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New century wolf conservation and conflict management

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New century wolf conservation and conflict management

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Editorial: New century wolf conservation and conflict management

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Editorial on the Research Topic
New century wolf conservation and conflict management

Introduction

Gray wolves (*Canis lupus*) are among the world's most charismatic, iconic yet feared carnivores (Lopez, 1978). Wolves evoke strong and often polarizing reactions of love and hate, and are involved in intense conservation conflicts (Mech, 2012). What are the keys to wolf conservation? Answering this question is deceptively challenging yet pressing because the legal status and management authority for wolves is shifting in many regions, which creates opportunities and challenges. How can ecology, social sciences, environmental history, and conservation ethics help meet this challenge? Additionally, there is an increasingly complex understanding of the ecological importance of wolves, which contributes to the valuation of wolves, and is a primary rationale for their continued restoration and conservation. How can this understanding contribute to more efficient and effective conflict management?

In this editorial, we revisit information published as contributions to this Special Issue by 86 authors across 18 peer-reviewed articles. We invited submissions to create an article collection focused on 21st century wolf conservation and conflict management. Our goal was to create a forum for relevant discussion around this theme and gather novel open-access studies, enabling readers to be informed about research that makes a difference in sustaining wolf populations and managing wolf-human conflict. Wolves inhabit diverse ecoregions across socio-cultural landscapes that supplied this topic with a unique opportunity to consolidate studies that can provide comparative insights into human-carnivore relationships worldwide. As a consequence, we were especially interested in submissions from authors who represent a diverse and global contribution.

This editorial is a prelude to the Special Issue, organized across geographical scales: Asia, Europe and North America, to provide an overview of the major challenges and resolutions for wolf conservation across the globe. We conclude by discussing geographical and systemic biases to wolf research and the peer-review process that can have serious implications for information dissemination and consequent management of wolves.

Perspectives from Asia

Four articles represented perspectives from Asia, three from the Indian subcontinent and one from Russia.

Poyarkov et al. provided a much-needed overview of wolf research in Russia, covering multiple aspects ranging from population status, predation ecology, behavior to physiology.

India is home to ancient wolf lineages, the Indian and Himalayan wolves, which represent important evolutionary significant units (Sharma et al., 2004; Hennelly et al., 2021). Both these lineages inhabit critical and vulnerable habitats. Jhala et al. show that the Indian wolf typically inhabits open forests, arid and semi-arid grass and scrublands, and agro-pastoral landscapes. Many of these habitats are traditionally considered "wastelands" and thus, Jhala et al. documents loss of prime wolf habitat in the Western and North Western parts of India owing to severe habitat transformation. This is coupled with wolf hybridization with feral dogs and population disjunction from linear infrastructure such as roads. However, Jhala et al. found wolf distribution in areas where they had been previously exterminated or were not found—a source of conservation optimism for the species in India. The species distribution models in Jhala et al. should be used as the "first-cut" for assessing Indian wolf distribution with a need for finer, more intense data for policy decisions at local scales.

Apart from habitat transformation, the major threat to wolves in India is their reliance on domestic livestock as a major food source, as shown by all the 3 contributions from the Indian subcontinent. Mahajan et al. records livestock depredation probability of Indian wolf to be very high. They found that shepherds wield negative and hostile feelings towards wolves owing to such losses, and ensuing retaliatory killings severely threaten the wolves. Mahajan et al. suggests that appropriate and prompt monetary compensation for livestock-depredation as well as raising awareness about wolves through education and sensitization can alleviate such conservation concerns.

Sonam et al. address retaliatory killing of wolves with some hope, especially in trans-Himalayas wherein they discuss a community level conservation initiative. In this specific region, pastoralists traditionally use hunting pits (*shandongs*) to bait, capture, and kill wolves that prey on their livestock. Through an extensive survey, Sonam et al. identified multiple such pits and by working with the community as well as religious leaders of the area, have been successful in neutralizing some of the pits. Furthermore, this project has been successful in consecrating the pits by building Buddhist *stupas* near them, thereby providing some levels of socio-cultural insurance against wolf-killing practices. However, Sonam et al. warns that the neutralization of *shandongs* alone could be counterproductive by facilitating more livestock predation by wolves. The authors propose a combination of neutralizing efforts with other strategies that mitigate negative human-wolf interactions and promote coexistence. The future of wolves in Asia thus hangs in a delicate balance wherein their proximity to humans is a boon (food source) and a bane (habitat alteration, direct persecution, and hybridization with human commensals such as feral dogs).

Perspectives from Europe

Seven articles in this collection were from European studies, consolidating topical diversity and breadth of foci. Studies ranged from understanding depredation patterns in areas with recolonizing wolves to responses of humans towards wolves and vice-versa, and dialogues related to wolf-conflict management.

Wolves are re-colonizing many agricultural and livestock dominated areas in Europe, leading to potential and realized conservation conflicts arising from depredation, as well as multiple management disparities. Ordiz et al. reviewed current management policies, implications and fallacies encompassing wolf conservation in Spain, and provided a roadmap for effective conservation. Mayer et al. showed that depredation of sheep in Denmark mainly occurred by dispersing wolves in areas with low availability of ungulate prey and high densities of sheep. Khorozyan and Heurich showed that sheep density was an important factor explaining losses to wolves in Germany, and that the number of adult wolves did not affect sheep losses while the expansion of the wolf population did. Both these studies suggested that lethal management will not be an efficient method to decrease depredation events and suggest non-lethal interventions.

Flykt et al. expanded upon the concept of the "landscape of fear" to describe how wolf presence in livestock areas can elicit stress responses from livestock owners themselves, creating a "landscape of stress". The paper lays out a framework based on physiological research to provide a detailed description of the domains of stress response reported by sheep breeders in Sweden.

The recolonization of wolves in Denmark during the last decade after 200 years of absence has caused conflicts over wolf management. Hansen et al. conducted a social experiment with citizens living in or nearby the first wolf territory established in 2012. The focus of the project was to promote dialogue and joint fact-finding to create constructive communication about wolf management using a few rules regarding the form of the communication that the participants agreed upon. This dialogue method can be used as a tool when managing other wildlife conservation conflicts.

People who share space with carnivores often experience fear of encountering them, while carnivores can often be shy about human presence. Eriksen et al. developed a standardized protocol for evaluating the response of GPS-collared wolves to close encounters with humans, allowing the study of wolf responses to humans in relation to different wolf, anthropogenic, and environmental factors. Increased knowledge of wolf behavior when meeting people can help to demystify the relationship between wolves and humans in shared landscapes. This protocol was tested in a pilot study in four wolf territories in Scandinavia (Versluijs et al.), with results showing that wolves invariably avoided humans. The majority of the wolves fled when approached by humans and no wolves were observed or heard during the trials. Further approach trials within and between different wolf populations are needed to draw general conclusions of wolf behavior towards approaching humans and may improve coexistence between wolves and humans.

Perspectives from North America

Seven articles in this collection were from North American studies, with four focused on wolf ecology, two related to human attitudes towards wolves and a perspective article describing a Native American relationship with wolves.

Protected areas such as National Parks in North America provide insight into wolf ecology in areas with relatively low human impacts. In their analysis of long-term data from Isle Royale National Park, Hoy et al. presents results that suggest wolf predation likely acts as a selective force against genes associated with developing severe osteoarthritis in prime-aged moose. These findings support the benefits of allowing wolves to help regulate large ungulate populations and that intensively hunting wolf populations could affect this force of predation. Borg and Schirokauer analyzed long-term data from Denali National Park in Alaska, demonstrating that wolf populations can have increases in natality concurrent with population declines. When conditions favored an increase in ungulate population, the wolf population failed to respond numerically through social limitations imposed by territoriality. This highlights the importance of pack dynamics in regulating wolf population growth.

Other studies in North America focused on human impacts on wolves. Chakrabarti et al. examined long-term known fate from radio-tagged wolves in Minnesota, USA to determine temporal trends and age- and sex-specific survival rates. While survival rates have gone down over the years, they did not observe evidence that survival was markedly reduced during years when a regulated hunting and trapping season was implemented. Still, human causes resulted in ~66% of known mortalities. In southeast Alaska, USA, human hunting was a key regulator of both wolf abundance and deer abundance, as shown by Gilbert S. et al.. Importantly, it is likely that wolf predation in this region has provided an ecosystem service to the timber industry *via* reduced tree browsing by deer.

Human attitudes and perceptions have been and will continue to be critical to the health and persistence of wolf populations in North America. Schroeder et al. examined how specific identities (wolf advocate, hunter, environmentalist, nature enthusiast, farmer, trapper, and conservationist) related to political ideology, trust in a wildlife management agency, wildlife value orientations and attitudes about wolves. Hunters associated with a domination value orientation and conservative political ideology; a farmer identity was most strongly associated with wildlife management agency distrust and negative wolf attitudes; wolf advocates were most strongly associated with a mutualism orientation, agency trust, and positive wolf attitudes. They also found that a conservationist identity was positively correlated with all other identities, which indicates to management authorities that a conservationist, rather than an environmentalist, or hunter perspective may be supported by a broader constituency and increased trust in agency actions. Slagle et al. assessed wolf tolerance among the general public throughout the USA. Wolves are not an issue important enough to compel action to the majority of respondents, i.e., 55% did not intend to engage in either supportive or oppositional actions. This is a significant challenge to continental-scale carnivore conservation.

In contrast to the studies in this collection on multiple identities and perceptions of wolves at national levels, Gilbert J. et al. describe the identity and perception of wolves held by indigenous Ojibwe communities. In their perspectives article they review the relationship between Ojibwe people with *Ma'iingan* (wolf); this relationship maintains that *Ma'iingan* and the Ojibwe people are to be considered relatives, with intertwined fates. The authors use a case study of a recent wolf hunt in Wisconsin, USA to illustrate how the *Ma'iingan* and Ojibwe people have lived parallel histories that include the effects of colonization, population decline, and cultural losses. Such perspectives have historically been ignored or devalued by contemporary, western wolf management.

Conclusion

Wolves will continue to capture human hearts and minds through the next century and, as a consequence, wolf conservation will continue to challenge us. Without national, continental, or wide scale collective policies, wolf management is expected to be highly heterogeneous. For example, while we completed this Special Issue, wolves in the United States simultaneously received greater protection in the northern Great Lakes region and less protections in the northern Rocky Mountains region. Highly variable wolf policies across the globe warrants comprehensive wolf science and knowledge, to encompass a broad range of locations, subject areas, perspectives, and authors. With that in mind, we especially solicited article submissions from a diverse spectrum of researchers and managers that would hopefully represent a global contribution. While this Special Issue involved a diverse array of authors and Research Topics, it is dominated nearly two-to-one by contributions from European or North American studies compared to elsewhere. Such skewed contributions partially reflect unequal access to resources that support wolf/carnivore science and publication. Case in point, the first article submitted was a study on wolves from eastern Russia. That article was withdrawn due to lack of publication funds. While our best efforts to convince publishers to waive processing charges for that article failed, we were successful in waiving the publication charges for the contribution by Sonam et al., yet another perspective from the Global South where support for disseminating wolf science is not easily available. If we hope to collectively meet the challenge of wolf conservation for the next century, then we also have to look beyond the borders of typical wolf research and support wolf science in the broadest sense. Support for research and publication costs, especially to early career researchers, collaboration with and promotion of researchers beyond the dominating Euro-American perspective, and shifting wolf research foci beyond protected areas are important steps if we are to effectively and inclusively understand and manage wolves in the next century.

Author contributions

SC and JB conceptualized the editorial. SC led the writing. All authors edited drafts, contributed to the writing of various sections, and approved the submission.

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Conflict of interest

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Large-Scale Sheep Losses to Wolves (*Canis lupus*) in Germany Are Related to the Expansion of the Wolf Population but Not to Increasing Wolf Numbers

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Recovery of predator populations triggers conflicts due to livestock depredation losses, particularly in Germany where the wolf (*Canis lupus*) population grows exponentially and livestock (especially sheep) losses raise public concerns and motivate the authorities to control wolf numbers. Yet, the effects of wolf numbers and alternative factors, such as abundance of prey and livestock, on livestock losses in this country are not investigated. In this study, we collected and analyzed data on the numbers of reproductive units of wolves (packs and pairs together) as a surrogate of adult wolf numbers, sheep killed by wolves, living sheep, red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*) in every German state and year from 2002 to 2019. We applied a negative binomial Generalized Linear Mixed Model (GLMM) to estimate the effects of these predictors on the numbers of sheep killed by wolves. We also examined the relationships between the percentages of killed/living sheep and the numbers of living sheep. Ranking of 63 models based on the Akaike information criterion revealed that sheep losses were determined by state, year, and number of living sheep, not by wolf numbers, at high precision and accuracy. The number of sheep killed by wolves increased consistently by 41% per year and by 30% for every additional 10,000 sheep, mainly in the north where most wolf territories are concentrated. This means that sheep are protected insufficiently and/or ineffectively. The percentages of killed/living sheep consistently increased by 0.02–0.05% per state and year, with the maximum percentage of 0.7%, on a backdrop of decreasing numbers of living sheep. In conclusion, we demonstrate that sheep losses in Germany have been driven by the expansion of the wolf population, not by wolf numbers, and by the number of sheep available. We suggest that Germany's wolf conservation policy should focus on alternative non-lethal interventions, enforcement and standardization of intervention monitoring, and promotion of wolf tolerance rather than on lethal control of wolf population size.

Keywords: carnivore, conservation intervention, effectiveness, GLMM, human-wildlife conflict, livestock, predator, recolonization

INTRODUCTION

The recovery of large predator populations and their return to the areas where they formerly were extirpated have been a fascinating result of long-term and dedicated conservation efforts (Chapron et al., 2014; Hamilton et al., 2020). However, apart from satisfaction and enthusiasm, these processes also bring high costs of co-existence and co-adaptation between humans and predators in a new reality (Carter and Linnell, 2016; Bergstrom, 2017; Kuijper et al., 2019; Boronyak et al., 2020; Cretois et al., 2021; Gervasi et al., 2021). Predators may trespass public places, frighten and in exceptional cases attack people, affect human behavior and lifestyle, and inflict financial losses by killing livestock, damaging crops, reducing productivity of stressed livestock, and increasing workload and anxiety of affected people (Barua et al., 2013; Steele et al., 2013; Widman et al., 2019; Khorozyan and Waltert, 2020). Human-predator conflicts have also been fueled by non-economic reasons such as intrinsic fear, traditions, superstitions, and other socio-psychological factors even when damage is negligible or none (Pooley et al., 2016). Thus, perceptions and tolerance are no less important than tangible losses in transforming human-predator conflicts into human-predator co-existence (Pătru-Stupariu et al., 2020). All these aspects make human-predator conflicts a long-lasting challenge for biodiversity conservation and local livelihoods, which needs to define the key factors that underlie a problem, specify factor-specific solutions, and mobilize human and other resources for their practical applications (van Eeden et al., 2018; Khorozyan and Waltert, 2019; Sutherland et al., 2020).

All this is very relevant to the recovery and recolonization of wolves (*Canis lupus*) in Germany from Poland. Beginning from 2000 when the first pair of wolves was established in eastern Germany's state of Sachsen (Saxony) until 2019–2020, the wolf population in the country has increased up to 175 territories, including 128 packs, 38 pairs, and nine individuals living in 12 out of 16 states (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2020a). Currently, only the city-states of Berlin, Hamburg and Bremen, and the smallest state of Saarland, do not have resident wolves. Wolf numbers in the country grow exponentially, on average by 28% per year, due to population expansion fostered by high mobility, reproductive potential and adaptability of wolves, prey abundance, and the presence of suitable corridors and stepping stones (Reinhardt and Kluth, 2016; Reinhardt et al., 2019, 2021; Plaschke et al., 2021). Therefore, it is not surprising that increasing losses of domestic livestock and farmed game species are associated with increasing wolf numbers. Like elsewhere in Europe (Gervasi et al., 2021), most of the damage has been inflicted on sheep, which make about 80% of all livestock and farmed game species killed annually by this predator in Germany (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2017, 2018, 2019, 2020b). In 2019, 2894 domestic animals and farmed game, including 2476 sheep, were killed by wolves (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2020b). However, the contribution of domestic animals and game to prey biomass consumed by wolves does not exceed 2% and the main prey are the wild ungulates such as the roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) (Ansorge et al., 2006; Wagner et al., 2012; Reinhardt et al., 2021).

The soaring numbers of wolves and domestic animals killed by them in Germany make a general impression that these numbers are causally correlated (Kaartinen et al., 2009) and that lethal control of wolf numbers is the most obvious intervention to be used to keep losses down (Straka et al., 2020). The German public acceptance of wolf and positive attitudes are generally high, but the recognition of associated risks is also rising (Lehnen et al., 2021). For example, the proportion of respondents supporting wolf killing increased from 56% in 2015 to 65% in 2018, with more support coming consistently from men, northern states with most wolf records, older (>60 years) people (NABU, 2015, 2018), and from those who adhere to human domination over nature (Hermann et al., 2013; Straka et al., 2020). Information sources shape public opinions on wolves and their killing in Germany; therefore, they should prevent and counteract disinformation, avoid one-sided views, exaggerations and stereotypes, and provide only reliable and evidence-based information (Arbieu et al., 2019; Lehnen et al., 2021).

In 2019, the German Parliament issued an amendment to the federal nature conservation law allowing to ease the killing of wolves in response to livestock depredation (Deutscher Bundestag, 2019). This document downgrades the permitting threshold from "considerable damage" to "serious damage," allows killing until no further losses are inflicted what may lead to the destruction of full packs, and does not mention the use or monitoring of alternative non-lethal conflict mitigation measures (Deutscher Bundestag, 2019; Kiffner et al., 2019). These conditions probably do not comply with the EU Habitats Directive, which is the main legal framework to protect wolves and other biodiversity in Europe (Epstein et al., 2019; Köck, 2019). Thus, human–wolf conflict over depredation transforms into a political human–human conflict between stakeholders (Köck, 2019) and makes the achievement of human–wolf co-existence a top priority for Germany's conservation agenda (Kuijper et al., 2019; König et al., 2020; Führes, 2021). More information is urgently needed to reach this goal to understand whether wolf numbers are indeed a strong determinant of livestock losses or other factors can be more relevant. Livestock losses can be inversely related to the abundance of wild prey, making depredation common in prey–lean areas (Newsome et al., 2016), or increase with the numbers and, hence, availability of livestock (Hanley et al., 2018). Scientific research on this topic using modeling approaches appears to be a timely and much needed work to do and report to conservation decision-makers in Germany.

In this study, we tested three hypotheses that sheep losses in Germany are (1) higher in states where wolf numbers are higher, and wolf number is the primary determinant of sheep losses, (2) higher in states where the abundance of wild prey (wild boar, roe deer, and red deer) is lower, and (3) higher in states where the numbers of sheep are higher. We define the most critical predictors of sheep losses to wolves and consider them in light of mitigation of escalating human–wolf conflicts in the country.

TABLE 1 | The set of the best model ($\Delta AIC_c < 2$) and six low-ranked models of the number of sheep killed by wolves (*Canis lupus*) in Germany in 2002–2019, which altogether attain the cumulative model weight of 1.

Model	AIC_c	ΔAIC_c	w_i	x	F	p
state + year + No. living sheep	804.550	0.000	0.747	1	69.035	< 0.001
				2	96.856	< 0.001
				3	10.944	0.002
state + year + No. wild boars	808.452	3.902	0.106	1	624.746	< 0.001
				2	53.632	< 0.001
				3	5.646	0.020
state + year	809.008	4.458	0.080	1	119.353	< 0.001
				2	71.119	< 0.001
state + year + No. reproductive units	811.241	6.691	0.026	1	122.243	< 0.001
				2	15.858	< 0.001
				3	0.991	0.323
state + year + No. red deer	811.748	7.198	0.020	1	120.289	< 0.001
				2	53.726	< 0.001
				3	0.231	0.632
state + year + No. roe deer	811.921	7.371	0.019	1	63.712	< 0.001
				2	71.514	< 0.001
				3	0.315	0.577
year + No. reproductive units + No. roe deer	818.452	13.902	0.001	1	17.690	< 0.001
				2	18.043	< 0.001
				3	6.769	0.011

Abbreviations: AIC_c, Akaike Information Criterion corrected for small sample size; ΔAIC_c, delta of AIC_c; F, F statistic; p, significance level; w_i, model weight; x, predictor of the model (first if 1, second if 2, and third if 3).

MATERIALS AND METHODS

Data Collection

We compiled a database encompassing the data for each year from 2002 to 2019 for each state of Germany where wolves were recorded. We selected this period of time because the earlier (2001) and later (2020) years contained missing values and we excluded these years to equalize sample sizes and make depredation models comparable in the ranked model set (Symonds and Moussali, 2011; see section "Data Analysis").

The numbers of wolf packs and pairs were retrieved from the Federal Documentation and Consultation Centre on Wolves (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf, DBBW[1]). Annual wolf monitoring has been conducted in Germany from May 1 to April 30 and then its results are agreed upon and finalized in autumn (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2020c), thus making wolf data valid for the year of that autumn. As the wolf population size in Germany is unknown, we calculated the number of reproductive units (packs and pairs together) as a surrogate of the number of adult wolves capable of killing livestock.

We collected the numbers of sheep killed by wolves from official reports of livestock depredation losses for 2016–2019 (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2017, 2018, 2019, 2020b) and from the information letter 18/10110 of the German Parliament for 2002–2015 (kindly provided by K. Steyer, Federal Agency for Nature Conservation/Bundesamt für Naturschutz, BfN). The numbers of living sheep were obtained from the database of the Federal Statistical Office of Germany, GENESIS v. 4.3.1.U2-2020[2]. The annual numbers of red deer, roe deer and wild boars officially hunted in states were retrieved from Wildlife Information System of German States (Wildtier- Informationsystem der Länder Deutschlands) v. 7.9.260 produced and maintained by German Hunting Association (Deutscher Jagdverband e.V[3]). The numbers of hunted individuals have been used officially as the indicators of actual population sizes of these three ungulate species. All these methods of data collection are standardized, the process of monitoring is continuous, and this information is used nationwide as the official, most reliable and best available one.

Data Analysis

We estimated how the response variable of the number of sheep killed by wolves was affected by the following potential predictors per state and year: state (integer nominal variable), year, number of reproductive units of wolves, number of living sheep ($\times$10,000 individuals), number of red deer, number of roe deer, number of wild boars, number of sheep/red deer, number of sheep/roe deer, and number of sheep/wild boar. To avoid data dredging, we set the actual number of predictors used in the analysis as a maximum of one-tenth of the number of data cases (Grueber et al., 2011), selecting the most meaningful predictors for this. Each case represented a row of response and predictor data in the dataset. As the response variable was a count

[1] https://www.dbb-wolf.de

[2] https://www-genesis.destatis.de/genesis/online

[3] https://wild-monitoring.de/cadenza

statistic, we checked for Poisson distribution and found it to be inappropriate due to overdispersion (Kolmogorov–Smirnov $Z = 5.804$, $p < 0.001$, mean = 98.99, variance = 16,978.32). Therefore, we applied a Generalized Linear Mixed Model (GLMM) with negative binomial distribution and log link (Koper and Manseau, 2009; Coelho et al., 2020). We ran an array of models with the main effects of one, two and three predictors in order to keep the most parsimonious models, avoid overfitting and foster interpretability of models (Chatterjee and Simonoff, 2013). We ranked models according to the Akaike Information Criterion corrected for small sample size (AIC_c), with the best models being selected as those having $\Delta AIC_c < 2$ and the highest model weights w_i toward 1 (Symonds and Moussali, 2011). We measured w_i also for the most important predictors by summing up w_i of models containing them. The effects of predictors were determined from their slopes (β) and the significance of their difference from zero at $p = 0.005$. We set the significance level at a much more conservative level than conventional $p = 0.05$ to increase the strength and reproducibility of results and to minimize the occurrence of false negatives and positives (Benjamin et al., 2018). Odds ratio $\exp^{\beta}$ was measured as the effect size and we also considered its 99% confidence interval resultant from a conservative p-value. Odds ratio indicates an increase if > 1 (e.g., by 20% if it is equal to 1.20), decrease if < 1 (e.g., by 60% if it is 0.40) or no change if = 1 (Lesniak et al., 2018; Khorozyan, 2020). Although information-theoretic and hypothesis testing approaches are conceptually different and their concurrent use is debated for long (Qian, 2014), we checked the AIC_c-based best models for statistical significance to be sure that they are indeed robust and not selected as the best out of all bad models (Poudyal et al., 2016).

The precision of the best GLMM models was estimated by plotting 99% confidence intervals of predicted values and overlapping them with original values of the number of sheep killed by wolves. These models were validated by 10-fold cross-validation and the accuracy of their predictions was estimated by calculation of mean root-mean-square error (RMSE) ± standard error (SE) from 10 random training/test sub-samples (Coelho et al., 2020; Khorozyan, 2020). SE was used as a measure of variation throughout the study.

We fitted linear regression (Chatterjee and Simonoff, 2013) to examine annual trends in percentages of killed/living sheep and numbers of living sheep in states with >5 annual data. Annual changes in these percentages and numbers of living sheep were determined from the slopes (β). All statistical analyses were conducted in IBM SPSS Statistics v. 26 (United States).

RESULTS

Our dataset consisted of 79 cases and, therefore, we used seven predictors: state, year, number of reproductive units of wolves, number of living sheep, number of red deer, number of roe deer, and number of wild boars. The running of 63 GLMM models led to one best model, in which the number of sheep killed by wolves was best explained by the German state, year, and number of living sheep (**Table 1**). The dataset is available in the **Supplementary Material**.

From this best GLMM model, significantly more sheep were killed in the northern states of Germany which were recolonized by wolves first in 2000–2008 (Sachsen, Sachsen–Anhalt, Brandenburg and Mecklenburg–Vorpommern) than in the southern ones (Baden–Württemberg and Bayern) compared to the central state of Thüringen (**Table 2** and **Figure 1**). The number of sheep killed by wolves increased consistently by 41% per year and by 30% for every additional 10,000 sheep (**Table 2**). So, annual sheep losses increased consistently over time along with the recolonization of states by wolves, but regardless of wolf numbers. The most important predictors of sheep losses were year (w_i = 1.000) and state (w_i = 0.999), followed by the number of living sheep (w_i = 0.747). This model had high precision (adequate coverage by 99% confidence intervals, **Figure 1**) and high accuracy (mean RMSE = 42.47 ± 0.66, which is much lower than the mean number of sheep killed per state and year = 98.99).

The next six models, which incremented w_i of the model set to the maximum of 1, were weak and showed only slight effects of the numbers of reproductive units of wolves and their prey on sheep losses to wolves (**Table 1**). The weights of these predictors were low: 0.106 for the number of wild boars, 0.027 for the number of reproductive units, 0.020 for the number of red deer and 0.019 for the number of roe deer.

The numbers of living sheep significantly decreased over years in Brandenburg [−5265.3 ± 894.8 sheep/year, R^2 = 0.759, $F_{(1,11)}$ = 34.628, $p < 0.001$], Sachsen [−5305.8 ± 437.3 sheep/year, R^2 = 0.902, $F_{(1,16)}$ = 147.200, $p < 0.001$] and Sachsen–Anhalt [−3792.6 ± 793.6 sheep/year, R^2 = 0.717, $F_{(1,9)}$ = 22.836, p = 0.001]. These numbers stayed stable in Mecklenburg–Vorpommern [−2420.2 ± 812.2 sheep/year, R^2 = 0.470, $F_{(1,10)}$ = 8.879, p = 0.014] and Niedersachsen [1204.8 ± 783.2 sheep/year, R^2 = 0.283, $F_{(1,6)}$ = 2.366, p = 0.175] (**Figure 2**). The percentages of killed/living sheep significantly increased in all these states by an average of 0.03 ± 0.01% per state and year (range 0.02–0.05%, mean R^2 = 0.75 ± 0.04, n = 5, all $p \leq 0.001$) (**Figure 2**). The maximum percentage of killed/living sheep was 0.44 ± 0.07% per state and year (range 0.25–0.67%, n = 5), with the upper estimate of 0.67% being also the maximum for all our dataset.

DISCUSSION

This study has clearly demonstrated that sheep losses to wolf attacks in Germany were not related to the numbers of adult wolves or prey, but were determined by states, years, and numbers of living sheep. Sheep losses tended to increase by 41% per year and by 30% for every additional 10,000 sheep regardless of wolf numbers, but they were higher in the north, where most wolf territories are concentrated (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2020a; Reinhardt et al., 2021). These patterns were well predictable and appeared to be precise and accurate (**Figure 1**). Thus, our study rejected the first two hypotheses (a positive and main effect of wolf number and an inverse effect of prey numbers on sheep

TABLE 2 | The best model ($\Delta AIC_c < 2$) output of the effects of state, year, and number of living sheep (×10,000 individuals) on the number of sheep killed by wolves in Germany.

Predictor	β	SE (β)	*t*	*p*	OR (99% CI)
Intercept	−685.75	70.47	−9.73	< 0.001	
BW	−4.15	0.80	−5.19	< 0.001	0.02 (0.00–0.13)
BY	−6.27	1.15	−5.44	< 0.001	0.00 (0.00–0.04)
BB	3.11	0.61	5.13	< 0.001	22.50 (4.50–112.56)
HE	1.29	0.84	1.55	0.127	3.64 (0.40–33.39)
MV	2.45	0.66	3.69	< 0.001	11.59 (1.99–67.41)
NI	0.91	0.47	1.91	0.060	2.48 (0.70–8.71)
NW	−0.33	0.38	−0.85	0.396	0.72 (0.26–1.99)
RP	−0.31	0.58	−0.53	0.599	0.74 (0.16–3.45)
SN	3.30	0.62	5.34	< 0.001	26.98 (5.25–138.55)
ST	2.33	0.65	3.59	0.001	10.23 (1.84–57.01)
SH	−0.61	0.68	−0.89	0.377	0.55 (0.09–3.30)
TH*	0				
Year	0.34	0.03	9.84	< 0.001	1.41 (1.28–1.54)
No. living sheep	0.26	0.08	3.31	0.002	1.30 (1.05–1.60)

Abbreviations: β, slope of model; CI, confidence interval; OR, odds ratio; p, significance level; SE (β), standard error of slope; t, t statistic.
States: BW, Baden–Württemberg; BY, Bayern; BB, Brandenburg; HE, Hessen; MV, Mecklenburg–Vorpommern; NI, Niedersachsen; NW, Nordrhein–Westfalen; RP, Rheinland–Pfalz; SN, Sachsen; ST, Sachsen–Anhalt; SH, Schleswig–Holstein; TH, Thüringen.
**The β of Thüringen is set to zero due to redundancy.*

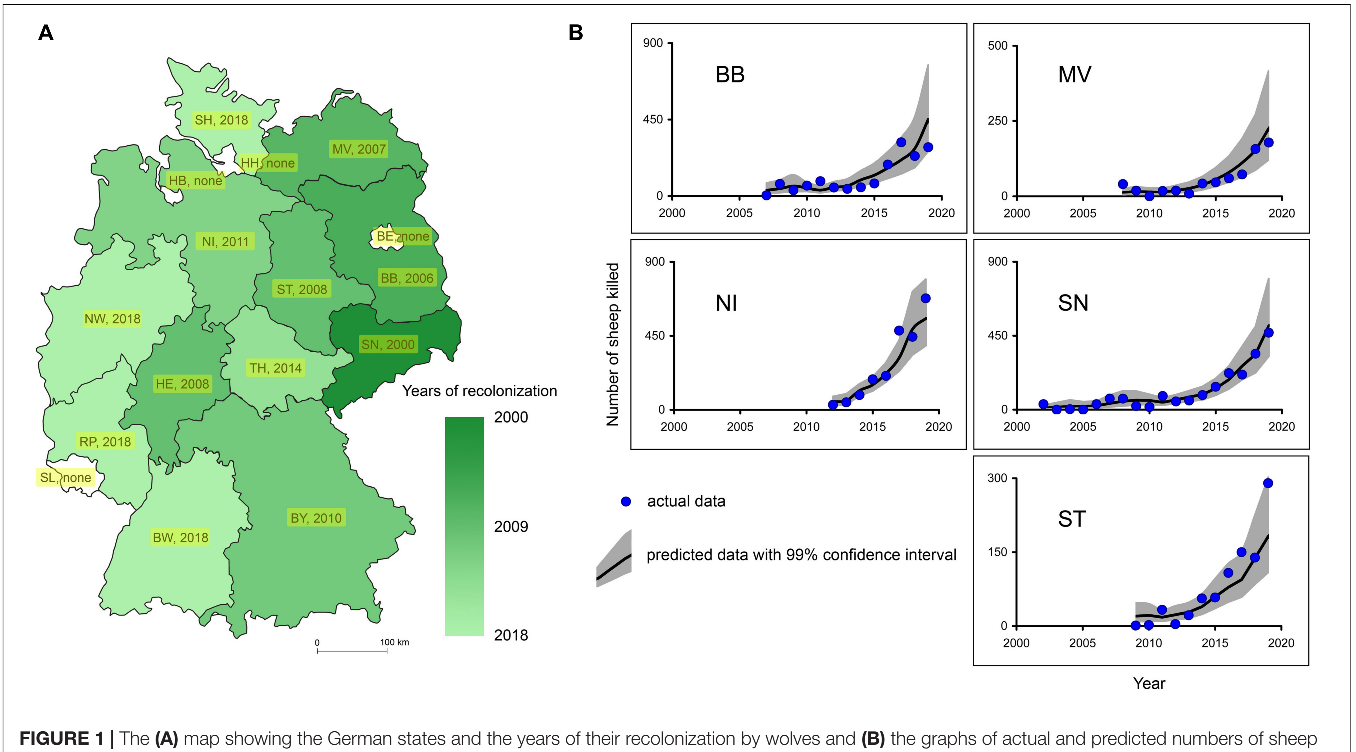

FIGURE 1 | The **(A)** map showing the German states and the years of their recolonization by wolves and **(B)** the graphs of actual and predicted numbers of sheep killed by wolves in states over years. The graphs include only the states with >5 annual data. States: BB, Brandenburg; BE, Berlin; BW, Baden–Württemberg; BY, Bayern; HB, Bremen; HE, Hessen; HH, Hamburg; MV, Mecklenburg–Vorpommern; NI, Niedersachsen; NW, Nordrhein–Westfalen; RP, Rheinland–Pfalz; SL, Saarland; SH, Schleswig–Holstein; SN, Sachsen; ST, Sachsen–Anhalt; TH, Thüringen. Map: adapted from https://www.freevector.com/map-of-germany.

losses) and supported the third one (a positive effect of sheep number). Our results mean that an increase of sheep depredation by wolves is progressing simultaneously all over the country along with the expansion of the wolf population. Additionally, they imply that sheep in Germany are protected insufficiently and/or ineffectively and killed more in sheep-rich states where chances to encounter and kill a sheep are higher.

In contrast to other studies where wolf number was the best predictor of sheep losses (Kaartinen et al., 2009), our result could be caused by highly variable predisposal of wolves

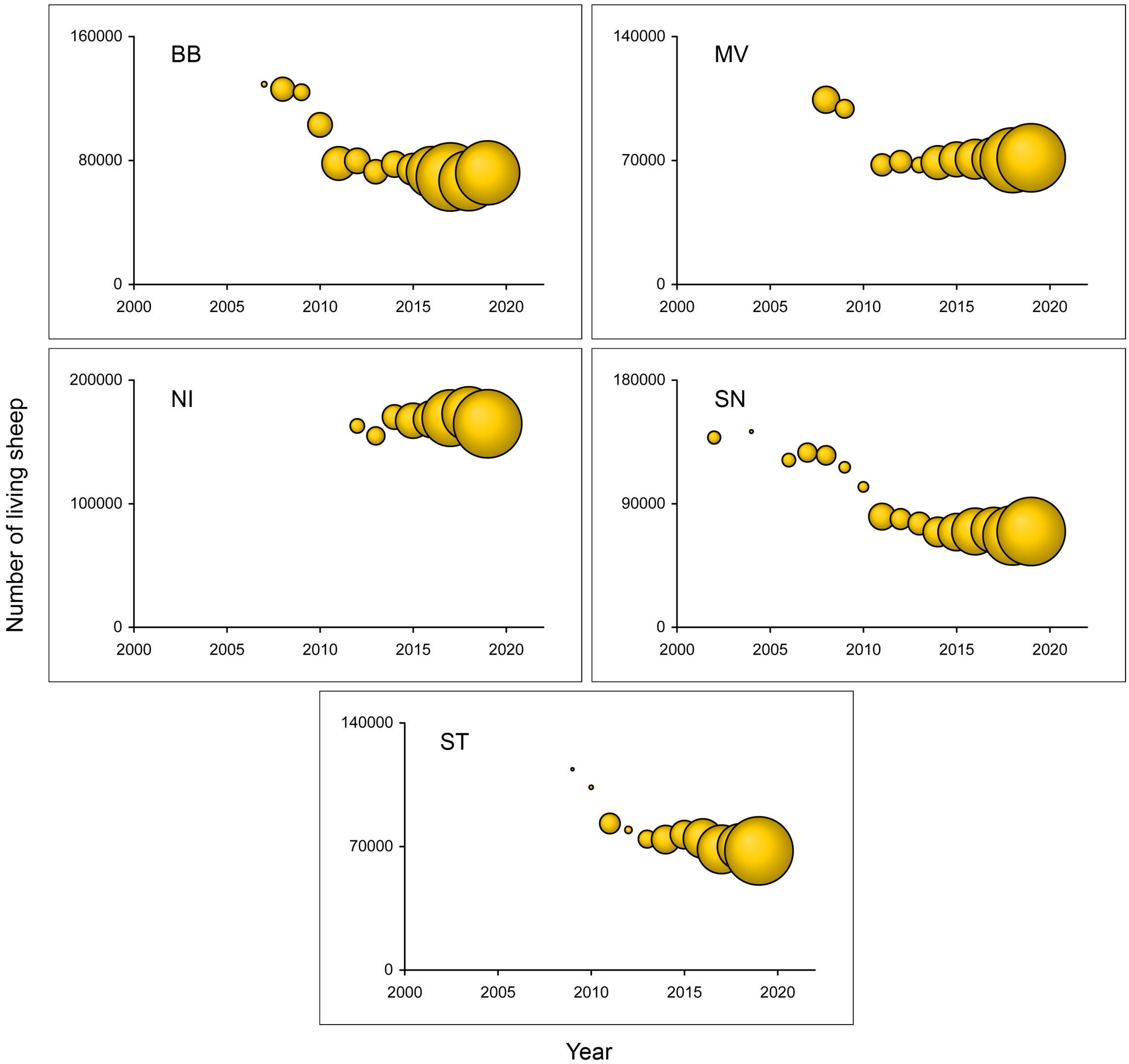

FIGURE 2 | An increase of the percentage of killed/living sheep (bubble diameter) in relation to changes in the numbers of living sheep in German states over years. The graphs include only the states with >5 annual data. States: BB, Brandenburg; MV, Mecklenburg–Vorpommern; NI, Niedersachsen; SN, Sachsen; ST, Sachsen–Anhalt.

to sheep killing. As wild prey is abundant in Germany and wolves can survive without attacks on livestock (Reinhardt et al., 2021), some problem individuals can be notorious for killing disproportionately high numbers of livestock (surplus killing) and thus cause variation in depredation rates. One of the best-known examples of such problem wolves in Germany was a male which killed over 40 sheep in 2019 in a newly recolonized state of Schleswig–Holstein (**Figure 1**; Anonymous, 2020) where only two territorial wolves were, and are still, living (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2020a). Possible existence of high-risk depredation hotspots (Treves et al., 2011) also may ensure geographical variation in sheep losses and requires in-depth research (I. Reinhardt, pers. comm.). As the wolf population size is not so high yet in the country, individual and spatial variation in livestock killing vs. no-killing cases will remain significant.

Our results closely agree with those of large-scale studies of wolf depredation on sheep in Europe (Gervasi et al., 2021) and cattle and sheep in several US states (Wielgus and Peebles, 2014; re-analyzed by Poudyal et al., 2016). It was found out that wider wolf distribution and higher sheep numbers were the main determinants increasing the numbers of sheep killed by wolves and then compensated (Gervasi et al., 2021) and the numbers of wolf breeding pairs analogous to breeding units in our study did not affect losses of cattle and sheep (Poudyal et al., 2016). Predator number can be a weak predictor of sheep losses at large scales, but play a more important role at local scales of management units where more wolves have higher chances to kill more sheep. Distribution is a geographical factor indicating the presence of wolves, which increases over time in recolonizing species, rather than a numerical factor of wolf numbers. Meantime, as the exposure to predators becomes longer, sheep losses tend to decrease due to co-adaptation of predators and local societies (Gervasi et al., 2021). This is a good perspective for Germany where sheep losses are still on the rise as the wolf recolonization is "young," but they are expected to recede over time with the wolf population approaching its carrying capacity (Fechter and Storch, 2014) and farmers protecting their livestock and becoming more tolerant (Cretois et al., 2021). Imbert et al. (2016) also report that livestock protection and stabilization of wolf packs lead to the decline of livestock losses over time.

Another significant result of this study was that the percentages of killed to living sheep increased over the years on a backdrop of decreasing sheep holdings in German states (**Figure 2**). This decline in sheep holdings is in accordance with decreasing sheep stocks in Germany and many other European countries for political and economic reasons (Linnell and Cretois, 2018). This trend aggravates financial losses incurred by sheep breeders and may serve as a solid ground for the agricultural sector to lobby for lethal control of wolf numbers. In this case, the wolf may become a symbol of tensions between biodiversity conservation and agricultural development agenda and a scapegoat for a failure of the authorities to support sheep farming (Chapron and López-Bao, 2014). However, conservation policy related to wolf and other large predators is unlikely to be uniform across Europe due to inherent cultural, environmental, and socio-political differences between its countries (Gippoliti et al., 2018).

We show that the percentages of killed/living sheep in German states increased by only 0.02–0.05% per year and the maximum percentage was nearly 0.7%. Considering negligible levels of damage and the economic capacity of Germany to compensate this loss, we think that the national and regional conservation policy should continue to pay compensations and subsidize the use of livestock protection interventions as it does now (nearly 9.5 million Euro spent in 2020, Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2021). However, compensation and subsidy payments are not a sustainable solution when wolf numbers are rapidly increasing and proper monitoring of intervention effectiveness is lacking (Boitani et al., 2010). Therefore, more efforts should be taken to (1) search and apply alternative, previously untested non-lethal interventions (Reinhardt et al., 2012; Bruns et al., 2020); (2) enforce and standardize the mechanisms of monitoring and troubleshooting of the use of interventions (Bundesamt für Naturschutz [BfN], 2019; Kamp, 2021); and (3) promote wolf tolerance through outreach education (Straka et al., 2020) and professional training of the most vulnerable groups such as livestock (especially sheep) owners, hunters, tourists, and other nature lovers.

