site characteristics, and we developed resource selection functions using GPS collar data from mule deer and mountain lions to examine the relative roles of predation risk and forage conditions on habitat selection of adult female mule deer. Our first objective was to determine if mule deer in our study area faced a trade-off between forage conditions and predation risk from mountain lions, the primary predator of adult deer in our study area. If this trade-off existed, we sought to examine how spatio-temporal variation of predation risk, biomass and nutritional quality of forage, and other habitat characteristics might affect mule deer resource selection. We expected mule deer to deal with the forage–predation risk trade-off in a context specific manner related to seasonal changes in forage conditions and variation in risk. We also expected that mule deer responses would vary by diel period, with responses to forage and predation risk most pronounced during the crepuscular periods when mule deer typically forage and by predation risk during crepuscular and nighttime periods when mountain lions are most active. We expected that during winter, mule deer would adjust habitat selection to prioritize acquisition of nutritional resources even at the cost of incurring higher predation risk from mountain lions. We expected that during the summer fawning season, female mule deer would prioritize reducing exposure to predation risk even at the expense of foraging opportunities in spite of the higher energy demands due to lactation. We also predicted that mule deer would increase selection for higher forage quality/quantity in areas of lower predation risk, and select for poorer forage conditions when predation risk is high. Finally, we expected that wildfire-burned areas would be a source of high quality forage and a risky area given that the post-fire recovery of woody browse that composes the bulk of mule deer diets can be used as stalking cover by mountain lions.

Materials and methods

Study area

We studied a non-migratory deer herd in the Gallinas Mountains area of the Cibola National Forest (Figure 1), near Corona, New Mexico. Elevation ranges from 1,912 to 2,631 m. Mean annual precipitation is 42.5 cm (± SD = 11 cm), with approximately 46% falling during the monsoon season from July to September (Climate data from Corona, NM, ca. 17 km east of the study area; elev. 2,054 m; WRCC, 2014). Average annual snowfall is 69.4 cm (± SD 47 cm). Average daily high and low temperatures are 7.6°C and −5.2°C, and 27.6°C and 11.6°C in January and June, respectively. Based on long-term precipitation and temperature data, seasons were designated as spring (April–June), summer (July–September), and fall–winter (October–March), which approximately corresponded with pre-parturition, parturition/lactation, and post weaning/reproduction, respectively.

Only a few natural perennial water sources exist in the form of small springs surrounded by thick vegetation and rough terrain. The majority of perennial water sources are developed water catchments and dirt livestock tanks. Vegetation communities range from grasslands (10% of study area) at lower elevations, transitioning to pinyon-juniper (*Pinus monophylla* [*P. edulis*]–*Juniperus* spp.) woodland (30% of study area) at mid-elevations and ponderosa pine (*Pinus ponderosa*) forests at upper elevations (34% of study area) with scattered patches of Douglas fir (*Pseudotsuga menziesii*) and Engelman spruce (*Picea engelmannii*) at the highest elevations and on north facing slopes. Shrublands composed of Gambel oak (*Quercus gambelii*), wavyleaf oak (Quercus undulata), buckbrush (*Ceanothus fendleri*) and mountain mahogany (*Cercocarpus montanus*) were interspersed within the pinyon-juniper woodlands and ponderosa pine forests. Approximately 25% (29 km^2) of the core study area was burned by stand-replacing wildfires within 17 years of our study (15 km^2 in 2001, and 14 km^2 in 2004). These burned areas remained in an earlier successional stage (i.e., shrubland) than the rest of the study area and were dominated by woody deciduous shrubs (i.e.,

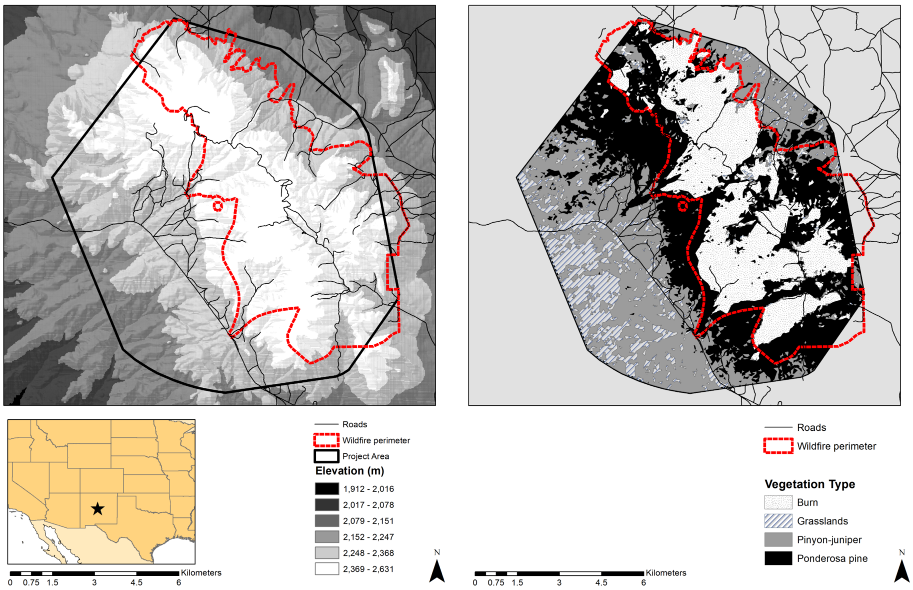

FIGURE 1
Mule deer and mountain lion study area in the Gallinas Mountains, central New Mexico USA. Left panel depicts the elevation gradient in the study area, while the right panel shows the vegetation types. Project area boundary, roads, and wildfire perimeter are depicted on both panels.

buckbrush, oak, and mountain mahogany) that typically compose most of mule deer diets in the region.

Cattle ranching occurred on both private and public lands year-round. Big game and wild turkey (*Meleagris gallopavo merriami*) hunting was common, as was occasional use of the area by other recreationists; legal deer harvest was restricted to adult males. In the Gallinas Mountains, the primary predator of adult mule deer were mountain lions. Annual survival rates of adult female mule deer in the Gallinas Mountains varied between 0.73 and 0.86 with 39% (n = 7) of mortalities of collared mule deer attributed to mountain lion predation, 28% (n = 5) from malnutrition, 5% (n = 1) due to other causes; cause of death for 27% (n = 5) of collared deer mortalities was undetermined (Kay, 2018). Mountain lion kill rates averaged 0.85 deer/week with 67% of mountain lion kills being mule deer (Kay, 2018). Additional predator species of neonatal deer included black bear, bobcat (*lynx rufus*) and coyote (*Canis latrans*). A resident elk (*Cervus canadensis*) herd was also present.

Animal capture and handling

In January–February 2015, we captured 43 adult female mule deer (> 2 years old) via netgun or dart gun fired from a helicopter. We physically restrained deer captured via net gun and immobilized darted deer with 0.03 mg/kg carfentanil + 0.7 mg/kg xylazine, reversed with 3 mg/kg naltrexone + 0.125 mg/kg yohimbine or 0.15 mg/kg thiafentanil + 1 mg/kg xylazine, antagonized with 2 mg/kg naltrexone + 0.125 mg/kg yohimbine. From April 2015 through June 2016, we also darted an additional 14 adult female mule deer from the ground to re-deploy collars from deer that died during the study. These deer were primarily immobilized with 1.5 cc BAM (butorphanol 27.3 mg/ml, azaperone 9.1 mg/ml and medetomidine 10.9 mg/ml), and reversed with 3 cc atipamezole (25 mg/ml) and 0.5 cc of naltrexone (50 mg/ml), or occasionally with thiafentanil (0.15 mg/kg) + xylazine (1 mg/kg), and antagonized with naltrexone (2 mg/kg) and yohimbine (0.125 mg/kg). We fitted 31 deer with GPS store-on-board collars, while 26 were fitted with VHF collars. We programmed GPS collars with a 5-hr fix interval to assess habitat selection patterns in relation to forage conditions and predation risk from mountain lions. We used VHF-collared deer to locate foraging sites of mule deer and for survival and cause-specific mortality (CSM) monitoring (see Kay, 2018 for details of survival and CSM results).

We placed GPS-Iridium collars on mountain lions to investigate prey composition, kill site characteristics, and to model landscape-scale predation risk. We utilized a combination of foot snares and hounds to capture and collar 5 adult mountain lions (3 female, 2 male). We immobilized lions using ketamine (3.0 mg/kg) and medetomidine (0.07 mg/kg) reversed with atipamezole (0.375 mg/kg). We programmed GPS collars on mountain lions with a 3-hr fix interval and transmitted the data every 1–3 days through the Iridium satellite system. All capture and handling procedures were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol #2014-041).

Habitat selection covariates, forage conditions and predation risk

Human disturbance, water, and topography

We mapped all open roads, human developments and perennial water sources using a combination of existing GIS data, satellite imagery, and ground data. We checked perennial water sources monthly throughout the study to ensure they consistently had water available. Ephemeral sources were not included in our analyses. We calculated distance from roads, developments, and perennial water in ArcGIS Desktop version 10.6 (Esri, Redlands, CA). We expected that mule deer would select areas closer to perennial water during summer, but that water would have less or no influence on habitat selection during winter and spring.

We used USGS digital elevation models with 30 x 30 m resolution to determine slope (degrees), aspect, and elevation (m). We converted aspect to eastness and northness using sine and cosine transformations, respectively resulting in values between −1 and 1, where −1 is west or south and 1 is east or north. We estimated vector ruggedness measure (i.e., terrain ruggedness; VRM) with the digital elevation model and a 19 x 19 pixel moving window in ArcGIS (Sappington et al., 2007). We created a topographic position index (TPI) using the digital elevation model with a 15 x 15 pixel moving window to categorize the study area as drainage, hill slope, or ridgetop (Jenness, 2006). A 15 x 15 moving window for TPI better represented the major landforms (i.e., drainages/valleys, hillsides, and ridges) in the study area than the 19 x 19 window used for VRM. Rather than bin the TPI values into a categorical covariate, we left the data as a continuous variable where positive values corresponded with ridgetops, values near 0 were slopes, and negative values corresponded to valleys or drainages. Based on previous research, we expected that mule deer and mountain lions would select for areas with intermediate terrain ruggedness, and that mule deer would select north facing slopes in summer due to higher forage abundance, but would avoid north aspects in winter due to deeper snow. We obtained percent tree canopy cover from the National Land Cover Database (Homer et al., 2004).

Vegetation cover type, forage characteristics and stalking cover

We classified vegetation type using existing data from the US Geological Survey (USGS) Gap Analysis Program (Lowry et al., 2005). Vegetation maps were condensed and reclassified into 4 vegetation types: pinyon-juniper woodland, ponderosa/mixed conifer forest, grassland, and burned areas. We confirmed vegetation map accuracy on the ground by randomly locating 200 points within the study area. We visited each point to ensure the correct classification rate for the vegetative communities was > 90%. We classified fire history as burned or unburned within 17 years prior to data collection, with the two largest stand-replacing wildfires occurring in 2001 and 2004 (MTBS Data Access: Fire Level Geospatial Data, 2017). We expected mule deer to select for vegetation types (i.e., pinyon-juniper woodland and burned areas) providing a combination of security cover and high forage abundance (Pierce et al., 2004; Watkins et al., 2007; Roerick et al., 2019; Johnston and Anderson, 2023). However, areas with security cover utilized by mule deer can also be used as stalking cover by mountain lions, so we expected that there would be a trade-off between access to high quality foraging areas and using risky areas with high concealment cover for mountain lions or low visibility for mule deer. We also expected that mule deer access to forage in areas with low visibility would be moderated by landscape-scale predation risk from mountain lions (see below).

We sampled 100 m transects throughout the study area to measure horizontal visibility as an index for stalking cover and to estimate edible forage biomass (i.e., grasses, forbs, and current year's growth, leaves and twigs <5 mm in diameter for browse), digestible energy and digestible protein content. Our forage sampling targeted plant species that were known to contribute >2% of seasonal mule deer diets and were confirmed with microhistological analysis (see Supplementary Material 1 for details; Kay, 2018). Stalking cover is the inverse of horizontal visibility (m) at a given point based on concealment cover (e.g., terrain or vegetation features) where a higher value indicates increased visibility, hence low stalking cover.

We developed generalized linear models in R (R Core Team, 2023) to estimate forage biomass, digestible energy and digestible protein (g/m^2) and horizontal visibility across the study area based on spatial and temporal attributes from the vegetation transects. Covariates included vegetation type, elevation, canopy cover, ruggedness, topographic position, slope and aspect. We also compiled 250 x 250 m Moderate-Resolution Imaging Spectroradiometer raw reflectance data for each 8-day period during the study and calculated the Normalized Difference Vegetation Index (NDVI) for each 8-day period (NASA LP DAAC, 2015). We then calculated the mean NDVI values and NDVI rate of change (ΔNDVI) for each season and transect location (Pettorelli et al., 2011).

We pooled the data on horizontal visibility (i.e., inverse of stalking cover) across the two years and divided it into seasons (i.e., spring, summer, winter), whereas we ran separate models for each season in each year for edible forage biomass, digestible energy and digestible protein (See Supplementary Material 1 for details). We examined pair-wise correlations between covariates and did not include correlated variables (i.e., $r \geq |0.65|$) in the same model. We also assessed multicollinearity of the most supported models by calculating variance inflation factors (VIF). We then created GIS surfaces for horizontal visibility, forage biomass, and biomass-specific estimates of digestible energy and protein utilizing raster calculator in ArcGIS based on topographical and vegetative geospatial data and their respective coefficients included in top models (Supplementary Material 1 Tables 1.1–1.6). These raster layers were created at 30 x 30 m resolution and used as predictor variables for mule deer habitat selection.

Mountain lion predation risk

We created a predation risk index for mountain lions that incorporated both a resource selection function (RSF) and probability density functions using kernel estimators (Hebblewhite and Merrill, 2007); separate predation risk indices were estimated for each season and diel period. To estimate the RSF, we censored the first 5 days of GPS collar data post-capture to avoid potential behavioral anomalies resulting from capture. We then generated 5 random points for each GPS location within a 99% kernel home range created from all mountain lion locations using the adehabitat package (Calenge, 2006) in program R (R Core Team, 2023). We used civil twilight times obtained from the US Naval Observatory (2014) to classify diel periods as night, day, and crepuscular, with the crepuscular periods being three hours after civil dawn and three hours before civil dusk; we coded data by season and diel period. Based on previous research on mountain lion habitat selection, we included canopy cover, horizontal visibility, TPI, slope, northness, VRM, distance to human structures and roads, and elevation as predictor variables in a suite of *a priori* models for our mountain lion RSFs (Robinson et al., 2015; Blake and Gese, 2016; Dellinger et al., 2020; Peterson et al., 2021; Supplementary Material 2 Table 2.1). We expected that mountain lions would select habitat characteristics that would enhance hunting success, including areas with high vegetation concealment cover and low horizontal visibility (i.e., high canopy cover, low visibility, north facing slopes and higher elevations with higher vegetation biomass) and topographic features that would facilitate hunting (i.e., steep slopes, terrain ruggedness) and movements (e.g., ridgelines and drainages). We also expected that mountain lions would avoid areas near roads and other human developments. We expected that some habitat characteristics could have non-linear relationships with resource selection of mountain lions, and that this may vary by season or diel period. Therefore, we evaluated preliminary models using Akaike's Information Criterion corrected for small sample size (AIC$_c$) and AIC$_c$ weights to compare structures with both linear and quadratic terms for slope, canopy cover, VRM, elevation, and horizontal visibility (Supplementary Material 2 Table 2.1). Preliminary analyses indicated that canopy cover, specifically intermediate levels of canopy cover, was highly predictive of landscape-scale mountain lion habitat selection so a quadratic term for canopy cover was included in all mountain lion RSF models. For a couple of diel/seasonal periods, the model with only linear terms for elevation, VRM, and visibility performed as well as or better than the model with the quadratic terms and we incorporated these into the model structures we evaluated. We scaled continuous covariates by subtracting their mean and dividing by two standard deviations (Gelman, 2008) and only included covariates in the same model that were not collinear (e.g., $r < |0.65|$ and VIF <4.0). We estimated RSF coefficients for lions using mixed-effects logistic regression including a random intercept for individual lions (Breslow and Clayton, 1993; Gillies et al., 2006) with lme4 (Bates et al., 2015) in R (R Core Team, 2023). We used AIC$_c$ to evaluate model support for each season and diel period model set, and used multi-model averaging for parameter estimates when there was model uncertainty (i.e., > 1 model had $\Delta AIC_c \leq 2$; Burnham and Anderson, 2002). We evaluated competitive models for uninformative parameters and models with uninformative parameters were discarded (Arnold, 2010). We used five-fold cross-validation (Boyce et al., 2002) to evaluate predictive performance of the most supported models.