In spite of subsidies provided by German states to apply livestock protection interventions, primarily electric fences, in many cases these interventions are used loosely and reluctantly (Kamp, 2021), their monitoring is insufficient, and most of the livestock are still unprotected. As a result, wolves learn to overcome interventions, habituate and make them ineffective. This requires a standardization of legally framed government-farmer relationships and intervention monitoring procedures across the states responsible for implementing wolf management plans. As agricultural workers and hunters are dominated by men (Hermann et al., 2013), and men are more inclined to support wolf killing (NABU, 2015, 2018), education and training should be designed to target the men's audience and tailored to their age, background and mentality. These activities should be carried out in adherence to the management plans of German states and the standardized framework of actions and their specifications which was published by the network of German non-governmental conservation organizations (Kucznik et al., 2020).

As this study was conducted at a large scale of all Germany, we suggest that its results and extrapolations are valid only at this scale, and at smaller scales sheep losses can depend on factors that we did not consider. Therefore, more information on wolf–sheep relationships is required at medium and fine scales, such as the roles of protection interventions, local sheep and wolf densities, landscapes, infrastructure, and other factors. This research will be a very timely and important contribution to the maintenance of wolf recovery and local livelihoods in European human-dominated landscapes where large predators demonstrate a remarkable comeback.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

Both authors conceived the ideas, designed methodology, led the writing of the manuscript, contributed critically to the drafts, and gave final approval for publication. IK collected and analyzed the data.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.778917/full#supplementary-material

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Wolf Conservation and Management in Spain, An Open Debate

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Wolf management in Spain is remarkably different at regional scales. South of Douro river, wolves are protected, north of Douro wolves can be hunted, and culling occurs on both sides. After a formal request to include wolves in the Spanish Red List of Threatened Species, wolves have been "listed," but not as a vulnerable species. Recreational hunting will no longer be a wolf management option, while culling is still allowed. We describe the process to raise wolf protection at the state level, and the factors that should be relevant to guide apex-predator management. Restricting lethal control and favoring predator-prey interactions by reducing livestock depredation should be more feasible with an overarching policy that is binding over the whole range of the species in Spain.

Keywords: human-wildlife conflict, large-carnivore conservation, management, protected species, wolf-listing process, wolves

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INTRODUCTION

Large carnivores are recolonizing former grounds in Europe (Chapron et al., 2014) and North America (Bruskotter and Shelby, 2010), yet carnivore recovery pace and success vary across regions. In central Europe, wolf recovery has been quite fast in Germany (Reinhardt et al., 2019), and wolves even reproduced in Denmark for the first time in ~200 years, although poaching may prevent further expansion (Sunde et al., 2021). In northern Europe, the Scandinavian wolf population started its recovery in the 1990s, but nowadays wolves are more numerous in Sweden than in Norway due to differences in policy (Bischof et al., 2020).

In southern Europe, wolves were eradicated from many countries and, where they persisted, they reached historical minimums and population bottlenecks in the 20th century. Wolves were at their nadir in ~1950–1970 in Italy (Zimen and Boitani, 1975) and Spain (Quevedo et al., 2019). Recently, wolves have shown a faster recovery in Italy, expanding into neighboring countries (Galaverni et al., 2016), while the Iberian wolf population of Portugal and Spain has shown a different trend (Torres and Fonseca, 2016; Quevedo et al., 2019).

In Portugal, wolves are still declining (Torres and Fonseca, 2016). In Spain, a wolf population estimate in 1986–1988 counted 294 packs in ~100,000 km^2 (Blanco et al., 1992), and a study in 2012–2014 reported 297 packs in a similar range, beyond some variation in the south of Douro river (MAGRAMA, 2016). In any case, the range is far from the ~440,000 km^2 (most of the Iberian Peninsula) occupied by the species until the 19th century (Rico and Torrente, 2000) (**Figure 1**). The wolf population in Spain, ~80% of the Iberian population, partially recovered in the 1970–1980s, but the expansion and recovery pace has stagnated compared to the recent and faster recovery in other European areas. The last wolves in southern Spain are likely extinct, and the NW Iberian population is isolated from other European populations (Quevedo et al., 2019).

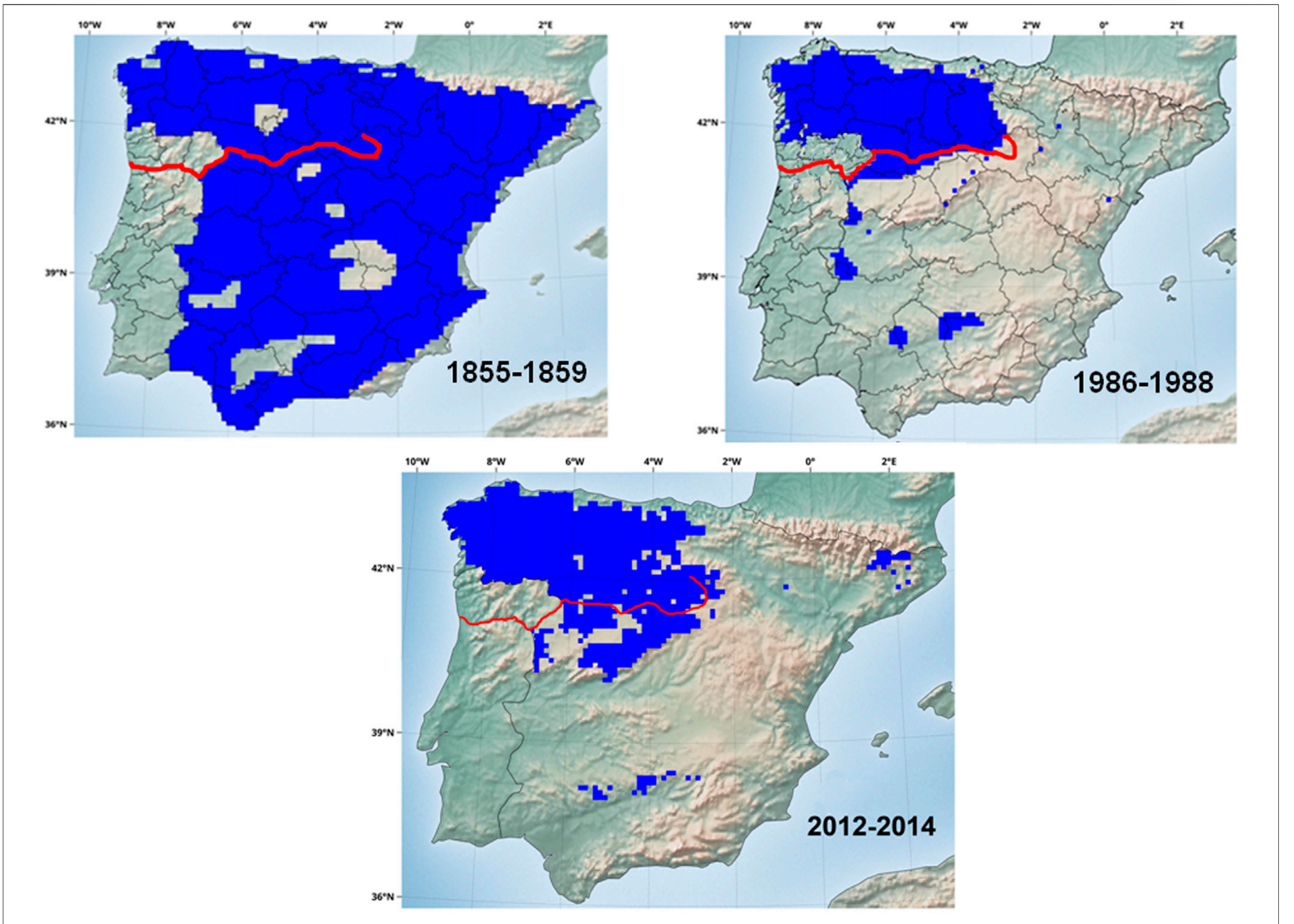

FIGURE 1 | Wolf range in Spain in 1855–1859 (adapted from Rico and Torrente, 2000), in 1986–1988, and in 2012–2014 (adapted from Blanco et al., 1992 and MAGRAMA, 2016, respectively). Douro river, which has been dividing wolf management regimes in Spain, is also shown (red line). We projected the original maps on a 10 km UTM grid size for a more standardized overview in terms of accuracy and comparison of range size.

Wolf management in the Iberian Peninsula is very fragmented and complex. Wolves are protected in Portugal, whereas different management regimes occur in the administrative regions of Spain that support wolves. Spain is divided into 17 regions (and two autonomous cities), a political and administrative division after the Spanish Constitution of 1978, with implications at multiple levels. There are national laws on, for instance, education, public health, and environmental management, but regional governments have independence and the responsibility to make their own regulations. South of Douro river, wolves are listed in Annex II and IV of the EU Habitats Directive, whereas wolves are listed in Annex V north of Douro (Quevedo et al., 2019). Legal hunting in some regions and culling both north and south of Douro occur, e.g., 623 wolves were legally killed in Spain in 2008–2013, 29 of them in areas with strict protection. In contrast, no wolf was legally killed in 2008–2013 in Portugal (Quevedo et al., 2019), but poaching occurs (Torres and Fonseca, 2016). Lethal management of wolves in Spain may limit wolf dispersal and population expansion (Quevedo et al., 2019).

In this scenario, there has been a formal request by an NGO (*Association for the Conservation and Study of Iberian wolves*, ASCEL) to the Spanish government, to include wolves in the Spanish Red List of Threatened Species as a "vulnerable" species or, alternatively, as "listed" (details below). This would eliminate the fragmented management scenario and would apply the protection of wolves to all of Spain. If wolves were granted that national protective status, *1*) lethal control and recreational hunting would not be a wolf management option any longer and, *2*) the inclusion in that List should trigger the drafting of a Wolf National Conservation Plan to promote long-term wolf viability.

We explain the process following the request to consider wolves as a vulnerable species, describing the reasoning for the request and the reactions from various stakeholders. We also highlight the factors and scientific data that in our opinion should be most relevant to guide the conservation-oriented management of an apex predator.

INSIGHTS INTO THE LEGAL FRAME OF WOLF MANAGEMENT IN EUROPE AND SPAIN

Conservation and management plans based on the trophic importance and key ecological role of large carnivores (and wolves in particular) have gained support in different ecosystems

(Hebblewhite et al., 2005; Terborgh and Estes, 2010; Ordiz et al., 2021). In Europe, the Bern Convention (Council of Europe 1979) and the Habitats Directive (European Union 1992) set the stage for wolf management in EU countries, which must use those rules to guide the drafting of national legislation.

In theory, wolves have been a protected species in Spain since it joined the European Union and Bern Convention in 1986. As an EU member, Spain also implemented the Habitats Directive (1992) that used the Douro river as the boundary between two distinct management zones, but there was not a Spanish national law drafted from the Directive until 2007 (Ley 42/2007). This law also created a Spanish Red List of Threatened and Protected Species (Royal Decree 139/2011). That list includes 77 mammals; 25 are "Vulnerable" and eight are in the "Endangered/Extinction risk" category, thus they are subject to more proactive protection, while 44 species are just "Listed" and their management follows less stringent regulation. For instance, the "Endangered" and "Vulnerable" categories of the IUCN Red List are included under the Spanish law, whereas being listed in Spain is not equivalent to other IUCN categories, such as Least Concern or Data Deficient.

Wolves in Spain were only "Listed" in some specific regions-provinces (most Spanish regions include several provinces). In 2011, the Sierra Morena (southern Spain) wolf subpopulation was listed and later (2019), the entire wolf range south of Douro river was also listed. North of Douro, wolves have not been listed until now, and management regimes vary widely among regions. Wolf hunting, hunting and culling, only culling, or no lethal management occur in different regions north and south of Douro, with varying management laws at the regional level (Quevedo et al., 2019). A reason for such complexity, which causes many wolf packs in mountain ranges between regions to be both protected and subject to hunting simultaneously (merely depending on the side of the mountains where they are roaming at a time), is that the national government holds the responsibility to interpret EU laws and set main guidelines at the state level, but regional governments are responsible for the actual management of biodiversity, including wolf management.

REASONS TO REQUEST THE LISTING OF SPANISH WOLVES AS VULNERABLE SPECIES

In Spain, any citizen or association can promote the inclusion of a species in one of the specific categories of protection under "Ley 42/2007," providing supportive arguments. The proposals are addressed to the corresponding Spanish ministry (*Ministerio para la Transición Ecológica y el Reto Demográfico,* MITECO). A form to fill in the request is available at the website of the ministry. It includes compulsory fields and additional ones (*see* **Supplementary Table S1**).

The legal criteria to include a species on the Spanish Red List were approved in 2017 and are based on the IUCN requirements to classify endangered species. The association (ASCEL) that requested the national protection of wolves in Spain argued that the species fulfills the sub-criterion B3, which states that a species must be included as "Vulnerable" in the list when it has experienced a strong range reduction in historical times (>50% loss of its historical range in the last 100 years), and when there is available habitat for its occurrence, the species is recovering, but it does not occupy 50% of the historical range yet (Spanish Official Bulletin 65).

OFFICIAL STEPS AND REACTIONS TO THE REQUEST

The Official Process and Its Outcome

The administrative process to be listed under RD 139/2011 is defined by law and includes several steps, and the competence to assign or modify the protection category of a species lies with the ministry (MITECO). Two committees, two commissions, public consultation processes, and representatives of the different regions are involved in the assessment process. First, the request by ASCEL (October 2019) was evaluated by a national scientific committee, which includes 19 researchers and biodiversity specialists designated by the Spanish government. This committee is an advisory group for MITECO, for the different regions, and for another committee. The scientific committee recommended (February 2020) the listing of wolves in Spain, but abstained from recommending its inclusion as a vulnerable species. The decision was based on a lack of peer-reviewed papers that analyzed the historical change in wolf range in Spain in the 20th century. Based on that assessment and according to the established process, MITECO arranged a technical report and made a decision (March 2020) that agreed with that of the scientific committee: the entire wolf population in Spain would be "Listed" (thus expanding the listing of wolves south of Douro river to the northern portion of the population), but without granting the species the more protective, "Vulnerable" status.

MITECO had to present that wolf listing proposal to the second committee, the "National Wildlife Committee," with members of public agencies, and to a third one, the "National Commission for the Natural Heritage and Biodiversity." The latter includes one representative of MITECO and one from each regional government and autonomous city (i.e., one member from MITECO and 19 from regions and cities). A lack of consensus on wolf listing by that commission (February 2021) triggered two voting processes, which ultimately decided wolf listing (nine supportive votes, eight against it, one abstention, and two did not vote). The regions with ~90% of the Spanish wolf population (Galicia, Asturias, Castille and Leon, and Cantabria), whose wolf management is largely based on lethal control, *via* culling and/or hunting, voted against wolf listing. Basque Country, where wolves are protected since 2020, also voted against it. Three regions (Catalonia, La Rioja and Aragón) with sporadic wolf presence and regions without wolves voted for wolf listing.

Next and to accomplish the Law 50/1997, MITECO submitted the wolf listing decision to a first, public consultation; a mandatory, yet not binding step. There were 5,635 responses; 2,446 private persons plus legal entities supported wolf listing, 3,138 were against it, 51 were classified as no preference, and the rest were out of date. Afterwards, MITECO submitted the wolf listing decree draft to the "National Council for the Natural Heritage and Biodiversity" (May 2021) to collect opinions and update the draft. This council includes 57 members of the Spanish and regional governments and stakeholders, including farmers, hunters, conservation and environmental associations, unions, professional associations, etc. In May 2021, MITECO launched a new public consultation process to assess the wolf listing decree draft, receiving 84 responses; 29 from legal entities (political parties, private companies, agricultural-farming unions, NGOs, and regional and local administrations), and 55 from citizens. The regions that include virtually all Spanish wolves submitted statements to discard the wolf listing decree. In July 2021, MITECO requested opinions about the wolf listing decree draft to its Technical General Secretary and other governmental agencies, collecting responses from the Ministry of Territorial Policy and Public Function and the Ministry of Agriculture, Fisheries, and Food. Finally, MITECO requested a judgment from the "Spanish Kingdom Council," the highest advisory board, which assesses if rules are in accordance with the overarching Spanish Constitution. As of 20 September 2021, the wolf listing order has been published by MITECO (*Orden TED/980/2021*), modifying RD 139/2011 to include the whole wolf range in Spain as Listed. The rule has been in force since 22 September, and it implies that wolf recreational hunting is no longer a management option. That rule includes two additional provisions: *1*) removal of individuals may be granted by regions if depredation preventive actions did not work, control does not negatively affect the favorable conservation status of the species, and the occurrence of significant damage to livestock on the affected farms is justified, taking into account possible recurring or significant damage; and, *2*) The Strategy for the conservation and management of wolves in Spain will be approved before 31 December 2021, publishing it in the website of the ministry and in the Spanish Official Bulletin, as requested by Ley 42/2007.

Social Reactions

Interactions between wildlife and people are often named "human-wildlife conflict." However, conflicts often involve groups of people with different opinions on wildlife, i.e., they are rather "human-human" conflicts over conservation goals (Redpath et al., 2013). Large carnivores can affect some human activities and trigger mixed perceptions from stakeholders (Redpath et al., 2013; Ordiz et al., 2021). Large carnivore management, especially wolf management, plays out in heated debates over the range of the species (Mech, 1995; Clark et al., 1996; Skogen and Krange, 2003; Treves and Karanth, 2003; Bergstrom et al., 2009; Redpath et al., 2017), and Spain is no exception.

Some hunters, farmers, and regional administrations overlapping the wolf's range oppose the Spanish wolf listing, and some stakeholders have claimed they would fight in court against a listing decision. According to them, wolves do not need further protection, the MITECO decision is random, there is no scientific or legal evidence supporting wolf listing, the ongoing regional wolf management plans secure long-term wolf conservation, and the Spanish wolf population shows a "favorable conservation status." The latter is not true according to the last EU Commission report (EU, 2019). Altogether, they claim that the national protection of wolves would lead to "overpopulation" and would increase livestock damage. Nowadays, ~7,000 wolf attacks affecting ~11,000 livestock heads are claimed annually in Spain and ~2.5 million € are paid to compensate presumed losses (data extracted from regional sources, e.g., from technical reports and online information), with huge variation among regions. Only some regions compensate depredation (Fernández-Gil et al., 2016).

There is also a fragmented scenario among wolf conservation supporters, further illustrating the human-human nature of these issues. Some seek for wolf classification as "Vulnerable," as ASCEL had requested, to stop lethal control by hunting or culling, while others support the wolf "listing" to avoid recreational hunting, but would permit culling of individuals (as stated in the additional provisions of the recently approved rule), and still others oppose rising wolf protection, arguing that it might increase poaching in retaliation, eventually causing collateral damage to other species.

WHAT SHOULD ACTUALLY MATTER TO MANAGE AN APEX PREDATOR?

Large carnivore persistence or recovery in human-dominated landscapes has resulted from a mixture of carnivore resilience to persecution, conservation-oriented legislation, and socio-economic changes in human societies in recent decades that led to abandonment of rural areas, among other factors (Chapron et al., 2014; Cimatti et al., 2021). In this context, top-down application of legislation that remains consistent after the successive interpretation from European to national and then regional levels, and solid methods for population monitoring and forecasting (Bischof et al., 2020), seem crucial for conservation and management. Reliable numbers should help soften the crossfire among stakeholders typically engaged in large-carnivore debates.

Large carnivores are keystone species that can trigger multiple effects on ecosystems, with predation being the mechanism driving that ecological role. For wolves to play it, populations should be as close as possible to their ecological carrying capacity, because single individuals should not be expected to play an equivalent function as that of populations (Ordiz et al., 2013; Ordiz et al., 2021 and references therein). Nevertheless, large carnivores are often considered to be conflict-prone species, and human factors play an important role in the decision-making process and management of carnivore populations (Olson et al., 2015; van Eeden et al., 2018; Marino et al., 2021; Salvatori et al., 2021). Scientific data for carnivore management is a must, but it is not enough to manage predators effectively; social acceptability and multidisciplinary approaches are equally important (Brewer and Clark 1994; Wallace, 2003; Treves et al., 2009; Woodroffe and Redpath, 2015), as illustrated by the long administrative process triggered by the request to rise wolf protection in Spain. Indeed, a list of overarching variables to be considered in a proper problem definition of the large-carnivore conservation issue includes: the cultural history involved in carnivore-human coexistence, the valuation and attitudes towards carnivores, the ecology of the species, the management systems and jurisdictions, and the policy process (*see* Clark et al., 1996 for a detailed list of subvariables). We envision an analysis with these variables in a theoretical policy framework as a next step, because it would be useful to forecast future trends of the wolf-human context and to guide management plans.

These premises set a trade-off for apex predator management. It should imply the least human intervention on the species, while reducing conflict with human interests to the largest possible extent. From a demographic perspective, large carnivore management should aim at minimizing lethal control. Even hunted populations can be close to carrying capacity, but that likely depends on the arrival of immigrants from neighboring areas (Suba et al., 2021), which is not feasible for isolated populations, such as wolves in the Iberian Peninsula. Granting wolves in Spain a level of protection that prevents the regular use of hunting as a management tool should favor self-regulation of the population. Reducing lethal management should improve wolf conservation status and favor connectivity within the Iberian Peninsula and beyond (Quevedo et al., 2019). Connectivity and dispersal would favor genetic recovery of European wolf populations, which have suffered severe bottlenecks and still have low effective population sizes (Sastre et al., 2011; Hindrikson et al., 2016), a conservation problem shared elsewhere with other species (e.g., Taron et al., 2021).

Furthermore, prevention of damage to livestock is crucial to avoid conflict and reduce social pressure for carnivore lethal management (Ordiz et al., 2021). Lethal control does not necessarily reduce depredation, as shown in different areas, including Spain (Fernández-Gil et al., 2016). Accessibility to free-ranging livestock favors wolf attacks in Spain, thus efficient livestock protection should be compulsory if extensive grazing continues to be promoted by European Union's Common Agricultural Policy (CAP) (Recio et al., 2020). Besides reducing conflict, livestock protection would also allow densities of natural prey and predator-prey interactions to become main determinants of wolf carrying capacity and the population size needed for them to play their ecological role (Ciucci et al., 2020).

CONCLUSION

Large carnivores and their management are controversial worldwide, as illustrated by the long-term wolf delisting process in USA (Bergstrom et al., 2009; Barber-Meyer et al., 2021; Treves et al., 2021). Lethal control of wolves is often used as a "biopolitical" action to affect social values, supposedly producing social tolerance for wolves (Anderson, 2021). Yet, granting wolf hunting does not necessarily favor wolf acceptance (Pepin et al., 2017). In some areas, social values that traditionally considered predators as vermin still allow lethal management of wolves, even in small populations dependent on immigration from neighboring areas (Sollund and Goyes, 2021).

Hunting and culling of wolves and economic compensation for damages attributed to the species are the main tools of wolf management in Spain, omitting, deliberately or not, demographic and ecological components that should also matter for apex predator conservation. The present case in Spain highlights the factors that are arguably important for carnivore conservation and management in human-dominated landscapes. Besides sociological aspects (to improve acceptability by the public and to include sociological variables that go beyond the ecology of the target species) and demographic considerations (to collect reliable data on population size and trends), other important issues include: *1*) recovering historical ranges (which are far from being recolonized by wolves in Spain, a key issue in relation to the national rule of the protective request to consider the species as "vulnerable"), *2*) considering the ecological function of apex predators from a holistic point of view for ecosystem recovery and, *3*) avoiding fragmentation and a too flexible application of environmental regulations at progressively lower administrative levels. Under an unambiguous legal framework, all of these factors should be included in a multidisciplinary, theoretical framework that would favor practical management and, ultimately, the long-term population viability of wolves.

Although conservation and management plans based on the ecological role of wolves have gained support in different ecosystems (Hebblewhite et al., 2005; Ordiz et al., 2021), further steps are needed to put theory in practice, a concern that applies for wolves in Spain and for this and other species elsewhere. Restricting wolf lethal control and favoring natural predator-prey interactions by reducing depredation on properly protected livestock should help achieve the goals mentioned above; namely, favoring the recovery of the species and its role in nature and its acceptability by the general public. For wolves in Spain, these goals should be more feasible with an overarching Spanish wolf policy that is binding over the whole range of the species. The recently approved listing decision raises wolf protection to the national level, but preventing livestock depredation will be crucial to avoid conflict and, in turn, that the culling continues to be widespread over wolf range.

AUTHOR CONTRIBUTIONS

AO conceived the idea with input from DC and JE and wrote a first draft of the manuscript, with some sections further elaborated by JE. AO, DC, and JE wrote and revised subsequent versions of the manuscript and approved its submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.781169/full#supplementary-material

Supplementary Table 1 | Compulsory fields required in a formal request to include a species in the Spanish lists of protected species or to modify its protection status (left column), and summary of the information included in the request to rise wolf protection (right column). Source of the official form (left column): Spanish *Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO)*. Source of the wolf information (right column): Request submitted by the *Association for the Conservation and Study of wolves* (ASCEL) to include wolves on the list.

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Occurrence and Livestock Depredation Patterns by Wolves in Highly Cultivated Landscapes

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Attacks by large predators on livestock are an important driver of conflicts. Consequently, knowledge about where predators occur, where livestock depredation takes place and what factors influence it will aid the mitigation of stakeholder conflicts. Following legal protection, wolves (*Canis lupus*) in Central Europe are recently spreading to areas dominated by agriculture, bringing them in closer contact with livestock. Here, we analyzed habitat selection and livestock depredation rates of 43 wolves identified by genotyping on the Jutland peninsula, consisting of mainland Denmark and the northernmost German federal state Schleswig-Holstein. Occupancy by resident wolves correlated positively with forest and other non-forested semi-natural land cover (habitat for natural ungulate prey), whereas occupancy by non-resident wolves correlated with increasing forest cover and sheep density. The latter effect likely reflected increased sampling probability of highly mobile dispersers killing livestock. We recorded 565 livestock depredation events (85 in Denmark and 480 in Schleswig-Holstein), of which 42% (55 in DK and 185 in SH) could be assigned to 27 individual wolves based on DNA evidence. Livestock (mostly sheep) were killed by wolves in 16% of the study area. Our results indicate that wolves mostly killed livestock as a context-dependent response, i.e., being dispersers in agricultural areas with low availability of wild ungulate prey and high livestock densities, and not because of behavioral preferences for sheep. Moreover, the livestock depredation was lower in areas with livestock protection measures (implemented in areas with established pairs/packs). We conclude that while wolf attacks on livestock in established wolf territories generally can be reduced through improvement of fences, livestock depredation by non-resident wolves in agricultural areas constitutes a bigger challenge. Albeit technically possible, the economic costs of implementing predator-proof fences and other preventive measures in such pastoral areas infrequently visited by wolves will be considerable. Experiences so far further indicate that lethal removal of identified "problem wolves" may be inefficient in practice.

Keywords: ***Canis lupus*, human-wildlife conflicts, large carnivores, livestock protection, *Ovis aries*, predation, spatial ecology**

INTRODUCTION

Following severe historic persecution leading to the absence of large carnivores in many areas of Central Europe during most of the nineteenth and mid-twentieth century, large carnivore populations have increased over recent decades (Chapron et al., 2014). The gray wolf (*Canis lupus*) has received legal protection in the 1980s in most European countries, and has since increased its geographic range (Nowak and Myslajek, 2016; Reinhardt et al., 2019). In general, wolves can persist in human-modified landscapes as long as human tolerance and policy are favorable (Boitani and Linnell, 2015; Reinhardt et al., 2019). Apart from legal protection and supportive public opinion, the main factors for large carnivore recovery (Chapron et al., 2014), habitat suitability for wolves has increased over the last two decades in some European areas, including Central and Northern Europe, which is correlated with decreasing human population density and increasing forest cover (Cimatti et al., 2021). Moreover, wolf occurrence depends on social status, with wolf pairs/packs occupying higher-quality habitats characterized by lower anthropogenic impacts like forests, whereas dispersing individuals can be found in a broad array of habitat types (Nowak et al., 2017).

The natural recolonization process by wolves has resulted in socio-political conflicts that may jeopardize conservation outcomes if not adequately managed. One of the most challenging conservation issues is that wolves predate on livestock, especially when they have returned to areas (after long periods of absence) where people are not habituated to animal husbandry practices that prevent damage (Linnell, 2013). Consequently, wolf predation on livestock can lead to social conflicts between conservationists, farmers and other stakeholder groups (Bautista et al., 2019). Livestock damage is often restricted to few farms (Gazzola et al., 2008), and depends on landscape structure and availability of natural prey (Treves et al., 2004; Suryawanshi et al., 2013; Imbert et al., 2016). Additionally, the social status or family history of individual wolves can affect livestock depredation rates. For example, in Northern Italy dispersing wolves killed more livestock compared to resident pairs and packs (Imbert et al., 2016). Sometimes single individuals or packs are responsible for disproportionately high livestock damage, which often results in public pressure for such "problem individuals" to be culled. From a management perspective, it is essential to identify why wolves predate on livestock. They either do so because of the ambient settings (being in the wrong place) or due to individual behavioral inclinations to kill livestock (compared to other individuals in the same setting) (Linnell et al., 1999). This distinction is important, because the EU Habitats Directive only allows lethal management of the latter type of wolves, whereas losses caused by normally behaving wolves must be solved otherwise, e.g., through protective measures. Prey specialization is a well-recognized phenomenon in generalist predators (Araújo et al., 2011; Dickman and Newsome, 2015) and problem-behaviors are known to vary individually (Swan et al., 2017), which might be transferred socially from parents to offspring, as shown in Grizzly bears (*Ursus arctos*) (Morehouse et al., 2016). However, to our knowledge, individual versus context dependent variation in livestock depredation rates have not been rigorously analyzed in wolves.

Importantly, livestock depredation by large carnivores can impact the attitudes of different stakeholder groups, which can influence effective conservation (Dressel et al., 2015). In Europe, attitudes toward large carnivores tended to become more negative with perceived increases in large carnivore abundance and risk of damage, especially in areas where people have to co-exist with large carnivores (Ericsson and Heberlein, 2003; Eriksson et al., 2015). Hence, to reduce conflict levels, keeping damage to livestock at low levels is important (Bautista et al., 2019). To do so, it is crucial to gather knowledge on wolf distribution and habitat use (Reinhardt et al., 2019; Cimatti et al., 2021), impact of livestock density on colonization patterns, as well as identifying spatial centers of livestock predation. Moreover, it is important to evaluate existing livestock protection measures (Eklund et al., 2017).

In this study, we investigated patterns of wolf settlement and predation on livestock in Jutland peninsula, one of Europe's most intensively cultivated regions, consisting of the northernmost German federal state Schleswig-Holstein (SH) and mainland Denmark (DK). We hypothesized that wolf settlement would generally be associated to land cover and human impact, as previously shown (Cimatti et al., 2021), and predicted that wolf occupancy increased with increasing forest and heathland cover (and other natural areas), and with decreasing human impact (human population density and road density). Additionally, we hypothesized that wolf occupancy depends on the social status of wolves, and predicted that non-residents (dispersers), occur in more landscape types than resident wolves (Nowak et al., 2017).

We then investigated depredation rates on livestock by individual wolves and related these patterns to sheep density, land cover, season, wolf social status, and livestock protection measures. Specifically, we predicted that livestock depredation rate decreases with increasing forest and heathland cover, because these land covers are associated with higher abundance of wild ungulates (Borowik et al., 2013), and depredation rate increases in areas with higher densities of sheep that are unprotected by predator-proof fences. Further, we predicted that non-resident wolves have higher livestock depredation rates compared to residents, because (1) non-residents occur more frequently in landscapes that facilitate livestock depredation, and (2) possibly because they are more prone to kill livestock due to unfamiliarity with the local area and/or inexperience. We also tested the extent to which implementation of livestock protection measures (predator-proof fences) lead to a decrease in livestock depredation rate. Finally, we evaluated the magnitude of individual variation in livestock kill rates. If wolf predation on livestock is primarily determined by ambient conditions and social status we expected little individual variation in depredation rates, whereas substantial individual variation should remain if personality and individual behavior had a major influence on a wolf's inclination to kill livestock.

MATERIALS AND METHODS

Study Area and Wolf Population Monitoring

The 470-km long Jutland peninsula belongs to Schleswig-Holstein (SH) and Denmark (DK; **Figure 1**). SH and Hamburg cover an area 16,430 km^2, inhabited by 4.47 million people (average population density: 272 per km^2), and are covered by 68% farmland, 13% forest, 10% developed, and 9% other land cover. The Danish region of Jutland (29,778 km^2, 2.58 million people, average population density: 87 people per km^2) is covered by 61% farmland, 13% forest, 12% developed, 10% heathland, and 4% other land cover. Jutland connects to the Central European mainland through a 60-km wide stretch between the North Sea and the Baltic Sea down to the city of Hamburg. In SH, the majority of the human population is located in the southern part of the state that connects to the federal states Niedersachsen and Mecklenburg-Vorpommern.

Since the Central European wolf population (to which the wolves in Jutland belong) established in the border region between Eastern Germany and Poland around year 2000 (Nowak and Myslajek, 2016; Reinhardt et al., 2019), wolves have been surveyed by means of genetic markers, enabling to identify individuals and to reconstruct their origin and dispersal paths

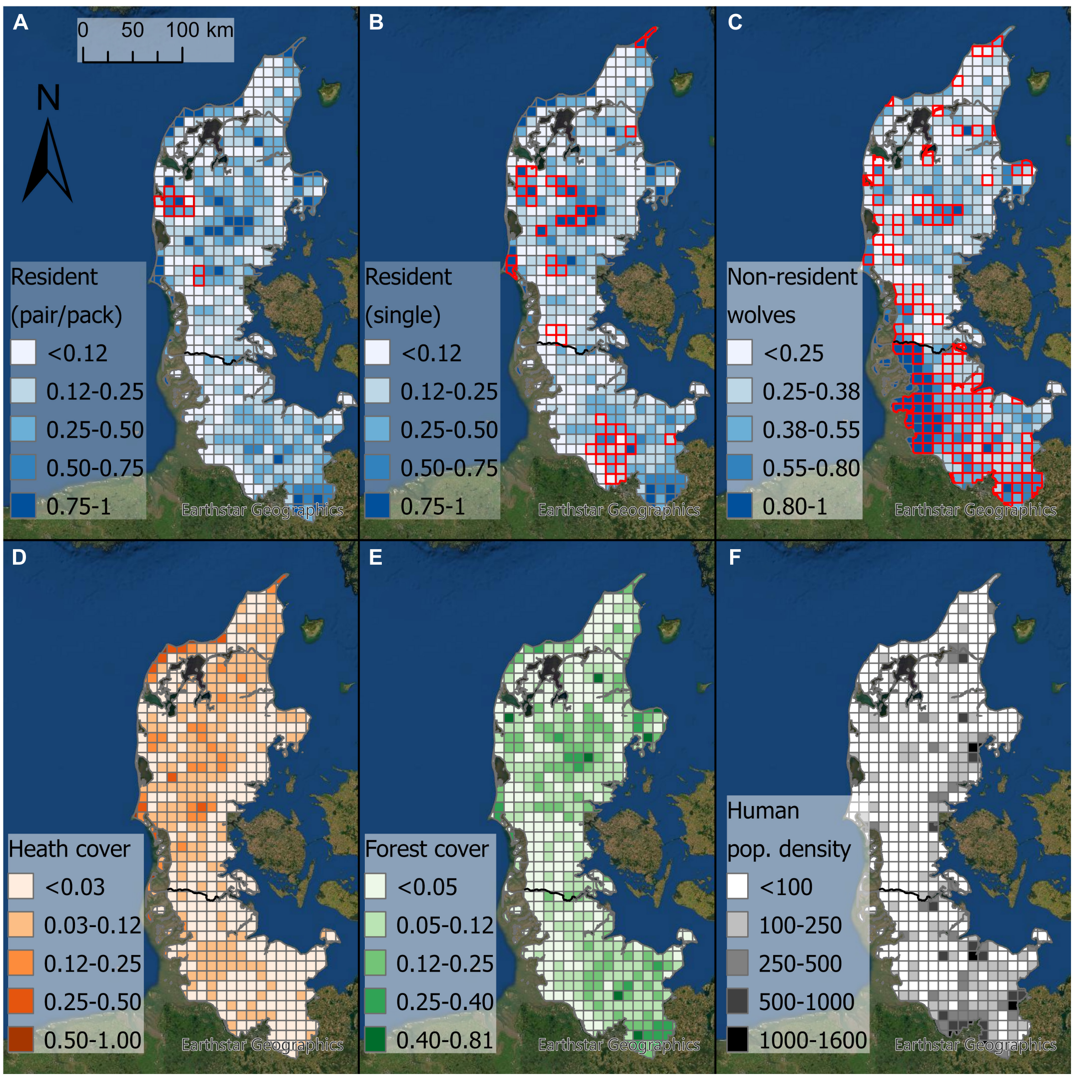

FIGURE 1 | Maps depicting our study area in Jutland separated into 598 grid cells. Red borders show grid cells with observations of **(A)** resident wolf pairs/packs, **(B)** single residents, and **(C)** non-resident wolves. The blue shading depicts the predicted probability of grid cell occupancy by resident wolves [**(A,B)** pairs/packs and single residents were merged for the analysis], and non-resident wolves **(C)**. **(D)** Proportion of heathland cover (and other non-forested semi-natural areas in SH) per grid cell. **(E)** Proportion of forest cover per grid cell. **(F)** Average human population density (people per km^2) per grid cell. The black line represents the border between Denmark in the north and Schleswig-Holstein in the south.

(Andersen et al., 2015). Governmental agencies and research institutions systematically sample DNA from scats, dead wolves, and livestock kills both in DK and SH. In SH, where sheep farming is common and only recently starting to adapt to wolf presence, livestock depredation has contributed to most genotype identifications. In DK, where wolves kill livestock less frequently, monitoring is primarily undertaken by DNA analyses of scats (Sunde et al., 2021). Because there is only a single wolf observation before 2012 (a roadkill from SH in 2007), we defined the period of our study from 2012 to the first quarter of 2021. Wolf observations were categorized according to the SCALP (Status and Conservation of the Alpine Lynx Population) criteria (Reinhardt et al., 2015), and we only used C1 observations, defined as unambiguously confirmed observations based on facts, for our analyses. Wolves were categorized as being resident when they were observed for ≥6 months in the same area (either as single resident or as wolf pair/pack), and non-residents (usually dispersers) when they were observed <6 months in the same area (Reinhardt et al., 2015). Observations that could be not assigned to an individual wolf were generally coded as non-residents unless we had strong evidence that they were part of a wolf pack/pair (e.g., based on their spatial location).

Land Cover, Human Population Density, and Sheep Density

We created 598 10 km × 10 km grid cells over the entire study area as observational unit to model wolf occurrence (**Figure 1**), because this size provides a trade-off between information precision and the average home range size of wolves (Chapron et al., 2014; Milanesi et al., 2017; Cimatti et al., 2021). We downloaded land cover data of 2018 from the CORINE land cover database[1], and categorized the 44 land cover types into seven biologically relevant categories: (1) built up areas, (2) grassland, (3) cropland, (4) forest, (5) heathland and other (semi)natural land cover (hereafter heathland), (6) water, and (7) other land cover (**Supplementary Table 1**). For each grid cell we estimated the proportion of forest and heathland (**Figure 1**), as these land cover types were previously shown to be important for wolves (Sunde and Olsen, 2018). Because there is very little heathland in SH, we additionally included land cover types that were analogous to heathland in DK, based on habitat monitoring data from the Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein[2]. These land cover types included bushes, woody vegetation outside forests, natural non-forest vegetation not in agricultural use, dune vegetation, moors, and swamps (**Supplementary Table 1**). We downloaded vector data of roads from the open source database OpenStreetMap[3]. We only included larger roads (motorways, primary, secondary, and tertiary roads), and intersected these roads with the grid cells to calculate the road density (m road per ha) in each grid cell. Moreover, we obtained data on human population density at 30 arc-second horizontal resolution from the Socioeconomic Data and Applications Center from the Gridded Population of the World (GPW), v.4 dataset for 2020[4]. We then calculated the mean human population density for each 10 km × 10 km grid cell using the "Zonal Statistics as Table" tool in ArcGIS Pro. As a measure of livestock densities, we focused on sheep, because they made up the bulk of livestock kills (see section "Results"). Sheep numbers were obtained on municipality level from the Danish central animal register[5] for DK and from the Statistikamt Nord[6] for SH. Using these numbers, we calculated the sheep density for each municipality (mean ± SD = 0.04 ± 0.06 sheep per ha, median = 0.02, range = 0–0.63 sheep per ha).

Livestock Depredation Patterns

A livestock depredation event was defined as an event where one or more livestock individuals (at the same place within the same day) were killed by a wolf, based on DNA evidence either with (43% of cases) or without (47% of cases) identification of an individual genotype (Reinhardt et al., 2015; Thomsen et al., 2020). To estimate individual livestock depredation rates, we used observations between 1 January 2017 and 15 August 2021, because both countries systematically sampled DNA from saliva left on livestock suspected to be killed by wolves during this period (which was not the case prior to 2017). The individual livestock depredation rate of wolves was estimated as genetically verified predation events relative to the number of days a given wolf was estimated to occur in a given area (grid cell), i.e., the number of livestock depredation events per individual wolf per day. To fill gaps between consecutive observations, we assumed that a wolf would stay in the grid cell where it was observed until the next observation. For example, if a wolf was first observed in grid cell A, and 10 days later in grid cell B to appear in grid cell C after another 5 days, we allocated ten observation days to grid cell A and five observation days to grid cell B. If the observation in grid cell A was based on a DNA profile from a sheep kill, we entered the data as one observation day with livestock depredation and nine observation days without livestock depredation. Accordingly, if the second registration in grid cell B was not based on a predation event (e.g., feces), we recorded 5 days without livestock depredation for grid cell B. For wolves that were not observed for more than 1 year, we assumed that their continued presence was highly unlikely, and estimated the likely day of disappearance as the last observation date plus the average observation interval until its disappearance, adding those days to the last observation (Sunde et al., 2021). We acknowledge that it is not realistic that wolves (especially non-residents) always stayed within the same grid cell for the whole period until the next observation, but consider this approach reasonably unbiased, because observation intervals were short (mean ± SD: 9 ± 13 days in SH and 17 ± 28 days in DK). We obtained 234 observations of identified wolves based on DNA

[1]https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download

[2]https://www.schleswig-holstein.de/DE/Fachinhalte/B/biotope/Downloads/kartierschluessel.pdf?__blob=publicationFile&v=2

[3]https://download.geofabrik.de/europe

[4]https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-adjusted-to-2015-unwpp-country-totals-rev11/data-download

[5]https://chr.fvst.dk

[6]https://www.statistik-nord.de

profiles sampled from different livestock depredation events and 689 observations from other sources (**Supplementary Table 2**), corresponding to 11,960 (88%) observation days in DK and 1,695 (12%) in SH.

Statistical Analyses

Grid Cell Occupancy

We modeled wolf occupancy per 10 km × 10 km grid cell in Jutland, by fitting linear models using Generalized Least Squares of the R package "nlme" (Pinheiro et al., 2017) that allow to account for spatial autocorrelation. For each grid cell, we counted the number of 3-month periods (annual quarters) with confirmed wolf observations out of the total number of quarters monitored (37 quarters from 2012 to 2021) as response variable (i.e., the proportion of quarters with wolf observations). We did this separately for resident wolves (single residents, pairs and packs) and non-residents, because they might select for different land cover and prey (two separate analyses; **Supplementary Table 3**). As predictor variables, we included the proportion of forest, proportion of heathland, road density, averaged human population density, and sheep density. We modeled spatial effects within an error term, using a spherical function for the correlation matrix (consisting of the x and y coordinate of the top-right corner of each grid cell) of the errors (Beale et al., 2010). Model fitting was performed with restricted maximum likelihood. We scaled all numeric variables (mean = 0; standard deviation = 1) to obtain comparable estimates. There was no collinearity among predictor variables, defined as variance inflation factors (VIF) >3 and Pearson correlation >0.7 (**Supplementary Figure 1**; Zuur et al., 2010), and no overdispersion in the models. For model selection, we created all possible combinations of the dependent variables using the R package "MuMIn" (Barton, 2016), including five candidate models based on biological hypotheses, a full and a intercept only model (**Supplementary Table 3**). We selected the most parsimonious model based on Akaike's Information Criterion corrected for small sample size (AICc; Wagenmakers and Farrell, 2004). Parameters that included zero within their 95% confidence interval were considered uninformative (Arnold, 2010). We assessed the models' predictive performance based on the receiver operating characteristics, analyzing the area under curve (AUC; Fielding and Bell, 1997). AUC assesses the discrimination ability of the models and its value ranges from 0.5 (equaling random distribution) to 1 (perfect prediction). AUC values >0.75 correspond to high discrimination performances (Fielding and Bell, 1997). As the registered grid cell occupancy depended on wolves present in a grid cell being registered, especially in highly mobile individuals, the result of the occupancy analysis might have been biased toward landscape features that correlate positively with observation frequency (e.g., sheep density that correlates with livestock kill rates), whereas spatial sampling biases was less of an issue for resident individuals that roam within the same few grid cells.

Livestock Depredation Rate

We analyzed depredation rate, using individual days as observation unit (1 = days on which a livestock depredation event by an individual wolf was recorded within a given grid cell *versus* 0 = days without livestock depredation). We ran generalized linear mixed models using the R package "spaMM," with a binomial response distribution, and fitting the data with a Matérn correlation model (including the x and y coordinate of the top-right corner of each grid cell as autocorrelated random-slope term) to account for spatial autocorrelation (Rousset, 2017, 2021). To quantify (and test for) individual variation in livestock depredation rates, we included wolf ID as random effect. If certain individuals would have particularly high livestock depredation rates relative to the spatial, seasonal and social circumstances, they would appear as significant outliers. As fixed effects, we included the proportion of forest and heathland cover as predictors of wild ungulate densities, sheep density (all three measures were calculated on grid cell level), season (winter: December–February, spring: March–May, summer: June–August, fall: September–November) to test if wolf predation on livestock changes seasonally, sex, and social status (**Supplementary Table 4**). Initially, we also included the two-way interactions of social status with the proportion of forest and heathland cover and with sheep density, to test if depredation rates differ between residents and non-residents depending on land cover and livestock prey availability. However, we could not achieve model convergence including the interactions and thus ran separate models for resident and non-resident wolves (**Supplementary Table 4**). There was no collinearity among predictor variables in any model (**Supplementary Figure 2**). We scaled all numeric variables (mean = 0; standard deviation = 1) to obtain comparable estimates. We again created all possible combinations of fixed effects, including candidate models based on biological hypotheses, and selected the most parsimonious model based on AICc (**Supplementary Table 4**).

Additionally, we created a categorical variable describing livestock protection measures. This included three levels: (1) SH, where – apart from the district in the very southeast – no funds for preventative livestock protection measures were available until March 2019, (2) no protection measures in DK, and (3) protection measures in place in DK. The protection measures in DK were governmental initiatives to prevent wolf attacks on sheep, typically implemented by predator-proof fences (at least 110 cm high to prevent wolves from entering enclosures) after repeated attacks from resident wolves inside "wolf management zones"[7]. Because livestock protection measures were usually implemented after the establishment of a wolf pair/pack, the protection measures and wolf social status were highly correlated (Pearson correlation = 0.87; **Supplementary Figure 2**). Consequently, we excluded this variable from the above analysis, but describe the daily depredation rate by wolves before *versus* after the establishment of the wolf management zone for the subset of wolves whose ranges intersected a wolf management zone in DK. The zone was initially established on 330 km^2 in February 2017 and then expanded to 1,730 km^2 in April 2021 (another zone was established in 2019, but there were only three wolf observations in the area and no recorded livestock attacks).

[7]https://fvm.dk/nyheder/nyhed/nyhed/miljoeminister-praesenterer-nye-tiltag-for-at-forebygge-ulveangreb/

RESULTS

Occupancy Patterns

Over the 10-year period from 2012 to 2021, 43 wolves (29 males and 14 females) were identified by genotyping (from 1,793 confirmed observations) in the Jutland peninsula. The number of wolves and wolf observations in the region gradually increased from 2012 to 2021 (**Supplementary Figure 3**). Of the males, 11 were members of a pair or pack, seven were single residents, and 26 were non-resident (the social status of 12 individuals changed during the study period), and of the females, eight were members of a pair or pack, four were single residents, and eight were non-resident (the social status of four individuals changed). Moreover, 30 individuals were immigrants from Central Europe and 13 were born in DK (7 in 2017, 6 in 2019). Non-residents accounted for 586 observations (503 in SH and 83 in DK), single residents for 381 (97 in SH and 284 in DK), and members of pairs/packs for 826 observations (all in DK; **Figure 1**).

Resident wolves were observed in 63 grid cells (pairs and packs were observed in 10 grid cells, 2% of the study area, and single residents in 60 grid cells, 10% of the study area). Grid cell occupancy by residents was positively associated with increasing forest (estimate ± SE: 0.24 ± 0.06; 95% confidence interval: 0.12–0.35) and heathland cover (estimate ± SE: 0.22 ± 0.06; 95% confidence interval: 0.09–0.34; **Figure 2** and **Supplementary Table 3**). Human population density, road density, and sheep density were not included in the best model and uninformative in the full model. Based on a 50% predicted probability of resident wolf occurrence in a given grid cell (during the entire study period), 15.9% of the study area was predicted to be suitable for the establishment of resident wolves. Non-resident wolves were observed in 143 grid cells (24% of the study area), and their grid cell occupancy was positively associated with an increasing proportion of forest cover (estimate ± SE: 0.16 ± 0.04; 95% confidence interval: 0.08–0.23) and increasing sheep density (estimate ± SE: 0.24 ± 0.05; 95% confidence interval: 0.14–0.34; **Figure 2** and **Supplementary Table 3**). The proportion of heathland cover, human population density, and road density were not included in the best model and uninformative in the full model.

Livestock Depredation Patterns

From 2012 to August 2021, 85 livestock depredation events from DK and 480 from SH were attributed to wolves (**Table 1**). In DK, 88% of the depredation events were on sheep, with an average of 5.4 ± 6.5 (SD) individuals killed per depredation event. In SH, sheep comprised 98% of all livestock attacks (the number of individuals killed per attack was not consistently reported). The 565 livestock depredation events occurred in 99 grid cells (16% of the total area; **Figure 3**), with 337 events (60%) located within 16 grid cells (13 in SH, 3 in DK) with >10 livestock depredation events each.

From January 2017 to August 2021 (when depredation events were systematically reported), we could assign 234 depredation events (55 in DK and 179 in SH) to 25 individual wolves based on DNA evidence (out of a total of 37 individually identified

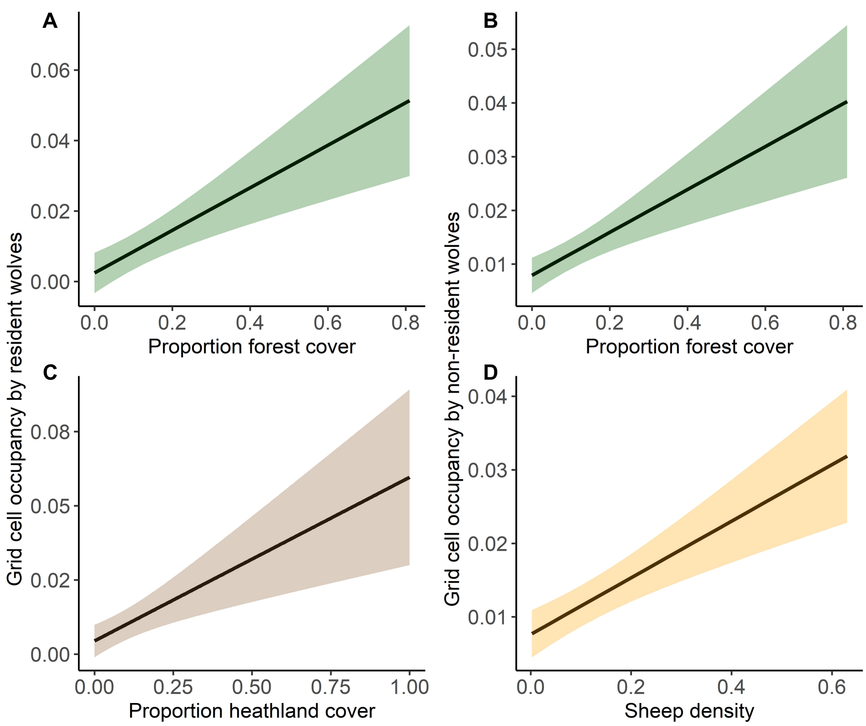

FIGURE 2 | Predicted grid cell occupancy by resident wolves (left panel) in relation to **(A)** forest cover, and **(C)** heathland cover, and by non-resident wolves (right panel) in relation to **(B)** forest cover, and **(D)** sheep density. 95% confidence intervals are given as shading.

TABLE 1 | The number of confirmed livestock depredation events and number of individuals killed (Denmark) or sampled (Schleswig-Holstein) by wolves between 2012 and 2021.

Prey species	Denmark		Schleswig-Holstein	
	Depredation events	Livestock killed	Depredation events	Livestock sampled
Sheep	75	461	468	899
Cattle	6	6	12	22
Pony	1	3	0	0
Fallow deer (captive)	3	8	0	0

For Schleswig-Holstein, we report the number of sampled individuals, because the exact number of individuals killed was not always recorded.

wolves). Of these depredation events, 25 were caused by pair or pack members (all in DK), 78 by single residents (17 in DK, 61 in SH), and 137 by non-residents (13 in DK, 118 in SH; **Table 2**). Three male siblings (GW900m, GW924m, and GW932m), born in DK in 2017, were responsible for 108 (46%) of the depredation events assigned to individuals. All three individuals dispersed to SH in 2018 where they stayed for 3–16 months before either dispersing out of the state (GW900m: 19 January–22 March 2019, 19 livestock attacks during this period; GW924m: 8 July 2018–21 October 2019, 64 attacks) or disappearing (GW932m: 6 May–27 August 2018, 17 attacks). GW924m was categorized as single resident after establishing in a fixed area in SH, whereas the other two individuals were categorized non-residents. After 10 months in SH, wolf GW924m was categorized as a "problem wolf" by the federal state office for nature conservation after it had overcome predator-proof fences several times. Despite a shooting permit being issued, the wolf lived on in SH for additional 6 months before dispersing south, where it died in a traffic collision in Niedersachsen 3 months later.

On average, individual wolves were registered killing livestock every 0.005 ± 0.007 (SD) days in DK compared to every 0.136 ± 0.135 days in SH. In other words, wolves were recorded to predate on livestock on average 1.8 times per year in DK and 49.6 times per year in SH, corresponding to a 27 times higher individual livestock depredation rate in SH than in DK. Moreover, livestock depredation rates differed among individuals of different social status, being highest for non-residents in SH and lowest for pairs/packs in DK (**Table 2**). The aforementioned three individuals (GW900m, GW924m, and GW932m) were

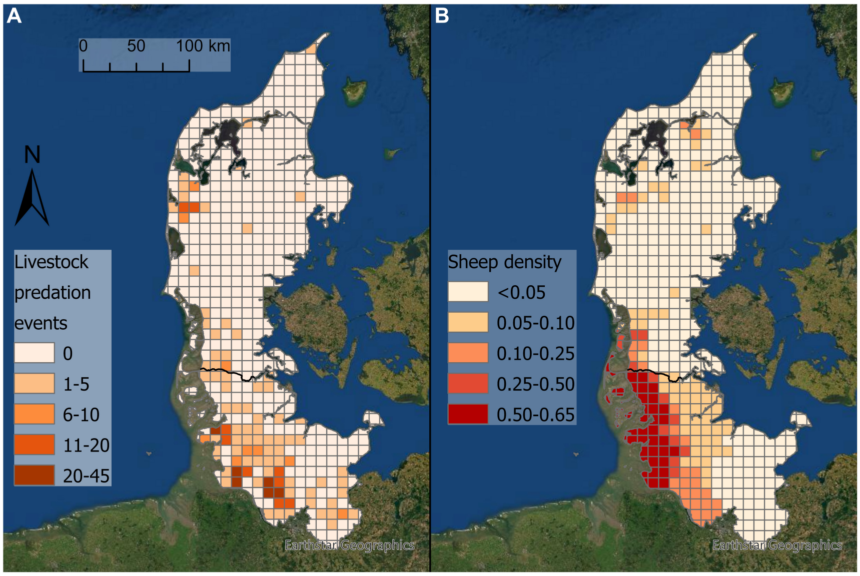

FIGURE 3 | (A) Distribution of 565 livestock depredation events in Jutland peninsula attributed to wolves by state authorities, 2013–August 2021. **(B)** The sheep density (number of individuals per ha) per grid cell in Jutland peninsula. The black line represents the border between Denmark in the north and Schleswig-Holstein in the south.

TABLE 2 | The number of individual wolf observation days (of identified individuals), livestock depredation events (number, events per day, events per year), and number of individuals from January 2017 to August 2021 separately for non-residents, single residents, and pairs/packs in Denmark and Schleswig-Holstein.

Social status	Country	Observation days	Predation events	Predation events per wolf per day	Annual predation events per wolf	Individual wolves
Non-residents	Denmark	948	13	0.014	5.0	8
Single residents	Denmark	3308	17	0.005	1.9	5
Pairs/packs	Denmark	7704	25	0.003	1.2	9
Non-residents	Schleswig-Holstein	982	118	0.120	43.9	22
Single residents	Schleswig-Holstein	713	61	0.086	31.2	1

registered killing livestock every 0.21, 0.13, and 0.12 days, respectively, once they had dispersed to SH.

The probability of wolf depredation on livestock (on a given observation day) was best explained by sex (lower in females, but uninformative), season (highest in winter and lowest in summer), proportion of heathland (negative correlation), proportion of forest (negative uninformative correlation), and sheep density (positive uninformative correlation) (**Table 3** and **Supplementary Table 4**). Social status (resident *versus* non-resident) was not included in the best model and uninformative in the full model, indicating that after accounting for the land cover variables, sheep density, and spatial autocorrelation, there was no statistical difference between predation rates of resident and non-resident wolves. The estimated random effect (wolf ID) differed significantly from zero for six individuals (**Figure 4**). Two individuals had lower depredation rates than expected by the fixed effects and four had higher depredation rates (including the officially declared "problem wolf" GW924m), with the latter four wolves accounting for 96 (41%) of all livestock depredation events. The random effects of GW924m's two siblings did not significantly differ from zero (**Figure 4**). Depredation rates by resident wolves were better predicted by our analysis (AUC: 0.93) than depredation rates by non-residents (AUC: 0.85). The probability of resident wolf depredation on livestock was lowest in summer (though seasonal differences were generally small), decreased with increasing proportion of heathland, and increased with sheep density (**Table 3**, **Supplementary Table 4**, and **Figure 5**). Proportion of forest was included in the best model, but uninformative (**Table 3** and **Supplementary Table 4**), and sex was not included in the best model and uninformative in the full model. The probability of non-resident wolf depredation on livestock was best explained by season only, but this effect was uninformative (**Table 3**, **Supplementary Table 4**, and **Figure 5**). The proportion of heathland and forest, sheep density, and sex were not included in the best model and uninformative in the full model.

In the area where a wolf management zone was established in 2017 (and expanded in 2021), 17 livestock depredation events were assigned to identified wolves (all members of a pair or pack). Daily depredation rate decreased from 0.009 (two depredation events during 220 wolf days) before the establishment of the zone to 0.002 (15 depredation events during 7175 wolf days) after the zone had been established (estimate ± SD: −3.88 ± 1.39; 95% confidence interval: −6.59; −1.16). Within the wolf management zone, no attacks were registered within intact and functional predator-proof fences to date.

TABLE 3 | The estimate, standard error (SE), lower (LCI), and upper (UCI) 95% confidence interval for the analysis of wolf predation rate, separately for (1) all individually identified wolves, (2) resident wolves, and (3) non-resident wolves.

(1) Predation rate by all identified wolves

Parameter	Estimate	SE	LCI	UCI
Intercept	−5.37	0.72	−6.78	−3.96
Season spring	−0.17	0.26	−0.68	0.33
Season summer	**−0.69**	**0.28**	**−1.25**	**−0.14**
Season winter	0.49	0.26	−0.01	0.99
Sex male	0.85	0.47	−0.06	1.76
Proportion forest	−0.26	0.15	−0.55	0.03
Proportion heathland cover	**−0.89**	**0.37**	**−1.60**	**−0.17**
Sheep density	0.13	0.12	−0.10	0.36

(2) Predation rate by resident wolves

Parameter	Estimate	SE	LCI	UCI
Intercept	−5.84	0.47	−7.03	−4.88
Season spring	0.05	0.33	−0.60	0.71
Season summer	**−1.56**	**0.39**	**−2.36**	**−0.82**
Season winter	0.15	0.31	−0.46	0.77
Proportion forest	−0.34	0.22	−0.83	0.06
Proportion heathland cover	**−2.20**	**0.52**	**−3.30**	**−1.22**
Sheep density	**1.09**	**0.49**	**0.07**	**2.17**

(3) Predation rate by non-resident wolves

Parameter	Estimate	SE	LCI	UCI
Intercept	−3.86	0.69	−6.60	−1.31
Season spring	−0.38	0.39	−1.19	0.43
Season summer	0.42	0.41	−0.40	1.25
Season winter	0.79	0.44	−0.13	1.69

The season "fall" was used as reference level. Informative parameters are in bold.

DISCUSSION

Our data suggest that resident wolves in Jutland settled in habitats with high forest and heathland cover (habitat mostly found in DK), whereas grid cell occupancy by non-residents was positively associated with sheep density and forest cover. Further, resident wolves killed fewer livestock per day than non-residents. This was likely related to dispersers occurring in a much wider geographical area with a broader range of landscape types and more often in the southern part of the peninsula, where sheep are more abundant and thus available as prey. Importantly, the variation in individual livestock predation rates was largely related to spatial patterns of wolf occurrence and environmental settings, and less to individual variation and social status, suggesting that livestock depredation was generally context dependent rather than the result of personality differences (such as individuals selecting for livestock). Differences in land cover and sheep density explain why the total number of livestock attacks was almost 6-fold higher in SH than in DK, despite ca. four times more wolf observation days in DK compared to SH. Hence, so far livestock damage inflicted by residents appears to be manageable, which might also be related to the introduction of governmentally supported livestock protection initiatives in areas where wolf pairs/packs established (Gervasi et al., 2021; Oliveira et al., 2021), whereas dispersing individuals pose a greater challenge. Below, we discuss how our findings can be used to predict the future expansion of wolves and to manage livestock depredation in cultivated landscapes.

Occurrence Patterns

Overall, wolves were more likely to occur in grid cells with high forest cover. The pattern of resident wolves selecting grid cells

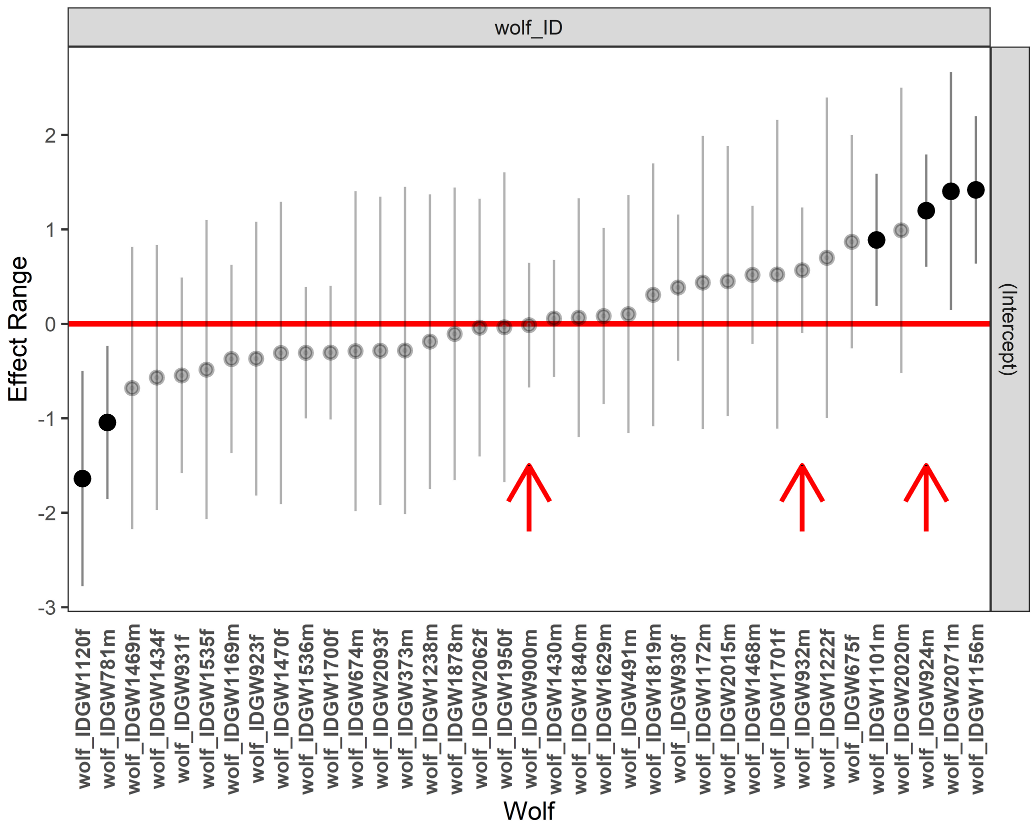

FIGURE 4 | Estimated random effect (of each individual wolf) of the model describing the daily livestock depredation rates by individual wolves in Jutland peninsula (landscape and season as fixed effects). The red arrows indicate the three male siblings that contributed 45% of all livestock attacks. Mean estimates are shown as dots, and 95% confidence intervals as bars. Intervals that do not include zero are in bold.

with high coverage of forest and heathland was in accordance with habitat selection patterns from other European countries (Jędrzejewski et al., 2008; Fechter and Storch, 2014; Nowak et al., 2017; Grilo et al., 2019). Forest is positively associated with wild ungulates (Borowik et al., 2013), the main prey of wolves in Central Europe, which explains why wolf grid cell occupancy increased with forest and heathland cover (Sunde and Olsen, 2018; Roder et al., 2020). Our model predicted that about 16% of the region's grid cells, almost all of them positioned in DK, could be considered suitable for wolf establishment. Lack of suitable habitat in SH explains why so few individuals stayed resident in SH, and in such cases not permanently. However, once higher quality habitats are occupied, wolves might nevertheless establish territories in lower quality habitats (Nowak et al., 2017).

Our models performed slightly worse in explaining grid cell occupancy by non-resident wolves compared to residents, suggesting that predicting the occurrence of dispersing wolves is challenging because they often traverse landscapes unsuitable for settlement (Blanco and Cortés, 2007). From a methodological perspective, we argue that the occurrence patterns of resident wolves provide a reliable representation of their true occupancy in the study area, as resident wolves were usually registered multiple times within each 3-month period. Moreover, at least in DK where the majority of the resident wolves were registered, resident wolves were monitored actively, independently of passive registration based on livestock kills (in DK 7% of all wolf observations came from livestock depredation events). In comparison, monitoring of non-resident wolves was more prone to be biased toward areas with high livestock densities where the per capita livestock depredation rate is higher. This is especially true for SH, where >90% of wolf observations came from livestock depredation events. In this light, the positive association between non-resident wolf occupancy and sheep density may reflect disproportionately high sampling frequency of highly mobile dispersers in quadrates with high sheep density (where the probability of killing sheep as opposed to wild prey is higher), rather than dispersers being attracted to areas with high sheep density.

Livestock Depredation

As only 64% (DK) and 39% (SH) of genetically registered livestock depredation events from 2017 to 2020 could be assigned to wolf individuals, and not all livestock attacks may be sampled genetically, the depredation rates estimated from individually assigned kills likely underestimate true depredation rates. Livestock kills without a genetically assigned predator individual could in theory also be caused by undetected wolves that lived in the region before they were registered,

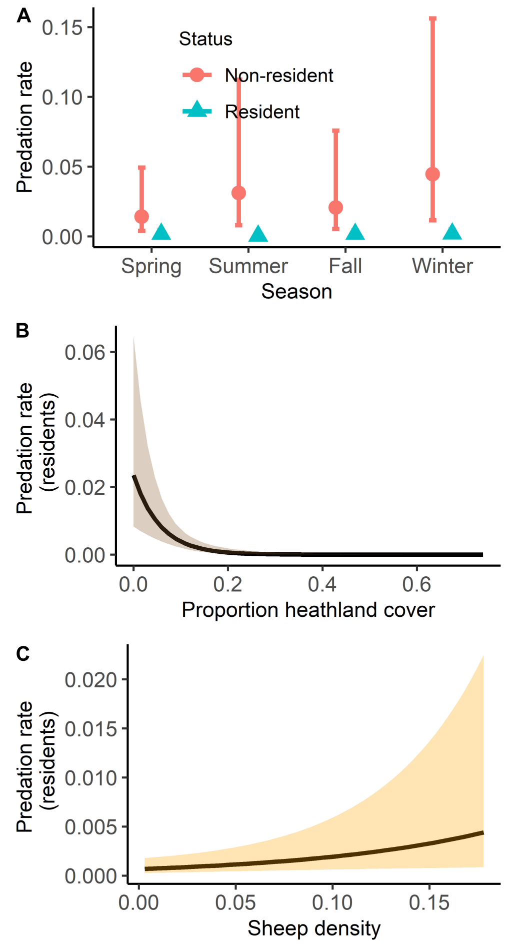

FIGURE 5 | Predicted probability of daily depredation events by individual wolves on livestock in relation to **(A)** season, shown separately for resident and non-resident wolves. Moreover, the predicted probability of daily depredation events by resident wolves on livestock in relation to the **(B)** proportion of heathland cover and **(C)** sheep density. Mean estimates are shown as dots **(A)** and lines **(B,C)**, and 95% confidence intervals as bars **(A)** and shading **(B,C)**.

hence underestimating the number of wolf observation days and consequently overestimating individual depredation rates. However, we consider this potential bias rather small due to the high observation frequency and detection rate of wolves in the region (Sunde et al., 2021).

Despite DK harboring >80% of the wolves in the region, measured in wolf observation days, the total number of livestock attacks in SH was six times higher than in DK. The annual livestock depredation rate of wolves estimated for DK (approximately two depredation events resulting in eight dead animals per wolf per year if estimated from assigned kills) was slightly above the median for European countries at roughly ∼5 kills per wolf per year (Linnell and Cretois, 2018). In contrast, the annual depredation rates in SH of approx. 50 livestock depredations per wolf per year in our study period based on individually assigned livestock kills exceed the highest reported livestock depredation rate from any European country (Norway: 34 sheep and goats killed per wolf per year 2012–2016) (Linnell and Cretois, 2018).

Our analysis suggests that differences in depredation rates were mainly attributed to spatial differences where residents and non-residents occurred, i.e., related to land cover (more forest and heathland in DK) and sheep density (more sheep in SH), than to social status *per se*. Lower depredation rates in DK were likely also related to the implementation of local protective measures (predator-proof fences) after which livestock depredation decreased. This result is in line with previous findings that predator-proof fences can be a successful livestock protection measure in areas were wolf pairs or packs establish (Reinhardt et al., 2011; Gervasi et al., 2021; Oliveira et al., 2021), although our data have to be taken cautiously due to the limited sample size. Livestock depredation by wolves decreased with increasing heathland, but surprisingly not forest. Areas that sustain wild ungulate prey, like heathland and forest (Kuiters and Slim, 2002; Borowik et al., 2013), are generally selected by wolves (Lesmerises et al., 2012; Milleret et al., 2019). It is therefore conceivable that availability of heathland buffered livestock attacks because the proportion of time wolves spent in these habitats correlated positively with their availability. Conversely, areas with very low coverage of forest and heathland likely forced wolves to cross open land with sheep pastures more often than would be the case in areas with more (semi)natural land cover. This is especially true for dispersers attempting to establish a territory, thereby roaming over large areas. The different depredation rates among individuals of different social status (being highest in non-residents and lowest for members of pairs/packs) were largely explained by differences in where residents and non-residents occur. Moreover, we cannot exclude the possibility that lack of familiarity with an area might influence the propensity of non-residents to attack livestock, as shown in other areas and species (Mizutani, 1993; Linnell et al., 1999). Independent of the proximate mechanism, increased predation on livestock in areas with reduced availability of natural prey and increased availability of livestock was also shown in other areas (Suryawanshi et al., 2013; Imbert et al., 2016). We have no clear explanation why livestock depredation rates by resident wolves were higher during winter and lower during summer, but it might relate to prey switching related to the presence of dependent offspring. These seasonal patterns contrast with other studies that found increased livestock depredation during summer (Bradley et al., 2015) and fall (Iliopoulos et al., 2009), respectively, and might be caused by geographic differences in seasonal variation of wild and livestock prey availability.

Even though three individuals were responsible for 45% of the livestock depredations, only for one of them (GW900m), the number of kills per day was more than 10% higher than the average for all wolves in the region and its residual predation rate (adjusted for landscape context) did not differ from the average for all wolves. Hence, the total number of livestock killed by these individuals was mainly caused by the time they stayed in SH. Even though the individual declared as problem wolf (GW924m) had a residual predation rate significantly above average, it was only ranked third in residual predation rate of all individuals in the analysis. This result suggests that even though some individual variation is identifiable in our model, individual preferences appeared to explain a minor part of individual livestock depredation rates compared to the effect of landscape context with no clearly identified outliers that could be ubiquitously assessed as "problem individuals" that were particularly prone to kill livestock [type-II problem individuals following the terminology by Linnell et al. (1999)].

Accordingly, from a management perspective, at least in this study area, removal of identified "problem individuals" would not (or only marginally) reduce local livestock depredation rates more than removal of any other wolf in the same place.

CONCLUSION

Our results indicate that the wolves in Jutland mostly killed livestock as a context-dependent response, i.e., being dispersers in agricultural areas with low availability of wild ungulate prey and high livestock densities, and not because of behavioral preferences for sheep. Consequently, the removal of so called "problem individuals" likely will not be a viable long-term solution to reduce local livestock depredation rates. From a technical perspective, the incidence that GW924m lived on for 6 month in SH after a shooting permit was issued before finally dispersing from the region, also indicates that targeted lethal management efforts is an inefficient tool to reduce livestock depredation in cultivated landscapes. We conclude that while wolf attacks on livestock in established permanent wolf territories generally can be prevented through improvement of predator-proof fences, livestock depredation by vagrants in pastoral areas where wolves do not settle permanently constitutes a bigger challenge. As the number of vagrant wolves in pastoral habitats like western Schleswig-Holstein is linearly related to the number of wolf packs in the Central European wolf population, a number that is still increasing, depredation rates are likely to increase further in the coming years. Thus, if reducing livestock depredation rates of wolves is a management goal, preventive livestock protection measures, such as predator-proof fences, should be considered in areas where frequent wolf occurrence is likely.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are publicly available. This data can be found here: doi: 10.13140/RG.2.2.16625.61289.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the search for and sampling of genetic material from wolves involved non-intrusive methods that did not affect the sampled subjects. Active monitoring efforts at all times followed the stringent procedures and obligations imposed by the states' laws and regulations for activities on public and private land.

AUTHOR CONTRIBUTIONS

PS achieved the funding. PS, MM, and KO conceived the ideas. MM analyzed the data. MM and PS led the writing of the manuscript. JM and BS were coordinating and conducting wolf monitoring in Schleswig-Holstein. KO, CV-S, and PS were responsible for the monitoring in Denmark. CN was responsible for genetic analyses of samples from Germany and partly from Denmark and organized the register of genotyped wolves in Central Europe. MH and PT were responsible for genetic analyses in Denmark since 2017. All authors provided input to the manuscript and its revised versions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.783027/full#supplementary-material

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"Landscape of Stress" for Sheep Owners in the Swedish Wolf Region

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Farmers who keep livestock in large carnivore areas are exposed to threat of predation directly impacting on finances and workload as well as the associated psychological stress indirectly impacting on farmers well-being. So far, little is known about such stress responses. The concept of "stress" or "stress reaction" is often used as an undifferentiated umbrella concept for the experience of negative emotional episodes. However, the stress reactions could be divided into cognitive, physiological, and behavioural aspects. This study aimed to develop and apply a theory-based approach to identify stress responses among sheep farmers in the Swedish "wolf-region." A thematic analysis of interviews conducted with sheep farmers showed ample support for stress responses among the informants in relation to large carnivores and their management, although the interviews were conducted with a different focal topic. The findings support the idea that stress responses could be categorised into cognitive, physiological, and behavioural aspects. This distinction would help to identify and fully understand the cumulative impact of stress from the presence of large carnivores on farmers' well-being.

Keywords: stress, cognitive, physiological, behavioural, wolf

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INTRODUCTION

According to evolutionary theory human stress responses have evolved in parallel with other mammals over millions of years (e.g., Adolphs, 2013; Nesse et al., 2016). Despite that stress responses are elicited by different stimuli for different species, the stress responses are at least functionally similar between species. That is, to help the individual out of potentially harmful situations. Also, the perceived imminence of a threat will shift physiology, vigilance and behaviour across species (see e.g., Fanselow and Lester, 1988; Davis, 1996; Fernandes et al., 2013). Here we will make a parallel to a lesson to be learned from wildlife ecology.

In the new century of wolf conservation, multiuse landscapes with human-wolf co-occurrence have become a central setting for conflict management. Interdisciplinary approaches are needed to see such systems as a unity that integrates humans as well as domestic and wild animals (Lischka et al., 2018). This study conceptualises human stress responses in the Swedish wolf range ecological system through the conceptual ecology of fear (Brown et al., 1999). The ecology of fear posits that impact of predators on prey animals is not limited to direct predation. Rather, the presence of predators in an ecosystem will at all times influence the behaviours of prey animals by forcing a reallocation of time and energy from preferred behaviours (such as feeding and reproducing) to predator avoidance behaviours and vigilance (Lima and Dill, 1990; Brown et al., 1999), inducing physiological and neurobiological costs to the prey animal (Zanette and Clinchy, 2019). The reestablishment of wolves (Canis lupus) in Yellowstone national park illustrates the concept, as increasing levels of vigilance in elk and bison is observed in areas with wolves in comparison to areas without wolves, generating a "landscape of fear" for the prey (Laundré et al., 2001). This effect was particularly pronounced in females caring for their young, likely reflecting a cost-benefit evaluation in relation to the prey's or the protégé's vulnerability (Laundré et al., 2001).

Following the same ecological reasoning for predators in multiuse landscapes, such as wolves on the Scandinavian peninsula, a landscape of fear may cause wolves to avoid areas with human settlements and activity (Carricondo-Sanchez et al., 2020). Nevertheless, attacks on livestock and pets do occur (Frank et al., 2021), making people fear for the safety of pets and livestock (Frank et al., 2015). In such an interaction, wolves and humans alike can be considered the feared or fearful party in this socio-ecological system (Lischka et al., 2018). In this context, we will focus on the individual human perspective and use a basic psychological approach focusing on the fundamental responses to describe this "multiuse landscape of stress," applying it on the sheep owners in the Swedish wolf range. The use of *stress* instead of *fear* is because the concept of stress in psychology encompasses a wider variety and blends of vaguely defined negative emotions (Lazarus, 1993). Stress is here referring to a response that from an evolutionary perspective has evolved to help the individual to handle threats. Human stress responses have evolved over millions of years, together with that of other mammalian species (Adolphs, 2013). Therefore, just as the wild prey, humans may respond to the mere presence of wolves with changes in behaviour, vigilance (cognition), heart rate, and other physiological responses (Lima and Dill, 1990; Brown et al., 1999; Zanette and Clinchy, 2019).

The elicitation of stress in humans, whether physical or mental, is based on appraisals in relation to the individual's goals (i.e., to what extent is a stimulus threatening the goals of the individual) based on the individuals' experience during the course of their lifetime (Arnold, 1960). Following Leventhal and Scherer (1987) such appraisal processes are made at different levels of cognitive elaboration, from automatic processing till highly cognitively elaborated processes, reflecting ontological learning in the specific cultural setting of the individual. Highly cognitively elaborated processes are therefore likely to involve people's social context and the related values and norms of their society belonging.

From the psychological perspective, interactions between people and wildlife may take many shapes. Interactions may, as with species in an ecological system, occur either as direct interaction in an encounter situation or as indirect interaction based on memories of previous personal experiences, stories about other people's experiences, or on new information. People who live within wildlife ranges are likely to be consciously and/or non-consciously affected by their experiences of wildlife in their daily life. These experiences could be perceived as both positive and/or negative. The latter are often triggered by feelings of insecurity due to unsafe conditions, exposure to danger, risk, or fear (for a review see Methorst et al., 2020).

In areas with wolves, sheep owners are particularly susceptible to direct and indirect wolf interactions. Similar to the vulnerability of female elk and bison with young offspring in Yellowstone's wolf areas (Laundré et al., 2001), livestock farmers care for their livestock, and are expected to become more vigilant at the presence of potential threats to their animals. Direct interactions with wolves may imply financial losses if sheep are injured or killed. However, the sheep owners' concern for the welfare of their animals may also imply that indirect interactions, in which the mere perception of the presence of wildlife or reflection on previous experiences and learning, can trigger negative thoughts and feelings (Eklund et al., 2020). Notably, these "intangible effects," are more likely to be associated with negative attitudes toward large mammals, which also includes large carnivores (Kansky and Knight, 2014) such as wolves.

The number of people directly affected by wolf predation on sheep, cattle, and dogs in Sweden is limited to roughly some hundred per year (for sheep $\sim$ 200 people) according to Frank et al. (2019). However, the number of people who are indirectly affected is substantially larger as the mere thought of a predation event may elicit stress, involving emotions of anxiety, fear, anger, worry, despair, and sadness. This stress can be expressed through a combination of various subjective experiences and physiological and behavioural responses.

The occurrence of stress and its impact on farmers', also including sheep owners', mental well-being has been observed worldwide (Hagen et al., 2019; Yazd et al., 2019). Sources of stress have been attributed to heavy workload and financial issues, as well as to concerns over potential threats to animals (Yazd et al., 2019). In Scandinavia, the growing wolf population is recurrently pointed out as a source of stress to sheep owners by the farming associations (LRF [The Federation of Swedish Farmers], 2013). Zahl-Tanem et al. (2020) investigated stress among Norwegian sheep owners in relation to wolf areas and wolf attacks. In this particular case, stress levels were impacted by the farmers' attachment to their livestock, their lack of control in reducing their own stress after predation events (combined with a lack of trust in the authorities), and their perceived need to make changes to their everyday lives in order to handle the ambient pressures caused by the presence of wolves.

Sheep owners who lived in areas where sheep had been lost to wolves during the past 5 years scored significantly higher on psychological stress than did farmers without sheep production in these areas, as well as sheep owners elsewhere in Norway (Zahl-Tanem et al., 2020). Sheep owners who had experienced wolf attacks, also reported in follow-up interviews that they had experienced sleeplessness, guilt, and a constant state of anxiety. These results may not be directly transferable to Swedish conditions due to the different sheep farming practices employed in the two countries. However, stress among Swedish livestock keepers including sheep owners has also been described in a recent report from the Swedish Environmental Protection Agency (Sjölander-Lindqvist et al., 2021). This report indicated that a larger percentage of sheep owners put up protective fences than other livestock owners. However, the reported reduction of worries and stress was at best only partial for those using these fences. Thus, there are indications that stress could be trigged by perceived risks of direct interactions with wolves also in the Swedish context. However, due to the relatively lower risk of a direct interaction in an attack on the sheep (which are to a greater extent free ranging in Norway, but kept in enclosures in Sweden), it is reasonable to assume, that the stress is often elicited by the mere awareness that wolves may be present in the vicinity.

Considering sheep owners as part of the same social-ecological system in which wolves occur, we can depart from established psychological theory on human stress and describe a theoretical framework that facilitates understanding and systematic documentation of wolf-induced stress on sheep owners. The paper is divided into two parts. First, we present a framework based on psychological research on stress responses. Starting with a brief history of the use of the concept of stress, we introduce the current terminology, we describe the concepts of stressor (e.g., the stimulus causing the stress in the individual) and how the stressors can be acute or ambient, and how effect of low intensive stressors over time can accumulate. We also outline how stress responses can be expressed within three different domains: Behavioural, Cognitive, and Somatic. Second, we apply the framework on information collected in focus groups discussions among sheep owners in Sweden to illustrate the impact that carnivores have on the "landscape of stress." Moreover, we outline different aspects of the stress caused by the perceived threat by wolves.