We created a 99% kernel density estimate for mountain lions using Home Range Tools in ArcGIS (Rodgers et al., 2007; Supplementary Material 2 Figure 2.1). Total predation risk was calculated as the product of the season by diel period RSF and kernel density functions (Hebblewhite and Merrill, 2007). This GIS surface was then scaled to values ranging from 0 to 1 using a linear stretch equation (Lillesand and Kiefer, 1994) and utilized as a predictor variable that represented landscape-scale mountain lion predation risk, or the relative probability of mule deer encountering a mountain lion for the mule deer habitat selection analysis (Supplementary Material 2 Figure 2.2). We set multiple camera traps and snares across the study area in travel corridors and at locations where we observed lion sign. Additionally, we conducted foot surveys for mountain lion sign 2–6 days/week (during spring, summer and fall), set cameras on mountain lion kills, and traveled the road network in winter to look for tracks in the snow. Collared lions frequently showed up on cameras, and we detected their tracks often during surveys (verified by matching up GPS collar locations to tracks). All mountain lion sign observed at cameras and during track surveys were associated with collared lions; we did not detect any uncollared lions during our study period.

Mule deer resource selection

We used GPS collar data to develop RSFs for mule deer at the landscape and within home range scales (2^{nd} and 3^{rd} order; Johnson, 1980). We omitted the GPS locations for the first 5 days post-capture. We then determined habitat availability at the landscape scale by amalgamating the GPS locations from all mule deer over the entire study period and estimated 99% seasonal kernel home ranges with the adehabitat package (Calenge, 2006) in program R (R Core Team, 2023). For the within home range scale, we similarly estimated 99% seasonal kernel home ranges for each mule deer. Within the landscape-scale and individual kernel home ranges, we generated 5 random locations for each GPS location from collared mule deer. We selected predictor variables for RSF models based on previous research and mule deer life-history traits (Ager et al., 2003; Pierce et al., 2004; Bishop et al., 2009; Monteith et al., 2014) and used a combination of remote sensing and on-the-ground methods to gather data on habitat characteristics.

We used a similar approach to model mule deer habitat selection as described above for mountain lions. We used mixed-effects logistic regression and included a random intercept for individual deer (Breslow and Clayton, 1993; Gillies et al., 2006) with lme4 (Bates et al., 2015) in R (R Core Team, 2023). Prior to analyses, we tested predictor variables for collinearity and standardized all continuous predictor variables. Due to temporally changing habitat conditions, we conducted all habitat selection analyses on a seasonal and diel basis. We developed *a priori* model sets to assess resource selection of mule deer relative to predation risk, forage conditions, and habitat characteristics (Supplementary Material 3 Table 3.1). Forage availability and nutritional quality are two common currencies used to assess nutritional constraints on herbivore foraging and habitat selection. Therefore, we developed model structures that included covariates related to predation risk and other non-forage-related habitat characteristics. We then added either edible forage biomass or forage protein content to these base models for seasonal mule deer habitat selection to determine which forage metric (biomass vs. protein content) was most related to seasonal habitat selection (Supplementary Material 3 Table 3.1). We did not use digestible energy content of forage in our mule deer RSF models because forage biomass and digestible energy content were highly correlated (all $r > 0.9$). Additionally, our models predicting digestible energy content of forage using transect and geospatial covariates performed worse (all $r^2 = 0.45$) than our models for edible forage biomass ($r^2 = 0.70$) and digestible forage protein ($r^2 = 0.73$; Supplementary Material 1 Table 1.1). We therefore compared seasonal models of mule deer habitat selection with forage protein content to those with edible forage biomass (along with other predation risk and habitat covariates). We selected top models utilizing AIC_c to determine which predictor variables best explained mule deer habitat selection. We then used five-fold cross-validation to evaluate the performance of top-ranking models (Boyce et al., 2002).

Vegetation type appeared to be an important factor for deer in our study area due to the quantity and quality of forage. However, continuous nutritional covariates (i.e., edible biomass and digestible protein; Supplementary Material 1 Figures 1.1–1.2) were not independent of vegetation type, and therefore we used continuous forage metrics in the resource selection analysis to reduce the number of parameters estimated and simplify interpretation. Horizontal visibility was also related to vegetation type with the lowest visibility in burned areas, intermediate in pinyon-juniper and ponderosa stands and highest in grasslands (Supplementary Material 1 Figure 1.3). To assess broad selection patterns by mule deer with respect to vegetation type, including wildfire-burned areas, we analyzed mule deer selection for specific vegetation types using wi function (design II data) in the adehabitatHS package in R (Calenge, 2006) to calculate selection ratios of vegetation types (Manly et al., 2002).

Characteristics of mountain lion kill sites and mule deer foraging sites

To further examine forage–predation risk trade-offs, we collected data at mountain lion kill sites to determine the habitat characteristics that best predicted the likelihood of an area being a kill site (e.g., higher predation risk, lower visibility). To identify potential kill sites for field visitation, we evaluated GPS clusters (Knopff et al., 2009; Ruth and Murphy, 2010) using a cluster detection code and mountain lion GPS collar data (Kindschuh et al., 2016) in R (R Core Team, 2023). Potential clusters or predation events were defined as ≥ 2 GPS points within 200 m of each other that were recorded within a 72-h period (Anderson and Lindzey, 2003). We also used radio-collared deer killed by lions during our study in this analysis. We determined cause of death by field necropsy (Kay, 2018). We skinned the head and neck of each deer to examine potential subcutaneous hemorrhaging (hemorrhaging distinguished predation from scavenging) and we palpated all extremities for physical trauma and signs of predation. Additionally, we searched the mortality site for other indicators of predation such as predator tracks, feces, drag marks, or cache piles.

At each kill site where we confirmed the location of a carcass, we backtracked from the cached carcass until we found a point where we felt confident the prey had first fallen in the predation sequence.

These points were located by observing tracks of both mountain lions and prey, as well as other signs found in the surrounding area (e.g., broken vegetation, hair and blood). We defined this as the actual kill site and measured micro-habitat characteristics at this location. While this point may not represent exactly where the deer was when the attack initiated, it is probably closer to the attack site than where the cached carcass was located during field visits. Laundré and Hernández (2003) reported that mountain lions typically made contact with a deer within 10 m of its initial pursuit location, and that mule deer traveled from 10–15 m after initial contact. If we did not have high confidence that our estimated attack location was where the animal first fell, we did not survey the site. From the determined site, we then generated a random location between 100 and 550 m away at a random azimuth to use as a matched-paired random point. We selected the minimum of 100 m to avoid potential overlap of sampling between kill and random sites and the maximum 550 m distance was based on vegetation heterogeneity in the study area. At both kill sites and random sites, we classified the dominant vegetation type within a 50-m radius, measured horizontal visibility and estimated edible biomass of forage species using the modified comparative yield method and dry weight rank multipliers using two quadrats (1 m^3) in each cardinal direction (8 total) at 10 and 20 m from the kill or random site (t'Mannetje and Haydock, 1963; Haydock and Shaw, 1975; Mazaika and Krausman, 1991; Marshal et al., 2005). We then estimated biomass-specific digestible protein and digestible energy based on nutritional content analyses of forage samples (See Supplementary Material 1 for details on visibility and forage sampling).

To evaluate habitat characteristics associated with mule deer foraging sites, we used telemetry to track collared deer during crepuscular hours. When we located undisturbed foraging deer, we recorded the location and returned within a week to record micro-site characteristics. We never used the same deer twice when locating foraging sites. Similar to lion kill sites, we also generated a paired random point within 100–550 m from the foraging site. Data collected at foraging sites were the same as for mountain lion kill sites.

We then used conditional logistic regression with the clogit function in the survival package in R (Therneau and Lumley, 2015) to evaluate a suite of *a priori* models (Supplementary Material 4 Table 4.1) to determine which habitat characteristics best predicted mountain lion kill sites and mule deer foraging sites. Biomass and digestible energy content estimates of forage were highly correlated at both kill sites ($r = 0.88$) and foraging sites ($r = 0.84$), so we only included biomass and forage protein content in modeling mountain lion kill sites and mule deer foraging sites. We used AIC_c to evaluate model support and used multi-model averaging across all models for parameter estimates when there was model uncertainty (i.e., > 1 model had $\Delta AIC_c \leq 2$; Burnham and Anderson, 2002).

To determine if mule deer were forced to make a trade-off between forage and predation risk, we tested for correlation between forage biomass, protein, digestible energy content and horizontal visibility estimates from our transect locations where we sampled forage conditions and horizontal visibility. We extracted our mountain lion predation risk index to transect locations. If a correlation between forage and predation risk metrics existed, we utilized parameter estimates from our top deer habitat selection models to evaluate how mule deer in our study area approached this trade-off.

Results

Mountain lion habitat selection

In 8 of the 9 model sets, there was a clear top model. Mountain lion habitat selection was broadly similar across seasons and diel periods (Supplementary Material 2 Table 2.2–2.3). Five-fold cross-validation analyses indicated that the most supported model for each model set performed well ($\rho > 0.80$ for top models).

Mule deer habitat selection

Landscape scale

The relative probability of use for mule deer at the landscape scale was best explained by terrain ruggedness, distance to water, northness, mountain lion predation risk, horizontal visibility and interactions between predation risk and horizontal visibility. There was relatively strong support for the highest-ranking seasonal RSF models in each diel period ($w_i \geq 0.7$). When there were competitive models (e.g., $AIC_c \leq 2.0$) in the model sets, the two highest ranking models had similar structures with differences generally related to the presence or absence of interaction terms between mountain lion predation risk and horizontal visibility or between mountain lion predation risk and either forage protein content or edible forage biomass (Supplementary Material 3 Table 3.2). Five-fold cross-validation indicated that the most supported model for each season and diel period performed well ($\rho > 0.91$ for the most supported models). Mule deer disproportionately selected areas previously burned by wildfires over every other vegetation type across all seasons and diel periods (Supplementary Material 3 Figure 3.1); wildfire burned areas had higher edible biomass and protein content for woody browse, but some of the lowest horizontal visibility (Supplementary Material 1 Figures 1.1-1.3).

At the landscape scale, mule deer consistently selected for areas with lower visibility (i.e., increased stalking cover), intermediate ruggedness, areas near perennial water, and south-facing aspects (Supplementary Material 3 Table 3.3; Figure 2). The main effect of predation risk was in the most supported models in all 9 model sets (Supplementary Material 3 Table 3.2), although for some seasons and diel periods, the confidence intervals for main effect of predation risk included 0 (Figure 2). More importantly, interaction terms between predation risk and forage protein content and predation risk and horizontal visibility in these same models, indicated that spatial and temporal heterogeneity in mountain lion predation risk across the landscape (Supplementary Material 2 Figure 2.2) influenced mule deer habitat selection by moderating the influence of forage protein content and horizontal visibility. We also observed significant interactions between terrain ruggedness and horizontal visibility (Supplementary Material 3 Table 3.3).

During spring and summer, RSF models including forage protein content were more supported than those with edible

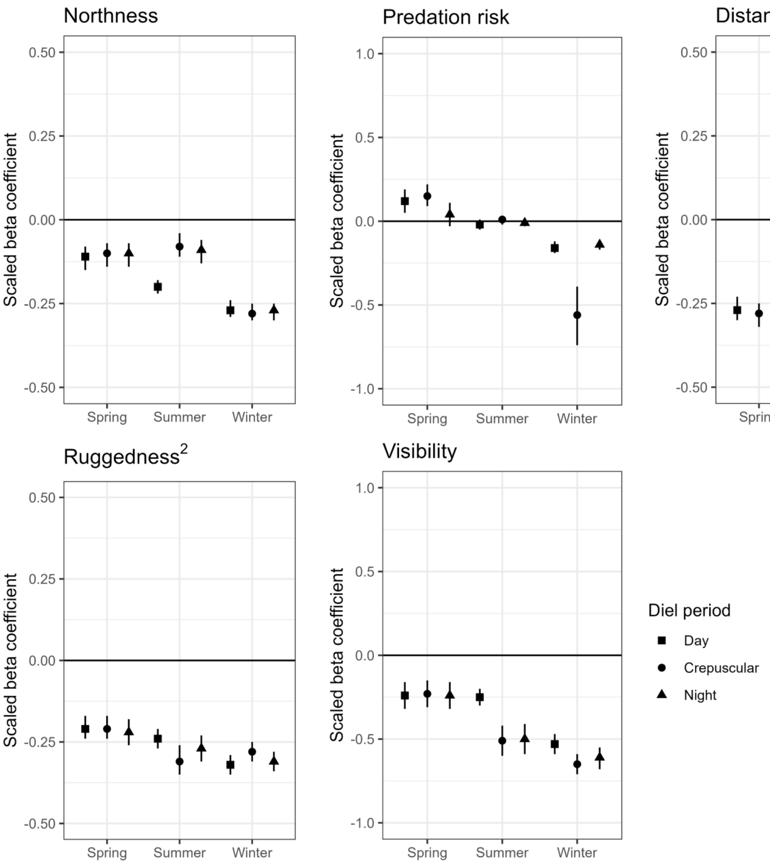

FIGURE 2
Standardized beta coefficient estimates and 95% confidence intervals for resource selection functions at the landscape scale for adult female mule deer in the Gallinas Mountains, New Mexico, 2015–2016. Covariates include northness, mountain lion predation risk, distance to perennial water, quadratic terrain ruggedness, and horizontal visibility (inverse of stalking cover). Note that the axes for the scaled beta coefficients depicted on each panel may be on different scales.

forage biomass. However, during winter, models with edible forage biomass were the most supported models during the day and nighttime, with the model with forage protein content ranked highest during the crepuscular periods (Supplementary Material 3 Table 3.2). During all seasons at the landscape scale, the relative probability of selection for mule deer increased with increasing forage protein content (g/m^2) but mountain lion predation risk had a dampening effect on this response with greater increases in the relative probability of selection by mule deer as predation risk decreased (Figure 3; Supplementary Material 3 Figure 3.2).

We also found an interaction between horizontal visibility and mountain lion predation risk, but when present in the top models, the nature of this relationship varied across seasons. During the daytime in spring, the relative probability of selection decreased with increasing mountain lion predation risk, but less so when visibility was lower; however, confidence intervals were wide (Figure 4A). Whereas during summer, the relative probability of selection increased with mountain lion predation risk when visibility was high, but decreased when visibility was low (Figure 4B). During day and night time in winter, relative probability of selection increased with increasing predation risk when visibility was high, but declined when visibility was average to low (Figures 4C, D; Supplementary Material 3 Figure 3.3D, E).

Relative probability of selection for mule deer generally decreased with increasing horizontal visibility, but the influence of horizontal visibility depended on terrain ruggedness (visibility × VRM interaction) in all diel periods. During spring, selection was highest at low visibility when terrain ruggedness was highest (Supplementary Material 3 Figure 3.4A–C). Similarly, in summer and winter, terrain ruggedness moderated the effects of horizontal visibility on the relative probability of selection (Supplementary Material 3 Figure 3.4D–I).