A THEORETICAL FRAMEWORK

Stress as a General Response

The use of the concept of stress in psychology derives from physics, and originates from the Latin word *stringere*, which mean to tighten, or to tie around tightly. Selye (1993) introduced stress in psychology in the 1930s (originally referred to as General adoption syndrome (GAS), or Biological stress syndrome). Selye (1993) considered stress, as a non-specific response constituting of a bodily response that was the same independently of what triggered it, meaning that the stimulus could be either physical or mental. This general response was described as an activation of the body to help the individual to maintain ongoing activities, or to try to go back to an activity that had been interrupted (Feuerstein et al., 1986). This idea of stress as a broad concept is still relevant in psychology and has a broad use in society. Thus, it is important to recall that the stress is referring to a response that from an evolutionary perspective has evolved to help the individual to handle threats, but that in many circumstances for humans in society of today the stress response may be irrelevant, as the context is different compared to when the reaction evolved (see e.g., Nesse et al., 2016). Although stress involves a broad range of negative emotions, the emotion of fear is often a main ingredient (Steimer, 2002; Adolphs, 2013).

Stressors

Despite that the stressor varies due to ontological learning in the specific cultural setting of the individual, stressors elicit the same kind of basic stress responses. When no stressor (/threat) is present or expected, the individual (humans, as well as most other mammals) will engage in their preferred activity. However, as soon as the individual experiences a probability of encountering a stressor (e.g., threat), different aspects of the preferred activity will change. As an example, foraging could become more efficient/rushed in between episodes of heightened vigilance when an encounter of a stressor is considered probable (Fanselow and Lester, 1988). Such a behavioural response would have evolved to help the individual handle the stressor by directing attention toward the stressor, assuming that the cost of the behavioural change is less than that of being eaten by the carnivore. That is, the frequency, location, time of the day for the activity or some other aspect will change to reduce the probability of encountering the stressor.

Acute Respectively Ambient Stressors

Stress could be triggered either by an abrupt change in the environment (acute stressor), or by a slow or accumulative increase over time (stressor). The experience of how close in time or space the stressor is (i.e., the imminence) will affect the following response (Fanselow and Lester, 1988; Maren, 2007; Fernandes et al., 2013; Löw et al., 2015). The sudden onset by an acute stressor may result in a stress response that helps the individual manage the stressor. An example of an acute stressor for a sheep owner could be if the sheep are attacked by a wolf. Here, the stress response would imply actions that result in deterring the wolf from killing more sheep. When the sheep are saved from the wolf attack, the sheep owners' acute stress would be temporally relieved.

On the contrary, a slow increase in a number of different demands and threats may instead accumulate low intensity physiological effects of the stress response(s), for example, muscle aches from low intensive muscle tension. This is often the case with the presence of so-called ambient stressors, such as low intense stimuli in the environment (e.g., presence of background noise and air pollution, Glass and Singer, 1972). The presence of wolves in the landscape may constitute an ambient stressor to the sheep owner, which could on its own be manageable, but could be detrimental if it occurs alongside other stressors.

Cumulative Stress

The theory on cumulative stress can explain why the wolf, as an ambient stressor which co-occurs with other stressors, can have a large impact on the sheep owner's psychological well-being. This theory suggests that low intensive exposure to several ambient environmental stressors, in parallel or temporally close in time, can result in negative effects on psychological well-being (Evans, 1996), because the mental cost of handling one stressor reduces the capacity to handle an additional stressor (Baum et al., 1982). As such, stressors within different domains must be considered in parallel (Evans et al., 2012). As an example, sheep owners are subject to a number of different stressors in their daily life (see Yazd et al., 2019). Such stressors are, for example, filling out government forms, bad weather, adjusting to new government regulations and policies (McGregor et al., 1995), concerns about the future of the farm, outsiders not understanding the nature of farming (Kearney et al., 2014), and these stressors have been shown to negatively affect psychological wellbeing among farmers (Yazd et al., 2019). This means that if a sheep owner is already concerned about the financial situation and heavy workload, regardless of the risk of an attack, the mere presence of wolves in the surrounding landscape could exponentially increase the amount of stress the sheep owner experiences (Zahl-Tanem et al., 2020). The cumulative effect of the various stressors must therefore be considered in order to fully understand farmers' stress responses to the presence of wolves. Cumulative effects of stress should be understood both as the presence of stressors (e.g., the perceived imminence of wolf attacks or workload associated with implementation of protective measures), and as the absence of coping ability to reduce the effect of the stressors (e.g., social support, financial compensation etc.). Intrusive thoughts about wolves as a looming threat of an encounter (direct or vicariously *via* the livestock) add to the stress response and are likely to impact on perceived quality of life.

Three Domains of Interlinked Stress Responses

Similar to the responses of wild prey with changes in behaviour, vigilance (cognition), and physiological responses to wolves (Lima and Dill, 1990; Brown et al., 1999; Zanette and Clinchy, 2019), human stress responses can also be categorised into three domains: Behaviour, Cognitive, and Physiological responses (**Figures 1**, **2**). The three response domains are interconnected and may occur simultaneously or as direct consequence of one another. However, a response in one domain may be more salient in one situation to one person than to another person, or to the same person in another situation.

To illustrate the close interlinkage of stress responses we will slightly shift the focus from the broad concept of stress to one specific emotional part of stress, fear. A situation where a person perceives a stressor that is appraised as involving some type of threat triggers fear. Fear stimulates *behaviours* that have provided an evolutionary advantage for the individual to handle the situation. That could be through fight or flight. The behaviour is accompanied by *physiological changes* (Fanselow and Lester, 1988; Fanselow, 1994), and changes in the possibilities for higher *cognitive functioning* in humans such as simple decision making (e.g., Flykt et al., 2013). These interlinked responses have been described as a defence cascade (Kozlowska et al., 2015). If a fight or flight response is not possible in a specific situation, or might not relieve the experience of an increased probability of encountering the stressor, the response may translate into an intrusive thought that takes mental resources from attention to other issues and thus impair learning and memory. Below we take a closer look at the domains of stress responses.

Behavioural Responses

The human stress responses can be categorised into *operational* and *non-operational* (i.e., made to obtain a goal or not) behaviours. Operational behaviours can be further divided into functional (i.e., enable the individual to handle the situation to some extent, to reach the goal of avoiding the threat) and non-functional (i.e., will not help the individual to handle the situation) behaviour. When faced with the stressor there will be a freezing response that might be too small to experience by the naked eye, but that could still be measured (Davis, 1996).

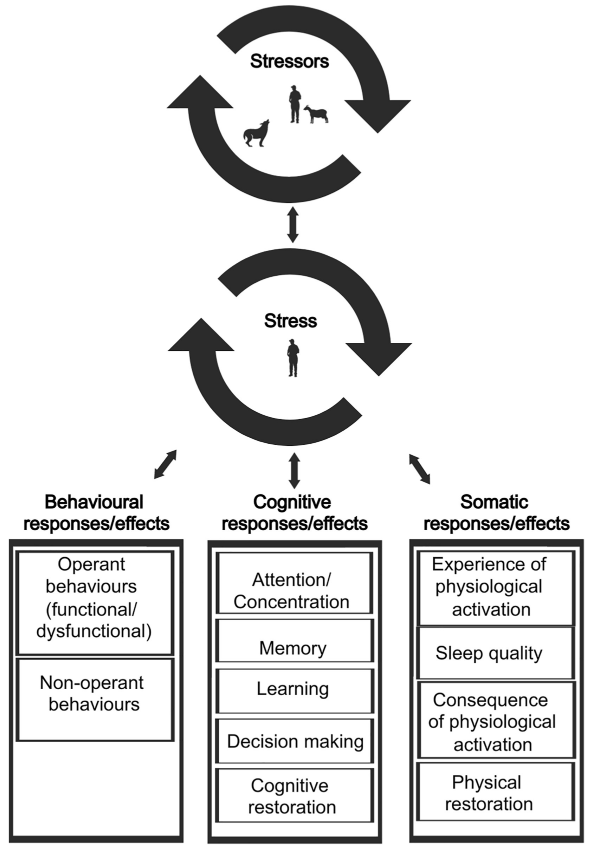

FIGURE 1 | The theoretical model with the three different response domains of stress responses: behavioural, cognitive, and somatic. Each domain is divided into subcategories.

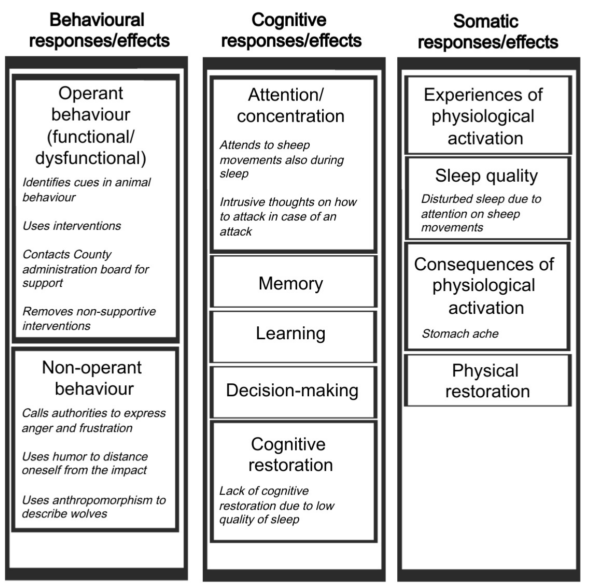

FIGURE 2 | The results from the analysis. Not all subcategories have annotations, as these aspects of the stress response were not reported during the group discussions.

Freezing is a muscle tension intended to prepare the individual for initiating an abrupt action that is aimed at increasing the distance to the stressor by fleeing from, or when flight is not an option attacking (/handling), the stressor (Azrin et al., 1967) when it gets too close.

Cognitive Responses

Cognitive aspects of the stress responses can be expressed as problems with *attention*, *memory*, and *learning* (Kausche and Schwabe, 2020), as well as decision-making (Starcke and Brand, 2012). As an example, exposure to a threat (e.g., large carnivores, or other animals experienced as threats/stressors) also requires mental resources which in turn reduces speed and accuracy of relatively simple tasks (e.g., Flykt and Bjärtå, 2008; Flykt et al., 2013). This is coherent with the fact that that humans blood flow in the prefrontal cortex (a region associated with cognitive control, see Miller and Cohen, 2001) decreases during intensive stress (Garcia et al., 1999). The frequencies of cognitive responses will indicate the possibility for *cognitive restoration*.

Physiological Responses

Physiological or somatic aspects of the stress responses can be a direct experience of *physiological activation*, such as an increase in heart rate (Tyra et al., 2020), sweaty palms (Boucsein, 1992, p. 284–285), and a shortness of breath (Kreibig, 2010), but can also be experienced as *consequences of physiological activation*, such as muscle tension (Bird et al., 1985), stomach pain (Brobeck et al., 2007), and headaches (Nash and Thebarge, 2006). Reduced *sleep quality* (Åkerstedt et al., 2012; Cardoso and Ramos, 2018) could also be a result of stress in the somatic/physiological domain. A prolonged stressor that cannot be relieved in fight or flight actions, but that lingers over a long period of time, results in an accumulation of stress and could result in muscle aches and other physiological consequences, as well as a lack of physical restoration. One reason for why such an accumulation occurs for sheep owners in wolf areas, is that they are regularly exposed to stimuli associated with the wolf that triggers the stress response (e.g., by seeing tracks, scratches, or remains of prey carcasses), but rarely encounter the wolf itself. These behaviours are all related to physiological effects, for example an increase in sweat gland activity and blood pressure and changes in heart rate. The frequencies of these responses will indicate the possibility for *physical restoration*.

AN EMPIRICAL APPLICATION OF THE FRAMEWORK: METHODS

This section reports on the application of the theoretical framework to focus group interviews carried out among sheep owners in large carnivore areas in Sweden.

Participants and Procedure

Interviews were conducted as three focus group meetings with sheep owners in the spring of 2016. All participants were active sheep breeders within the regions that represent the main distribution range of lynx and wolves in Sweden. Participants owning small herds held on average 50 ewes (range 10–120), participants with medium herds held on average 136 ewes (range 60–300), and participants with large herds held on average 345 ewes (range 130–500). Participants were recruited through the Swedish sheep breeders' association, where a contact person on the board was asked to suggest participants based on their geographical location and the size of their herd. Focus groups were held in three different counties, including participants with smaller herds in Uppsala, medium sized herds in Värmland, and larger herds in Örebro county. All three counties are in the south-central parts of Sweden, an area mainly dominated by a mosaic landscape of agriculture, lakes, and boreal forest production.

Because the participants of each group were active in the same region, and within the same organisation, they were familiar with each other since before and appeared comfortable in sharing their experiences in the group setting. The interviewer ensured all were actively participating in the discussion and that no single participant dominated the discussion. There were 4–5 participants in each group, and the semi-structured interviews lasted approximately 2 h following an interview guide. In total, 10 female and 3 male sheep owners participated in the focus groups, and the average age was 49 years (range 32–61). The main focus of the interviews related to the animal owners' views on using various interventions intended to prevent large carnivore attacks on their sheep (see Eklund et al., 2020). The reason for including participants with various sized herds was that they were expected to face differing challenges in relation to intervention use, which was the main focus of the interviews. However, discussions relating to the contextual appraisals of direct interaction with carnivores spontaneously occurred. Also, the interviews did not specifically focus on wolves, but large carnivores in general, nevertheless the wolf had a pronounced role in the discussions. An event covered in media at the time of the interviews, which was likely salient among the sheep owners and may have influenced the focus on wolves, was the conflict that occurred between the wildlife managing authorities and a large sheep farm in another county. There, the authorities had filed a report on "lack of animal protection" against the farm which had suffered major losses of sheep to wolves. This event was brought up by the sheep owners as a horrific example of wolf management, or as a contrast to their positive experience with the authorities in their counties. All interviews were recorded and transcribed verbatim using Atlas TI 7.0.

Analysis

We took a deductive approach in our analysis of the interview material. A theoretical framework based in previous research guided the creation of thematic codes on three levels of detail (**Figure 1**). The first level related to the mentioning of stress or other words describing negative emotions, the second level to the mentioning of behavioural, and cognitive or somatic/physiological responses. The third level of detail related to specification of these responses. Stress would in some instances relate directly to interactions with large carnivores but in are other situations related to indirect responses to carnivore management interventions as previously described by Eklund et al. (2020). Codes were therefore specified as direct or indirect in relation to carnivore interactions.

Intercoder reliability was established by a parallel coding of approximately half an interview, i.e., 1/6th of the total transcribed interview material, undertaken by two co-authors (AF and AE). The initial inter-coder agreement was 72%, and with uncertainties discussed between the two co-authors, inter-coder agreement reached 93%. The remaining uncertainties were discussed with a third co-author (MJ). This discussion highlighted the need for creating an additional coding-theme relating to consequences for social interactions. Several of the uncertainties brought to this discussion specifically related to problematic social communication following carnivore interactions.

RESULTS/FINDINGS

The Presence of Reported Stress and Other Words for Negative Emotion

Sheep owners used word like stress and other negative emotion words (worry and anxiety) in relation to wolves and other large carnivores. The sheep owners describe the summer as the time of the year when they would expect the least stress from taking care of the sheep, as the sheep are out grazing in the pasture and only need daily supervision and water. The summer is thus expected to represent a welcome break from the extra work of feeding and cleaning out in the stables. Yet, with the return of the large carnivores, keeping the sheep in the summer pasture is also described as a time which is associated with worry and anxiety. It is during this time that the sheep are kept further from the house and stables and are at higher risk of being predated. This stress would likely not be described as an acute onset of stress, but rather illustrates the prolonged sense of anxiety that would come from an ambient stressor.

> *"... it was perhaps a month before we were set to release. . .release them [the sheep]. It's a bit stressful too, because essentially they [the tracked wolves] were coming closer and closer. And then I saw. . .after I was out tracking, because we had had some snow, and then I became even more concerned because I had tracks all around my yard. . ."* (Värmland)

These citations illustrate how the mere presence of wolves and other large carnivores are appraised stressors, which goes in line with the findings in previous studies (Yazd et al., 2019; Sjölander-Lindqvist et al., 2021). In the participants' references to the stressor they talk about stress as closely connected to feelings such as worry and anxiety (Lazarus, 1993).

> *"The entire summer is one prolonged agony"* (Örebro)

> *"You can never quite describe that worry"* (Örebro)

The onset of such negative emotional outcomes may stimulate behavioural reactions to deal with the stressor and reduce the negative emotion. Worry has for instance been identified as a link between the experienced carnivore presence and behavioural adjustments used to cope with the threat (Eklund et al., 2020).

Operant Behaviours

The expanding carnivore populations have resulted in an increased vigilance among sheep owners. Such increased vigilance is part of an operant behaviour directed at handling the situation, for instance through attempts of identifying cues in the animals' behaviour and predict the risk of a large carnivore attack:

> *"Because you always go around listening and being attentive: Is the herd unsettled? In a way it should not be? How are they grazing, how are they standing? Have they herded together? And you kind of register all of those things a lot more than you used to"* (Örebro)

To cope with the threat of attacks and in order to reduce stress, sheep owners report using a variety of interventions including carnivore deterring fences and night-time confinement, lambing indoors, removing carcasses and similar attractants as well as the use of scaring devices. In situations where large carnivores have been observed in the vicinity of the farm or pastures, or when attacks on sheep have occurred, the sheep owners may contact the county administration board for support. The use of some interventions, such as keeping animals in small night pens, are undertaken to prevent repeated carnivore attacks subsequent to an initial depredation event. It should be noted that although the interventions intended to prevent large carnivore attacks on sheep are provided as tools for sheep owners coping with the large carnivore threat, the interventions themselves can sometimes evoke additional stress for sheep owners if the intervention is unsuitable for their life situation or provide an increased awareness of threat. This implies cumulative stress. In such cases a functional operant behaviour to reduce the experienced stress can be to remove the intervention, although it contradicts the aim of reducing the threat of an large carnivore attack.

> "*I got to borrow three of them [sound deterrents], and that scream is really powerful and loud. And because there are two different sounds. . .And considering the fact that I work in shifts and so on, no. . .no I just couldn't handle it. . ..I became nervous in the middle of everything. I just said: "these are going XXXX down!" You know, don't get me wrong, because it was a really good thought that they [the county administration board] offered me, "I think you should use this." Well that's great, really great you know, but I just can't handle hearing "huhhh, it just went off" and then you quickly run up to the bedroom window and sort of hang there halfway out the window and check, there's that one, there's that one. . .which one of them just went off? And then you need to scan the perimeter. . .and we're talking a few hundred meters distance and you go "damn, the binoculars are in the kitchen." Well it's like. . .it was really stressful!"* (Värmland)

In many cases the reported operant behaviours, such as intervention use, are direct attempts initiated by the sheep owners themselves to cope with the worry of an attack with or without a preceding predation event having occurred. These behaviours include the use of interventions previously mentioned as well as increased supervision of the sheep. The sheep owners themselves describe the behaviours as an urge to do something, whether the behaviour should be regarded as functional or dysfunctional is dependent on if the behaviour have any actual effect on reducing the risk of large carnivore attacks or not:

"I try to walk with the dogs. I have no idea if it matters but I think that if they [the wolves] walk here, then at least it might smell of dogs. Around the pastures like that, when I'm out walking them anyway – [Do they care about it?] – I have no idea" (Örebro)

*"Every night, when I need to take the dogs out for a walk anyway, I walk around the entire yard. But it's really just my own belief that it might leave behind some tracks that will prevent something [*large carnivores*] from entering. I don't have any proof that it works or not though. But I do it anyway since I'm going out anyway, I might as well walk around. . ." (Uppsala)*

Operational behaviours are here viewed as the use of different interventions. For example, putting up carnivore deterring fences and having the livestock indoors during the night. These behaviours, aiming at reducing the possibility of a wolf attack decreased stress, albeit moderately.

Non-operant Behaviours

Some of the behavioural responses that sheep owners employ to reduce the onset of stress cannot clearly be defined as operant behaviours. One example would be to, refrain from a earning a desired income from rental grazing on other people's land. Such "business" is considered a potential income and an opportunity to contribute to maintaining an open landscape outside of the own property. However, letting the sheep graze on someone else's land also implies less control over the well-being of the sheep, and the worry prevents the owners from letting the sheep go. This behaviour corresponds to changes in strategies to avoid the stressor in the Fanselow and Lester (1988) model for threat imminence. The mere knowledge that a threat may occur results in a changed behavioural pattern, in this case to not have the livestock too far from oneself. Without the perceived risk of large carnivores attacking the animals there would be no reason to refrain from letting the sheep for rental grazing. Further non-operant behaviours may include calling the appropriate authorities simply to express the experienced anger and frustration. This behaviour does not directly handle the situation with the wolves but may be explained by the fact that imminent threats reduce the blood flow in the prefrontal cortex, (Garcia et al., 1999) thereby reducing the possibilities for elaborated mental activity. The need for action might be larger than any premeditated idea with the phone call to the authorities. However, if the phone call could result in a calm discussion about possible and acceptable interventions, it might turn into an operant behaviour.

Some behavioural responses to the negative emotions and stress are clearly non-operant in relation to handling the threat of a large carnivore attack on the sheep. Coding of the interview material revealed a social dimension of such behavioural expressions, either as emotional outbursts or as the anxiety of stirring up a fuss. The negative emotions and stress may thus have indirect consequences for social relations, and examples were provided for such social interactions with partners, peers, and authorities:

"Well it is the county administrative board that. . .serve us [information about interventions]. When I'm pissed off then I call them" (Örebro)

"...but when he came home then he [partner] says – I don't dare to tell you this" –"We...I think we had a wolf in front of us on the track. . ." (Värmland)

Another non-operant response for dealing with the stress that large carnivore situations evoke can be to use humour to distance oneself from the impact that the situation has had. Although this behaviour is non-operant for dealing with an actual carnivore-sheep interaction situation, it could provide a means to deal with the emotional onset and generate a sense of control in the social (interview) setting. During the interviews, humour was repeatedly used when describing stressful situations with large carnivores, as sheep owners were highlighting the absurdness of behaviours and reactions, evoking laughs and giggles in the focus group. Anthropomorphism was used to describe wolves with names or behaviours. When talking about self-experienced negative events or being exposed to unpleasant stimuli people might smile, or even laugh (Marci et al., 2004; Ansfield, 2007; Hess and Bourgeois, 2010; Flykt et al., 2021). Thus, using humour when talking about large carnivores may be a form of emotion regulation (Gross, 1998).

"And I've seen wolf, so I have! Yeah, I was going out. . .yes in a crossing at home. . .I was driving to a hockey game, that's when I met what was Mr. Wolf. That's a bit so. . ." (Värmland)

"They [wolves] are so scared. We've seen them. They are, well they don't get off the road. Because we have. . .They're. . .if there are two poles like this they don't like to go between two poles like this. . .because maybe they think there's wire between them. Really scared. They walk past and say "howdy howdy" to the sheep and it's not like. . .Yeah but seriously. . .yeah we've seen them. They stood outside and watched when the friend [the sheep dog] herded sheep inside the fence. They were standing on the road like this and were kind of checking like "oooh, that's exciting." But I mean, if they come inside and start taking, then there is no fence that will be able to stop them" (Örebro)

Using humour when talking about pressing matters is non-operational as it will not handle the problem per se. However, it might be a way of emotion regulation (see e.g., Gross, 1998) to reduce the intensity of negative emotions. Thus, a humoristic approach should probably not be regarded as that the situation being fun or even as the retrospective aspects of being amusing, but rather as a way to handle the situation without being overwhelmed with negative feelings.

Cognitive Effects

The interview material revealed some examples of how the potential carnivore presence and interaction generated cognitive stress responses among sheep owners, particularly in relation to attention/concentration, potential effects on the memory (Kausche and Schwabe, 2020), and lack of cognitive restoration. Effects on learning and decision-making as a direct result of carnivore presence were not identified from the interviews in our case study. That is not to say that there are no such aspects of stress in these situations, but rather that associations between wolf activity in the learning or decision-making were not as salient to the interview persons as other cognitive effects.

One adaptation that sheep owners use to relieve the intruding thoughts and in order to get some sleep is to supervise the sheep during the night as well. By fitting one of the sheep with a collar and bell and keeping the bedroom windows open, the sheep owners attempt to keep their attention on the sheep herd's movements when they are sleeping also. A sheep owner pointed out that while this may have consequences for the quality of sleep (and cognitive restoration) at least then there is some sleep.

*"Starting when the sheep are let out in the pasture, then *participant* and *partner* sleep with open windows, and open doors. No, but the windows are open. And it... then it depends on which side of they yard they are at. And it's because we put a bell on one of the ewes. And we do that partly to hear what sound it makes, and you do that even while you are sleeping. So I don't know how well you sleep, but at least you sleep. But you do hear it, yeah you do. If it moves, and then it's supposed to...well it makes a certain sound when they are just grazing. And if it's quiet it means they are lying still. And if it starts sounding an awful lot like this, then it means you need to get up to check on what's going on? (Laughter) And you wake up.*

The vigilance for sounds of wolf presence indicates that intrusive thoughts are easily triggered and that some sheep owners in the interview materials were sensitised to certain sounds. With such sensitisation triggering potential catastrophic appraisals and intrusive thoughts, cognitive restoration would be hard to achieve. That sensitisation to certain aspects of the environment occurs are essential for most mammals, humans are no exception. However, if the triggers are not specific enough, many sounds trigger an orientation toward the sound, which may have accumulative negative effects over time (see e.g., Lovibond et al., 1993).

Somatic/Physiological Effects

Some examples of sheep owners experiencing a physiological activation or consequences of physiological activation were provided in the interviews. These included a sense of feeling bad or experiencing a stomach ache at times of stress or negative emotions, also associated with a lack of cognitive restoration.

> *"It's like a lump in the stomach when we release the animals. Yeah, and that anxiety can never be described. And I don't think any animal owner can say that it's calm and pleasurable anymore..." (Örebro)*

> *"I'm retiring now. And now I've waited many years to see if my daughters, or one of them, would like to take over. And then I just got to a point where I thought....no, I don't want any of my daughters to take over. It's devastating. They...they'll go under. It's not possible. They can't take over. They will not be able to cope with it, physically psychologically that is. It's insane" (Örebro)*

GENERAL DISCUSSION AND CONCLUSION

The application of a theoretical framework, based in the established basic psychological research on stress, reveals that sheep owners in focus group discussions about large carnivores describe the presence of wolves and other large carnivores primarily as an ambient stressor. In similar contexts the effects have previously been addressed as intangible or psycho-social effects of large carnivores (Kansky and Knight, 2014; Sjölander-Lindqvist et al., 2021), which we are able to describe in more detail from a basic psychological perspective. Owning sheep in a large carnivore area appears to imply stress of a relatively low intensity, but that is present over a prolonged period, i.e., an ambient stressor. This on top of many other stressors of daily life for farmers and animal owners will accumulate stress, especially if the potential to take action to safeguard the animals and/or the opportunities to obtain relief and restoration are limited (Evans et al., 2012). The sheep owners reported such alarming, but not surprising, experiences as the constant perception of threat that the wolves represent. This is particularly evident during summer times when the sheep owners' anxiety may cause reduced possibility for cognitive restoration. Although stress induced by wolves may be the onset of acute stress in response to a single event, for example in case of an attack, it seems highly relevant to take the perspective of cumulative stress.

In the literature on "landscape of fear" (e.g., Laundré et al., 2001) predators are understood to have a similar impact on co-occurring species, i.e., they elicit fear not only through direct interactions and predation, but also indirectly by causing vulnerable prey to reallocate time toward safer, but from an energetic and reproductive point of view less preferred, options. Here we show that the same effect may also apply to humans, in our case study illustrated by sheep farmers in the Swedish wolf range. While natural prey may reallocate time to spend more time on the lookout for approaching carnivores, sheep farmers may keep their windows open to listen for unsettled herds. While prey animals may move into open fields with hesitance, sheep owners experience a lump and anxiety in their stomach when releasing their sheep in the field. Although the indirect effect of carnivore presence is similar for humans and natural prey species alike (Clinchy et al., 2013), for humans it may be more appropriate to use the term "landscape of stress" to illustrate the indirect effects on, for instance, sheep owners' everyday life. Even though humans are not directly comparable to other species in some ways, all mammals share much resemblance and millions of years of evolution (see Nesse et al., 2016). It is therefore highly plausible that psychological understandings of different domains of human stress responses, such the one presented here, are helpful to further understand reactions and behaviour in a framework of the ecology of fear.

The unique contribution of the present work is that our analysis goes beyond reported stressors and stress, and makes use of a psychological theoretical framework adapted to provide a detailed description of different domains of stress responses. Behaviours, operational as well as non-operational, somatic/physiological reactions, and cognitive responses were identified. Drawing on well-established theory on human stress, the framework can be applied also to other human wildlife interactions. A limitation of our work is that it is solely based on interviews. It might be that reports on behaviour are more easily communicated and therefore reported in a group discussion than somatic/physiological reactions or cognitive responses. Psychology offers a broad range of standardised methods used to capture stress responses in the domains of somatic/physiological reactions, such as cardiovascular measures, and cognitive effects. Further studies would benefit from complementing interviews with established questionnaire batteries, cognitive tests and physiological measures. The distinctions of the sheep owners stress responses into the three domains helps to more closely tie the cumulative stress in response to large carnivores to the psycho-physiological processes involved. It thereby becomes possible to gain a more nuanced understanding of the potential health and well-being outcomes for sheep owners in wolf/large carnivore areas.

The "landscape of stress" for sheep owners when coexisting with wolves and other large carnivores suggest that sheep owners' behaviour is somewhat similar to behaviour described for prey in the ecology of fear (Laundré et al., 2001). They respond to the carnivore presence and change their behaviours in accordance with the experienced probability of a predator attack. Such changes will be adaptive as long as the behavioural changes are proportional to the probability of an encounter. One emerging question is if the landscape of stress is similar to the landscape of fear based on the cognitively elaborated appraisals made by humans involving higher cognitive functioning as well as cognitive bias. That is, despite the possibility to logical reasoning there is no need that these higher mental processes should overrule evolutionary more old processes. Humans might overestimate the probability of an encounter or attack and thus have stronger responses than necessary based on the actual probability. It should be noted that all anxiety disorders are to the ground an overestimation of threat encounters, and the lifetime prevalence of anxiety disorders in humans is >30% (Bandelow and Michaelis, 2015). This overestimation of threat encounters could involve a number of factors associated with appraisals based on ontogenetic learning coloured by the prevailing vales and norms of their society. Humans will, on the other hand, be much more capable of modifying both their situation and the environment in the landscape of stress to a much larger extent than a prey animal will ever be capable of, thus providing a greater control over the situation. However, the higher cognitive functions in humans also provide opportunity to dwell on the possible ways of dealing with the threat, which might result in a prolonged exposure to intrusive thoughts and elaborations. Such thoughts may act as ambient stressor and to the cumulative stress.

Although the coexistence between humans and large carnivores in multiuse landscapes imply other challenges than those between prey animals and wolves in areas such as Yellowstone national park, there are also striking similarities (Clinchy et al., 2013). Here we focus entirely on the responses of the individual farmer to the large carnivore as a stressor, but in a next step, it is also plausible that the responses that sheep owners have to their stress of large carnivores can have consequences or cascading effects on the species composition in the landscape. When sheep farming is closed down, or if sheep are gathered in fields near human settlements, trees, bushes and grasses take over the abandoned grazing areas and the abundance and species richness of flowering plants and herbs diminish. This can have severe effects for pollinators and biodiversity conservation in the Swedish landscapes (Winsa et al., 2017; Rotchés-Ribalta et al., 2018). Interventions to prevent carnivore attacks on sheep may also impact other species, carnivore deterring fences will for instance limit the movements of various medium and large sized wildlife (Woodroffe et al., 2014), and livestock guarding dogs may have a local impact on target and non-target wildlife including mesopredators such as foxes and badgers (Smith et al., 2020). Thus, the landscape of stress could, just like the landscape of fear, imply cascading effects for biodiversity and species richness/abundance on a landscape level. Moreover, also social processes may be altered in the landscape of stress. It can be speculated that time for nurturing social relationships decrease, the social interaction with family members might get tense due to underlying stress (Novaco et al., 1991), and in turn breaking down relationships. Another possible social effect of the landscape of stress might be more intense polemic interactions between different interest groups. By incorporating psychological theory with an ecological concept, we can better understand the systems in which humans and carnivores live. These are not separate worlds, but rather they are depicted by different scientific perspectives providing multiple views of one system, where interactions occur and where carnivores influence humans and humans influence carnivores (Carricondo-Sanchez et al., 2020) at some level of coexistence. This type of interdisciplinary understanding of coexistence provides a starting point for the new century of wolf conservation.

This study shows that stress affects behaviours, cognitions, and physiological activity and that this becomes apparent even when the focus is not on stress. Apart from introspection of experience of states that humans would label stress, this study show that other sources of information are available for gaining a more nuanced picture of stress responses. Thus, this indicates that investigation of stress responses could and should address all components of stress. Despite that humans by some are considered as more cognitively developed, some basic psychological processes could be parallel to processes in other mammals. In the present case that a landscape of fear in prey animals can transpose to a landscape of stress for sheep owners in wolf areas.

DATA AVAILABILITY STATEMENT

The data analysed in this study is subject to the following licenses/restrictions: Anonymised and transcripted group interview data in Swedish could be granted for appropriate purposes. Requests to access these datasets should be directed to JF, Jens.Frank@slu.se.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the Local Legislation and Institutional Requirements. Written informed consent was obtained from the patients/participants.

AUTHOR CONTRIBUTIONS

AF and AE drafted the different parts of the first version of the manuscript. All authors have rewriting and restructuring the first draft to its present form.

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A Community-Based Conservation Initiative for Wolves in the Ladakh *Trans*-Himalaya, India

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We describe a pilot community-based conservation initiative for wolves *Canis lupus* that involves (i) voluntary deactivation of traditional trapping pits called *Shandong*, (ii) commitment to wildlife conservation by the local community, and (iii) collaborative construction and consecration of a *Stupa* (Buddhist shrine) in the vicinity of the *Shandong* as a symbol of conservation and repentance for past hunting. People and wolves have a complex relationship, in part shaped by predation on livestock, which can have severe impacts on livelihoods in pastoral societies. Consequently, wolf conservation often evokes strong and polarizing reactions. To control wolf populations, livestock herders across the *Trans*- Himalayan and Tibetan regions use different types of traps. *Shandong* is a relatively large, widely used traditional trapping pit with inverted funnel-shaped stone walls, usually built near villages or herder camps. Typically, a live domestic animal is placed in the pit to attract the wolves. Once the wolves jump into the pit, the funnel shaped walls prevent them from escaping, and trapped wolves are usually stoned to death. In an extensive survey covering over 25,000 sq. km, we enumerated 94 *Shandong* in 58 of the 64 surveyed villages in Ladakh between June 2019 and March 2020. Thirty of these had been used to kill wolves within the past 10 years, while 7 had been destroyed. *Shandong* that were not in use were of poorer condition. Since 2017, we have worked with community members, local monks, and the region's religious leaders to support the neutralization of the *Shandong* while preserving their structure, and assisted the communities to build *Stupas* and to consecrate them. Our pilot efforts with three communities appear to generate pride locally, and hold promise for promoting wolf conservation in Ladakh and in large parts of *Trans*-Himalayan and Tibetan regions that share similar cultural settings.

Keywords: trapping pits, predators, livestock, conflict, culture

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INTRODUCTION

Humans and wild animals have long-standing, complex and variable relationships (Bhatia et al., 2020). These relationships are often multi-faceted, manifested in dynamic behaviors, attitudes, and emotions that may simultaneously range from negative, neutral, to positive especially in the case of large carnivores (Treves and Naughton-Treves, 1999; Bhatia, 2021). Large carnivores typically specialize in feeding on ungulates, and, consequently, livestock represent a potentially suitable prey that have typically high density, predictable distribution, and reduced anti predatory abilities (Zohary et al., 1998; Johansson et al., 2015; Mishra et al., 2016a; Samelius et al., 2021). Retaliatory or preventive killing of large carnivores in response to predation on livestock is a global conservation challenge (Treves, 2009; Van Eeden et al., 2018; Williams et al., 2020).

The *Trans*-Himalayan region, including the Tibetan plateau and its marginal mountains, is a vast rangeland system (>2.6 million km^2), which has been home to traditional livestock grazing for several millennia (Mishra et al., 2001, 2002). These rangelands are also home to large carnivores, including snow leopards *Panthera uncia*, wolves *Canis lupus* (Álvares et al., 2019) and Eurasian Lynx *Lynx lynx*. Livestock depredation by large carnivores and their retaliatory or preventive killing is an important livelihood and conservation concern in the region (Mishra, 1997; Berger et al., 2013; Suryawanshi et al., 2013; Aryal et al., 2014; Home et al., 2017; Lyngdoh et al., 2020). People in the region are reported to have a particularly negative attitude toward wolves (Suryawanshi et al., 2013; Bhatia et al., 2020). Compared to other sympatric large predators, wolves can be perceived to be particularly dangerous because of their greater visibility, howling behavior and pack living (Kellert et al., 1996; Eriksson et al., 2015).

Wolves are one of the few top and wide-ranging predators across the *trans*-Himalayan region. Hence, they could serve as indicator and umbrella species of this ecosystem (Suryawanshi et al., 2013). They also have various deep-rooted associations with local people as reflected in local folklore (Kusi et al., 2020; Bhatia et al., 2021). Traditionally, the people of the *trans*-Himalayan region have used various means to protect their livestock against wolf attacks (Singh et al., 2013; Bhatia et al., 2021). Amongst the most prominent means of trying to control wolf populations is a traditional trapping pit, locally called the *Shandong* (derived from *Shangku* which is the wolf in vernacular, and *dong* meaning trap). Other means of persecuting wolves have also been traditionally employed in the region, including leg-hold traps, but their current use and spread is unknown (Pers. Comm. RD). *Shandong* are large pits typically built near villages or herder camps, and have inverted funnel-shaped stone walls (**Figure 1**). People typically bait the trap with a live domestic animal to attract wolves. Once inside the pit, the funnel-shaped walls prevent the wolves from escaping and the trapped wolves are usually stoned to death (Ghoshal et al., 2018). Officially, the persecution of wolves is forbidden under the country's wildlife protection laws (Indian Wildlife Protection Act, 1972; Ramesh, 1999).

Here, we describe in detail a pilot community-based conservation effort that involves voluntary neutralization of the *Shandong* by local communities (reported in brief by Ghoshal et al., 2018). To better understand the extent and use of *Shandong* in Ladakh, we also present the results of a survey of 64 villages covering over 25,000 sq. km. in Leh District of Ladakh. Our work has the potential to promote wolf conservation in Ladakh and other parts of the *Trans*-Himalaya with similar cultural settings. This is particularly relevant as in this region, the Buddhist religion plays an important role in people's lives and also in wildlife conservation (Li et al., 2014).

FIGURE 1 | A *Shandong* or traditional trapping pit for wolves with inverted funnel shaped walls. An agro-pastoralist village is seen in the background. Photo Credit: Rigzen Dorjay.

MATERIALS AND METHODS

Study Area

The Indian *Trans*-Himalaya lies mostly above 3,500 m, with temperatures ranging from c. 30°C in summer to −30°C in the winter. The region has a limited growing season (May–September) resulting in low primary productivity (Chundawat and Rawat, 1994). The Union Territory of Ladakh is India's largest *Trans*-Himalayan cold-desert region. The large carnivore assemblage includes snow leopards, wolves and Eurasian lynx, and the wild large ungulate assemblage includes Bharal *Pseudois nayaur*, Ibex *Capra sibirica*, Urial *Ovis orientalis*, Tibetan Argali *Ovis ammon* and Tibetan Wild Ass *Equus kiang*. Unlike most other parts of India, these wildlife populations are spread across the landscape and not confined to protected areas. Local communities living in this low-productivity, highly seasonal region have evolved a distinct lifestyle and culture, and have traditionally been pastoralists and agro-pastoralists (Singh et al., 2013). Predominantly, Eastern Ladakh (namely Changthang) is inhabited by transhumant pastoralists, whilst the remaining area is home to agro-pastoral communities (Murali et al., 2020). For this work, we worked with both transhumant pastoralists and agro-pastoral communities. High instances of livestock depredation especially by snow leopards and wolves are reported from large parts of Ladakh (Jackson and Wangchuk, 2004; Namgail et al., 2007).

Since the 1960s, Ladakh has had a strong military presence which has facilitated expansion of road network. The region opened for tourism in 1974, with particularly rapid growth in the past two decades (Dollfus, 2013). Expansion of defence, tourism, and developmental infrastructure, along with implementations of wildlife management and laws, have led to rapid socio-economic and cultural changes in Ladakh (Dollfus, 2013).

Field Surveys

Surveys were carried between June 2019 and March 2020. Our initial intention was to carry out the project across c. 60,000 km^2 covering both districts within Ladakh namely, Leh and Kargil. This area is comprised of six blocks: Changthang, Kargil, Nubra, Rong, Sham and Zanskar and *c.*200 villages. These blocks aren't the legal administrative blocks of Ladakh, rather, they are local delimitations. Logistical challenges due to the COVID-19 pandemic necessitated a prioritization of three of the six initial study blocks. The blocks of Changthang, Rong, and Sham were selected based on evidence from literature and knowledge of livestock herders, Wildlife Protection Department Officials, and research scholars who confirmed these blocks to be where wolves predominately occurred and had negative interactions with people (Mallon, 1991; Namgail et al., 2007; Srivathsa et al., 2020). These blocks covered c. 25,000 sq.km in the Leh district of Ladakh.