Within home range scale

The most supported models for mule deer habitat selection at the within home range scale had similar model structures as the most supported models at the landscape scale (Supplementary Material 3 Tables 3.2, 3.4). Five-fold cross-validation analyses indicated good model performance for the highest-ranking model for each season and diel period ($\rho > 0.78$ for the most supported models). At the within home range scale, mule deer habitat selection was related to terrain ruggedness, distance to water, northness, forage conditions and predation risk (Figure 5; Supplementary Material 3 Table 3.5). Similar to landscape scale, there were significant interactions between predation risk and forage protein content, predation risk and edible forage biomass, and terrain ruggedness and horizontal visibility.

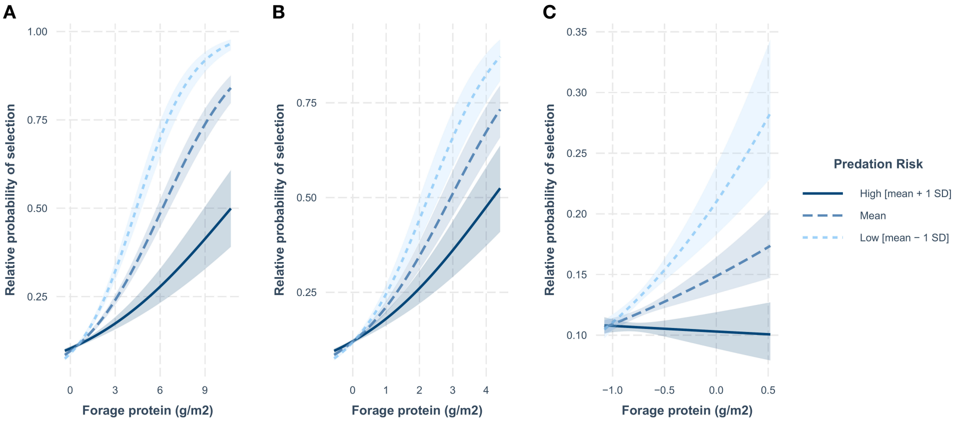

FIGURE 3
Predicted relative probability of selection by mule deer at the landscape scale in relation to forage protein content (g/m^2) as a function of mountain lion predation risk during **(A)** spring, **(B)** summer, and **(C)** winter crepuscular diel periods in the Gallinas Mountains, New Mexico, 2015–2016. Confidence bands are 90% confidence intervals. The relationship between predicted relative probability of selection and forage protein content are plotted for three levels of mountain lion predation risk (mean predation risk [mean], low predation risk [mean – 1 standard deviation SD] and high predation risk [mean + 1 SD]). Note that the axes for the relative probability of selection depicted on each panel may be on different scales.

Some interactions between predation risk and horizontal visibility had confidence intervals that included 0 (Figure 5; Supplementary Material 3 Table 3.5). During spring and summer, models with forage protein content had more support than those with edible forage biomass. In winter, models with edible forage biomass were more supported compared to similar models with forage protein content (Supplementary Material 3 Table 3.4). The relative magnitude of parameter estimates within model sets was lower at the within home range scale than the landscape scale for VRM and VRM^2 during summer and winter, and for distance to perennial water and north-facing aspects for all seasons and diel periods (Supplementary Material 3 Table 3.5).

At the within home range scale, relative probability of selection was highest at intermediate ruggedness (Figure 5). During spring

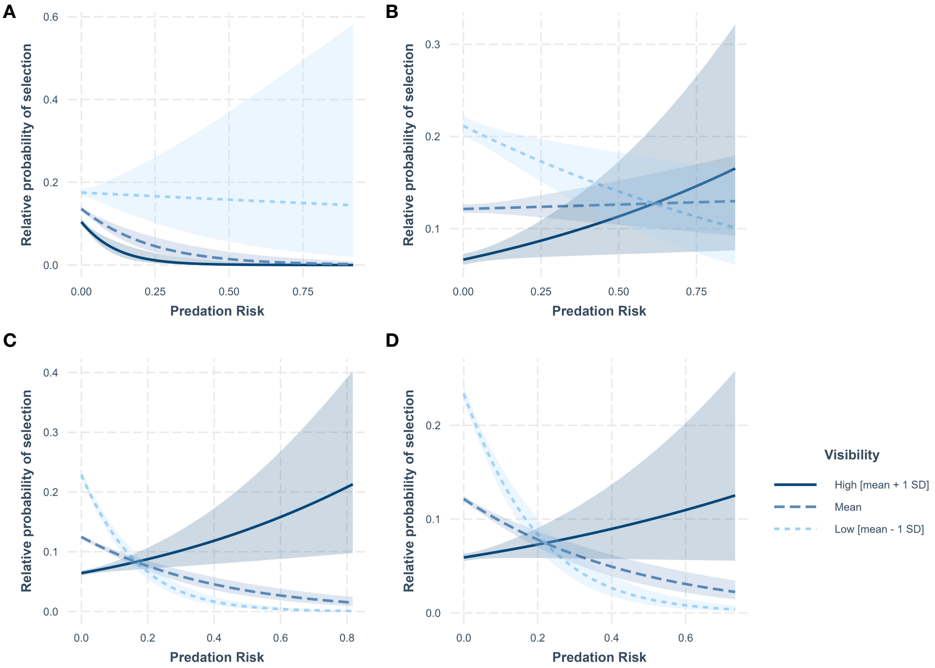

FIGURE 4
Predicted relative probability of selection by mule deer in relation to mountain lion predation risk as a function of horizontal visibility at the landscape scale during **(A)** spring – day, **(B)** summer – crepuscular, **(C)** winter – day, and **(D)** winter – night diel periods in the Gallinas Mountains, New Mexico, 2015–2016. Confidence bands are 90% confidence intervals. The relationship between predicted relative probability of selection and mountain lion predation risk is plotted for three levels of horizontal visibility (mean visibility [mean], low visibility [mean – 1 standard deviation SD] and high visibility [mean + 1 SD]). Note that the axes for the relative probability of selection depicted on each panel may be on different scales.

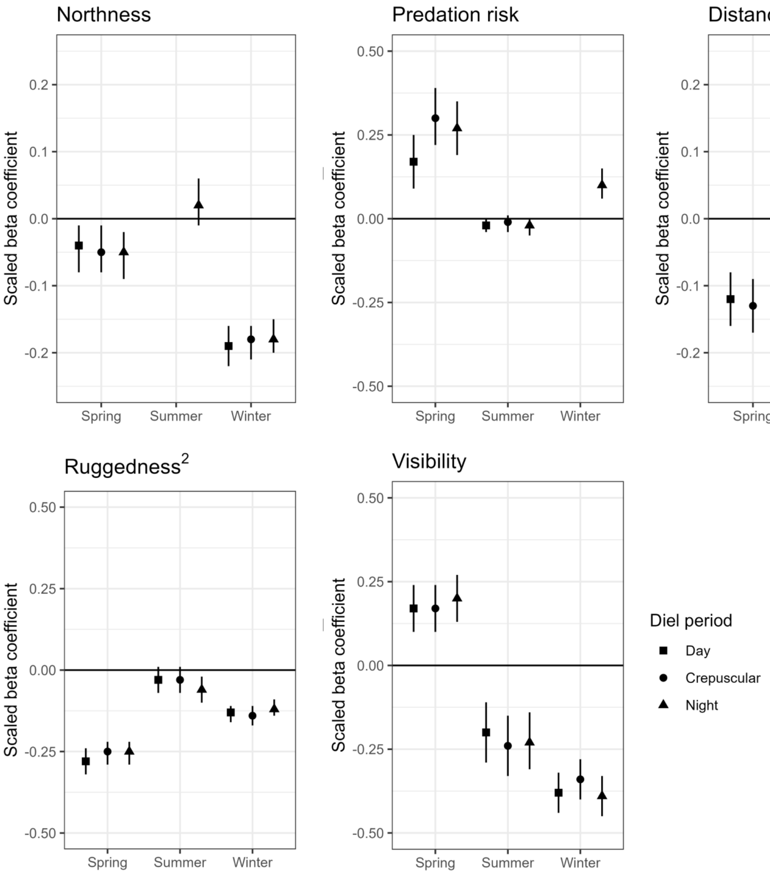

FIGURE 5
Standardized beta coefficient estimates and 95% confidence intervals for resource selection functions at the within home range scale for adult female mule deer in the Gallinas Mountains, New Mexico, 2015–2016. Covariates include northness, mountain lion predation risk, distance to perennial water, quadratic terrain ruggedness, and horizontal visibility (inverse of stalking cover). Some panels are missing coefficient estimates for some predictor variables because those variables were not in the most supported model for that season. Note that the axes for the scaled beta coefficients depicted on each panel may be on different scales.

and winter, mule deer selected areas closer to perennial water and avoided north-facing slopes. During summer, selection increased slightly as distance to water increased (Figure 5; Supplementary Material 3 Table 3.5). At the landscape scale, relative probability of selection increased with decreasing visibility, whereas at the within home range scale, selection increased in spring with increasing visibility (Figure 5; Supplementary Material Table 3.5).

The effect of forage protein content on relative probability of use showed a similar pattern of being moderated by mountain lion predation risk, although there was substantial overlap in the 90% confidence intervals (Supplementary Material 3 Figure 3.5A–C). During spring, relative probability of selection increased with forage protein content. However, during summer, the relative probability of selection for mule deer decreased with increasing forage protein content, but with greater declines in the relative probability of use in areas with high predation risk (Supplementary Material 3 Figure 3.5D–E); however, 90% confidence intervals overlapped. During winter, the relative probability of selection was related to edible forage biomass rather than forage protein content, with mule deer selecting areas with higher forage biomass (Supplementary Material 3 Table 3.5). During nighttime in winter, the influence of forage biomass on relative probability of selection depended on predation risk, with mule deer selecting areas of higher forage biomass at higher levels of mountain lion predation risk (Figure 6).

The influence of horizontal visibility on relative probability of selection also depended on terrain ruggedness in all diel periods at the within home range scale. During spring, the relative probability of selection decreased with increasing visibility in areas with low terrain ruggedness and increased in areas with high ruggedness (Supplementary Material 3 Figure 3.6A–C). During summer, the relative probability of selection decreased with increasing visibility for average and high terrain ruggedness (Supplementary Material 3 Figure 3.6D–F). In winter, the relative probability of selection was highest in areas with low visibility when ruggedness was high, but the relative probability of selection decreased with increasing visibility for all levels of terrain ruggedness (Supplementary Material 3 Figure 3.6G–I).

Kill and foraging site microhabitat characteristics

We were able to identify 33 kill sites and 22 foraging sites. The top model predicting kill sites included horizontal visibility and digestible

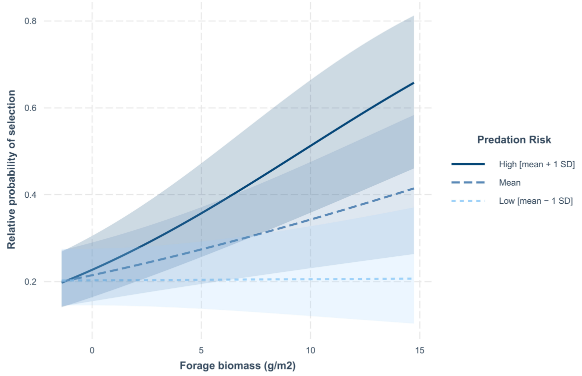

FIGURE 6
Predicted relative probability of selection by mule deer in relation to forage biomass at the within home range scale during the winter crepuscular period in the Gallinas Mountains, New Mexico, 2015–2016. Confidence bands are 90% confidence intervals. The relationship between predicted relative probability of selection and forage biomass is plotted for three levels of mountain lion predation risk (mean predation risk [mean], low predation risk [mean – 1 standard deviation SD] and high predation risk [mean + 1 SD]).

protein of forage (g/m^2; Supplementary Material 4 Table 4.2). Although there was some model selection uncertainty, horizontal visibility was in all models that carried any model weight (Supplementary Material 4 Table 4.2). Sites were less likely to be a kill site as horizontal visibility increased (i.e., stalking cover declined); there was more horizontal cover in areas where deer were killed by lions (Supplementary Material 4 Table 4.3). A site was 34% less likely to be a kill site with each 1-meter increase in visibility. Mean [95% CI] horizontal visibility at kill sites was 10.47 m [9.53–11.41 m] compared to 14.43 m [12.8–16.06 m) at random points. Digestible protein (g/m^2) was also positively associated with kill sites, but parameter estimates overlapped zero. Mean forage protein was almost 5 times higher (9.60 g/m^2 ± 1.87 SE; range 0.45 to 49.1 g/m^2) at kill sites compared to random sites (1.93 g/m^2 ± 0.282 SE; range 0.08 to 8.16 g/m^2).

There was model uncertainty for mule deer foraging site models (Supplementary Material 4 Table 4.4); the highest-ranking models included edible forage biomass (g/m^2), horizontal visibility, and digestible protein (g/m^2). However, the parameter estimates for digestible protein and horizontal visibility included 0. The probability of a location being a foraging site was best explained by available forage biomass (Supplementary Material 4 Table 4.5). As edible forage biomass increases by 1 g/m^2, the odds of a site being a foraging site increases by 2.2%. On average, foraging locations contained 229% (250.08 g/m^2 ± 15.7 SE; range 128.7 to 433.6 g/m^2) more edible forage biomass compared to matched paired sites (75.91 g/m^2 ± 10.02 SE; range 9.03 to 202.64 g/m^2). Available forage protein at foraging sites was 7.6 times (11.99 g/m^2 ± 1.97 SE; range 0.46 to 39.02 g/m^2) higher than random paired sites (1.39 g/m^2 ± 0.28 SE; range 0.03 to 4.55 g/m^2). Mean horizontal visibility at foraging sites was 12.6 m [9.26–11.23 m]) compared to 10.2 m [10.98–14.18 m]) at random sites.

Trade-off correlations

There was an inverse relationship between edible forage biomass and horizontal visibility at our forage and horizontal visibility transects ($n = 112$) during all seasons (winter: $r = -0.521$, $P < 0.001$; spring: $r = -0.573$, $P < 0.001$; summer: $r = -0.627$, $P < 0.01$). Digestible energy (winter: $r = -0.485$, $P < 0.001$; spring: $r = -0.544$, $P < 0.001$; summer: $r = -0.609$, $P < 0.001$) and protein (spring: $r = -0.473$, $P < 0.001$; summer: $r = -0.522$, $P < 0.001$) were also negatively correlated with horizontal visibility with the exception of forage protein during winter (winter: $r = -0.045$, $P = 0.636$). Diel landscape-scale mountain predation risk indices had a moderate negative association with horizontal visibility during spring crepuscular ($r = -0.202$, $P = 0.037$), spring night ($r = -0.252$, $P = 0.009$), and summer night ($r = -0.327$, $P < 0.001$); there was no relationship for all other seasonal-diel periods ($r < -0.076$, $P > 0.436$).

Edible forage biomass during summer was positively associated with the nighttime mountain lion predation risk ($r = 0.462$, $P < 0.001$), and negatively correlated during winter for all diel periods (r range -0.208 to -0.268, all $P < 0.031$); forage biomass and mountain lion predation risk were not associated during spring. Digestible energy at sampling points was positively correlated with our nighttime mountain lion predation risk index during summer ($r = 0.329$, $P < 0.001$), but digestible energy was not correlated with diel predation risk indices during spring (all $r \leq 0.172$, all $P \geq 0.076$). There were moderate negative correlations with diel predation risk during winter (day: $r = -0.203$, $P = 0.035$; crepuscular: $r = -0.194$, $P = 0.044$; night: $r = -0.268$, $P = 0.005$). Digestible protein content of forage was positively correlated with diel mountain lion predation risk during nighttime in spring ($r = 0.367$, $P < 0.001$) and summer ($r = 0.462$, $P < 0.001$), but was negatively correlated with diel predation risk indices in winter (day: $r = -0.209$, $P = 0.030$; crepuscular: $r = -0.223$, $P = 0.020$; night: $r = -0.203$, $P = 0.035$).