The surveys involved visiting each of the 64 villages in the study area and interacting with local key informants to map the location of all the *Shandong*. We did not use a pre-set questionnaire, though our main questions pertained to the location of *Shandong* and the last time the community had used one to trap wolves. The conversations revolved around the *Shandong* and human-wolf interactions in the area. Sixty-four key-informants (one from each village), typically community elders involved in past or present livestock rearing and serving as the village head, were interviewed. Before asking for information, oral consent was taken from each key-informant and the conversation was held in *Ladakhi* which is the local Tibetan dialect. As it is illegal to kill wolves, it was possible that key-informants might not share information about the *Shandong*, particularly given the social desirability bias (Grimm, 2010). To address this bias, we spent time building relationships with each key-informant in each survey village. We assured them that our intention was not to persecute or cause difficulty for anyone (Newing et al., 2011). Having local team members who spoke the local language (*Ladakhi*) helped in gaining the trust of the respondents as well. Village locations were obtained from the local district office in Leh (capital of Ladakh). With verbal consent from them, we visited all the *Shandong* around each village, accompanied by the key informants, recorded the GPS location, and categorized each *Shandong* as active or inactive based on the state of the structure and information provided by the key informants. We recorded the time a *Shandong* was last used in either one of the following time periods: over 20 years ago, 10–20 years ago, and within the last 10 years. A significant geo-political conflict (Kargil war) that occurred approximately 20 years before our surveys provided a temporal reference point that all respondents could relate to (Chari, 2009). This provided for relatively comparable time estimates among the respondents. Each *Shandong's* condition was assessed qualitatively using likert-scale type categories (Joshi et al., 2015; **Table 1**). We determined the use of each *Shandong* based on a combination of its condition and key informant information (see **Table 2** for the likert-scale type categories). We also engaged in informal conversation with elders and youth to understand the nature of human-wolf interactions in the area and gauged their willingness on working together to discontinue wolf hunting by neutralizing the existing *Shandong*.

TABLE 1 | Shandong condition categories used during the qualitative assessment.

Condition–Likert scale	Qualitative description
Destroyed–1	The structural form that is characteristic of a *Shandong* (e.g., **Figure 1**) didn't exist as it was torn down, rendering the structure unusable.
Very bad–2	Large portion of the *Shandong* was dismantled and/or damaged, although its characteristic shape was discernible. While its use was unlikely, with some repair, it would be usable.
Bad–3	Parts of the *Shandong* were dismantled and/or damaged, although its characteristic shape was evident. While its use was likely, with some upkeep, its effectiveness and longevity would likely increase.
Good–4	Large portion of the *Shandong* was intact and likely maintained regularly for its structure and use.
Don't know–5	None of the above descriptions were discernible for the *Shandong*. This was generally the case when we knew a *Shandong* existed but couldn't reach it for reasons such as restriction of access due to snow.

Key-informant interviews suggested that Shandong in bad and very bad condition and those that were destroyed would not be able to trap wolves effectively.

TABLE 2 | *Shandong* use categories in the qualitative assessment.

Use–Liker scale	Description
Absent–1	No *Shandong* existed in the village during the survey.
Don't know–2	*Shandong* present in the village but insufficient information was available to determine if it was in use or not.
In use–3	*Shandong* present and were being used to trap wolves.
Not in use–4	*Shandong* present but were not being used to trap wolves currently.

The field surveys were led by two of our team members who are local *Ladakhis* (RD and SL), from the Sham and Rong regions, respectively. Both had been involved in livestock herding in the past. Conversations were all conducted in *Ladakhi*, a local dialect of Tibetan. Throughout the surveys, we respected the sanctity of local traditions, even if some of them were harmful toward wildlife. No gathered information was shared or compromised to prevent any possible persecution or maligning of the local people involved.

Data Analysis

We used the Pearson's Chi-squared test of independence to test if the usage of *Shandong* was linked to their condition. We expected *Shandong* in good conditions to be in use, unless other social, economic or ecological factors prevented or rendered their use unnecessary. Additionally, we tested if the *Shandong* in use (i.e., those used in the previous 10 years) were clustered in space. To do so, we calculated the nearest neighbor distance for each *Shandong*

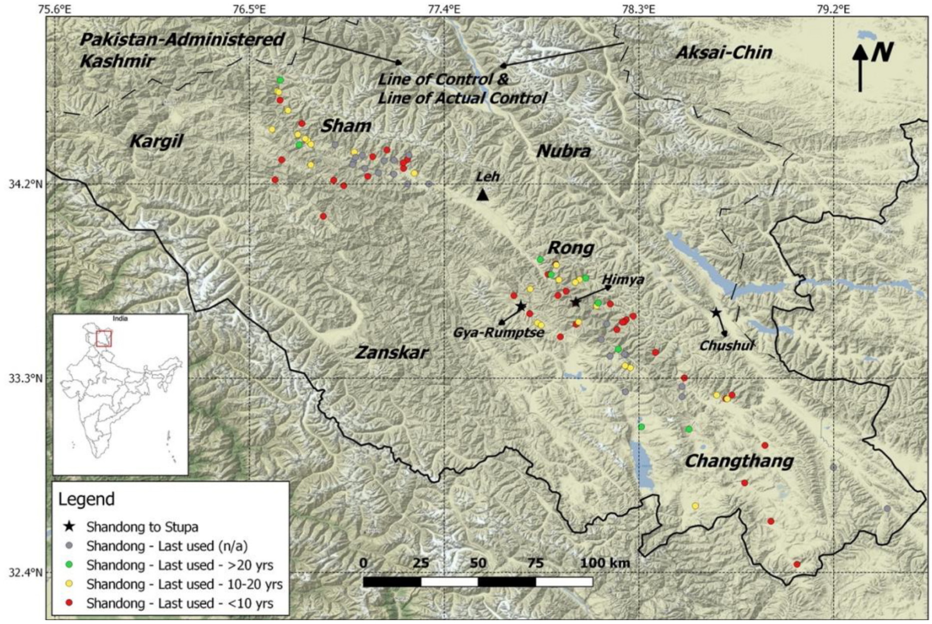

FIGURE 2 | Map showing *Shandong* locations and use. Locations depicted by stars are where *Shandong* have been neutralized. The colors correspond to the time the *Shandong* was last used. Green = Last used >20 years ago, Yellow = Last used 10–20 years ago, Red = Last used <10 years ago and Gray = Last used not known. The Line of Control and Line of Actual Control indicate the present military control line along international borders.

pair and compared this distance for recently used and not in use *Shandong*. We expected spatial clustering of *Shandong* that were in use as we expected neighboring communities to share similar wolf abundance and retaliatory practices.

RESULTS

Status of Shandong in Ladakh

We recorded 94 *Shandong* spread across the three surveyed blocks in Ladakh–Rong (n = 32), Sham (n = 39), and Changthang (n = 23) in 58 of the 64 surveyed communities (**Figure 2**). The highest number of *Shandong* in a village was five. According to the information from our key informants, some *Shandong* may have been used to trap and kill 10–20 wolves over the previous 20 years. Thirty-seven *Shandong* were reported to have been used within the past decade (years 2010–2020), of which fifteen were currently active (**Figure 3**). Thirty-four *Shandong* had not been used in the past decade and were not being actively maintained, many of which were in a poor condition (**Figure 3**). For the remaining 23 *Shandong* we couldn't determine the last time they were used (**Figure 2**). *Shandong* that were not in active use were poorer in their condition (Pearson's Chi-squared test of independence: X-squared = 55.604, df = 6, p-value = 0.02).

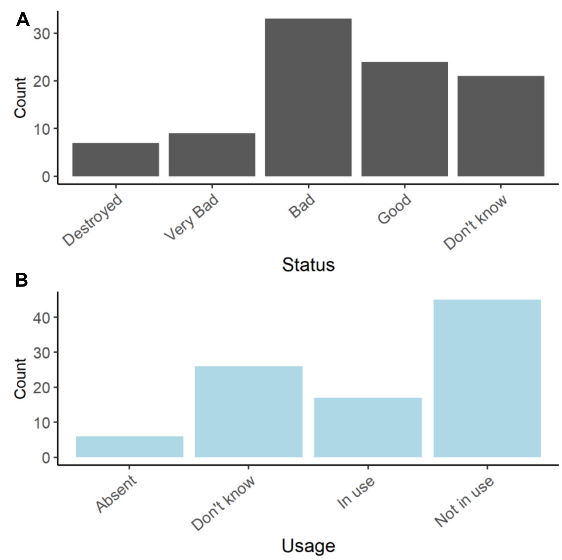

FIGURE 3 | Panel graphs showing **(A)** the status and **(B)** the usage of *Shandong* across the study area.

Distribution Pattern of Shandong

We found that *Shandong* that had been in use recently had a significantly lower nearest neighbor distance when compared to the nearest neighbor distance of a randomly selected pairs of *Shandong*. *Shandong* that were in use before the last decade did not show signs of clustering relative to the recently used ones (**Figure 4**).

Conservation Initiative

In 2017, we (CM and KS) initiated discussions with the local community members and their political representatives from the pastoral village of Chushul about the possibility of neutralizing

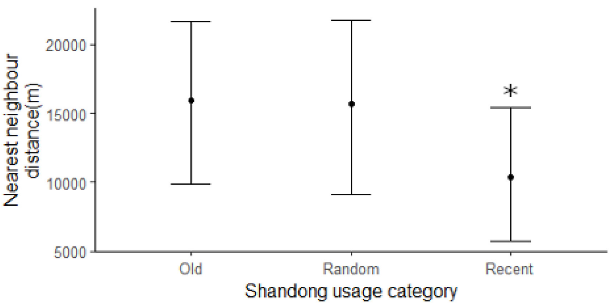

FIGURE 4 | *Shandong* that were used in recent times (<10 years ago) were clustered in space as shown by the significantly lower nearest neighbor distance. Error bars show 95% bootstrapped confidence intervals. * indicates statistically significant difference in the bars.

their *Shandong* while preserving and maintaining them as part of the cultural heritage. We also initiated discussions about the initiative with influential religious leader and scholar His Eminence Bakula Rangdol Nyima Rinpoche and sought his views and advice on the possibility of symbolically building a *Stupa* (a Buddhist religious symbol) at the *Shandong* site. A *Stupa* is a mound-like or hemispherical structure which contains relics like idols, religious text, or the remains of Buddhist monks/nuns. They may be used as a place of meditation (Sharma, 2013). The shape of a *Stupa* supposedly represents the Buddha and there is belief that a *Stupa* may represent the five purified elements according to Buddhism: (i) the base, often a square, represents the earth, (ii) the hemispherical dome/vase represents water, (iii) the conical spire represents fire, (iv) the upper parasol represents air, and (v) the dissolving point represents wisdom. Buddhists across Ladakh circumambulate the *Stupas* as an important ritual and devotional practice (Dorjey, 2016). In certain areas of Ladakh, *Stupas* also play an economic role in the community by attracting tourists.

The Chushul community was enthusiastic about the possibility of neutralizing the *Shandong*, committing to conservation, and under the Rimpoche's guidance, collectively building a *Stupa*. We had started interacting with the Chushul community in the year 2017 as part of our work on assisting livestock herders to produce relatively sustainable "snow leopard friendly" cashmere. This involves assisting them to adopt wildlife friendly herding management and other practices. In June 2018, the Chushul community neutralized all the four *Shandong* in their area and built a *Stupa* next to one, as a commitment toward conservation and in repentance of past hunting. These *Shandong* had been active in the past. The neutralizing of the *Shandong* is done by removing a few stones from the structure, which creates a passage for any trapped animal to escape, while preserving the traditional architectural structure. This can be labor and time intensive task and various community members including the herders, youth groups, women and local monks usually take part in it. The structure is maintained to respect the tradition and cultural heritage of the communities. The *Stupa* helps integrate Buddhist principles of compassion toward all living beings. Thus, this effort strengthens the links between culture, livelihoods and conservation. While we supported the cost of building the *Stupa* including identifying and appointing experienced masons, the community members voluntarily contributed funds as well relics to be placed inside the *Stupa*. This *Stupa* was publicly consecrated in June 2018 by Rangdol Nyima Rinpoche. In the meantime, one of us (KS) had similar discussions with the community of Rumptse in the Gya-Miru region within the Changthang block of Ladakh, with whom we have had a conservation partnership since 2006. This community agreed to neutralize their *Shandongs* and built a *Stupa* in the year 2019. Before proceeding with on-ground activities, we (AB, CM, KS, RD, KRS) sought advice from another religious leader who is revered by this community, His Eminence Drukpa Thuksey Rinpoche of Hemis Monastery. He supported our efforts and performed the consecration of the *Stupa* in September 2019.

We had video recorded the process of *Stupa* building and consecration in both the Chushul and Rumptse communities, and these were converted into an awareness film by contracting a Ladakhi filmmaker. The film has been made publicly available[1] and is being used to spread awareness among other communities (**Figure 5**). In the year 2021, we (KS, CM) completed negotiations with the community of Himya for neutralizing their two *Shandongs* and build a *Stupa*. This *Stupa* was consecrated in September, 2021 by His Eminence Drukpa Thuksey Rimpoche.

Our informal interactions with people in all three communities has revealed considerable pride and a sense of gratification amongst community members for having been involved in this initiative, and we believe that this has made sustainable impact in terms of renewed support for wolf conservation. Anecdotal evidence suggests that no wolves have been killed in the region since the conversions of the *Shandong*. Nevertheless, we acknowledge that to robustly test the efficacy of this conservation initiative, data on metrics such as reduction in wolf hunting cases and perceptions and attitude of people toward wolves would be needed.

Approach to the Conservation Initiative

In our *Shandong* to *Stupa* conservation initiative, we followed the PARTNERS (Presence, Aptness, Respect, Transparency, Negotiation, Empathy, Responsiveness, and Strategic Support) Principles approach for community-based conservation (see Mishra et al., 2017 for detailed definition of each principle).

In all three partner communities that have neutralized their *Shandong*, we built long-term relationships with multiple visits and interactions (following the principles of **Presence**, **Respect**, **Transparency**, and **Empathy**) before the actual conservation interventions were initiated. Amongst other learnings, this helped us understand that the intention behind killing wolves was purely to protect their livestock (**Respect**, **Empathy**). We did not entertain or pursue any wish to penalize community members involved in hunting wolves, nor did we seek to destroy the *Shandong* which represent an important part of the cultural heritage (**Aptness**, **Respect**, **Transparency**). This background and understanding helped us to conceptualize the idea of neutralizing the *Shandong* and constructing a *Stupa* (**Aptness**).

[1] https://www.youtube.com/watch?v=bLW_5C6nOIE&t=415s

FIGURE 5 | A neutralized *Shandong* with a newly constructed *Stupa* adjacent to it. Photo Credit: Rigzen Dorjay.

Throughout the process, we disclosed our goals, purpose and intentions to the communities (**Transparency**). Even after multiple discussions, there would often be periods when community members were not available. It was important for us to accommodate their availability and timelines (**Responsiveness**), but also expect accountability as well as to be accountable ourselves for activities listed in formal agreements (**Negotiation**). Lastly, a community although a collective, is often a heterogenous mix of individual aspirations, thought processes, and opinions (Klein et al., 2007; Xu et al., 2009; Mishra et al., 2017). This is why we worked with different groups within the community including but not limited to the women's alliance, the herders and local monks, but also engaged with regional religious authorities and government representatives at both the conceptualization and execution levels of the intervention (**Strategic support**).

We also realize that neutralizing *Shandong* by itself doesn't address the issue of livestock predation and the negative human-wolf interactions. In each of the three communities that neutralized their *Shandong* (as indeed in the tens of our other partner communities), we have also assisted with multiple other initiatives such as livestock insurance and predator-proofing of corrals.

DISCUSSION

Shandong Abundance and Use

Our surveys documented a relatively high abundance of *Shandong* across the survey region, with 90% of the surveyed communities having one to five *Shandong*. Although some of them were no longer used or had been destroyed, many of the *Shandong* were well maintained and in occasional use. This is understandable as livestock herding is an important source of livelihood and integral part of the *Ladakhi* culture and lifestyle, and livestock losses to predators are difficult for people to absorb or tolerate due to economic and emotional setbacks (Namgail et al., 2007; Bhatia et al., 2020; Maheshwari and Sathyakumar, 2020). In parts of Ladakh, wolves reportedly account for disproportionately higher proportion of livestock losses that other sympatric predators such as snow leopard and lynx (Namgail et al., 2007).

Interestingly, we found that there was spatial clustering of *Shandong* currently in use, that could be indicative of conflict hotpots. Such hotspots can account for disproportionate persecution of wolves which requires immediate conservation attention. These hotspots appear to be in the Central Rong and Eastern Sham regions of Ladakh (**Figure 2**). We hope to engage in a similar manner as we did in Chushul, Gya-Miru region (including Rumptse) and Himya in these two regions as well (see sections "Conservation Initiative" and "Approach to the Conservation Initiative"). Nevertheless, further investigations are required into factors like declining wolf populations, presence of livestock compensation programs and decreasing livestock numbers (as seen in some parts of Ladakh).

Our interactions with key informants revealed that use and status of *Shandong* were impacted in part by factors beyond human-wolf interactions. Expansion of defence, tourism, and development infrastructure has led to rapid socio-economic and cultural changes in Ladakh (Dollfus, 2013; Sharma, 2019). We found places where *Shandong* had been dismantled and left unattended due to the availability of alternate livelihood sources like employment in the tourism sector, other than livestock. Additionally, a few *Shandong* were destroyed and hence rendered unusable due to flash floods. We also found two instances where *Shandong* had presumably been used against dogs. Wild felids like snow leopards are presumably able to get out of these structures should they fall in, and we didn't find any instance when they had been trapped in *Shandong*. There is little evidence to suggest that other methods are being employed to kill wolves (some of the last documented cases of wolf pups being killed at dens are nearly two decades old). Most respondents suggested that availability of guns and snares has seen a decline across many parts of Ladakh (Pers. Comm. RD).

Conservation Initiative

The cost of living with large carnivores, is often borne disproportionately by the communities co-habiting spaces with these predators (Salafsky and Wollenberg, 2000; Treves and Karanth, 2003). Exclusionary and top-down conservation approaches have tended to further alienate local peoples, turning potential conservation allies into adversaries (Lele et al., 2010). Conservation efforts have historically been perceived to be discriminatory against local people (Mishra et al., 2017). Respectful engagement of local communities as partners is critical in achieving long-term conservation outcomes (Holmes, 2007; Lejano et al., 2007; Bennett et al., 2017; Mishra et al., 2017).

Our conservation initiative is founded on and strengthens the links between culture, ecology, and conservation. However, this effort must not be viewed in isolation. Neutralization of *Shandong* by itself could have potentially negative outcomes by facilitating more livestock predation by wolves. This is why it is critical to combine the neutralizing of *Shandong* with other multi-pronged strategies that mitigate negative human-wolf interactions and facilitate human-wolf coexistence (Pretty and Smith, 2004). As mentioned earlier, with all the three partner communities involved in this pilot phase, we have assisted with multi-pronged efforts including livestock insurance (Mishra et al., 2003, 2016b), setting up village reserves (Mishra et al., 2016c), predator proofing of corrals, and other livelihood and conflict management initiatives. With such a multi-pronged approach, this initiative of neutralizing *Shandong* and gaining the communities' conservation commitment has the potential to be replicated and significantly improve the status of wolves in Ladakh and other parts of the Tibetan Plateau that share a similar culture.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

KRS, AB, and CM conceived the idea of the project. KS led the on-ground conservation interventions, while RD led the on-ground field surveys. MK and SL helped in data collection. MK, MS, and SS conducted the analysis. All authors contributed to the writing of the manuscript.

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frontiers in Ecology and Evolution

ORIGINAL RESEARCH
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The Role of Weather and Long-Term Prey Dynamics as Drivers of Wolf Population Dynamics in a Multi-Prey System

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As climate change accelerates in northern latitudes, there is an increasing need to understand the role of climate in influencing predator-prey systems. We investigated wolf population dynamics and numerical response in Denali National Park and Preserve in Alaska, United States from 1986 to 2016 under a long-term range of varying climatic conditions and in the context of prey vulnerability, abundance, and population structure using an integrated population modeling approach. We found that wolf natality, or the number of wolves added to packs, increased with higher caribou population size, calf:cow ratio, and hare numbers, responding to a 1-year lag. Apparent survival increased in years with higher calf:cow ratios and cumulative snowfall in the prior winter, indicators of a vulnerable prey base. Thus, indices of prey abundance and vulnerability led to responses in wolf demographics, but we did not find that the wolf population responded numerically. During recent caribou and moose population increases wolf natality increased yet wolf population size declined. The decline in wolf population size is attributed to fewer packs in recent years with a few very large packs as opposed to several packs of comparable size. Our results suggest that territoriality can play a vital role in our study area on regulating population growth. These results provide a baseline comparison of wolf responses to climatic and prey variability in an area with relatively low levels of human disturbance, a rare feature in wolf habitat worldwide.

Keywords: Alaska, *Canis lupus*, demography, natality, population dynamics, predator prey, survival, wolf

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INTRODUCTION

Considerable attention has been given to the role of predators, particularly large carnivores, in driving ecosystem dynamics. In a top-down role, predators can limit herbivore abundance and activity, reducing herbivory and subsequently allowing more plant diversity and biomass which in turn supports biodiversity in other biota (Hairston et al., 1960; Terborgh, 1988; Estes, 2005; Schmitz, 2006). Through these top-down forces, predators can be seen as important components of ecological health, providing ecosystem benefits via top-down trophic cascades (Berger et al., 2001; Miller et al., 2001; Ripple and Beschta, 2004; Terborgh et al., 2006). Through opposing bottom-up forces, primary productivity can regulate consumer population abundance and in turn, their predators (Caughley, 1976; Sinclair, 1977; Houston, 1982). Evidence of trophic cascades following predator reintroductions has fostered support for conservation of large carnivores as agents improving biodiversity (Miller et al., 2001; Ripple and Beschta, 2004, 2012; Estes, 2005; Schmitz, 2006; Ripple et al., 2014, 2016). Conversely, predators' top-down effects on ungulate populations are used as support for controversial predator control activities (Boertje et al., 1996; Titus, 2007).

Perhaps no large carnivore's role in driving prey populations has fostered more controversy than that of gray wolves (*Canis lupus*). Across their extensive range, wolf density appears to be linearly related to prey biomass, supporting the theory that wolf populations exist at densities limited by food supply (Fuller, 1989; Fuller and Murray, 1998; but see Vucetich et al., 2002; Fuller et al., 2003). This relationship suggests that at a global scale, wolf populations are limited by bottom–up forces driven by primary productivity and herbivore densities (Oksanen and Oksanen, 2000). However, there is substantial evidence suggesting that wolves exert top-down control of prey populations, as wolves can depress prey abundance over large spatial and temporal scales (Gasaway et al., 1983, 1992; Adams et al., 1995; Boertje et al., 1996, 2010; Crête, 1999; Mech and Peterson, 2006). The influence of top-down controls are difficult to tease apart from bottom up and climatic influences, even in manipulative experiments (Gasaway et al., 1983; Boertje et al., 1996; Vucetich et al., 2005; Keech et al., 2011; Valkenburg et al., 2016; Allen et al., 2017).

There is ample evidence that the role of top-down control of ungulates by wolves is nuanced, and factors such as weather conditions and prey age structure alter vulnerability of prey (McRoberts et al., 1995; Mech et al., 1998; Vucetich et al., 2005; Valkenburg et al., 2016). Ultimately, it is vulnerability to predation that determines which and how much prey is availability to wolves. Climatic factors play an important role in prey availability, as wolves tend to be more successful when winters are severe in terms of heavy snowfall and cold temperatures (Peterson and Allen, 1974; Peterson and Page, 1988; Mech et al., 1998). Snowpack affects the vulnerability of prey directly by covering possible food sources and restricting prey movement. Indeed, snow depth has been considered the most important landscape attribute affecting ungulate movement and mobility (Wallmo and Gill, 1971; Hugie, 1973; Telfer, 1978). Snowpack can also affect prey indirectly; for example, in years following severe winters, caribou are more susceptible to predation, in part because of poor nutrition during the natal period affecting the susceptibility of yearling caribou (Peterson, 1977; Mech, 1991). Ungulate availability can also fluctuate from a variety of factors in addition to snowpack such as disease, other climatic variables, available forage, and ungulate age structure (Klein, 1991; Valkenburg et al., 2016). When ungulates are in poor condition or exhibiting density dependent limitations, wolves may be the proximate but not necessarily the ultimate cause of ungulate mortality (Murie, 1944; Vucetich et al., 2005; Mech and Peterson, 2006). Therefore, the role that wolves play in exerting top-down controls and limiting ungulate populations is context dependent or may be compensatory.

Although wolves are considered obligate consumers of ungulates (Peterson and Ciucci, 2006), they are opportunistic predators and subsidies from alternate prey may play a role in wolf density and wolf-prey dynamics (Adams et al., 2010; Gable et al., 2018). Where available, hares (Lepus spp.) may be a particularly important prey for wolves during summer months (Mech, 2004; Haber and Holleman, 2013; Newsome et al., 2016). While pups are too young to travel with the pack in the summer, adult pack member range away from homesites (dens and rendezvous) to hunt for food and return to feed pups. Pack cohesion is lower in the summer (Benson and Patterson, 2015), perhaps because traveling separately increases efficiency in hunting smaller prey that is available in summer (Mech et al., 1998). In the High Arctic, wolves rely heavily on hares where the only other prey are muskox (Mech, 2004) and near 100% of pup survival variation is due to availability of small prey (Mech, 1995). Other studies have postulated about the role of hares in providing nutritional subsidy for wolves in a sub-arctic population, but the effect of hare abundance on wolf demographics has not been quantified (Murie, 1944; Mech et al., 1998; Haber and Holleman, 2013).

Much of what we know about wolf population dynamics and relationships between wolves and prey comes from long term studies (Mech, 1966, 1986; Mech et al., 1998; Smith and Bangs, 2009; Nelson et al., 2011). Long term studies are particularly important because the conclusions regarding predator-prey dynamics can drastically change based on the time-period studied (Nelson et al., 2011). Large terrestrial mammals can be difficult and expensive to study especially when they exist at low densities and are wide ranging (Estes, 1996) and these long-term studies represent a significant investment and body of work. The wolf population in and around Denali National Park and Preserve (hereafter, Denali) has a long history of research and relative protection from harvest (Murie, 1944; Mech et al., 1998). This makes the Denali wolf population unique worldwide and valuable as a conservation baseline (Borg and Burch, 2014; Borg et al., 2015).

We explored wolf population dynamics in Denali from 1986 to 2016 in the context of prey vulnerability and population structure using the powerful integrated population modeling approach developed by Schmidt et al. (2015, 2017). The overall goal of this study was to identify prey population characteristics associated with variation in wolf vital rates to better understand the relative roles of wolves and their prey as system drivers. A prior analysis of wolves in Denali documented a period with above average snowfall, high wolf populations and major changes in wolf and caribou numbers (Mech et al., 1998). In contrast, subsequent decades have been characterized by mild winters, a decreasing wolf population and increasing prey base. Here, we examine 30 years of variation in weather and prey populations to identify underlying decadal trends in these factors and their impacts on wolf demographics.

Our primary objectives were to: (1) estimate wolf vital rates for the study population, (2) quantify the effects of prey population size, productivity, and indices of vulnerability (i.e., winter weather) on wolf demographic rates, and (3) quantify the potential role of secondary non-ungulate prey resources (i.e., snowshoe hares) on wolf vital rates. We hypothesized that prey productivity and weather-driven prey vulnerability, rather than raw abundance, were the ultimate drivers of wolf population dynamics in the Denali ecosystem. Finally, we expected that snowshoe hares might play an important role in subsidizing wolf populations during cyclic population highs due to the large increase in available biomass during cyclic peaks. We expected that the overall numbers of hares and caribou in the current year would be representative of prey abundance, while snow depth and caribou fall calf:cow ratio in the previous year, would serve as indices of prey vulnerability. We based these assumptions on findings that young ungulates often comprise a large proportion of wolf diets (Murie, 1944) and that heavy snows increase the vulnerability of ungulates to predation by wolves (Mech et al., 1998, 2001).

MATERIALS AND METHODS

Study Area

The study area encompassed approximately 17,270 km^2 of wolf habitat primarily north and west of the Alaska Range in and adjacent to Denali National Park and Preserve (**Figure 1**) and ranged in elevation from 150 to 3,000 m. The eastern region of Denali contains habitat patches of boreal forest, high alpine, open gravel river bars, and willow-lined creeks. The western region of the park is more homogenous, dominated by relatively flat, lowland black spruce (Picea mariana) forest and long meandering rivers and wetlands.

The climate in Denali is sub-arctic and subject to wide variations in temperature and precipitation. On the north side of the Alaska Range, a snow-shadow effect predominates, resulting in low amounts of precipitation year-round and continental interior climate patterns generated by the High Arctic prevail in this region (Sousanes, 2006). At Denali headquarters (within the study area) temperature extremes range from 33 to −48°C. Daylight varies throughout the year with more than 20 h in June to 4 h in December. Summers are short and warm, and winters are long and cold with snow cover generally present October through early May. The average high temperature in July is 19°C, and the average low temperature in January is −21°C. Total annual precipitation is relatively low and averages ~ 38.2 cm. Most of the precipitation (20.5 cm) falls as rain during the summer months (Sousanes and Hill, 2017). Cumulative winter snowfall on the north side of the mountain ranged from 21 to 394 cm from 1986 to 2016 (**Table 1**; NOAA Regional Climate Centers, 2021).

Prey Numbers and Distribution

The diversity of habitat types in the eastern region of Denali supports resident populations of caribou (Rangifer tarandus), Dall's sheep (Ovis dalli), and moose (Alces alces) which constitute the main prey base for wolves in the region (Murie, 1944; Mech et al., 1998). High winds in the Outer Range (northwest of the Alaska Range) in winter months tend to result in wind-scoured ridges, leaving areas with relatively low snowpack and exposed vegetation. These conditions provide favorable wintering

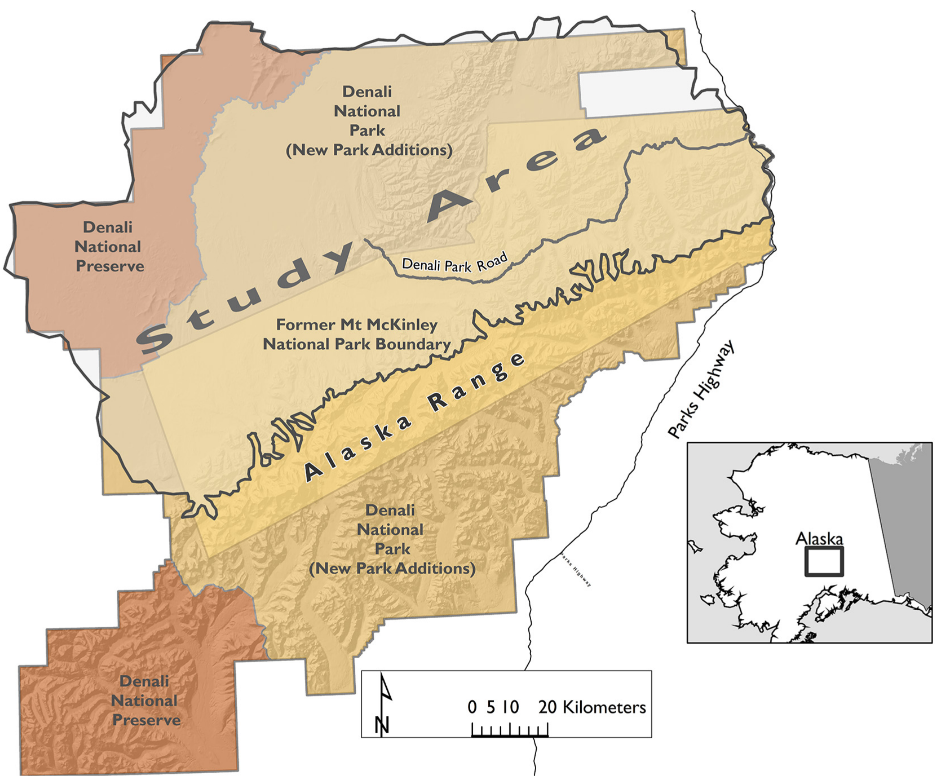

FIGURE 1 | Wolf project study area includes all areas north of the Alaska Range within Denali National Park and Preserve, Alaska, United States. The new park additions are north and south of the original park boundary (tan) and the Preserves are in the northwest and southwest (orange). The study area is denoted by shaded area.

TABLE 1 | Cumulative year snowfall and average winter temperature in Denali National Park and Preserve, Alaska, United States.

Year	Cumulative snowfall	Average winter temp °C
1986	128.3	−7.4
1987	120.7	−7.3
1988	246.4	−11.7
1989	225.8	−9.9
1990	394	−10.1
1991	322.6	−9.7
1992	394.2	−9.1
1993	280.2	−8.1
1994	177	−9.0
1995	165.9	−9.1
1996	181.9	−10.3
1997	169	−7.6
1998	110.3	−10.4
1999	296.2	−9.1
2000	150.1	−5.5
2001	190.5	−8.8
2002	78.7	−3.3
2003	175	−8.3
2004	235.7	−6.8
2005	146.8	−11.8
2006	97	−8.8
2007	161	−8.6
2008	178.1	−11.0
2009	119.4	−8.0
2010	205	−7.8
2011	27.4	−8.3
2012	31.5	−9.4
2013	21.4	−5.6
2014	113.3	−5.0
2015	211.8	−4.1
2016	181.1	−7.5

Data obtained from McKinley Park National Weather Service Cooperative Observer site near Denali National Park Headquarters. Cumulative snowfall from June of Year to July of Year+1, average winter temperature is from September (Year) to April (Year +1).

grounds for caribou, Dall's sheep, and moose (320 moose-equivalents/1,000 km^2, Adams et al., 2010). The western lowlands support lower densities of ungulates (primarily moose at 70 moose-equivalents/1,000 km^2, Adams et al., 2010), and salmon are an important food source for wolves in this region (Mech et al., 1998; Adams and Roffler, 2009; Owen and Meier, 2009; Adams et al., 2010). Throughout the study area, small mammals such as snowshoe hares and arctic ground squirrels are locally abundant and can represent a large amount of available biomass available to the predator community (Boonstra et al., 2001). Wolves in the study area are known to prey on snowshoe hares (Lepus americanus), Arctic ground squirrels (Spermophilus parryii), hoary marmots (Marmota caligata), beaver (Castor canadensis) and various birds (Murie, 1944; Mech et al., 1998). We used prey population data collected by concurrent studies in Denali (specified below) as covariates in our analyses to explain variation in wolf demographic rates.

Caribou

The caribou population in Denali is predominantly composed of members of the Denali Caribou Herd (DCH). The DCH exhibits a local seasonal migration of about 80 Km from summering and winter ranges. Calving season begins in late April and early May, with peak calving typically occurring synchronously in mid-May. Calving grounds are generally located in high elevations near glaciers and snowfields near the foothills of the Alaska Range, and winter range includes a large area of typically wind-swept slopes near the northeast corner of Denali (**Figure 2**).

The DCH has been monitored since 1984 and current protocols for monitoring the caribou population have been in place since 1986. Each year, caribou were captured by helicopter darting and radio-marked to monitor their survival, productivity and movements, and to aid in conducting composition surveys and herd counts (Adams and Roffler, 2009). Population estimates were derived annually from aerial composition and count surveys. For detailed methods on capture, radio collaring, composition, and population estimation see Adams and Meier (2018). Denali Caribou Herd size estimates from 1986 to 2016 ranged from 1,760 to 3,210 animals, with an average of 2,269 (SE 68.7) from 1986 to 2016. Calf:cow ratios ranged from 6.4 to 38 calves: 100 cows and averaged 19.6 calves:100 cows (SE 1.5, Adams, 2017).

Dall's Sheep and Moose

The Dall's sheep population in Denali occurred in alpine areas within the Alaska Range (**Figure 2**), and abundance estimates ranged from 1,374 to 2,288 during the course of our study. Sheep population estimates were obtained from aerial census in 1996 (Putera and Keay, 1998) and aerial distance sampling surveys in 2011 and 2013 (Schmidt and Rattenbury, 2013). Moose occurred in relatively low density throughout the study area, with greater density occurring in the north eastern region of the Denali (Owen and Meier, 2009; **Figure 2**). From 1986 to 2004, moose abundance estimates were obtained from aerial censuses using a stratified random sampling technique (Gasaway et al., 1986; Meier, 1986; Meier et al., 1991; Belant and Stahlnecker, 1997; Fox, 1997; Belant et al., 2000). Moose population estimates ranged from 1,104 to 2,168, averaging 1,677 (SE 121.0). Moose density estimates in the northern study area averaged 0.175 moose/km^2 (range: 0.13–0.24) and calf: cow ratios averaged 26 calves:100 cows (range: 0.22–0.39) (P. Owen, unpublished data).

Moose and sheep abundance data were too sparse for use as covariates in our analysis, although the available moose population estimates at least suggested a population trajectory similar to that of the caribou population (**Figure 3**). Salmon as a food source was assumed to be a relatively consistent seasonal subsidy (Adams and Roffler, 2010).

Snowshoe Hare

Snowshoe hares occurred throughout the study area, although relative abundance fluctuated wildly among years reflecting the regular 9–11 year population cycle of this species (Krebs et al., 2013). Relative abundance was indexed using the average number of adults observed per day during routine field work (McIntyre and Adams, 1999; McIntyre and Schmidt, 2012;

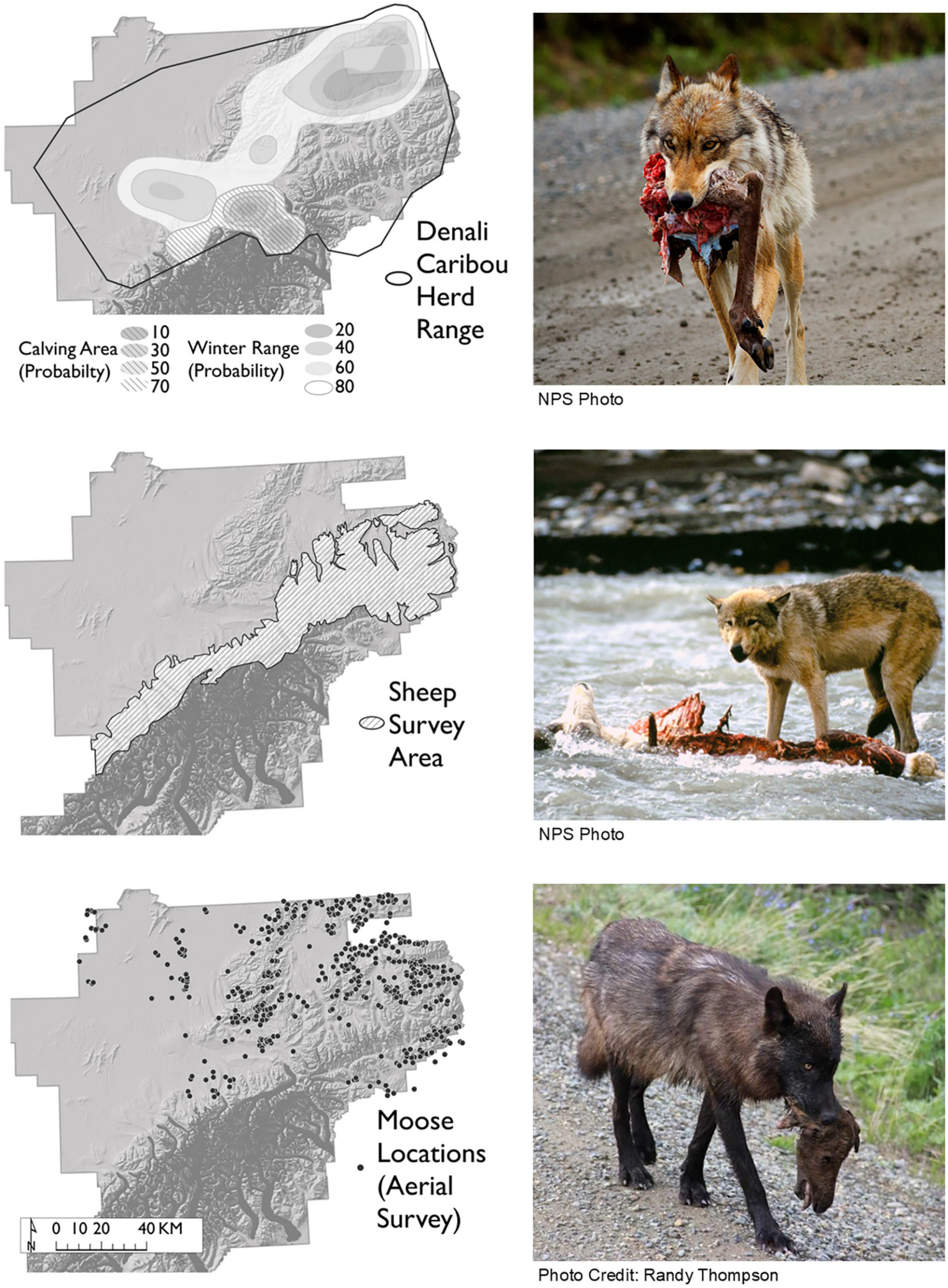

FIGURE 2 | Approximate distribution for three ungulate species that compose the main prey base for wolves within the Denali National Park and Preserve, Alaska, United States. Denali Caribou Herd range was derived from caribou distribution data from 1986 to 2007 (Adams and Roffler, 2010), calving distribution and winter range isopleths were derived from caribou location data from 1986 to 1996 (Schirokauer and Adams, unpublished data). Dall's sheep range is represented by the aerial survey area designed to cover a majority of sheep habitat. Moose distribution is indicated by the locations of moose groups located during aerial surveys conducted in November 2008 and 2011 (Owen and Meier, 2009; Meier and Owen, 2011). Corresponding photos show wolves feeding on each of the three ungulate species. Top two photos NPS Photos.