Discussion

Ungulates must acquire sufficient nutritional resources for survival and reproduction while also mitigating the risk of predation, thus habitat selection is influenced by spatial and temporal variation in predation risk and foraging conditions

(Schmidt and Kuijper, 2015; Kohl et al., 2018, 2019). These demands can lead to a trade-off when high quality foraging areas correspond with areas of increased predation risk (Lima and Dill, 1990; Ganz et al., 2022). We determined that this trade-off existed for mule deer in our study. Habitat selection by mule deer was influenced by forage availability and nutritional content at both the landscape and within home range spatial scales. However, the influence of forage conditions on habitat selection was moderated by landscape-scale encounter risk for mountain lions, the primary predator of adult mule deer in our study area. The influence of forage conditions on habitat selection by mule deer also depended on horizontal visibility as it related to stalking cover for mountain lions. Mule deer consistently selected wildfire-burned areas, which contained the highest biomass and forage protein content for browse species that composed the majority of their seasonal diets in our study area, as well as high biomass and protein content of herbaceous forages during spring (Kay, 2018). Wildfire-burned areas also had the lowest horizontal visibility, hence highest stalking cover for mountain lions.

One potential limitation of our study was that we were only able to capture and collar 5 mountain lions. However, given the size of our study area and typical densities of mountain lions in the western US, we believe that we had all resident mountain lions with home ranges overlapping our study area fitted with collars. We maintained camera traps in areas with conditions frequently used as travel corridors by lions and we conducted sign surveys (track and snow) a couple times a week across our study area. All sign that we detected matched up with GPS collar data from our sample of mountain lions and we did not detect any collared deer mortalities attributable to mountain lion predation that were not associated with mountain lions we had fitted with collars.

Changes in forage biomass and nutritional content interact with herbivore dietary demands including previous and current year's nutritional reserves (or deficiencies therein) to determine the influence of forage conditions on habitat selection. Forage conditions influenced mule deer habitat selection at both spatial scales in our study, but whether forage biomass or protein content were in the most supported RSF models varied seasonally. At the landscape scale, mule deer strongly selected for areas with higher forage protein content in spring and summer, with forage biomass replacing forage protein content in the winter during day and night. At the within home range scale, forage protein content was positively related to mule deer habitat selection in spring. Seasonal climatic patterns drive inter-annual changes in forage availability and nutritional content, with nutritional quality of forages declining during winter. In our study, winter RSF models at the within home range scale suggested that forage biomass, rather than protein content of forage was more important. During winter, forage protein content was substantially lower with little spatial variation, while biomass declines were far less pronounced but with more spatial variation in biomass across the vegetation types in our study area. Consistent with our predictions on the influence of diel period, when we detected diel differences in the magnitude of the parameter estimates for forage metrics, the relative magnitude of those parameter estimates was reduced (i.e., had less influence on habitat selection) during the day when mule deer would typically be resting or ruminating. However, as predicted, our metrics of forage conditions had a larger influence on habitat selection during crepuscular periods when deer typically feed (Beier and McCullough, 1990; Ager et al., 2003; Morano et al., 2019).

Merems et al. (2020) reported that forage conditions had a strong effect on landscape-scale habitat selection by mule deer in Oregon, but forage had a reduced influence at smaller scales because of the availability of high quality forage within the home range resulting from selection at broader spatial scales. However, we observed that the relative magnitude for the forage parameter estimates were similar across spatial scales in spring and summer, indicating that forage conditions were a key driver of habitat selection at both scales. During the growing season, forage protein content would be expected to have a strong effect on habitat selection at the larger spatial scale given the importance of forage quality on enhancing nutritional condition, supporting the energetic demands of milk production, and recovery of nutritional reserves following winter and gestation (Monteith et al., 2013, 2014; Merems et al., 2020). During summer, forage protein content had a strong, positive influence on mule deer habitat selection at the landscape scale; however, at the within home range scale, mule deer avoided areas with the highest protein content, likely because these areas were associated with higher predation risk. Previous research has demonstrated that predation risk for vulnerable neonates may result in maternal habitat selection focused more towards neonate survival rather than enhancing maternal nutritional condition. For example, female bighorn sheep (*O. canadensis*) select areas with poorer foraging conditions and reduced predation risk compared to areas used by males, thus females enhance fitness via offspring survival (Festa-Bianchet, 1988; Bleich et al., 1997). Similarly, white-tailed deer (*O. virginianus*) in Florida that selected areas with higher quality forage during fawning were more likely to be killed by Florida panthers (*P.c. coryi*), whereas those that selected recently burned areas with both lower predation risk and good foraging conditions had higher survival during fawning (Abernathy et al., 2022). Deer in the Gallinas Mountains appeared to employ risk-mitigation strategies at times when the influence of forage protein content on habitat selection was reduced in areas with increased predation risk, particularly during the summer when adult female deer would be expected to be supporting neonates. Although we were unable to capture and collar fawns to determine fawn survival or fawn at heel status for our collared adult deer, pregnancy rates during our study were ≥89% indicating that most of our collared adult female deer likely had fawns each year (Kay, 2018).

Mule deer utilized spatio-temporal strategies and risk-conditional behavior to reduce predation risk, and at times selected suboptimal foraging areas with lower predation risk. Mule deer selection of areas with higher forage protein content was constrained at the landscape scale by encounter risk for mountain lions, such that increasing encounter risk was associated with diminished selection for areas containing high forge protein content. Similar interactions were reported for elk in Montana (Paterson et al., 2022). The moderating effect of mountain lion encounter risk on selection for areas with high forage protein content was particularly pronounced during the spring and summer at the landscape scale when mule deer would be expected to select for forages with high protein content (Anton et al., 2022). We found that influence of the main effect of landscape-scale encounter risk for mountain lions on mule deer habitat selection was inconsistent across seasons. During winter, mule deer avoided areas with high encounter risk for mountain lions at the landscape scale, but selected for areas with higher encounter risk during spring at the within home range scale. However, we also documented an interaction between landscape-scale encounter risk for mountain lions and horizontal visibility in some seasons with mule deer selecting for areas with reduced encounter risk for mountain lions when horizontal visibility was lower. During spring when mule deer selected for areas with higher encounter risk at the within home range scale, they also selected for areas with higher visibility. Many other large herbivores have been observed to detect when predators are in the area and alter their habitat selection in order to reduce predation risk (Creel et al., 2005; Winnie and Creel, 2007; Valeix et al., 2009; Padié et al., 2015). Because they rely on habitat attributes that increase kill success, predation risk from stalking predators may be more predictable than coursing predators (Preisser et al., 2007). Thus, mule deer may be responding to both direct cues related to previous encounters with mountain lions as well as indirect cues related to variability in vegetation cover and other terrain features used by mountain lions as stalking cover. When high quality foraging areas correspond with spatial variation in encounter risk for mountain lions, but also have conditions that provide stalking cover that could increase risk of kill success, prey responses may be more nuanced than simply avoiding areas of increased predator activity or shifting active periods to times when their primary predators are less active.

Mule deer generally selected for areas with reduced horizontal visibility, likely because those areas contained the highest biomass and protein content for woody browse. Mountain lions also selected for areas with reduced visibility. However, the effect of horizontal visibility on mule deer selection depended on terrain ruggedness. At the landscape scale, the highest relative probability of selection for mule deer was for areas of low horizontal visibility when terrain ruggedness was highest. However at the within home range scale, the nature of the visibility–terrain ruggedness interaction on mule deer habitat selection differed during spring when mule deer selection increased with increasing visibility when terrain ruggedness was high. Incidentally, spring was the only season when mule deer strongly selected for areas with increased encounter risk for lions at the within home range scale. Mule deer commonly select steeper and more rugged slopes than other ungulates to enhance predator avoidance or detection (Dellinger et al., 2019; Saudenmaier et al., 2021; Ganz et al., 2022). Our landscape-scale results are consistent with mule deer exploiting terrain features as a predator avoidance mechanism by selecting steeper or more rugged slopes when stalking cover was lower (i.e., visibility was higher). Selection of areas with steeper slopes has been related to increased fawn survival for mule deer (Bonar et al., 2016). However, mule deer use of more rugged areas would be a better predator avoidance strategy for coursing rather than stalking predators (Bonar et al., 2016; Dellinger et al., 2019). Mountain lions commonly select for areas with topographic complexity that also provide stalking cover (Robinson et al., 2015; Blake and Gese, 2016; Peterson et al., 2021), which may enhance kill success (Elbroch et al., 2013).