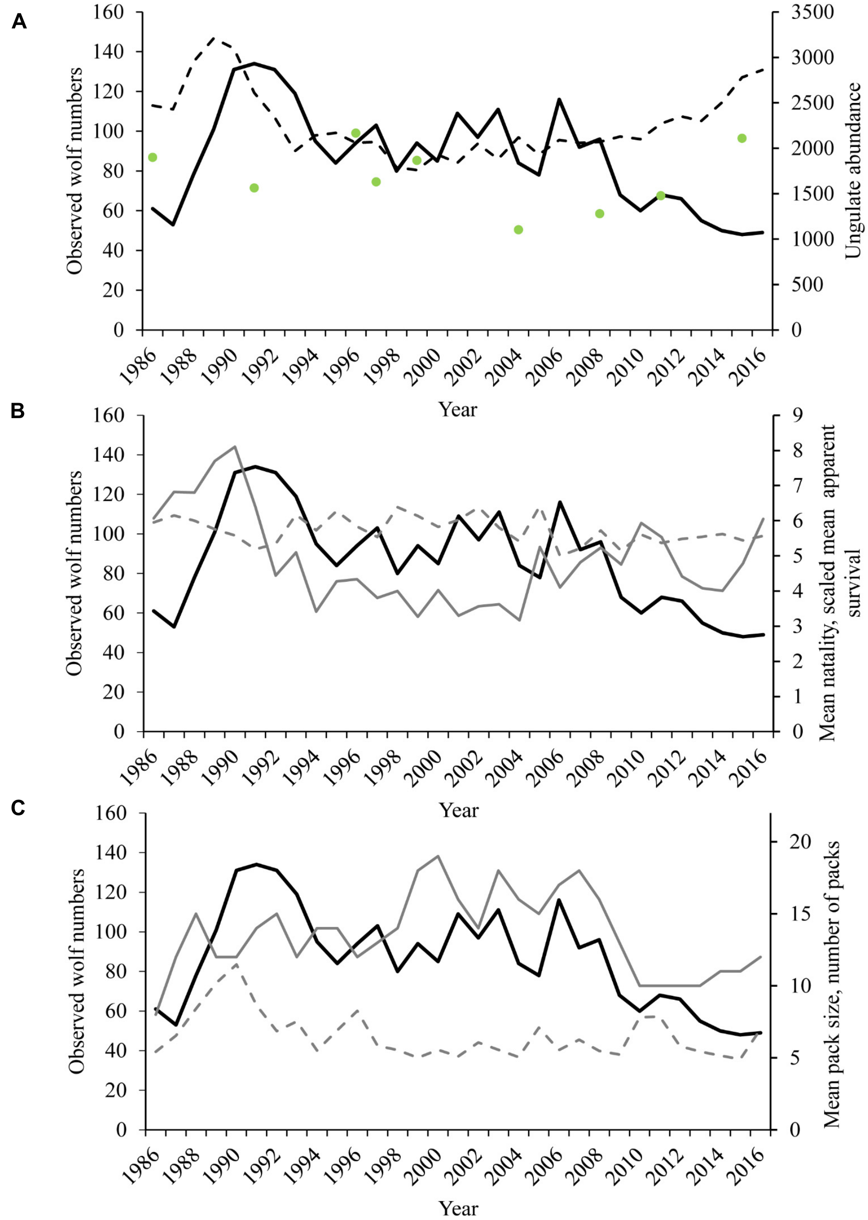

FIGURE 3 | The annual minimum number of wolves known to exist (solid black lines) and **(A)** Estimates of caribou (dashed line) and moose (green dots) abundance and **(B)** Mean natality (solid gray line), scaled mean apparent survival (dotted gray line, scaled apparent survival = mean apparent survival multiplied by a constant [8]) and **(C)** number of packs (solid gray line) and mean pack size (dotted gray line) in Denali National Park and Preserve, Alaska, United States from 1986 to 2016.

Schmidt et al., 2018a). There was considerable variation in the amplitude of the cycle peaks, with the third hare peak observed during our study period (2006–2009) being approximately fourfold larger than the previous two peaks (Schmidt et al., 2018b).

Data Collection

There is a long history of wolf research and monitoring in Denali, with research beginning in 1939 (Murie, 1944). The use of radio-telemetry for tracking and monitoring packs began in 1986 (Mech et al., 1998), and the wolf population has been continuously monitored since that time. While the wolf population within Denali represents a wolf population with relatively little human exploitation (Mech et al., 1998; Adams et al., 2010), all areas outside of the Denali boundary were open to hunting and trapping (collectively called "harvest") under state regulation.

Beginning in 1986, we attempted to maintain collars on two or more wolves in each pack whose home range was mostly within Denali boundaries. Wolves were immobilized by darting from helicopters and collared following protocols described in Meier et al. (2009). From 1986 to 2016, 421 individual wolves were captured and radio-collared (radio-marked) with very high frequency (VHF) collars. From 2003 to 2016, 86 of the VHF collars were equipped with GPS (Telonics, Mesa, CA, United States) which provided daily locations uploaded through the Argos or Iridium satellite system (Meier et al., 2009).

We noted estimated age and breeding status during capture and collaring operations (for details see Meier et al., 2009; Schmidt et al., 2017). Additional monitoring of collared wolves and pack mates during radio tracking flights through denning, pup-rearing and subsequent seasons allowed for additional confirmation of breeding status. In instances where breeding status was not noted (in early capture records), we identified breeders following the methods in Borg et al. (2015). Some packs were monitored during the course of the study after being captured in or near the study area but were ultimately determined to not reside within the study area. These packs were generally poorly monitored, due to lack of radio-tracking flights in their vicinity and were censored from our analyses. New and establishing packs were located during aerial tracking and efforts were made to radio collar members from each pack once considered to be a resident pack within the study area. A small number of wolves may reside in newly establishing packs at any given time prior to marking.

We located radio-marked wolves by VHF signal from fixed-wing aircraft roughly twice a month and recorded location, number of pack members, pelt colors, estimated age classes (if distinguishable), and any data on prey killed or eaten. We also recorded detailed information on mortality, den site location/use, and pack affiliation (Mech et al., 1998; Meier et al., 2009). Radio-marked wolves were lost from our study either due to mortality (e.g., natural, harvest, capture related, or unknown) or dispersal. We noted mortalities of collared wolves during aerial tracking and observation and (from 2003 to 2016) through weekly GPS data checks. Cause of death was determined through a field necropsy or by wildlife veterinary staff at the University of Alaska Fairbanks (UAF) or the Alaska Department of Fish and Game (ADF&G). Natural causes of death primarily included being killed by other wolves or starvation, but also included avalanches, drowning, or unknown causes. When carcasses were too decomposed to determine cause of death or both lab and field evidence were inconclusive, and there was no evidence of human interference, we recorded cause of death as "unknown natural" and fate was categorized as natural. Hunting and trapping were a primary source of human-caused mortality. A small number (n = 10) mortalities were attributed to capture events, either directly (e.g., dart injury) or indirectly (e.g., harvested or killed by other wolves while still sedated, or died from infection related to heart valve defect). We classified wolf fate to the unknown category when a fate could not be determined, either due to loss of contact or carcass recovery long after the mortality event.

The dispersal category included known dispersals of radio-marked wolves and instances where an entire pack "shifted" out of the study area. Pack shifts occurred when all known members of a pack moved from a previously held territory within the study area to new territory outside of the study area (n = 4). Packs outside of the study area were difficult to monitor due to logistical constraints, typically resulting in loss of contact with the pack. These members were censored from the time of dispersal or pack shift from the study population for the purpose of our apparent survival analyses.

Data Analysis

We estimated survival and natality rates using an integrated population modeling approach incorporating known-fate information from collared individuals and repeated counts of unmarked pack mates (Schmidt et al., 2015, 2017). We used the model structure presented by Schmidt et al. (2017) which combined cause-specific known-fate (Royle and Dorazio, 2008; Schmidt et al., 2010) and open N-mixture (Dail and Madsen, 2011) sub-models for the collar and count data, respectively.

Use of this integrated framework allowed us to make direct inference to the entire population of wolves in our study area, without relying on the assumption of a representatively marked subsample (Schmidt et al., 2017). This was important because suspected breeders were targeted for marking when possible and tended to accrue in the marked population over time due to higher survival and lower rates of dispersal. Most of the wolves in the population were unmarked, therefore formally including them in the analysis increased our power to assess annual variation in population parameters in the context of explanatory covariates. Finally, the integrated approach also accounted for temporal variation in resighting effort. This was important because variable weather conditions, funding, or other logistical challenges resulted in fluctuating sighting effort over time. Together these features provided much stronger inference than would be possible using simple known-fate data and unadjusted counts (Schmidt et al., 2015, 2017).

We estimated the probability of mortality and dispersal based on the collared subset of the population. We present estimates of true survival and dispersal as overall means because cause-specific losses were only available from our relatively small sample of collared wolves. Because the cause of loss (i.e., mortality vs. dispersal) was unknown for the much larger unmarked subset of wolves, we also estimated apparent survival, the probability of surviving and not dispersing, for the unmarked sample. We considered dispersal to be equivalent to mortality in terms of apparent survival because the individual was effectively lost from the population. We were primarily interested in the relationship between wolf population dynamics and a suite of covariates, which in the absence of cause specific mortality for the much larger unmarked subset of the population limited us to assessments of apparent survival.

Local dispersal events (i.e., an individual switching from one monitored pack to another or forming new packs) were observed in the marked sample throughout the study (n = 34) potentially affecting parameter estimates. We expect that these local dispersers would cause some upward bias in natality rates, and possibly limited negative bias in apparent survival rates. This is because while the local disperser was lost from the original pack, it was not lost from the study population. Some portion of the potentially negative pressure on estimates of apparent survival was likely mitigated by concurrent losses in the accepting pack during the interval between observations. Overall, local dispersals represented <10% of all losses of collared individuals, suggesting any bias would be limited (see section "Results").

In instances where contact with a radio-marked wolf was lost, the period after loss of contact was right censored. If there was a lapse in time between the interval in which the wolf was last seen alive and the interval when the mortality was detected, the timing of mortality was estimated (Royle and Dorazio, 2008). With the advent of GPS collars, determining the exact date of death was more accurate and therefore estimation of date of death was less frequent after 2003. For wolves that were collared and died in the same interval (month), we assumed they were alive on the first of the month prior to the collaring and died over the interval in which collaring occurred. Radio-marked wolves that were not a member of a pack, as indicated by one or more visual confirmations of the wolf alone and without evidence of affiliation with known packs or other individual wolves were censored from the survival analyses.

As in Schmidt et al. (2017), we formulated our model based on the biological year (BY) starting in May of the current year t through April of the following year t+1. Packs were open to additions over the May-August interval, reflecting primarily pups born in May and recruited over the 3 month interval (i.e., natality). While we assume that most of these additions were of pups, some additions may have resulted from dispersing adults being accepted into existing packs. We estimated monthly apparent survival throughout the BY as well.

Our model structure directly followed that of Schmidt et al. (2017). For collared individuals, the observed state, Y_{it}, is modeled as:

$$Y_{i,t} \sim Bern\left(Y_{i,t-1}\phi^{A}_{i,t-1}\right)$$

where the state for individual i at time t depends on the state at t–1 and apparent survival probability, $\phi^{A}_{i,t-1}$. The models for the probabilities of surviving, $\phi^{S}_{i,t-1}$, and not dispersing, $\phi^{D}_{i,t-1}$, can be written as:

$$logit(\phi^{S}_{i,t-1}) = x'_{i,t-1}\beta$$

$$logit(\phi^{D}_{i,t-1}) = x'_{i,t-1}\beta$$

$$\phi^{A}_{i,t-1} = \phi^{S}_{i,t-1} \times \phi^{D}_{i,t-1}$$

where $x_{i,t}$ are covariates and β are coefficients. For the counts of unmarked pack-mates, the surviving number of individuals, Sj, t, within each pack, j, as:

$$S_{j,t} \sim Bin\left(N_{j,t-1} - R_{i,t-1}, \phi^{A*}_{i,t-1}\right)$$

where $R_{i,t-1}$ indicates the number of individuals newly marked and then transferred to the known-fate sample. As above, we modeled $\phi^{A*}_{i,t-1}$ in 2 parts as

$$\text{logit}(\phi^{S*}_{i,t-1}) = x'_{i,t-1}\beta^*$$

$$\text{logit}(\phi^{D*}_{i,t-1}) = x'_{i,t-1}\beta^*$$

$$\phi^{A*}_{i,t-1} = \phi^{S*}_{i,t-1} \times \phi^{D*}_{i,t-1}$$

where $x_{i,t}$ is a vector of covariates and β^* represents the coefficients. Note that components of β and β^* were shared (i.e., data integration). The additions, $B_{j,1}$, to each pack, j, during the May–August interval can be written as:

$$B_{j,1} \sim Pois(\gamma_j)$$

where γ_j represents the number of individuals recruited into each pack. To include covariate information, $\boldsymbol{w}_j$, natality can be parameterized as:

$$\log\left(\gamma_j\right) = \boldsymbol{w}_j\boldsymbol{\rho}$$

where $\boldsymbol{\rho}$ represents the coefficients. The counts can be modeled as:

$$n_{j,t} \sim Bin(N_{j,t} - R_{jt}, p_{jt})$$

where the observed number of individuals, $n_{j,t}$, is a function of true abundance, $N_{j,t}$, minus any individuals transferred to the known-fate sample, R_{jt}, and detection probability, p. For packs and months when counts were not certain, we modeled p as a random effect allowed to vary by month. Please see Schmidt et al. (2015, 2017) for additional details on model structure and fitting. JAGS code for this implementation is available on FigShare (see section "Data Availability Statement").

We considered a suite of covariates that we expected to explain variation in apparent survival and natality rates. We began by assuming that the components of apparent survival would vary by month and that individuals identified as breeders would remain in packs at higher rates than other wolves (i.e., Schmidt et al., 2017). Breeder status was assigned to radio-marked individuals on a yearly basis. If an individual wolf was identified as a known breeder in year t, and died before whelping in year $t+1$, it was assigned as a breeder in year $t+1$. This was intended to apply the covariate of breeding status to an individual wolf's survival risk, regardless if it had the opportunity to breed in the given season.

We also included covariates related to prey abundance and availability: hares$_t$, herd size$_t$, calf ratio$_{t-1}$, and snow depth$_{t-1}$. Because pups are generally born in May, we considered hares$_{t-1}$, herd size$_{t-1}$, calf ratio$_{t-1}$, and snow depth$_{t-1}$ as potential covariates on natality, assuming that conditions prior to whelping would be related to natality. We also assumed that the loss of a breeder in BY$_{t-1}$ would negatively affect natality rates (Borg et al., 2015; Schmidt et al., 2017).

RESULTS

We monitored 8–19 wolf packs annually (**Table 2**) and analyzed data from 379 radio-marked wolves from 73 packs monitored between BY1986 -2016. Our sample included 194 (51%) females and 185 (49%) male wolves. Marked wolves remained in the sample an average of 1.5 years for a total of 1,151 collared wolf-years in the sample. All age classes were represented in the sample (**Table 3**) although older age classes were more frequent in the sample because collaring efforts targeted older individuals as they were more likely to stay within the study area. We identified 182 wolves as suspected or confirmed breeding members of the pack. On average, wolves were breeders in their pack for 2.8 years, with a maximum of 10 years.

TABLE 2 | Numbers of packs monitored and wolves marked with radio-collars for biological year (May–April) in Denali National Park and Preserve, Alaska, United States.

Biological Year	Packs	Collared wolves	Initial number	Mean pack size	Pack size distribution
1986	8	8	58	7.3	
1987	12	14	102	8.5	
1988	15	19	168	11.2	
1989	12	22	170	14.2	
1990	12	21	198	16.5	
1991	14	25	186	13.3	
1992	15	29	154	10.3	
1993	12	31	117	9.7	
1994	14	20	108	7.7	
1995	14	22	123	8.8	
1996	12	29	136	11.3	
1997	13	28	110	8.4	
1998	14	23	97	6.9	
1999	18	25	118	6.5	
2000	19	34	145	7.6	
2001	16	26	108	6.8	
2002	14	24	106	7.6	
2003	18	20	138	7.7	
2004	16	26	119	7.5	
2005	15	20	133	8.8	
2006	17	26	151	8.9	
2007	18	30	173	9.6	
2008	16	19	123	7.7	
2009	13	19	106	8.1	
2010	10	16	111	11.1	
2011	10	20	117	11.7	
2012	10	20	85	8.5	
2013	10	13	78	7.8	
2014	11	15	81	7.3	
2015	11	19	79	7.2	
2016	12	19	120	10.0	

Initial number is the estimated number of wolves (model-based) in all monitored packs in August, and mean pack size = initial number/packs. Pack size distribution shows fall pack counts for packs monitored in the study area, with a vertical bar for each pack and vertical height portraying relative pack size (vertical scale 0 to 33).

TABLE 3 | Number of wolves by estimated age at first capture in Denali National Park and Preserve, Alaska, United States between biological years 1986 to 2016.

Age class at first capture	Number collared
Pup (<12 months)	72
Yearling (12 – 24 months)	83
Adult (2 – 8 years)	212
Old (>8 years)	12
Total	379

In the collared sample, more wolves were lost to death by natural causes (i.e., intraspecific strife, starvation, drowning) than any other fate (52% natural causes, **Supplementary Figure 1**). Harvest-related mortalities, unknown cause of death, and losses from packs due to dispersal occurred at similar rates in the collared sample (harvest 15%, dispersal, 16%, **Supplementary Figure 1**). Capture-related mortalities were rare, only occurring in 10 out of 421 capture events. After accounting for unknown fates of dispersing wolves, the majority were ultimately harvested (49%, **Supplementary Figure 1**).

The probability of detecting unmarked wolves during pack counts was lower during the late summer/early fall months (May–September), corresponding to periods with little or no snow cover and the presence of obscuring vegetation (**Supplementary Figure 2A**). Probability of detection was consistently high in winter months, peaking in March when increased daylight hours, snow cover, and increased flight efforts related to capture operations improved detection. Monthly survival probabilities were high and relatively consistent throughout the year (**Supplementary Figure 2B**). Dispersal was more likely to occur in the summer (May–August) or late winter [February, corresponding to the pre-breeding season (Borg et al., 2015)] and was less likely during the early to mid-winter months (**Supplementary Figure 2C**).

Based on the basic integrated model with no covariates and no random effects, mean annual apparent survival probability was 0.65 (0.61, 0.68) for known breeders and 0.48 (0.45, 0.51) for other wolves (**Supplementary Figure 3**). Mean annual survival probability (dispersal excluded) for known breeders (0.68 [0.65, 0.72]) was slightly higher than estimates for other wolves (0.63 [0.59, 0.67]) and mean estimated annual dispersal probability was much lower for known breeders (0.05 [0.03, 0.07]) than for other wolves (0.24 [0.21, 0.29], **Supplementary Figure 3**).

Several covariates explained variation in wolf apparent survival. Cumulative snowfall in the preceding winter and higher calf:cow ratios in the DCH were associated with higher apparent survival in wolf packs (**Figures 4**, **5**). In contrast, the size of the DCH and the index of hare abundance were negatively related to apparent survival although the confidence interval for the effect of hare abundance slightly overlaps 0 (**Table 4** and **Figures 4**, **5**).

Metrics of prey abundance and availability also influenced wolf natality. Cumulative winter snowfall in the winter preceding was positively related to wolf natality (**Table 4**) with peak natality occurring following a winter of severe snowfall in winter 1989-90 (**Figures 6**, **7**). The DCH calf:cow ratio and herd size in the previous year were positively associated with the number of wolves added to packs in the spring. The index of hare abundance was also positively associated with wolf natality (**Table 4** and **Figure 7**). Conversely, the loss of a breeder in the preceding year decreased natality rates for wolf packs (**Table 4**).

Spring population estimates derived from the model ranged from 58 wolves at the start of the study in 1986 to a high of 198 wolves in 1990 following a dramatic increase in caribou herd numbers (**Figures 3A**, **8**). There was an interaction between mean pack size and the number of packs observed. In years with high prey availability, mean pack size increased, as seen following during a period of high snowfall in the late 1980s and early 1990s and again during the peak hare index around 2010 (**Figure 3C**). From the early 1990s to 2000s, the number of packs was high and variable, with relatively low variability in mean pack size (**Figure 3C** and **Table 2**).

DISCUSSION

We found a strong influence of climatic conditions in the form of cumulative snowfall on wolf survival, natality, and population size. Wolves experienced greater apparent survival and natality and population size increased during periods with more cumulative snow fall. We also found that survival, dispersal, and population size all declined as the caribou population grew, in direct contrast to the expectation that increased prey biomass should result in higher wolf population size (reviewed in Fuller et al., 2003). In addition, our findings provide evidence that non-ungulate prey can impact wolf population dynamics, subsidizing ungulate resources when abundant. Together these results clarify the nature of bottom-up effects in wolf -ungulate systems, indicating that the influence is not simply a density-dependent relationship between large ungulate prey and predator populations. Our work provides insights into the role of weather and secondary prey resources in driving wolf populations, and our results offer important context for wolf management and conservation, particularly in Alaska where wolf control is implemented widely.

One of the most important questions in the field of ecology, particularly wolf ecology, is how populations of predators affect those of their prey. Our findings are consistent with those from other components of the Denali ecosystem (Schmidt et al., 2018a,b) and previous work (Murie, 1944; Mech et al., 1998) suggesting that bottom-up forces play a large role in predator-prey dynamics in this system. While bottom-up drivers in food webs are linked to primary productivity, whereby increased primary productivity leads to increases in herbivores which leads to increases in predators (Paine, 1980), a more intricate food web paradigm may better explain the wolf-prey dynamics (Eisenberg et al., 2013).

We found that prey vulnerability affected wolf demographics in ways that were distinct from effects of prey abundance. Although measuring vulnerable prey biomass can be challenging (Fuller et al., 2003), in several systems key factors influencing vulnerability are so dominant that they provide relatively reliable indices of prey vulnerability. For example, in Isle Royale the number of moose 10 years and older has been shown to be a strong predictor of wolf population trends (Peterson, 1977; Peterson and Page, 1988) and evidence for bottom-up control (Sand et al., 2012). Previous work determined prey availability and corresponding trends in wolf populations in Denali were driven largely by snow depth (Mech et al., 1998), and indeed we found that greater snowfall in the preceding year increased survival and natality in the Denali wolf population (**Figures 5**, **7**). Additionally, we saw that increasing vulnerable prey as seen through higher calf ratios increased wolf survival and natality. This evidence supports the effect of prey base, moderated by factors that influence vulnerability, are strong drivers of the wolf demographic rates. Because ungulate prey face similar nutritional and mobility stressors with increased snow depth, snow depth is likely to be broadly applicable as an index of vulnerability across prey species in regions with seasonal snow cover.

While winter conditions can have immediate effects on prey vulnerability, our findings indicate that cumulate impacts over time may also be important. Prenatal nutrition can impact fetuses during severe winters and persist across additional generations (Zamenhof and Van Marthens, 1978; Mech et al., 1991; Messier, 1995), and consecutive winters with deep snowpack pose a cumulative effect on prey vulnerability (Mech et al., 1987; McRoberts et al., 1995; Messier, 1995). In general, weather conditions in the Denali study are have been mild since 1992, with several consecutive winters with low cumulative snowfall and very low number of days with snow on ground over 53 cm, and a consistent decrease in snow depth over time (**Table 1**). In conjunction, plant biomass (as measured by running NDVI) increased almost linearly through 2008 (Schmidt et al., 2018b). Recent increases in caribou and moose numbers (**Figure 3**) and the effect of improved nutrition coupled with decreased energetic costs in winter may be evidence that ungulates are in good condition, and thus harder for wolves to catch. Thus, reductions in ungulate vulnerability mediated through changing environmental conditions can release prey from low density, even in the presence of unregulated wolf numbers, as also seen in a

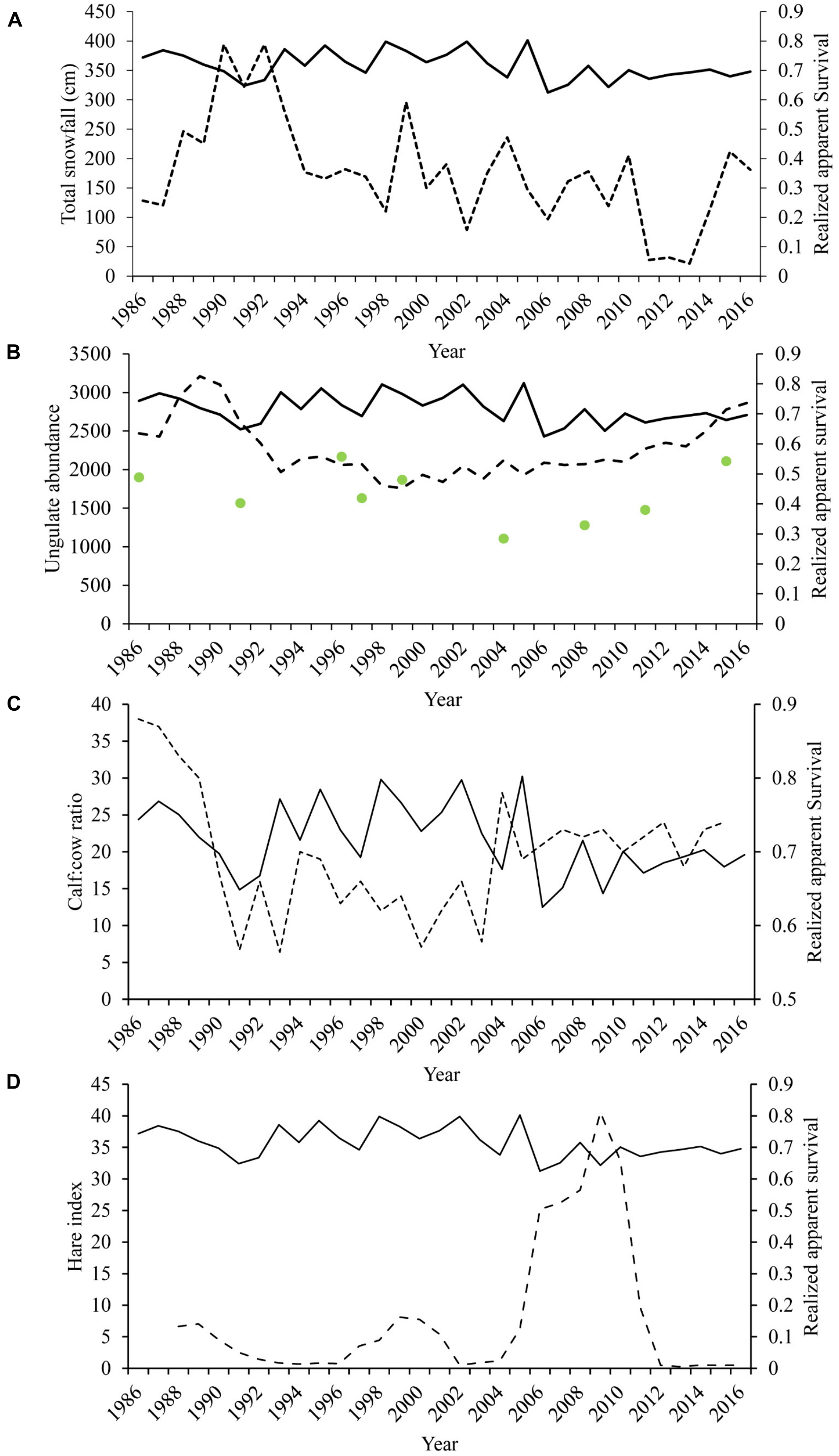

FIGURE 4 | Estimated annual apparent survival of wolves (a proportional combination of known breeders and wolves of unknown status) in Denali National Park and Preserve, Alaska, United States for biological years 1986–2016. Annual estimated apparent survival (solid lines) is plotted in relation to **(A)** total annual snowfall (in cm), **(B)** caribou (dashed line) and moose (green dots) abundance, **(C)** caribou cow:calf ratios (dashed line), and **(D)** the snowshoe hare abundance index (dashed line).

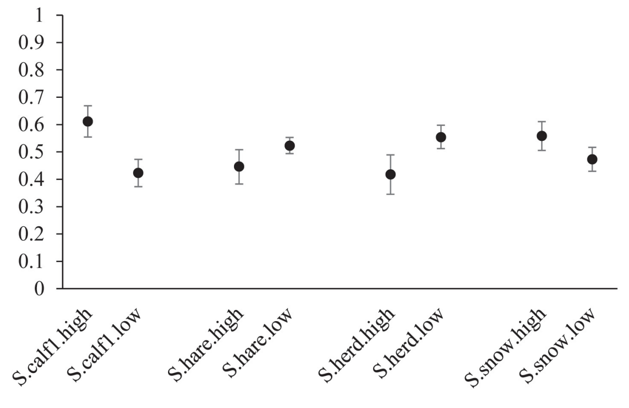

FIGURE 5 | Comparison of covariate values on estimated survival for wolves in Denali National Park and Preserve, Alaska, United States. Conditions included are: high caribou calf:cow ratio in the preceding year (S.calf.high), low caribou calf:cow ration in the preceding year (S.calf.low), high hare index in the current year (S.hares.high), low hare index in the current year (S.hares.low), high caribou herd size in the current year (S.herd.high), low caribou herd size in the current year (S.herd.low), high snowfall in the previous winter (S.snow.high), and low snowfall in the previous winter (S.snow.low). Values used represent the range of values observed during our study. Error bars represent 95% credible intervals. For each scenario all other covariates are held at mean values.

weather-related increase in the Forty-Mile Caribou Herd prior to implementation of wolf control actions (Boertje et al., 2017).

We found that when conditions allow for the increase in a resident caribou herd, as seen in the latter part of our study, wolf natality increased, yet contrary to expectations wolf population size declined (**Figures 3A,B**). Intrinsic social characteristics and territoriality may moderate wolf population response to growing prey populations (Fuller et al., 2003), and we speculate that territoriality in our study area may play a restricting role on population growth. The decline in wolf population size is attributed to fewer packs in recent years, rather than a decrease in mean pack size (**Figure 2C** and **Table 2**). As prey becomes harder to catch, wolf packs respond by increasing search distance for vulnerable prey, requiring increased territory sizes (Johnson et al., 2013). As growing ungulate populations are evidence of reduced ungulate vulnerability, this can result in increased wolf territory sizes and fewer packs within same area. The upper limit on the number of territories that can be supported effectively caps breeding by a cooperatively breeding social carnivore, limiting the influence of increased natality on population growth (Fuller et al., 2003). This limitation may be evidence of how territoriality can be a self-regulating mechanism for a population (Wallach et al., 2015).

Mean pack size has been proposed as an alternate to wolf density measures for tracking changes within a study area as density estimates alone are problematic (Schmidt et al., 2017). However, mean pack size and pack territory size or the number of territories that a given area can support must also be considered. As wolf natality and apparent survival increase in response to prey vulnerability, we expect mean pack sizes to increase, as seen following the increase in caribou vulnerability of the late 1980s and early 1990s and during the high hare peak around 2010 (**Table 2**). While mean pack size increases can lead to increases in population during these periods of increased prey vulnerability, during periods without dramatic shifts in prey vulnerability, the number of packs in the study area drives more interannual variation in the population (**Figure 2C**). The interaction between group size and number of groups, as mediated by food availability and environmental conditions is likely to be important for determining density for many social, territorial species.

The concurrent long-term studies on caribou and wolves in the Denali ecosystem allowed for a unique long-term analysis of predator-prey dynamics. The effects of other large ungulates and carnivores in this system were less clear due to lack of consistent data (see section "Materials and Methods"). Despite this limitation, wolf natality responded strongly to caribou numbers but was insensitive to an apparent moose increase in the mid-1990s (**Figure 6**). Although DCH abundance measures may reflect a relatively coarse metric of ungulate biomass (caribou comprised 39% of kills from 1986 to 1993, Adams and Roffler, 2010), it does provide a valuable index of change in the abundance of a key ungulate prey species for wolves in this system.

TABLE 4 | Parameter estimates for models evaluating the effect of covariates on wolf natality (number of wolves added to the population) and survival (number of wolves lost from the population) over three decades in Denali National Park and Preserve, Alaska, United States.

Parameter	β ± SE	2.5% CI	97.5% CI
Natality Model			
Cumulative Snow Fall	0.075 ± 0.0355	0.008	0.146
Hare abundance	0.065 ± 0.0316	0.090	0.237
Calf:Cow ratio in Denali Caribou Herd	0.164 ± 0.0371	0.002	0.126
Denali Caribou Herd Size	0.106 ± 0.0380	0.030	0.178
Breeder Loss	−0.315 ± 0.0774	−0.471	−0.166
Survival Model			
Cumulative Snow Fall	0.0719 ± 0.0336	0.005	0.137
Hare abundance	−0.063 ± 0.0336	−0.128	0.004
Calf:Cow ratio in Denali Caribou Herd	0.174 ± 0.0467	0.082	0.266
Denali Caribou Herd Size	−0.108 ± 0.0426	−0.190	−0.022

All parameters are estimated for covariates measured in year t-1 for natality.

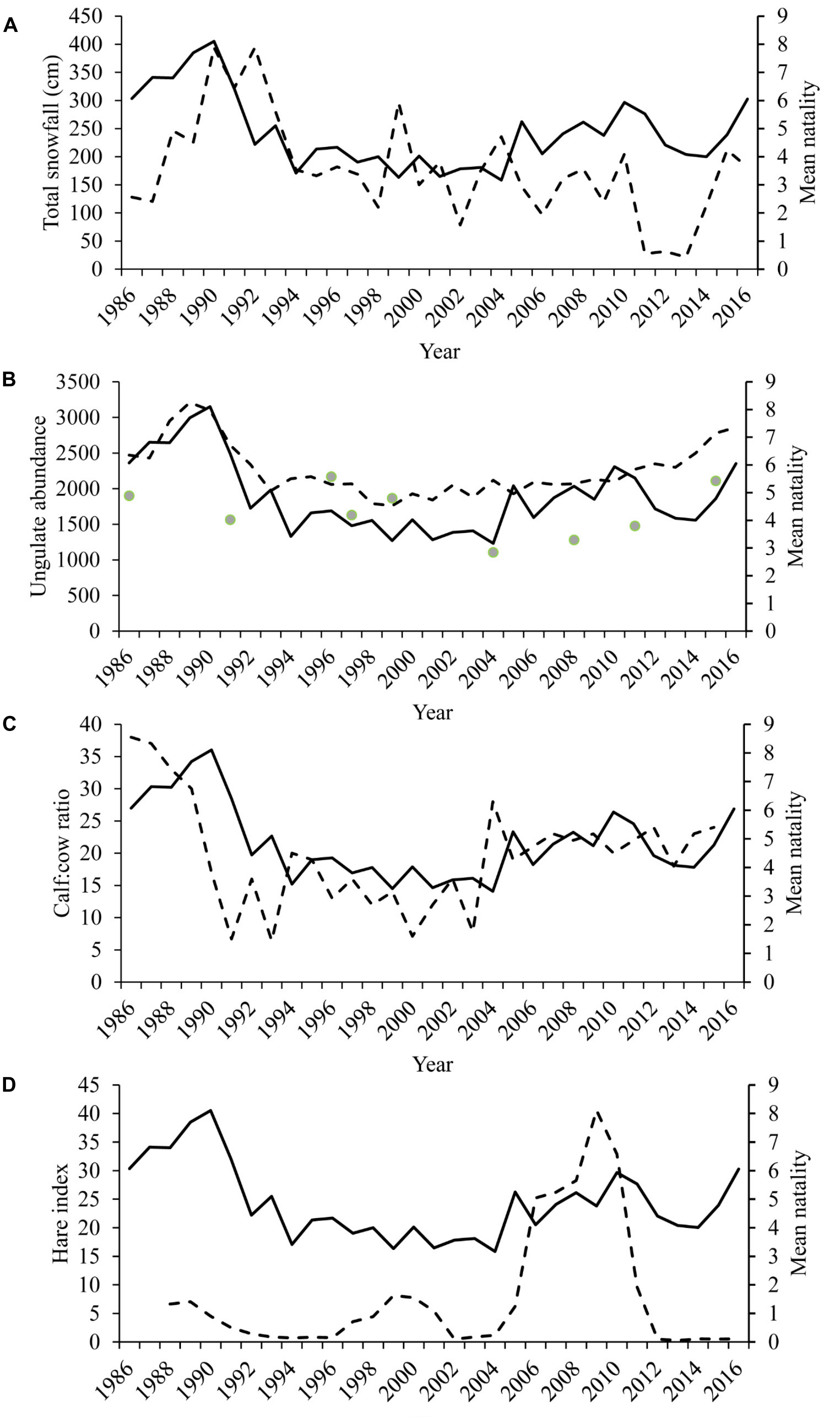

FIGURE 6 | Estimated mean number of individuals added to each pack annually (mean natality; solid line) in Denali National Park and Preserve, Alaska, United States for biological years 1986–2016. Natality (mean natality, solid line) is plotted in relation to **(A)** observed total snowfall (dashed line) in the winter immediately preceding each biological year, **(B)** caribou (dashed line) and moose (green dots) abundance, **(C)** caribou cow:calf ratio (dashed line), and **(D)** the snowshoe hare abundance index (dashed line).

We found evidence for the influence of secondary prey on metrics of wolf demographics as hare abundance prior to whelping had a strong effect on wolf natality rates. Previous work posited that high pup survival rate estimated in Denali may have be in part due to the presence of small prey such as ground squirrels, marmots, beavers, and hares during summer

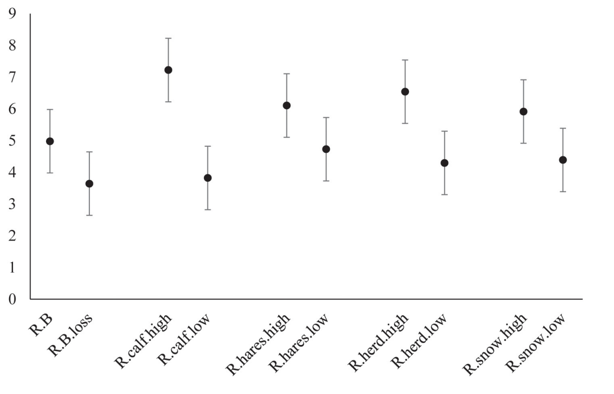

FIGURE 7 | Comparison of covariate values on estimated average number of individuals added to each wolf pack in Denali National Park and Preserve, Alaska, United States. Conditions included are: no breeder lost (R.B), loss of a breeder (R.B.loss), high caribou calf:cow ratio in the preceding year (R.calf.high), low caribou calf:cow ration in the preceding year (R.calf.low), high hare index in the preceding year (R.hares.high), low hare index in the preceding year (R.hares.low), high caribou herd size in the preceding year (R.herd.high), low caribou herd size in the preceding year (R.herd.low), high snowfall in the previous winter (R.snow.high), and low snowfall in the previous winter (R.snow.low). Values used represent the range of values observed during our study. Error bars represent 95% credible intervals. For each scenario all other covariates are held at mean values.

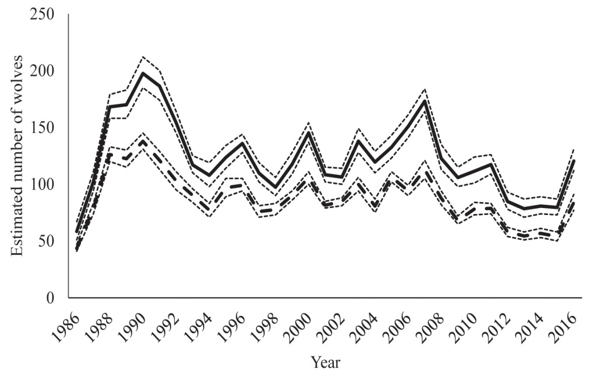

FIGURE 8 | Estimated number of wolves in study area population in Denali National Park and Preserve, Alaska, United States derived from model for spring (solid line) and fall (dashed line). Dotted lines around estimates indicate 95% credible intervals.

months (Mech et al., 1998; Haber and Holleman, 2013). Biologist Adoph Murie documented the use of hares by wolves in the 1940's and suggested that hares may play a significant role in subsidizing wolves (Murie, 1944). Nutritional condition of females at breeding and pregnancy determines litter size (Sadleir, 1969) and this principle applies to wolves (Boertje and Stephenson, 1992). Thus, hare abundance during this time period may result in improved prenatal condition of breeding females and increased litter size and early survival of pups (Sadleir, 1969; Boertje and Stephenson, 1992).

The influence of a secondary prey source such as hares on wolf natality further supports our findings implying that wolf productivity is otherwise limited by prey availability. The influence of primary productivity on subsequent hare abundance further supports the prevalence of bottom up processes (Schmidt et al., 2017, 2018a,b). Interestingly, apparent wolf survival decreased with increased hare numbers. It is possible that presence of hares may increase time individuals spend traveling alone during summer months as they take advantage of abundant small prey (Benson and Patterson, 2015) and time spent away from packs may increase mortality risk or dispersal. Alternatively, increased natality may put more pressure for provisioning on packs during the winter months leading to decreased survival or increased dispersal (Mech et al., 1998).

Comparing vital rates and predator-prey associations from our study in Denali to those in other areas with different management regimes (e.g., predator control) and prey population characteristics (e.g., migratory prey) can allow managers to make more informed and effective decisions regarding the conservation and management of both wolves and their ungulate prey in a variety of systems. Overall, annual apparent survival rates in Denali were relatively consistent (**Figure 5**). We found that apparent survival of breeding wolves was lower in Denali (0.68) than for breeding wolves in Yukon-Charley (∼0.8) or all wolves in Brooks Range (∼0.8), whereas survival for non-breeding wolves in Denali (0.63) was higher than that in Yukon-Charley (Adams et al., 2008; Schmidt et al., 2017). Models based on Yukon-Charley data suggested that apparent survival should be approximately 0.9 for breeding wolves and 0.6 for non-breeding wolves in interior Alaska (Schmidt et al., 2017). The finding that survival rates in the lightly harvested population of wolves in Denali was lower than expected for breeding wolves is intriguing. Intraspecific strife is the leading cause of natural mortality for wolves in Denali (Mech et al., 1998, this paper) and breeders may be at greater risk for mortality in these conflicts (Cassidy, 2013; Cubaynes et al., 2014; Cassidy et al., 2017) although more recent work suggests that breeders are associated with increased risk of attack but not necessarily mortality (K. Cassidy, pers. comm.). Prey base may also be implicated in the reduced survival of wolves in Denali, because when caribou are less vulnerable and wolves switch to sheep and moose (Murdoch, 1969; Mech et al., 1998), they may have greater risk of injury or mortality in hunting (Mech et al., 2015), especially as breeders take a leadership role in hunting (Mech, 2000; Peterson et al., 2002; MacNulty et al., 2011).

We found an inverse relationship between wolf natality and apparent survival. Because apparent survival is a composite of mortality and dispersal from the population, it was difficult to clearly determine if mortality or dispersal was increasing in response to increased natality. Interpack competition may act to increase both sources of loss from the population (Messier, 1985; Ballard et al., 1987; Peterson and Page, 1988; Gese and Mech, 1991; Boyd and Pletscher, 1999). However, dispersal and survival rates from the known fate collared sample indicates that dispersal, rather than survival was inversely correlated with natality rates. One hypothesis for this is that large litters increase interpack competition by putting more pressure on other pack members to leave or travel more, leading to higher dispersal and reducing apparent survival (Mech et al., 1998;

Adams et al., 2008; Smith et al., 2010). However, the timing of dispersal in our study coincided with the pre-breeding and breeding season, showing similarity with studies in the Brooks Range and Yukon-Charley (Adams et al., 2008; Schmidt et al., 2017) and suggesting that pressures due to breeding may predominate as precursors to dispersal.

Our results contribute to a growing body of evidence that environmental conditions may ultimately determine prey vulnerability and predator dynamics. Leveraging data from two concurrent, long-term studies allowed us to view predator-prey dynamics over a time scale commensurate with a changing climate. Global climate change is occurring more rapidly at northern latitudes (Intergovernmental Panel on Climate Change [IPCC] et al., 2013), underscoring the importance of understanding the mediating role environmental conditions play in a predator-prey-climate system.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://irma.nps.gov/DataStore/Reference/Edit/2288285 and https://doi.org/10.6084/m9.figshare.17054369.

AUTHOR CONTRIBUTIONS

BB conducted the data collection from 2010 to 2021, prepared the data, conducted the analyses, and wrote the manuscript. DS oversaw the biological program research and provided support and input on the wolf research project and this manuscript.

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Joshua H. Schmidt conducted the statistical analysis for the integrated wolf population model and provided considerable assistance with the manuscript. Layne Adams collected and curated the data on the Denali Caribou Herd from 1986 to 2016 and on the Denali wolves for 1986–2003. John Burch conducted wolf captures in Denali from 1986 to 2003. Tom Meier oversaw the Denali wolf research program and was the Biological Program manager from 2004 to his untimely death in 2012. This work is dedicated to Tom and his legacy of leadership and work in Denali. Stephan Arthur oversaw the Denali wolf research from 2012 to 2016. Carol McIntyre collected and provided the hare index data for analysis. Maggie MacCluskie, Kaija Klauder, and Laura Prugh all provided valuable insight, input, and editing that lead to significant improvement in the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.791161/full#supplementary-material

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Distribution, Status, and Conservation of the Indian Peninsular Wolf

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An understanding of the distribution range and status of a species is paramount for its conservation. We used photo captures from 26,838 camera traps deployed over 121,337 km^2 along with data from radio-telemetry, published, and authenticated wolf sightings to infer wolf locations. A total of 3,324 presence locations were obtained and after accounting for spatial redundancy 574 locations were used for modeling in maximum entropy framework (MaxEnt) with ecologically relevant covariates to infer potentially occupied habitats. Relationships of wolf occurrence with eco-geographical variables were interpreted based on response curves. Wolves avoided dense wet forests, human disturbances beyond a threshold, arid deserts, and areas with high top-carnivore density, but occurred in semi-arid scrub, grassland, open forests systems with moderate winter temperatures. The potential habitat that can support wolf occupancy was 364,425 km^2 with the largest wolf habitat available in western India (Saurashtra-Kachchh-Thar landscape 102,837 km^2). Wolf habitats across all landscapes were connected with no barriers to dispersal. Breeding packs likely occurred in ≈89,000 km^2. Using an average territory size of 188 (SE 23) km^2, India could potentially hold 423–540 wolf packs. With an average adult pack size of 3 (SE 0.24), and a wolf density < 1 per 100 km^2 in occupied but non-breeding habitats, a wolf population of 3,170 (SE range 2,568–3,847) adults was estimated. The states of Madhya Pradesh, Rajasthan, Gujarat, and Maharashtra were major strongholds for the species. Within forested landscapes, wolves tended to avoid top-carnivores but were more sympatric with leopards and dhole compared to tigers and lions. This ancient wolf lineage is threatened by habitat loss to development, hybridization with dogs, fast-traffic roads, diseases, and severe persecution by pastoralists. Their status is as precarious as that of the tiger, yet focused conservation efforts are lacking. Breeding habitat patches within each landscape identified in this study should be made safe from human persecution and free of feral dogs so as to permit packs to breed and successfully recruit individuals to ensure wolf persistence in the larger landscape for the long term.

Keywords: ***Canis lupus pallipes*, camera traps, radio telemetry, MaxEnt, home range, pack size, population estimate, wolf-large carnivore Interaction**

INTRODUCTION

Reliable information on the status, that is the distribution, population size, extent, and habitat contiguity between populations, are essential for the management of any endangered species (Sousa-Silva et al., 2014). This basic information is not available for many species, and conservation management is often based on educated guesses that can have direr consequences (Blake and Hedges, 2004) and is especially relevant for threatened species that occur outside of protected areas (Maron et al., 2018; Simmonds and Watson, 2019). Carnivores, due to their wide-ranging behavior, low density, and elusive nature, are one of the most difficult taxa to study (Garshelis, 1992). The status of many carnivores was assessed from indices, such as pug-marks for tigers and lions (Wynter-Blyth and Dharmakumarsinhji, 1949; Choudhary, 1970), simulated howls for wolves (Harrington and Mech, 1982), and golden jackals (Graf and Hatlauf, 2021), questionnaire surveys, and interactions with the local community (Jhala and Giles, 1991, Karanth et al., 2009). In the absence of any better approach, the information generated by these methods was often used for policy decisions and management actions. However, now with the advent of cost-effective modern technologies, such as camera traps and radio-telemetry, and analytical approaches, i.e., species distribution models (Sousa-Silva et al., 2014), better insights on species distribution and abundance and their determining factors are possible.

Indian peninsular wolves (*Canis lupus pallipes*) are an ancient lineage of wolves endemic to the Indian sub-continent (Sharma L. K. et al., 2004; Hennelly et al., 2021). They are considered endangered and are listed on Schedule 1 of the Wildlife Protection Act (1972). Several attempts have been made to evaluate their status locally (Jhala and Giles, 1991; Kumar and Rahmani, 1997; Singh and Kumara, 2006) and at the country scale (Shahi, 1982; Jhala, 2003; Karanth et al., 2009; Srivathsa et al., 2020). Earlier range maps and population estimates were based on ground surveys, information from local pastoralists, and knowledge of wolf ecology and their habitat (Shahi, 1982; Jhala and Giles, 1991; Kumar and Rahmani, 1997; Kumar, 1998; Kumar and Rahmani, 2000; Jethva and Jhala, 2004; Singh and Kumara, 2006; Kumar and Rahmani, 2008; Agarwala et al., 2010). Karanth et al. (2009) used expert knowledge, while Srivathsa et al. (2020) used a combination of data from field surveys, citizen science, and authenticated reports, while both studies used occupancy framework with eco-geographical and human footprint covariates to model wolf distribution across India.

In this study, we used data generated from the largest camera trap survey to date covering 121,337 km^2 (Jhala et al., 2020) in combination with wolf locations obtained from radio-telemetry and authenticated records as presence data to model species distribution. We subsequently estimate population size based on territory size and pack size estimates in occupied and breeding habitats. We evaluate wolf distribution and relative abundance with respect to other large competing carnivores and identify wolf stronghold populations that should be targeted for conservation to ensure wolf persistence in the larger landscape for the long term.

MATERIALS AND METHODS

The geographical extent of our study covered the entire range of Indian wolves within India. We modeled wolf distribution using the maximum entropy approach in maximum entropy framework (MaxEnt; version 3.4.1, Phillips et al., 2006) that uses machine learning from occurrence locations of the target species and background points along with ecologically relevant spatial environmental variables to develop statistical relationships (Elith et al., 2011). These relationships are then used to predict species occurrence across modeled space (Elith et al., 2011). We used a combination of methods to infer wolf presence locations. These were (a) extensive coverage of forested habitats across 20 Indian states by camera traps carried out by State Forest Department personnel and research biologists of the Wildlife Institute of India (Jhala et al., 2020). Camera traps with heat and motion detectors were deployed at 26,838 locations in 2018–2019 to cover a forested area of 121,337 km^2 (**Figure 1**). All photo captures of wildlife were geotagged and subsequently segregated into species. Camera trap locations that recorded wolf captures were used for modeling wolf distribution. (b) Since Indian peninsular wolves were known to use agro-pastoral landscapes (outside of forest habitats; Jhala, 1993) and since these areas were not camera trapped, we obtained records of wolf presence from Shahi (1982), Jhala (1993, 2003, 2007), Jhala and Sharma (1997), Kumar and Rahmani (1997), Jethva (2003), Habib (2007), Lokhande and Bajaru (2013), Saren et al. (2019), Ghaskadbi et al. (2021), Mahajan and Khandal (2021), Maurya et al. (2021), Sadhukhan et al. (2021), Sharma (2021), and Trivedi et al. (2021), and from radio-telemetry (Jhala, 2007) and geotagged records from Jhala Y.V. et al. (2021) to augment the camera trap data.

Since many of the radio-telemetry-based locations and other locations were clumped, we picked only one location for approximately every 5 km^2. This reduced the spatial redundancy of information in location data and we were left with 571 locations that were used for model building. Based on knowledge of wolf ecology and behavior (Mech, 1970; Jhala, 1993; Mech and Boitani, 2007), we hypothesized *a priori* that Peninsular Indian wolves would occur in semi-arid grasslands, scrub, and open forests with high ambient temperatures, would avoid areas of high human density but occur in rural areas with livestock husbandry, and would avoid areas having a high density of competing carnivores. The eco-geographical variables used in MaxEnt were as follows: (a) habitat characteristics (land use land cover, Normalized Difference Vegetation Index (NDVI), elevation, and ruggedness; (b) climatic factors (temperatures of coldest and hottest months, rainfall, and aridity); (c) human footprint indices (distance to night light, distance to roads, road density, and human modification index; (d) prey indices as livestock density, goat and sheep density, and cattle density, and (e) top-carnivore density (tiger and lion density across their range of occurrence) (**Supplementary Table 1**). Linear, quadratic, and product features available in MaxEnt were used in combination with representative variables from each of the above-mentioned eco-geographical variable categories. The models were assessed based on area under the curve (AUC) of receiver operator curves (ROC), specificity and sensitivity of the models, and testing the

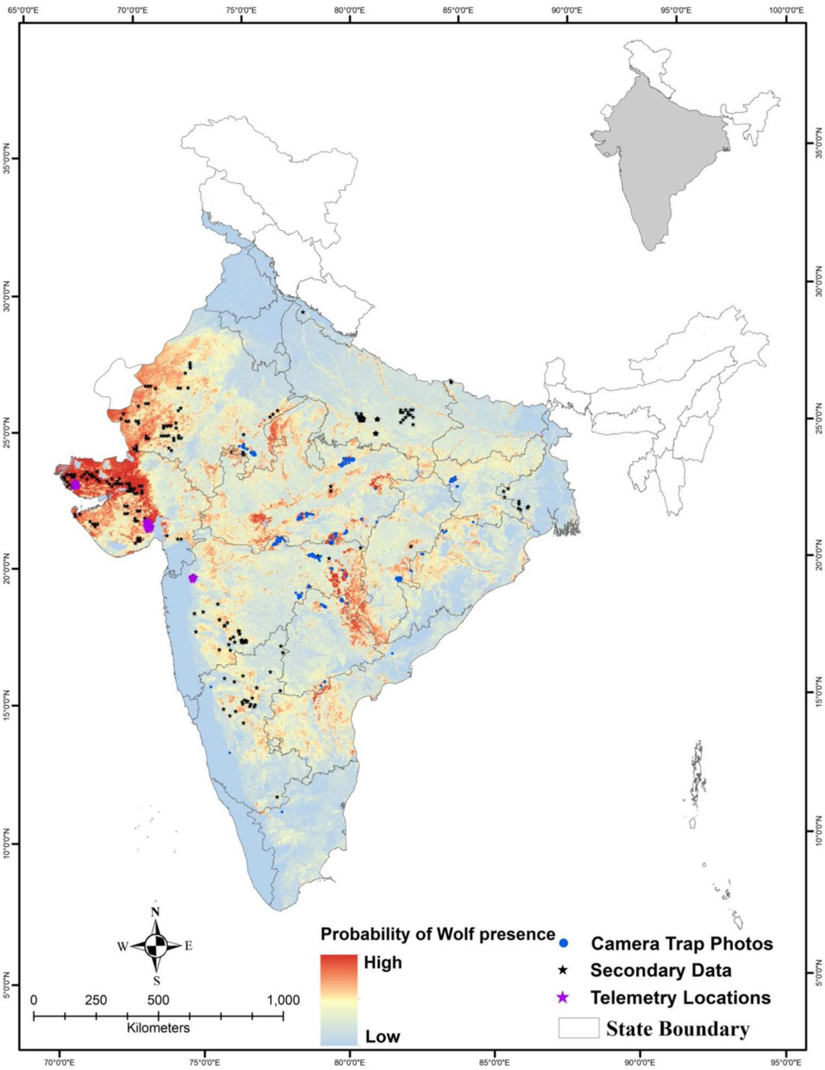

FIGURE 1 | Wolf distribution modeled in MaxEnt using presence locations with eco-geographical variables of human modification, climate, habitat, competing carnivores, and prey. Map inset shows region within India where wolf distribution was modeled.

model classification accuracy on 30% of the data that were not used for model building (Jiménez-Valverde, 2011). Best models were selected on the basis of model fit and parsimonious use of relevant ecological covariates that made ecological sense based on our *a priori* expectations (**Supplementary Table 1**). We used clog-log analysis (Phillips et al., 2017) to determine the probability value beyond which pixels had high wolf occurrence classification and below which wolves were likely absent to determine the area occupied by wolves. We also determined the pixel probabilities for 16 known breeding packs from 14 different areas spread across India and used one SD on the mean pixel values to address uncertainty in the cutoff values to determine occupied and breeding habitats.

Wolves are known to be territorial where neighboring territory areas overlap minimally (Jhala, 2003; Habib, 2007). Since 100% Minimum Convex Polygon territories of four wolf packs reported by Habib (2007) did not differ from 95% fixed kernel estimates of another eight radio-collared packs from three different sites (Jhala, 2007) (t-test, p = 0.9) we combined these estimates for our analysis to get better coverage of territory sizes from across India (**Supplementary Table 2**). We removed isolated wolf occurrence habitat patches that were <100 km^2 from further analysis as these would be too small to harbor wolves. We used data from 35 wolf packs for estimating adult pack size (**Supplementary Table 3**) to estimate the potential wolf population within areas of breeding habitat. Occupied areas outside of breeding habitats would hold dispersing individuals, old ousted pack members, and sub-adults biding their time to join packs or form their own packs (Packard and Mech, 1980). For areas that were above the MaxEnt clog-log probability value of occurrence but below the threshold of breeding packs, we used a conservative estimate of wolf density of less than one wolf per 100 km^2 (range between 0.75 and 0.5 wolves per 100 km^2).

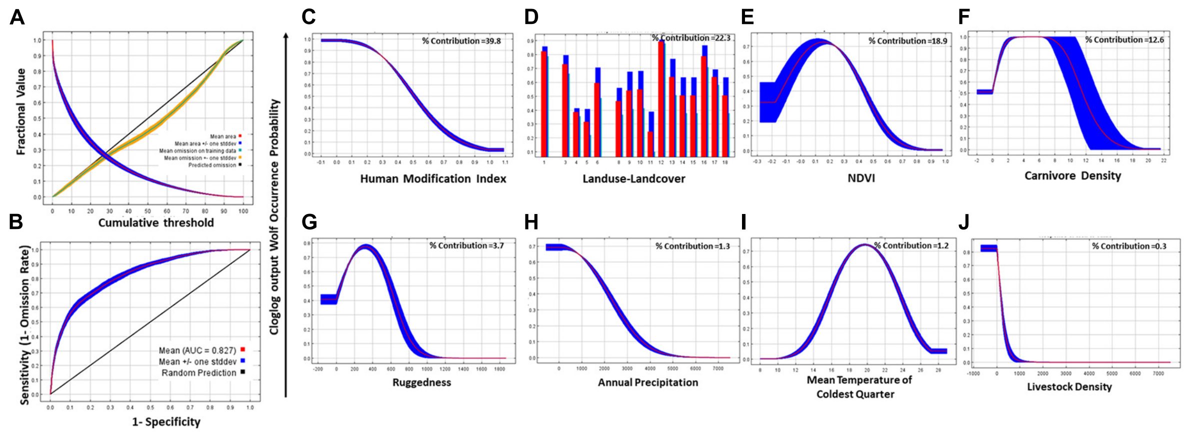

FIGURE 2 | Response curves of wolf occurrence with eco-geographical variables, their contributions, and model fit assessment obtained from 100 bootstrap runs of the best MaxEnt model. **(A)** Variation in the omission of model data and predicted area with increasing MaxEnt cumulative threshold values. **(B)** Receiver operating curve of test and training data. **(D)** Land use land cover classes were (1) arid scrub, (3) grassland, (4) agriculture, (5) settlement, (6) open, (8) water, (9) riparian, (10) evergreen open, (11) evergreen broadleaf, (12) deciduous broadleaf, (13) deciduous open, (14) mixed open, (15) evergreen broadleaf open, (16) deciduous broadleaf open, (17) scrub, and (18) coastal marsh. **(E)** Normalized Difference Vegetation Index (NDVI). **(F)** Carnivore density (density of tigers and lions) across their range in India.

To get a better understanding of species interactions within forested habitats, we computed relative abundance index (RAI, Carbone et al., 2001) as the number of photo captures per 100 trap days of wolves, dhole, leopards, and tigers and averaged these for all camera traps in 25 km^2 grids. We plotted wolf RAI against dhole RAI, leopard density, and tiger density from Jhala et al. (2020) and Jhala Y.V. et al. (2021) and inspected scatterplots, fitted models, and tested for linear correlations to better understand species interactions.

RESULTS

We obtained 34,858,623 photographs of wildlife from which 2,812 were of wolves from 313 camera locations. Published (34), other geo-tagged records (365), and radio-telemetry (2,612) contributed to a total of 3,324 wolf presence locations from across the range of the species in India (**Figure 1**). The best MaxEnt model was a good fit with an AUC of 0.83 and performed well in classifying 30% of the test data (**Figure 2**). Wolf occurrence was best explained by (1) climatic variables: (a) average rainfall, (b) average temperature of the coldest quarter; (2) habitat characteristics: (a) pre-monsoon NDVI, (c) land use and land cover; (3) Human Modification Index (maximum contribution to the model 40%); (4) prey availability in the form of livestock density; and (5) density of top-carnivores (**Figure 2**). As per our *a priori* predictions, wolves were tolerant of higher temperatures (**Figure 2** and **Supplementary Figure 1**), they preferentially occurred at semi-arid sites that had lower rainfall, higher temperatures, lower values of canopy cover (NDVI), avoided high human densities but their occurrence coincided with moderate livestock densities. As expected, the response of wolves to top-carnivore density was a right-skewed bell-shaped function, with wolves occurring in areas of low top-carnivore densities but declining at high top-carnivore densities (**Figure 2** and **Supplementary Figure 1**).

Wolf territory size was estimated at 189 (SE 23) km^2 (**Supplementary Table 2**). The total area above the threshold value obtained from clog-log analysis (p = 0.47 SE 0.0094) that could potentially be occupied by wolves after removing isolated areas that were smaller than 100 km^2 was 364,425 km^2 in India. The largest potential for wolf occupancy was in the contiguous Saurashtra-Kachchh-Thar landscape (102,837 km^2, **Figure 3**). Area suitable for breeding packs was estimated at 89,138 km^2 with the largest contiguous breeding habitats available in the Central Indian landscape (37,323 km^2, **Figure 3**). Considering an average adult pack size of 3 (SE 0.24) adult wolves (**Supplementary Table 3**) for breeding habitat and a density range from 0.75 to 0.5 wolves per 100 km^2 for occupied areas outside of the breeding habitat, the potential number of wolves in India was estimated at 3,170 (SE range 2,568–3,847). Besides the Saurashtra-Kachchh-Thar landscape, the other habitat patch that could potentially hold a population of > 150 wolves was Udanti Sitanadi-Indravati-Kawal-Tadoba (**Figure 3**). Shivpuri-Mukundara-Gandhi Sagar, Satpura-Betul-Melghat, Bandhavgarh-Sanjay, and Panna-Nauradehi were other areas that support good wolf populations. Madhya Pradesh supported the largest wolf population followed by the states of Rajasthan, Gujarat, and Maharashtra (**Table 1**).

Scatter plots of wolf RAI against dhole RAI, leopard, and tiger density categories in forested habitats (**Supplementary Figure 2**) showed that wolf relative abundance declined with an increase in competing for carnivore relative and absolute abundances. Declines in wolf photo-capture rates were sharper and statistically significant with an increase in tigers compared to that of leopard and dhole.

DISCUSSION

Assessing the status of widespread, low density, and elusive species, such as the wolf, is a difficult task (Kunkel et al., 2005).

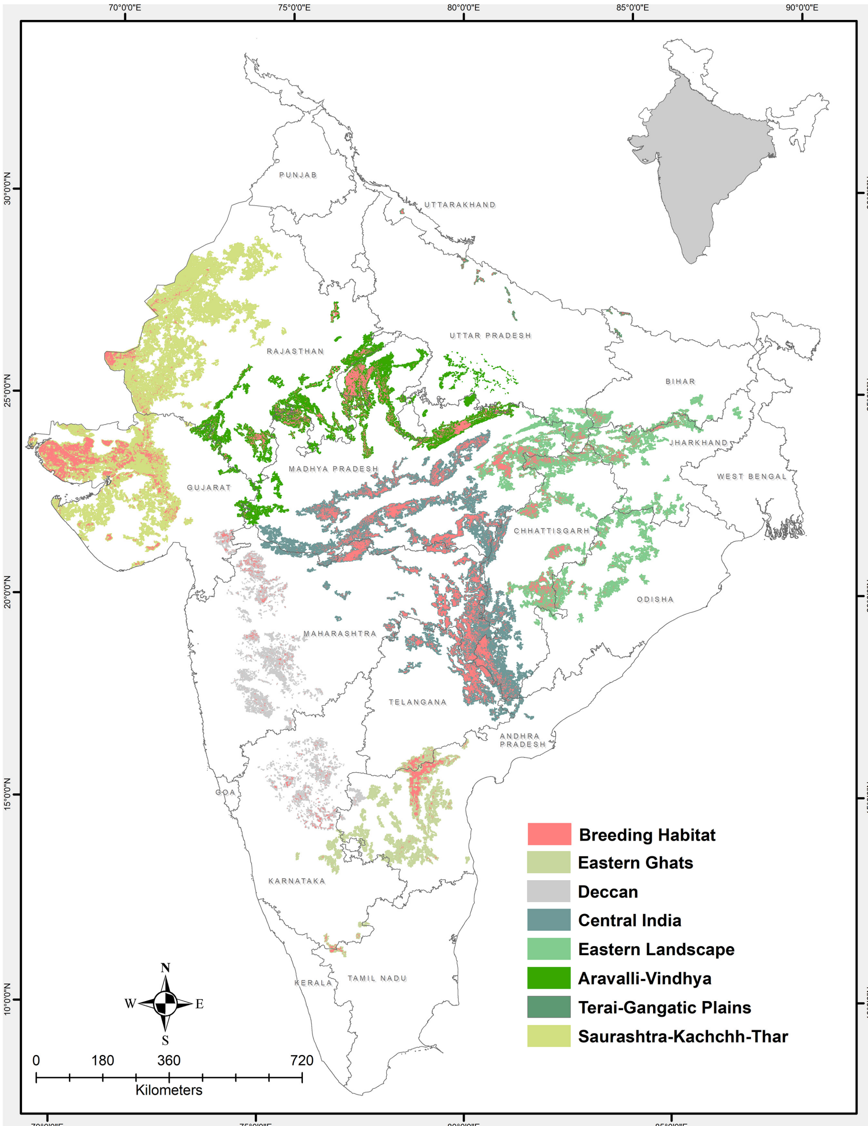

FIGURE 3 | Wolf-occupied landscapes and breeding habitats across India inferred from the MaxEnt models. MaxEnt, maximum entropy framework.

Shahi (1982) estimated the Indian wolf population at ≈800 individuals, while subsequent estimates were higher (2,000–3,000; Jhala, 2003) due to a better understanding of wolf distribution and ecology. The current assessment uses robust quantitative information of occurrence data (from large-scale geo-tagged camera trap, telemetry, and authenticated sightings) in combination with species distribution models with relevant eco-geographic covariates to evaluate wolf status. We use clog-log models with 100 bootstrap runs in MaxEnt (Phillips et al., 2017) to determine the threshold probability below which wolf occurrence was unlikely, to determine wolf-occupied area. Estimates based on models are only as good as the data used to build these models; with an extensive coverage of wolf location data from across their range, from varied habitats, and eco-climatic conditions, we believe that our model predictions are good (as also shown by model evaluation statistics). However, we caution that due to the clog-log threshold used to determine wolf occupancy, there will be some areas where wolves may be present and our model threshold failed to predict them or predicated wolf occupancy in areas of known absence. We believe that at the country scale, these small errors would not matter, but at local scales where conservation measures need to be implemented, deviations from the truth would make a large difference. Therefore, the wolf habitat suitability map provided in this article should be used as a first cut and subsequent ground validation of the model results eventually used for conservation investments and management. The current distribution (**Figures 1**, **2**) and population estimate (**Table 1**) are similar to earlier estimates and validate Jhala (2003) with better information and formal model-based analysis. In the past

TABLE 1 | State-wise estimated wolf population based on the MaxEnt model estimate of potential occupied, breeding habitat, average pack size of 3 (SE 0.24), and territory size of 188 (SE 23) km^2.

State	Occupied habitat (km^2)	Breeding habitat (km^2)	Population estimate (SE range)
Madhya Pradesh	81,734	25,979	772 (626–938)
Rajasthan	73,697	7,097	532 (428–416)
Gujarat	53,891	15,656	494 (401–600)
Maharashtra	40,114	14,453	396 (322–481)
Chhattisgarh	35,310	9,908	320 (259–389)
Andhra Pradesh	20,567	3,582	165 (133–199)
Telangana	15,046	6,165	156 (127–190)
Odisha	11,730	1,107	84 (68–102)
Jharkhand	10,499	1,641	82 (66–99)
Karnataka	9,545	1,238	72 (58–87)
Uttar Pradesh	7,659	1,299	61 (49–74)
Bihar	4,022	758	33 (26–40)

States of Tamil Nadu, Uttarakhand, West Bengal, and Haryana had sporadic wolf occurrence. Range is one SE of the mean.
MaxEnt, maximum entropy framework.

two decades, wolf populations seem to have colonized new areas while losing out in some of their strongholds. Wolves have been recently recorded from several areas from where they had been exterminated or were not known to exist in the recent past [e.g., Rajaji Tiger Reserve (Sharma, 2021), Bangladesh (Muntasir et al., 2021), Indian Sundarbans (Ghai, 2017), Valmiki Tiger Reserve (Maurya et al., 2021), and Kaveri Wildlife Sanctuary (Gubbi et al., 2020)]. While wolves have declined from their stronghold of Kachchh and parts of Rajasthan primarily due to persecution, hybridization with dogs, and development of fast traffic roads. The easternmost limit of the Indian wolf was the Sundarban mangrove forest (Ghai, 2017; Muntasir et al., 2021), there were no records of the Indian wolf from Assam and the North East States. No suitable occupied habitat was predicted in the states of Haryana and Punjab, possibly due to extensive and intensive agriculture, yet it is possible that wolves can also sporadically occur in these two states. It was believed that Indian peninsular wolves rarely used forested habitats (Jhala, 2003), however, as evidenced from the extensive camera trap data, wolves have been recorded from several forested areas of India (**Figure 1**). Notably, the tiger reserves of Mukundara, Kawal, Udanti Sitanadi, Melghat, Panna, Palamau, Bor, Kanha, Satpura, and Pench had a good number of wolf photo captures. Wolf photo captures from these tiger reserves were either from the buffer zone or from parts of the reserve that had relatively open canopied forests and scrubland habitats, and these parts had a relatively low density of tigers. Conserving a large carnivore outside of the realms of a protected area, especially when it has the propensity of predation on livestock, is a formidable task despite being protected by law (Woodroffe et al., 2006). Protected areas targeting wolves as a focal species for conservation were few (e.g., Mahuadanr, Hazaribagh, Gandhi Sagar, and Nauradehi wildlife sanctuaries). Therefore, documenting breeding wolf populations in some well-protected areas of India heralds well for the long-term conservation of Indian wolves. Earlier estimates of wolves from Gujarat and Rajasthan (Jhala and Giles, 1991) mapped their distribution and abundance based on extensive ground surveys and expert knowledge of local pastoral communities. These estimates were lower than the estimates reported herein. The MaxEnt-based analysis identifies habitats that meet the requirements for wolf occupancy based on the covariates used to build the model, human persecution can severely deplete wolf populations within suitable habitats as has been observed in Kachchh in recent times. Therefore, detailed ground surveys and radio-telemetry-based estimates of pack size, territory configurations, and sizes in selected sites are required to validate the population estimates obtained by model-based inference and for monitoring long-term population trends. Telemetry studies from mid-1990s to 2005 in the Bhal and Kachchh regions of Gujarat and Nashik (Jhala, 2007) and Sholapur in Maharashtra (Kumar and Rahmani, 1997; Habib, 2007; Habib et al., 2021) have shown that wolf populations were vulnerable to disease and persecution and fluctuated substantially (Jhala, 2003). Unfortunately, no long-term telemetry-based studies are being implemented on the Indian wolves at specific sites to monitor population dynamics. Source populations of wolves within each of the identified landscapes need to be monitored continuously through radio-telemetry to keep the *pulse of the population,* i.e., ensure that these populations are not declining, and if declining, identify site-specific threats so as to address them in a timely manner. As long as these source populations are secure within each landscape, they will recruit wolves that will disperse and occupy the larger landscapes. Efforts to reintroduce wolves from captive-bred zoo populations should only be considered after appropriate rewilding, evaluation of their behavior, and skills of hunting wild prey. Such wolves (if habituated to humans) can become a major cause of human-wolf conflict (Jhala and Sharma, 1997; Rajpurohit, 1999) and compromise the conservation of the entire species due to community backlash (Treves et al., 2006).

Response curves of wolf occurrence to eco-geographical covariates were in consonance with our hypothesis conforming to their behavioral ecology. Besides climatic and habitat characteristics, top carnivore densities contributed (12.6%) to explaining wolf occurrence. It has long been speculated that Indian wolves have likely been out-competed by other large carnivores that dwell in forested habitats (Jhala, 1993). The alternative hypothesis could be that Indian wolves evolved at a time when India was undergoing a dry spell (Sharma D. K. et al., 2004; Hennelly et al., 2021) and adapted to open semi-arid habitats and therefore now avoid thick forests. Wolves often occurred in the buffer zones of protected areas, but were rarely seen within the core areas of PA's that have high large carnivore densities even though habitats were suitable. For example, the habitats of Gir Protected Area and that of Ranthambore National Park were suitable for wolves (dry open canopied deciduous and thorn forests) and wolves occurred in the periphery of these reserves, but they were rarely seen in the core areas that have high lion and tiger densities, though these core areas abound in prey. While in protected areas, namely, Nauradehi, Gandhi Sagar, and Mukundara, that have similar habitats but do not have tigers or lions and dhole, wolves use most parts of these protected areas. These observations suggest that though Indian wolves may have specialized for open habitats, they were also likely limited by direct competition with other large carnivores. Since we had density estimates of only tigers and lions covering the full extent of these carnivores' range across India, we could use these for modeling wolf occurrence in MaxEnt (**Figure 2**). However, wolves were also likely limited by leopards and dhole. Leopards occur outside of forests as well (Daniel, 1996), while dholes are primarily forest dwellers (Johnsingh and Acharya, 2013) in tropical India. Since leopard, dhole, and wolf photo capture rates were available only from forested habitats, we restricted our analysis on their interactions to this habitat that was extensively camera trapped across India (Jhala et al., 2020). Wolves tended to avoid all three competing large carnivores but were more tolerant of leopards and dhole compared to tigers (**Supplementary Figure 2**).

The peninsular Indian wolf is an ancient lineage endemic to the Indian sub-continent (Sharma L. K. et al., 2004; Hennelly et al., 2021), its status is precarious and with only ≈3,100 adult individuals their population is as big as that of the tiger in India (Jhala Y. et al., 2021). Wolves are persecuted by pastoralists, threatened by diseases spread by dogs, and genetically swamped by a large feral dog population (Jhala, 2003; Vanak and Gompper, 2009; Srivathsa et al., 2019). Conserving wolves is a more formidable task compared to tigers, since the majority of their population resides outside the realm of protected areas and there are currently no focused efforts for conserving the species. For successful recruitment, all that wolves require, within the larger occupied landscapes that include several types of land use and cover, are small patches (5–15 km^2) of safe habitat for denning and rendezvous sites between December to March (Jhala, 2003). Besides the use of poison, the new multi-lane fast-traffic motorways being built through wolf habitats are a death knell for wolves and other threatened species and need careful mitigation to provide safe passage (Dennehy et al., 2021). Ensuring that breeding habitats are well protected would enable wolves to continue to persist in the larger occupied landscape. This study provides the required information for focused efforts to target and assist in their long-term conservation.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Data on pack size, territory size are included in the **Supplementary Material**, location data is provided in the figure. Since the precise location of Schedule 1 species under the Wildlife Protection Act is not possible to be provided in the public domain, therefore, wolf location data will be provided for genuine users based on reasonable requests to the corresponding author. Requests to access these datasets should be directed to corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the manuscript does not involve capture or handling of any animal and depends on secondary data that was generated with appropriate legal approvals as per the wildlife protection act.

AUTHOR CONTRIBUTIONS

YJ conceived the study, collected field data, did the data analysis, and wrote the manuscript. SS conducted data analysis and wrote the manuscript. QQ and SK contributed field data. All authors reviewed and commented on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.814966/full#supplementary-material

Supplementary Figure 1 | Relationships of wolf occurrence with eco-geographical variables when all variables were considered together in the model and with variables that were considered in explaining wolf occurrence but not used in the final model.

Supplementary Figure 2 | Three-dimensional and two-dimensional scatter plots of wolf relative abundance index (RAI) against tiger **(B,C)**, leopard **(A,B,D)**, and dhole **(A,E)**. Two-dimensional scatter plots show intensity and 95% ellipses of data distribution. Wolf RAI was negatively correlated with all three large carnivores but was statistically significant ($p < 0.01$) only for tigers.

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Tolerance for Wolves in the United States

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This study applies a psychological hazard-acceptance model to U.S. wolf conservation. Where most prior studies have focused on human populations most likely to interact with wolves (e.g., people who reside in wolves' range), we sought to model tolerance among the general public throughout the United States, with representative samples from two regions with ongoing recovery efforts (i.e., the Northern Rocky Mountains and Western Great Lakes) as well as the rest of the country. As opposed to typical, attitudinal measures of tolerance (e.g., wildlife acceptance capacity) we sought to model supportive and oppositional behavior among the U.S. public as a function of perceptions of risk, benefit, and control, trust in the U.S. Fish and Wildlife Service, and affect toward wolves. At the national level, results predict a moderate amount of the variance for tolerant, stewardship behaviors (r^2 = 0.22–0.25) and intolerant, oppositional behaviors to wolf conservation (r^2 = 0.14–0.22). Most respondents (55%) did not intend to engage in either supportive or oppositional actions, and 23% indicated a preference for wolf populations to increase nationally. These preferences varied slightly by sample region when weighted to reflect regional demographics, with about one in three respondents in the Northern Rocky Mountains preferring for wolf populations to increase (32%), and slightly fewer saying the same in the Western Great Lakes region (30%) and rest of the United States (27%). We performed a *post hoc* logistic regression to identify factors that predisposed U.S. residents nationally to engage in *any* behavior toward wolves (tolerant or intolerant). This analysis suggested that the perceived importance of the wolf issue was most predictive of intentions to engage in behavior relevant to wolf conservation. Analyses indicate high levels of tolerance for wolves nationally, some support for their restoration, and only small minorities engaging in oppositional behavior. With the recent shift to individual state-level management, a more diverse policy matrix will increase the importance of understanding how human tolerance for wolves varies spatially (at the local level), and what factors drive tolerance at both the individual and group level.

Keywords: carnivores, risk, hazard, benefit, trust, tolerance, wolves (*Canis lupus*)

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INTRODUCTION

In recent decades, large carnivores have begun to reoccupy parts of Europe and North America where they were previously eradicated (e.g., Chapron et al., 2014). As these species move into human-dominated landscapes, coexistence requires some degree of human tolerance of their presence and associated risks (Bruskotter et al., 2014). Indeed, in some cases, human-causes represent the overwhelming source of mortality for carnivores (Treves et al., 2017). Thus, a variety of recent scholarship has sought to address the question: *what makes people more or less tolerant of wildlife* (e.g., Carter et al., 2012; Slagle et al., 2012; Zajac et al., 2012; Browne-Nuñez et al., 2015; Inskip et al., 2016; Kansky et al., 2016; Marino et al., 2021). As large carnivores represent a novel hazard to many human populations, Bruskotter and Wilson (2014) adapted theory explaining individual-level variation in the "acceptance" of hazards (e.g., Siegrist, 2000; Siegrist and Cvetkovich, 2000) to explain variation in acceptance (or tolerance—we use these terms interchangeably here) of carnivores. Here we test a hazard acceptance model of carnivore conservation with a national sample in the United States, using the gray wolf as our model species.

Conventional wisdom suggests that charismatic megafauna can act as "flagship species"—animals that become symbols or rallying points for conservation action (Ducarme et al., 2013). However, large terrestrial mammals are also prone to conflict with humans' interests. Through normal expressions of behavior these animals represent potential threats to our crops, our pets and occasionally our lives (Nyhus, 2016). In the language of researchers who study risk, they are *hazards*. Studies on hazard acceptance indicate that acceptance is driven in large part by the perceived risks and benefits individuals associate with hazards (Siegrist, 2000; Visschers et al., 2011; Ascher et al., 2013), a finding that generally mirrors research on tolerance for wildlife (for reviews see: Kansky et al., 2016; Slagle and Bruskotter, 2019). Although describing acceptance in terms of risk and benefit implies a considered and rational cost/benefit approach to managing a carnivore species, in reality it is the human perceptions of these risks and benefits that matter (Slovic, 1987; Alhakami and Slovic, 1994; Siegrist, 2000), and these perceptions are not always objectively accurate (Slovic, 1999). While research on perceived risks and benefits related to carnivore conservation is recent, findings generally follow similar patterns as other environmental hazards in that higher risk perceptions correlate to lower acceptance (e.g., Riley and Decker, 2000; Zajac et al., 2012), and higher perceptions of benefits generally correlate to greater acceptance (e.g., Siemer et al., 2009; Carter et al., 2012). Where studies have employed more extensive models of tolerance for carnivores, perceptions of risk and benefit work in a converse relationship (as they do in other hazard contexts: Alhakami and Slovic, 1994), though perceived benefits may be as or more predictive of tolerance than risk perceptions across varied contexts of carnivore conservation (e.g., Carter et al., 2012; Slagle et al., 2012; Inskip et al., 2016).

Perceptions of risk and benefit are, in turn, affected by individuals' general feelings surrounding a hazard, also known as *affect* (Johnson and Tversky, 1983; Peters, 2006). Affect serves to bias subsequent judgments concerning hazards such that negative affect can increase risk perceptions and lower benefit perceptions, while positive affect can have the opposite effect (Finucane et al., 2000), with evidence of this in the tolerance literature (e.g., Slagle et al., 2012; Vaske J. et al., 2021). Affect as a heuristic enables us to sift through information and come to a decision more efficiently than an endless tabulation of pros and cons might (Peters, 2006).

Also critical to understanding perceptions of risk is one's perception of control over the hazard, where a perceived lack of control drives up risk perception (Slovic, 1987), and inhibits our intended behaviors (Armitage and Conner, 2001; Ajzen, 2002). The tolerance literature supports these findings, where lower personal control was associated with increased risk perceptions of black bears (*Ursus americanus*), and in turn, decreased acceptance of black bears in Ohio (Zajac et al., 2012). In Norway, residents that had lower perceptions of control found carnivore behaviors in general to be less acceptable (Kleiven et al., 2004), and sheep farmers with a higher sense of control had fewer negative attitudes toward carnivores (Bjerke et al., 2000). Focusing on tigers (*Panthera tigris*) in Nepal, local residents' lower perceived ability to adapt to or avoid risks was associated with a preference for fewer tigers (Carter et al., 2012).

Finally, in modern societies, citizens shift responsibility and management for hazards to local, state and federal agencies charged with mitigating risk on behalf of the public (think nuclear power, prescription drugs, or forest fires). Because the actions of these agencies affect how hazards are managed, they can also impact the extent to which hazards are judged as risky or beneficial. Specifically, trust in the agency acts as a decision-making shortcut, similar to affect, in that it simplifies our choices. When agencies are trusted, individuals tend to view hazards as less risky and more beneficial; when they are not trusted individuals tend toward the opposite (e.g., Siegrist, 2000; Siegrist and Cvetkovich, 2000; Zajac et al., 2012). Trust in the management agency is partially composed of calculative trust or confidence: do we believe the agency is capable in their management? If so, we entrust them with responsibilities ranging from saving endangered carnivores to protecting us from recovered carnivore populations. Similarly, trust as salient values similarity, also known as relational trust, is the perception that the agency holds the same values as we do in this issue and will act in a similar manner as we would. When we perceive a similarity, we trust the agency to do the right thing, whatever we perceive that to be, because we expect those who think like us to act like us. Relational trust is based in knowing the intentions of the agency and is resilient because of its basis in shared values.

Pulling together the antecedents of acceptance—trust, control, affect, risk, benefit—into a sequential model provides additional insight to how judgments concerning the acceptability of carnivores are made, particularly the relationships between these judgments (**Figure 1**). In prior work, we designed and experimentally evaluated outreach aimed at increasing these antecedents as a means of increasing tolerance. We found evidence of the causal nature of this framework in that messages focused on heightening a sense of personal control and perceived benefits increased reported acceptance of black bears in Ohio (Slagle et al., 2013).