Our evaluation of lion kill sites and mule deer foraging sites were consistent with our RSF results. Forage biomass proved to be the most important variable for predicting foraging site selection by mule deer, while stalking cover and forage protein content best distinguished mountain lion kill sites. Areas with more forage biomass and higher forage protein content also had the highest stalking cover, increasing the risk of being killed by a mountain lion following an encounter because stalking cover can increase the efficacy of ambush predators (Beier et al., 1995; Blake and Gese, 2016). These results further suggest that deer in our study area are making habitat selection decisions based on forage quality, but habitat selection was constrained by the increased cost of predation risk. This trade-off appears to affect mule deer in the Gallinas in that they may choose to forgo areas with superior foraging conditions thereby compromising nutritional benefit, or increase their risk of being preyed upon. Our kill-site analysis indicated that micro-habitat features are important predictors of predation risk, and that when combined with our RSF results indicates that deer may approach the forage–predation risk trade-off at small as well as large spatial scales. Past research has also shown that mountain lion hunting strategies generally operate on smaller spatial scales than coursing predators and mountain lions often select hunting areas based on the availability of stalking cover and prey (Murphy, 1998; Husseman et al., 2003; Blake and Gese, 2016). Due to limited time and resources, we were only able to visit a small number of kill and foraging sites, yet we were still able to detect biologically and statistically meaningful effects. Increasing the sample size of foraging sites and kill sites as well as increasing the number of paired random points may provide additional insight into drivers of predation risk and foraging behavior by ungulates.

Decades of fire suppression, logging, and overgrazing have altered the conditions of Southwestern forests resulting in increased densities of small diameter trees and fuel loads (Covington and Moore, 1994a). These changes have been associated with limited understory development, reducing forage for ungulates and other wildlife, and more frequent and severe wildfires (Covington and Moore, 1994b). Wildfire-burned areas can benefit ungulate nutritional condition and subsequent productivity (e.g., Proffitt et al., 2016). Changes in herbaceous forage for ungulates often occur immediately after prescribed or low-severity fires, but these changes are often short-lived, lasting only a few years (Hobbs and Spowart, 1984). The effects of high-severity fires can persist for longer periods (Bartos et al., 1994; Bataineh et al., 2006; Wan et al., 2014; Proffitt et al., 2016; Roerick et al., 2019; Fredriksson et al., 2023). High-severity, stand-replacing wildfires can result in dramatic changes in vegetation structure and species composition. Given sufficient post-fire recovery time, stand conversion from high-density conifer patches with little to no understory to open grasslands or shrublands can occur following high severity wildfires (Coop et al., 2020; Falk et al., 2022; Guiterman et al., 2022). This was the case in our study area where browse species that comprise a substantial portion of mule deer diets in the Southwest (including Gambel oak, buckbrush, and mountain mahogany; Boeker et al., 1972; Austin and Urness, 1985; Sandoval et al., 2005), responded favorably following two stand-replacing wildfires after the removal of conifer forest canopy. Deer in our study strongly selected for these burned areas, which contained the highest quantity and quality of forage. However, burned areas also had low visibility and higher stalking cover for lions. Ganz et al. (2022) similarly reported strong selection of moderate and high severity burns by mule deer in wildfire-burned areas in north-central Washington; however, deer in their study avoided areas with high burn severity and the oldest burns as predicted use by mountain lions increased. Thus, predation risk by lions had a moderating effect on mule deer use of wildfire-burned areas (Ganz et al., 2022).

How ungulates exploit a seasonally dynamic nutritional landscape underpins seasonal changes in body condition, ultimately influencing survival and reproduction (Keech et al., 2000; Bishop et al., 2009; Parker et al., 2009; Lamb et al., 2023). Merems et al. (2020) reported that female mule deer that used areas with the highest forage biomass and nutritional content entered winter in better nutritional condition. However, exploitation of the nutritional landscape can interact with varying predator composition and levels of predation risk (Monteith et al., 2014; Duquette et al., 2015). Ungulates incorporate the risks and rewards of the forage–predation risk trade-off into their behavioral decisions, which consequently affects their ability to survive and reproduce. Given the seasonal changes in forage availability and nutritional quality, and subsequent density-dependent effects when forage conditions decline, it is important to assess individual changes in nutritional status in relation to use of risk-prone versus risk-averse behavioral strategies. Deer that are in a poorer nutritional state in general or during periods when the quality of the nutritional landscape declines should be more likely to engage in risk-prone foraging and suffer from this trade-off (McNamara and Houston, 1986; Brown, 1999; Bastille-Rousseau et al., 2015; Rignos, 2015). More informative insights could be gained from future research that incorporates data on individual body condition and reproduction, and forage conditions when examining the indirect effects of predation, thus linking ungulate behavioral decisions to individual health and productivity as well as population vital rates. It is also essential to study resource selection at multiple spatial and temporal scales in order to fully explore variability in potential trade-offs and corresponding behavioral decisions made by ungulates to balance nutritional demands and risk of predation.

Habitat selection by ungulates, including mule deer, is often driven by the abundance and nutritional quality of forage because of the effects on fitness (Kie, 1999; Monteith et al., 2014). However, risk of predation influences not only where ungulates can safely forage, but also foraging efficiency, which is reduced when ungulates increase vigilance to mitigate risk of predation (Lima and Dill, 1990; Brown, 1999; Altendorf et al., 2001; Childress and Lung, 2003; Creel et al., 2014). Prey species sometimes sacrifice forage quality to alleviate predation risk, but may find ways to at least partially mitigate risk by selecting areas that still contain sufficient food or by foraging more efficiently (Lima and Dill, 1990; Hebblewhite and Merrill, 2009). The variable risk-dependent behavior we report show that mule deer behavioral decisions operated at and were influenced by factors at multiple temporal and spatial scales. These behavioral decisions can correspond to dynamic levels of individual body condition, predation risk, the presence of offspring, and climate-related changes in forage conditions (Kie, 1999; Lima and Bednekoff, 1999; Creel and Christianson, 2008; Basille et al., 2015; Rignos, 2015; Dupke et al., 2016). Deer in our study appeared to utilize a mix of strategies to balance nutritional requirements and predation risk at the landscape, within home range, and foraging areas scales.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Animal Care and Use Committee, New Mexico State University. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JC, JK, and SL contributed to conception and design of the study. JK and JC collected the data. JK and JC performed the statistical analysis. JK and JC wrote the initial draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1121439/full#supplementary-material

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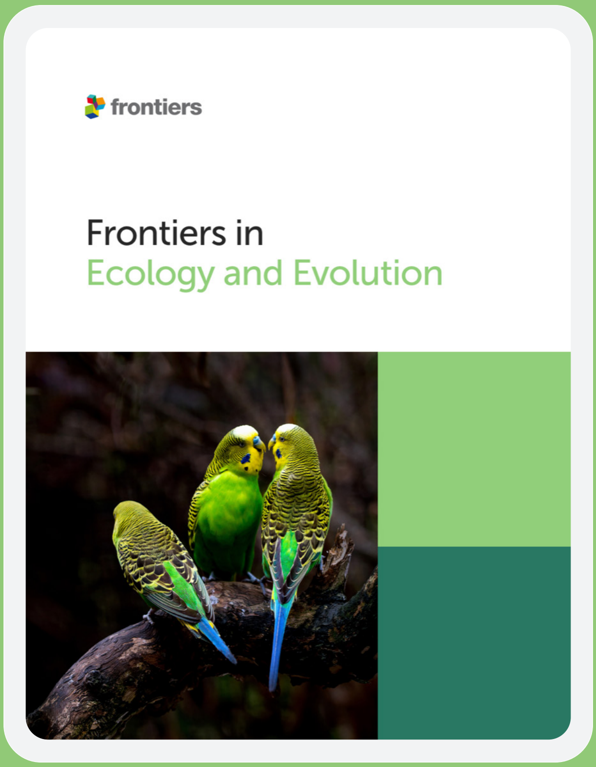

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