However, recently scholars have questioned the adequacy of relying on traditional, attitudinal measures of acceptance (e.g., attitudes or "Wildlife Acceptance Capacity") to gauge tolerance of wildlife (e.g., Bruskotter and Fulton, 2012; Heberlein, 2012; Brenner and Metcalf, 2020). Psychological researchers have long understood that a general attitude toward a *target* (general classes of entities such as peoples of certain nationalities or

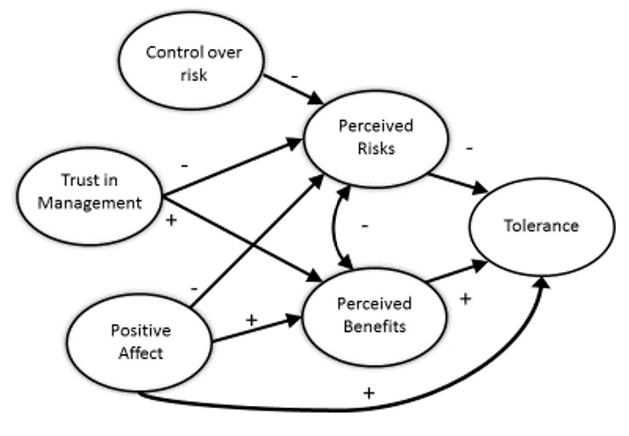

FIGURE 1 | Hypothetical hazard acceptance model, with signs indicating direction of relationships.

animals of a particular species) tends to be weakly associated with any instance of behavior, though the strength of association improves when broad classes of behavior are examined (Fishbein and Ajzen, 1974; Weigel and Newman, 1976). Bruskotter and Fulton (2012) argued that beyond the problem of prediction, single-item measures do not capture the broad array of actions people can take either in support of or opposition to carnivores. They proposed a behavioral measure, where researchers assess respondents intentions to engage in a broad range of supportive and oppositional actions. Slagle et al. (2012) demonstrated that, similar to attitudinal measures of acceptance, risk and benefit judgments can be useful for explaining intentions to engage in supportive and oppositional behaviors directed at carnivores. However, their study is limited in that it (i) did not contain all of the components of the hazard model discussed by Bruskotter and Wilson (2014), and (ii) relied on a sample of highly involved individuals (i.e., an "issue public"). Thus, in this study we seek to test the hazard-acceptance model of tolerance among a sample of the general public in the United States, using a behavioral measure of tolerance. We use gray wolves (*Canis lupus*) as a model species in this analysis. Gray wolves are an ideal model because they (i) are among the widest-ranging large, terrestrial carnivore (Wolf and Ripple, 2017); (ii) are capable of living near human settlement (Linnell et al., 2001; Mech and Boitani, 2003); and (iii) occasionally attack humans, our pets and our livestock (Linnell et al., 2001, 2021). Moreover, wolves have recently expanded into parts of their former ranges in Europe and the United States where they have not been for decades, prompting questions about how to coexist with this species (Bruskotter et al., 2014; Chapron et al., 2014).

MATERIALS AND METHODS

Sampling and Data Collection

We conducted an online survey of a representative sample from a panel maintained by GfK (now maintained by Ipsos), a marketing research firm. In order to approximate traditional mail samples, GfK recruits members via multiple contacts at their mailing address. To overcome coverage issues plaguing online samples due to a lack of internet access, GfK provides internet access to recruits that do not have access in exchange for their participation in the online panel. Recruits that already have internet access are compensated with points, which translate to roughly \$4–\$6 per month, a nominal remuneration unlikely to bias responses. GfK then draws a sample of respondents from their recruited panel members for study. Our samples were roughly evenly recruited from three regions of the United States: (1) The Northern Rocky Mountains, (2) the Western Great Lakes, and (3) the rest of the United States. To ensure sample representativeness at the national level, *post hoc* sampling weights were constructed using United States. Census Bureau data, accounting for respondent age, race and/or ethnicity, level of education, household income, census region, metropolitan area residence, and whether the respondent had household access to the Internet. Research on this method of sampling suggests that it is almost identical to telephone surveys (Berrens et al., 2003), but lacks other biases associated with telephone surveys (coverage bias due to cellphone use and social desirability bias; Chang and Krosnick, 2009; for more detail on panel construction, see Berrens et al., 2003; The GfK Group, 2013.

The Ohio State University's Office of Responsible Research Practices reviewed and approved the methods used in this research (protocol number 2013E0553). Prior to the full survey period, we pre-tested the survey instrument for function and length, and found it necessary to reduce survey burden. To achieve this, we limited respondents' assessment of trust in the USFWS to those respondents at least somewhat familiar with the agency. Respondents not at all familiar with the agency skipped to the next bank of questions, and thus were removed for SEM analyses due to data not missing at random. Additionally, responses to the 10-item bank of benefits and risks to wolf recovery were randomly assigned, such that each respondent received a random set of 8 of the 10 questions. These changes resulted in a final average survey length of 12.5 min. We gathered all responses using Qualtrics, an online survey platform, and the full survey period occurred over an 11-day period in February 2014. Respondents were contacted up to 3 times, twice by email and a final automated telephone call (for further details on this study, please see (Slagle et al., 2017).

There are several variables of interest in this study: affect, benefits, risks, control, trust, and tolerance (specific measures can be found in **Table 1**). Measurement of affect followed the method proposed by Peters and Slovic (1996, 2007), where respondents are asked to write down the first thought or image that comes to mind when considering wolves. They are then asked to rate on a bipolar scale how positive or negative they feel about what they wrote. To increase the measure's usefulness and follow existing literature, the measure was asked a second time, immediately following the question rating the first thought or image (Peters and Slovic, 2007).

Benefits and risks were measured by agreement with statements regarding various outcomes of a recovered wolf population (Bright and Manfredo, 1996; Slagle et al., 2012). Five statements described negative outcomes like depredation, effects

TABLE 1 | Factor loadings, unweighted and weighted descriptive statistics of items used to measure latent model variables.

Latent variables and items	Mean (W)	*SD* (W)	Skew (W)	Factor loading
Affect[a,e]	3.50 (3.57)	1.11 (1.03)	–0.33 (–0.28)	
When considering the first thought or image you just mentioned, how negative or positive do you feel about the thought or image?	3.59 (3.62)	1.26 (1.22)	–0.50 (–0.56)	–
When considering the second thought or image you just mentioned, how negative or positive do you feel about the thought or image?	3.41 (3.51)	1.28 (3.51)	–0.27 (–0.33)	–
Trust[b,e] I feel that the U.S. Fish and Wildlife Service. . .	3.52 (3.54)	0.94 (0.92)	–0.61 (–0.63)	
. . .Shares similar values as me.	3.50 (3.48)	0.90 (0.88)	–0.53 (–0.71)	0.54
. . .Takes similar actions as I would.	3.35 (3.35)	0.94 (0.93)	–0.41 (–0.53)	0.58
. . .Is trustworthy in their management of wildlife in the U.S.(c)	3.50 (3.52)	0.99 (0.96)	–0.58 (–0.63)	0.88
. . .Is capable in their management of wildlife in the U.S.(c)	3.55 (3.56)	0.97 (0.94)	–0.63 (–0.64)	0.83
Control[c,e] Please tell us how much you agree or disagree with the following. . .	4.84 (4.82)	1.15 (1.19)	–0.26 (–0.32)	
People can choose whether or not they are exposed to risks associated with wolves. (c)	4.63 (4.68)	1.59 (1.56)	–0.50 –0.47)	0.55
I can prevent conflict with wolves by taking precautions. (c)	5.04 (5.07)	1.49 (1.51)	–0.78 (–0.76)	0.87
This country is run by a few people in power and there is not much the little guy can do about decisions regarding wolves.	4.65 (4.57)	1.64 (1.65)	–0.35 (–0.36)	0.00
By taking an active part in political and social affairs, people can control the presence of wolves locally.	4.34 (4.31)	1.46 (1.47)	–0.42 (–0.56)	0.10
Risks[c] Allowing wolf populations to expand into other areas (outside of those areas they currently occupy) would. . .				
. . .Result in large numbers of wolf attacks on livestock	4.73 (4.57)	1.46 (1.50)	–0.27 (–0.25)	0.76
. . .Result in ranchers losing money	4.74 (4.65)	1.44 (1.45)	–0.30 (–0.29)	0.70
. . .Result in wolf attacks on humans	3.83 (3.81)	1.64 (1.67)	–0.08 (–0.67)	0.49
. . .Result in wolves wandering into residential areas	4.62 (4.66)	1.46 (1.42)	–0.36 (–0.30)	0.46
Benefits[c] Allowing wolf populations to expand into other areas (outside of those areas they currently occupy) would.				
. . .Help control coyote populations.	4.30 (4.34)	1.22 (1.12)	–0.31 (–0.61)	0.27
. . .Keep deer and elk populations in balance	4.52 (4.61)	1.56 (1.45)	–0.54 (–0.56)	0.57
. . .Increase tourism in areas where wolves have moved into	3.48 (3.51)	1.46 (1.42)	0.04 (–0.01)	0.29
. . .Preserve the wolf as a wildlife species	4.71 (4.75)	1.46 (1.41)	–0.53 (–0.54)	0.53
. . .Return the natural environment back the way it was	4.16 (4.18)	1.56 (1.55)	–0.35 (–0.45)	0.54
Supportive behavioral intentions[d]				
Below are a number of actions you could take in order to INCREASE wolf populations in the United States. Please indicate how likely or unlikely you are to.				
Write your congressperson in support of further wolf recovery efforts	1.93 (1.93)	1.16 (1.14)	0.95 (0.89)	0.86
Sign a petition in support of further wolf reintroductions	2.46 (2.57)	1.44 (1.45)	0.36 (0.24)	0.60
Contribute to an organization that supports further wolf recovery efforts	2.07 (2.12)	1.26 (1.26)	0.80 (0.72)	0.71
Post to Facebook or Twitter in support of wolves	2.07 (1.96)	1.23 (1.24)	1.12 (0.96)	0.51
Contact a wildlife manager/management agency in support of further wolf recovery efforts.	1.96 (1.99)	1.15 (1.15)	0.84 (0.80)	0.87
Oppositional behavioral intentions[d]				
Below are a number of actions you could take in order to REDUCE wolf populations in the United States. Please indicate how likely or unlikely you are to.				
Contact a wildlife manager/management agency to oppose further wolf recovery efforts.	1.73 (1.68)	1.08 (1.06)	1.30 (1.34)	0.90
Write a letter to your Congressperson to oppose further wolf recovery efforts	1.69 (1.65)	1.05 (1.00)	1.38 (1.28)	0.92
Contribute to an organization that opposes further wolf recovery efforts	1.68 (1.66)	1.07 (1.04)	1.38 (1.36)	0.79
Sign a petition to stop further wolf recovery efforts	1.93 (1.87)	1.28 (1.26)	1.08 (1.17)	0.66
Post to Facebook or Twitter in support of wolves*	1.62 (1.64)	1.03 (1.05)	1.46 (1.45)	0.45

*Weighted descriptive statistics are in parentheses. Items used in composite measures are marked (c). [a]Scale ranged from 1 (Very negative) to 3 (Neutral) to 5 (Very positive). [b]Scale ranged from 1 (Strongly disagree) to 3 (Neutral) to 5 (Strongly agree). [c]Scale ranged from 1 (Strongly disagree) to 4(Neither agree nor disagree) to 7 (Strongly agree). [d]Scale ranged from 1 (Very unlikely) to 3 (Undecided) to 5 (Very likely). [e]Mean and SD for composite variables are calculated using items followed by (c). *This item was mistakenly worded identically to support; however, factor loadings suggest respondents interpreted the question in light of the opening sentence referring to reductions, so it has been kept for analysis.*

on game species and rancher losses. Five statements described positive outcomes like a return of "naturalness," benefits of tourism, and "balanced" wildlife populations.

Control was measured through agreement with a series of four statements that assess both control over the risk from wolves themselves (adapted from Zajac et al., 2012), as well as control over the policy process (adapted from Johansson and Karlsson, 2011).

Agency trust was assessed through measures aimed at both relational trust and calculative trust in the U.S. Fish and Wildlife

Service (Earle, 2010). Salient values statements tapping relational trust focused on the extent to which an individual feels the agency in question shares their values and would take similar action (Earle and Cvetkovich, 1995; Cvetkovich and Winter, 2003). Confidence statements or calculative trust, was measured in statements regarding the agency's ability to manage wildlife.

Finally, tolerance for wolves was measured as the intention to perform a variety of politically relevant behaviors. Tolerance can be thought of as a continuous scale ranging from stewardship of wildlife to passive tolerance to active intolerant behaviors (Bruskotter et al., 2015). Here, tolerance is measured with a set of behavioral intentions to oppose and support wolf recovery, which are replicated from Slagle et al. (2012). These include writing one's Congressperson, signing a petition, and contributing to a non-profit organization. We added 2 more behaviors that might be more accessible or typical of the general public: contacting a wildlife manager and making a post to social media related to wolf conservation.

Model Measurement and Analyses

Testing the hazard acceptance model required measuring 6 latent variables via 30 survey items: trust, control, affect, risk, benefit, and tolerance (divided into support and opposition for purposes of analysis; **Table 1**). Latent psychological variables are impossible to measure directly, and as such, are observed through their influence on other human behaviors (here, responding to items on a survey questionnaire). Structural equation modeling allows for these latent—observed variable relationships to be maintained by building confirmatory factor analyses into the measurement models, while also testing for the theoretical relationships between the latent variables themselves (Schumacker and Lomax, 2004). Model fit was assessed using multiple indices, specifically the Comparative Fit Index (CFI), Root Mean Squared Error of Approximation (RMSEA), and the Standardized Root-Mean Squared Residual (SRMR). Following Diamantopoulos and Siguaw (2000) and Schumacker and Lomax (2004), RMSEA and SRMR values between 0.05 and 0.08 were seen as having "reasonable fit," while anything less than 0.05 was a "good fit." We sought CFI values of 0.95 or greater, but levels of 0.90 or greater were considered as having "reasonable fit" (Hu and Bentler, 1999).

Structural equation modeling requires data missingness to be explicitly handled prior to analysis, and this study explicitly contained data missing completely at random due to the need to reduce response burden (see "Sampling and Data Collection" section for detail). In order to apply weights approximating a national sample, we used linear interpolation method using ordinary least squares regression in IBM SPSS (IBM Corp, 2013) to recover planned missingness in benefit and risk (10 items total, between 20 and 24% missing completely at random), as well as random missingness in the remaining model variables (18 items total, between 2 and 6% missing at random). This method uses regression to model missing data for each respondent, imputing the value suggested by the regression line (Allison, 2003). After imputing the data in SPSS, it was transferred to R for all structural equation model analyses. Measurement confirmatory factor analyses and structural equation model analyses were performed in R using the lavaan and lavaan.survey packages (Rosseel, 2012; Oberski, 2014; R Development Core Team, 2016). We used weights generated by GfK to adjust our sample to approximate the demographics of the U.S. national population and investigate the generalizability of the hazard-acceptance model to a broader context. Descriptive analyses and *post hoc* regressions were performed in IBM SPSS (IBM Corp, 2013).

RESULTS

GfK contacted a total of 2,020 potential respondents and received 1,287 completed surveys for a response rate of 63.7%. Prior to weighting procedures, respondents were more female than male (46.0% male), majority white (83.5%), from metropolitan statistical areas (73.0%) and had internet access separate from GfK (84.5%). The average age was 50.8 years, and 50.9% of respondents reported a household income of less than $59,000 per year. Weights were created using demographics from the 2009 to 2011 American Community Survey conducted by the United States Census Bureau, and the minimal impacts of adding sociodemographic weights to descriptive analyses for observed variables can be seen in **Table 1**, where fairly small or non-existent changes to means, standard deviations, and skewness are evident. After national weighting, 30% of respondents preferred for wolves to increase nationwide, and when weighted to reflect regional demographics, about one in three respondents in the Northern Rocky Mountains preferred for wolf populations to increase nationwide (32%), with slightly fewer saying the same in the Western Great Lakes region (30%) and rest of the United States (27%).

Bearing the thresholds for factor loadings and model fit indices in mind, we aimed to ensure good measurement models while not discarding observed variables out of hand. We assessed affect with two items, which required an averaged composite measure rather than a latent variable model. Trust was measured via 4 items, and responses to these items was limited to those individuals who reported being at least somewhat familiar with the U.S. Fish and Wildlife Service. Still, a measurement model resulted in poor fit (CFI = 0.87, RMSEA = 0.46, SRMR = 0.07), but indicated high factor loadings (> 0.80) for the two items focused on trustworthiness and capability in management. These items were averaged for a composite measure of trust, or more specifically, calculative trust or confidence. Control was also measured through 4 items, resulting in marginally acceptable fit of the overall measurement model (CFI = 0.94, RMSEA = 0.15, SRMR = 0.05), but poor factor loadings for 2 items of < 0.10. Again, we created a composite measure for control by averaging the 2 items with factor loadings of > 0.50, measuring personal control over exposure to the risk and prevention of conflict with wolves. The remaining 4 latent variable measurement models (benefit, risk, support and opposition) all had acceptable fits for at least 2 of the 3 fit indices used here (CFI > 0.95, SRMR < 0.05), and factor loadings greater than 0.16 for each observed variable, and thus were maintained in full (**Table 1**).

The unweighted model achieved a reasonable fit for both support and opposition (support: CFI = 0.92, RMSEA = 0.06, SRMR = 0.06; opposition: CFI = 0.93, RMSEA = 0.06, SRMR = 0.06; **Figure 2A**), explained 25 and 22% of the variance, respectively, and all relationships were in the expected directions. Affect did not significantly predict opposition, but trust had a small relationship with risk (β = –0.13).

Finally, we tested the model on weighted, imputed data to understand the generalizability of such a model among a national public. Model fit dropped to a marginal fit for support and a poor fit for opposition (support: CFA = 0.89, RMSEA = 0.08, SRMR = 0.06; opposition: CFI = 0.86, RMSEA = 0.09, SRMR = 0.07; **Figure 2B**), and explained 22 and 14% of the variance, respectively. After weighting, the trust relationship with risk was reduced and no longer significant and affect no longer had a significant direct influence on support. While the model fit is poor for opposition, an interesting shift in the relationship between risk, benefit, and opposition occurs in this model: Risks and benefits are almost equally predictive of opposition (risk β = 0.23; benefit β = –0.19), where in the previous unweighted model the influence of benefits on support and opposition dwarfed the influence of risk (**Figure 2A**). It should be noted that the unweighted model would be more heavily influenced by the respondents from the Northern Rocky Mountains and the Western Great Lakes regions—i.e., places where wolves are present and, presumably, a subject of more regular discussion and debate.

Given the overall poor fit of the weighted model, we conducted *post hoc* analyses to determine which variables might predict *any* likely action regarding wolves nationwide. We combined supportive and oppositional intended behaviors into one measure, where all unlikely responses were coded as 0, and all neither or likely responses were coded as 1. After combining behaviors, we then collapsed them into a dichotomous variable where any respondents who were unlikely to take any actions were coded as 0, and all others were coded as 1. We then used composite mean measures of trust, control, risk, benefit, and affect, as well as region (Northern Rocky Mountains, Western Great Lakes, and the rest of the United States) and dichotomized perceived importance of the wolf issue (0 = not at all or slightly important, 1 = moderately or very important) to predict any likely intended behavior in a logistic regression using pairwise deletion to handle all missing data (**Table 2**). Analyses weighted for a national sample suggest that when perceptions of both risk and benefit are high, any action is more likely, and when importance is high, any action is more likely. All other variables in the model were not significant.

DISCUSSION

A variety of studies have demonstrated that perceived risks and benefits are important for understanding acceptance of wildlife.

TABLE 2 | Weighted logistic regression results predicting any likely or uncertain action reported by respondents (respondents unlikely to take any action coded as 0).

		95% CI for odds ratio		
Variables in model	**b**	**Lower**	**Odds ratio**	**Upper**
Risk of wolves	0.363*	1.264	1.438	1.635
Benefit of wolves	0.235*	1.085	1.264	1.474
Affect toward wolves	0.083	0.935	1.086	1.262
Trust as confidence in USFWS	–0.021	0.821	0.821	1.166
Control over risk	0.083	0.965	1.087	1.223
Region—NRM (reference: rest of U.S.)	0.671	0.594	1.956	6.439
Region—WGL (reference: rest of U.S.)	0.155	0.699	1.167	1.948
Dichotomized wolf interest (1–2 = 0, 3–4 = 1)	1.555*	3.452	4.737	6.501
Nagelkerke R^2	0.198			
Chi-square	$x^2(8) = 153.044$, $p < 0.001$			

*Respondents with no answers to trust questions removed from analysis. N = 931. *p < 0.01.*

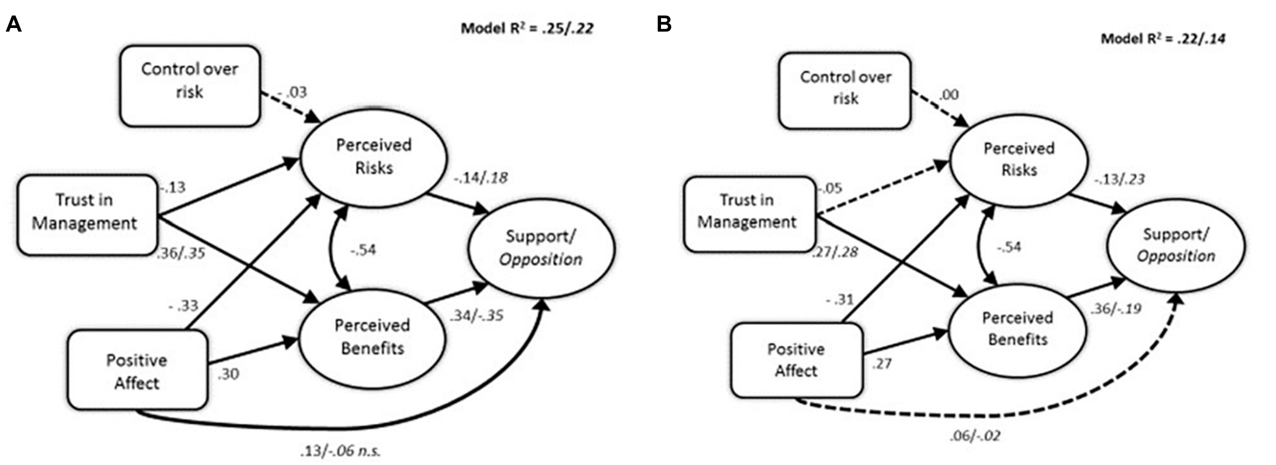

FIGURE 2 | Structural equation model coefficients estimated using unweighted data **(A)** and weighted data **(B)** imputed with linear interpolation for both support and opposition. Where different, the opposition model coefficients are in italics. Bolded lines represent pathways significant at the $p < 0.01$ level for both models, dotted lines represent non-significant paths in both models. Discrepancies in path significance between models is noted with n.s. following the appropriate path coefficient. Observed (directly measured) variables are in rectangles, while latent variables are in ovals.

However, studies of acceptance are often conducted among particular populations, i.e., those most likely to be impacted by a particular species. Moreover, it is unclear the extent to which the factors associated with attitudinal measures of "acceptance" are likewise associated with the broad classes of behavior (measured as intentions) that may impact the management of wildlife. Having demonstrated the usefulness of affect and perceived risk and benefit for explaining behavior in a sample of highly interested and involved individuals (see Slagle et al., 2012), we sought to determine the applicability of the full hazard-acceptance model among the general population of residents of the United States.

The structural model showed a reasonable fit to the data, predicting 22–25% of the variance in intentions to oppose or support wolf conservation, but became marginal to poor once weights adjusting for demographics within our sample were applied. While our model did not do nearly as well at explaining variance in behavior as it did among the interested and involved respondents, the explained variance is similar to other behavioral models. For example, a recent study found the Theory of Planned Behavior (TPB) and Value-Belief-Norm Theory explained 25 and 16% of variance, respectively, in willingness to pay for conservation of a specific park (López-Mosquera and Sánchez, 2012). Likewise, a recent meta-analysis of the TPB's application to another risk-related behavior (food safety), found model components explained 22% of the variance in intention (Lin and Roberts, 2020). Moreover, TPB studies typically take advantage of the "principle of compatibility" to align measures to refer to a specific target behavior, conducted at a specific time in a particular context (Ajzen, 2005). Unfortunately, while this alignment makes them ideal for understanding instances of a behavior, it also means they are not well-suited to understand broad classes of behavior. Our model performs similarly well to these models and is designed to be used with a broad class of behaviors of interest to conservationists.

At least a couple of factors potentially explain why our model performed less well among the general public (this manuscript) than in an interested public (Slagle et al., 2012). First, it is likely that geography dictates the relevance of a subject. In this case, geography determines who interacts with wolves under what conditions. We know that people generally acquire the various beliefs and attitudes they possess through repeated rehearsals, i.e., interactions with the target of the attitude or with other people over that target (see generally, Eagly and Chaiken, 1993). At the time this survey was administered, fewer than 10 states had gray wolf populations. Moreover, wolves tend to be in the least populated regions of states—meaning very few people are "exposed" to wolves as a hazard. As experience with wolves increase, we expect beliefs about them and the risks and benefits they pose to become practiced and thus, more stable and accessible in memory (Petty and Krosnick, 2014). Second, our study used a panel of paid respondents, which led to much higher response rates (> 60%) than are normally witnessed in traditional mail and phone surveys. While this could be an indication that our sample is more representative than these other surveys, non-response can act as a type of "filter" whereby un/less interested individuals are less likely to respond (Thomson, 1991). If interested individuals have more stable and accessible thoughts about wolves, we can expect greater associations between their risk/benefit perceptions and behavior (because lack of reliability attenuates statistical relationships; Block, 1963).

Although, all relationships were in the expected hypothesized directions, in every model, the impacts of trust and control on risk were minimal, and the direct effects of affect on behavior were minimal to non-significant. Trust was a moderate predictor of benefits in every structural model, and for every model save the weighted opposition model, benefits maintained a moderate relationship with both supportive and oppositional behaviors. Structural model fit for opposition was consistently poorer than that for support, and possibly related to the mildly non-normal nature of those observed variables. In essence, very few people indicated they were likely or very likely to perform oppositional behaviors (less than or equal to 14% for any given action). Indeed, 33% of our sample were unlikely or very unlikely to perform *any* of the behaviors we included in our study, although this means 67% were at least uncertain of whether they would act and at most very likely to act to influence wolf policy. This finding is consistent with other work on the general public's engagement in political behaviors meant to address environmental concerns (see Ballew et al., 2019 where the strong majority never contact policy makers about climate change).

Overall, this research suggests when placed in context with other models of human behavior, the hazard acceptance model provides similar insight into the way the general public approaches wolf management, and perhaps more broadly, carnivore management. Namely, that calculative or non-relational trust in the managing agency can increase the perceived benefits of the carnivores (for those familiar with the agency), and in turn, increase politically supportive behaviors.

One-third of our respondents were unlikely to perform any of the behaviors we assessed, and could be deemed "tolerant," in the sense that they are not choosing to impact wolves in any fashion (Bruskotter and Fulton, 2012; Bruskotter et al., 2015). Understanding inaction may be just as important for future research as understanding active stewardship or intolerance, and given the limitations of our final weighted models, we chose to explore this idea in a *post hoc* logistic regression. Results suggest that interest in the wolf issue is a primary driver of action. Interest was associated with both increased risk and benefit perceptions, as well as increased likelihood of engaging in *any* action.

Comprehensive measures of trust in the area of risk and decision making rely on different measures (Earle, 2010), however due to survey length, we chose to both limit the number of items used to measure it and allow respondents unfamiliar with the agency to skip the question of trust altogether. Excluding unfamiliar respondents from analysis resulted in a significant relationship between trust and benefit, suggesting for those familiar with an agency, greater trust could increase perceptions of benefits. This relationship was no longer significant once sampling weights were applied, calling into question the public's ability to make trust judgments due to a lack of familiarity and limiting generalizability of the finding. However, the relationship between trust and benefit remained throughout all iterations of the hazard acceptance model, emphasizing not only previous recommendations for agencies to include benefits as part of their outreach efforts to increase tolerance (Slagle et al., 2013; Bruskotter and Wilson, 2014), but also the importance of building trust with the public. The inverse relationship between risk and benefit indicates that an increase in perceived benefits could subsequently serve to lower risk perceptions and increase tolerance for carnivores both directly and indirectly. To increase trust, agencies, or other entities, might choose to emphasize their effectiveness in wolf management and any other successes in wildlife conservation. Here, greater trust related to greater perceptions of benefit, suggesting higher trust in the agency's ability to manage successfully may promote a greater belief in the benefits of wolf conservation.

While recent work suggests a critical role for emotions or affect in understanding wildlife interactions (Jacobs and Vaske, 2019; Vaske J. J. et al., 2021), similar assessments of models for tolerance either omit affect entirely (Lischka et al., 2020), or only assess it as worry or concern (Carter et al., 2012; Inskip et al., 2016). In a reduced model tested on a sample highly interested in and knowledgeable about wolves, a generalized affect measure had a direct effect on both supportive and oppositional behaviors (Slagle et al., 2012), suggesting a role for motivated reasoning among this group of political sophisticates (Taber and Lodge, 2006, 2016). With motivated reasoning, affect acts as a contagion in our minds, spreading throughout cognitive schema and influencing the way in which we consider new information. This influence comes mostly in the form of discounting information that disconfirms our existing biases and placing greater value on information that confirms our initial affective evaluation. Here, however, among a national sample, the expected relationships between affect, risk, and benefit were maintained in all the models, but the direct relationship between affect and conservation related behavior was either weak or unsupported. When affect was predictive of conservation behavior, it was positively predictive of supportive behavior in the present sample. Key to the differences between a national public and an engaged and informed issue public, the contagion effect of affect resulting in motivated reasoning is indeed more pronounced among political sophisticates like those represented by the issue public—those one might intuitively presume to be most immune to it but in fact are often the most subject to such effects (Kahan et al., 2012). Less engaged individuals on the wolf issue, and likely other carnivore conservation issues, may lack the existing strong affective reactions or cognitive schema that drive the potentially motivated reasoning of an issue public, and could give more careful consideration and cognitive effort to weighing risk and benefit, though this is admittedly rare (Taber and Lodge, 2016).

From a more practical perspective, no more than 13% of our respondents were willing to contact a wildlife manager or agency in support or opposition to wolf recovery. Informal conversations with wildlife managers and agency personnel suggest that they fret over being contacted by members of the public, and sometimes take such calls as reflective of the general population. Managers and the agencies they serve in would do well to maintain perspective regarding contacts from the general public—it was a very small group in our sample that would consider this a viable action for impacting a charismatic and heavily contested carnivore species. One might conclude that contact from constituents regarding lower profile species or issues probably represent an even smaller portion of the general public. While these contacts from the public could be interpreted as a sign of bigger issues, such interpretations should be investigated further before warranting major shifts in policy or protocol.

The hazard acceptance model demonstrated acceptable fit with unweighted data from a nationally representative sample, indicating that it is useful for explaining some of the individual choice to impact wolf conservation. Our unweighted sample would have more heavily reflected regional populations (i.e., Northern Rocky Mountains and Western Great Lakes), and likely provided a better fit due to the contextual relevance for these respondents. At the national scale, many of the respondents in our sample were unlikely to undertake any of the behaviors we investigated, suggesting either a passive tolerance of wolves on their part or that our list of behaviors needs to be more inclusive. Where Kansky and Knight (2014) found the most predictive strength in intangible and tangible risks when considering attitudes toward large mammals among nearby communities, we found tangible and intangible benefits to be better predictors of intentions to behave among a broader, spatially distant sample. We also note the important differences between measuring attitudes toward conservation and conservation-related behaviors—predicting human behavior is more difficult, but better links to existing social science theory can better guide policy makers, and allow for stronger linkages to conservation outcomes via impacts on policy. We echo previous calls for additional exploration of the importance of explaining benefits of carnivore conservation, and issue caution to managers heavily weighting the contacts they receive from the public, as this likely represents a very small portion of their constituents.

CONCLUSION

Public tolerance for wolves in a general public sample does not appear to be driven by positive or negative affect toward wolves, but rather by perceptions of the benefits of expanded wolf populations, which were moderately predictive of both oppositional, intolerant behaviors and supportive, tolerant behaviors. These benefits may also be driven by confidence or calculative trust in the agency's ability or those familiar with the managing agency. As might be expected by the compatibility principle, the hazard acceptance model tested at a large geographical scale here did not perform as well as similar models of tolerance at the state and local level, although it provides useful insights into the possibility of building acceptance through trust and perceived benefits even among a less engaged audience. We would expect that researchers and conservationists at the local level might find the model even more predictive and informative for public engagement around issues that are more proximal and relevant to a local population.

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 studies involving human participants were reviewed and approved by the Institutional Review Board at The Ohio State University. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

KS, RW, and JB equally contributed to conception and design of the study. KS performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Mediating Human-Wolves Conflicts Through Dialogue, Joint Fact-Finding and Empowerment

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Within a local and national context of escalating conflicts surrounding the management of immigrating wild wolves (*Canis lupus*) spreading from Germany into Denmark, we invited a group of citizens living in and nearby a Danish wolf territory to participate in an experiment called “The Wolf Dialogue Project”. The overall objective of the Wolf Dialogue Project was to explore the possibility of developing a productive alternative to the systematically distorted communication and “High conflict” that characterizes current wolf management, using a critical-utopian dialogue approach guided by Habermasian discourse ethic and a joint fact-finding process, that seeks to empower citizens to take on a shared responsibility for the commons. By purposefully not representing any strategic interests for or against wolves or the existing wolf management regime, the project offered a group of citizens the opportunity to formulate and communicate the problems and concerns they experienced, living in or nearby wolf territory. The project further offered the participating citizens the opportunity to develop counter measures and solutions to their experienced problems, through a facilitated process of social learning and empowerment. The duration of the dialogue project was two and a half years and included a demographic and political cross section of local citizens. Despite difficulties along the way, the outcome of the project was more profound than initially anticipated by the project team. Participants were initially very polarised, and some were opposed to the existing wolf management regime as well as governmental agencies, but they began taking on a collective responsibility guided by the common interest of their community, across individual differences. In addition, the process left a significant mark on the new wolf management plan recommended to the government by the Danish Wildlife Council in 2021. Far from all problems and conflicts were solved by the project, and new problems also emerged as a result of the project, but by bringing the commons of the participating citizens into focus, and applying a process of communicative rationality, joint fact-finding and the exploration of alternative futures, the project revealed the potential for social and environmental responsibility to emerge from sociopolitical empowerment.

Keywords: systematically distorted communication, discourse ethic, dialogue, commons, empowerment, interdiciplinary, wolves, wildlife conflicts

INTRODUCTION

Opposition to wolves and existing wolf management regimes among citizens living in or nearby wolf territories, is a well-described phenomenon in many countries (Nie, 2001; Linnel, 2013; Pohja-Mykrä and Kurki, 2014; Kaltenborn and Brainerd, 2016). The phenomenon is often exacerbated in areas where the wolf has remigrated after previous extinction, as is the case in many parts of Europe (Højberg et al., 2017; Mech, 2017; Skogen and Krange, 2020; Pettersson et al., 2021). In literature the opposition to wolves from people living in or nearby wolf territories is linked to high levels of cryptic mortality amongst wolves, indicating illegal killing (Liberg et al., 2012; Dressel et al., 2015; Kaltenborn and Brainerd, 2016; Suutarinen and Kojola, 2018; Sunde et al., 2021).

Wolf management is challenged by a lack of legitimacy, which is particularly pronounced in rural regions and communities near wolf territories. Being forced to accept wolves as a part of the environment, citizens in rural areas experience a marginalisation of their livelihood and everyday life situation in wolf management processes (Pettersson et al., 2021; Skogen and Krange, 2020; von Essen and Allen, 2017; Pohja-Mykrä and Kurki, 2014; Højberg et al., 2017). Traditional governance methods, based on the principles of liberal democracy, targeting predefined interests ("stakeholders"), such as nature conservationists, hunters, farmers, governmental agencies etc., at the expense of the common good, tend to reproduce the very problems they seek to solve (Hansen et al., 2016; von Essen and Hansen, 2015; von Essen). The wolf management conflict seems to leave behind a despair and apathy among responsible wildlife agencies, policymakers, wildlife managers and other scholars (Sonne et al., 2019; Treves and Santiago-Ávila, 2020).

Conservation and management conflicts are not restricted to wolves or other carnivores but arise in many different contexts when the conservation or management regime of a species and/or a landscape fails to recognise the existence of human interests, needs, values, and rationalities that differ from those of powerholders. While the approach taken by policymakers, agencies and other stakeholders is often determined by their strategic pre-defined objectives and by a rather instrumental approach to polity, other types of rationalities (interests, values, needs) are excluded as what has been referred to as the "blind spot of public institutions" (Hansen and Peterson, 2016; Kenter et al., 2021). Traditional governance strategies such as persuasion and consensus building via negotiations, combined with the use of legal means and–ultimately–law enforcement, may for a period of time suppress variables outside the existing power structures. Nonetheless, in certain contexts, conflicts, sociopolitical polarisation and/or violent expression may require alternative solutions (Hodgson et al., 2021; Niemiec et al., 2021).

Wolf-management is one such case where traditional governance strategies have failed or, at least seem to be insufficient to avoid escalating conflicts leading to a non-functioning and disrupted wildlife management (Gieser and von Essen, 2021; Niemiec et al., 2021). We launched the Wolf Dialogue Project (WDP) in august 2017 with the objective to explore the possibility of developing a more fruitful alternative to the systematically distorted communication, that has transformed wolf management into "High conflicts" in many places around the world (Ripley, 2021a). The project was partly funded by Aarhus University (AU), partly by a 300000 Danish Kronor grant–equivalent to approximately 45,000 USD, from the "15. Juni Fonden" (The 15th of June Fund) that supports art, nature conservation and health activities.[1] In contrast to the "pro- or con wolves"-focus of the public and social media, politicians, and interest groups engaged with the issue, we decided to focus on common direct and indirect impacts on the community resulting from wolves settling in the area, applying a critical-utopian dialogue approach based on a Habermasian discourse ethic and joint fact-finding process that empowers affected citizens. We did this by inviting citizens from a local community on the outskirts of the first wolf territory in Denmark in 200 years, giving them the opportunity to formulate and communicate the concerns and practical problems they experienced. Through the idea of "alternative futures" being possible, we further offered the participants the chance to foster and develop their own ideas for a future national wolf management plan, and to communicate concerns, problems, and ideas to responsible policymakers and governmental agencies.

In this paper we describe the context, process, and method applied in the WDP. We further present and discuss some of the internal as well as external results of the project, including the impact on the national wolf management debate, and we discuss challenges and pitfalls that we noted during the project. Finally, we conclude the paper by discussing how the approach in the WDP differed from more traditional governance approaches, what the chosen method offered, and where it did not succeed. We will not refer to the names or genders of specific local participants but will in some cases use aliases.

Background–Return of the Wolf

In 2012, the grey wolf (*Canis lupus*) returned to Denmark, approximately 200 years after the last known specimen was shot in 1813 (Trolle and Jensen, 2013; Pagh, 2018). Being a member of the European Union (EU), wolves are in Denmark, as in the rest of EU, protected by The Habitats Directive, Council Directive 92/43/EEC (European Union, 1992). In Denmark wolves belong to the annex IV which are species that require close protection.

Shortly after the wolves were first rediscovered in Denmark in 2012, researchers from Aarhus University (AU) identified 10 potential wolf habitats where wolfpacks were likely to settle (Madsen et al., 2013; Sunde and Olsen, 2018). One of these areas was the forest and heathland area of Stråsø in Western Jutland, in the vicinity of the small villages of Ulfborg, Vind and Idom. As predicted a male and female wolf established themselves in the Stråsø area during 2016 and 2017. Following the settlement of the two adult wolves, the first juveniles were observed in June 2017 (Sunde and Olsen, 2018).

[1]https://www.15junifonden.dk/.

Since 2012, at least 35 wolves have been identified in Denmark following a combination of wolves immigrating from Germany, and wolves being born in Denmark (Olsen et al., 2021). At least 10 wolves have disappeared without any trace, making Denmark the country with the highest cryptic mortality among wild wolves worldwide (Olsen et al., 2021; Sunde et al., 2021). In April 2018, the killing of one wolf was by coincidence caught on camera (The Guardian, 2018). A paper published in 2021 concluded that the only likely explanation of the high mortality rate in Denmark was illegal persecution (Sunde et al., 2021); a conclusion supported by a previously published paper documenting a high acceptance rate for illegal killings of wolves amongst landowners in rural areas (Højberg et al., 2017). Recent European studies have also identified illegal killings as a primary driver of wolf mortality (Musto et al., 2021; Nowak et al., 2021).

Within the Danish context, escalating conflict over wolves and wolf management has played out in public during the last 8–10 years, especially on social media, in newspapers, on radio and television. The conflict stems from the combination of fear for the safety of humans, especially children, and the frustrations of local hunters that they are now competing with wolves for the local population of red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Additionally, a relatively high level of sheep predation by wolves, and various circulating narratives about wolves in Denmark, e.g., that wolves are brought into the country by people and that the wolves are dog-wolf hybrids that are therefore not “real” wolves, drive the conflict surrounding wolf management. Several local actors, together with local and even national politicians, have expressed the viewpoint that people must now “take the law into their own hands” (Sonne et al., 2019).

METHODOLOGICAL APPROACH AND THEORETICAL FRAMEWORK

We labelled the research design developed and applied in the WDP, the “critical-utopian dialogue approach”. The design is rooted in the Critical-Utopian Action Research methodology (Egmose et al., 2000; Nielsen and Nielsen, 2006; Nielsen and Nielsen, 2016; Tofteng and Bladt 2020) with roots in Robert Jungk and Norbert R. Müllert’s Future Creation Workshops (Jungk and Müllert, 1981). Future Creation Workshops seeks to empower participants (citizens) on common matters, such as natural resources and future planning, through a mixture of deliberation, joint fact-finding, and the envisioning of alternative futures. In traditional participatory processes or public hearings, citizens are “invited into” a pre-defined strategic space with objectives pre-defined by various powerholders united by certain technical and instrumental ways of reasoning and–in case of conflicts–a language of systematically distorted communication (Elling, 2010). In those settings ordinary citizens rarely get the chance, to define or re-define the problems based on their own everyday life experience (Clausen, 2016).

The Future Creation Workshops attempt to create a space for the citizens themselves, not only to define the problems and the questions relevant from the perspective of their daily life and experiences, but also to imagine “alternative futures,” that is alternatives to those futures anticipated as given, unless we actively try to change the present trajectory (Jungk and Müllert, 1981). Combining elements from the Future Creation Workshops with experiences from Critical-Utopian Action Research, and guided by a Habermasian discourse ethic, joint fact-finding and exploration of “alternative futures,” we labeled our research design “the critical-utopian dialogue approach”.

An Alternative to the “Stakeholder” Approach

Traditional participatory processes are typically designed to give precedence to those actors and representatives–labelled “stakeholders”—who somehow have the power to influence decision-making and planning processes. From the 1990s and onwards the “stakeholder-approach” has become a widely used concept on environmental issues in public governance. However, the basic notion of “stakeholders” keeps participants “locked” in predetermined, strategic positions, hence making it difficult to find common solutions to common challenges (Clausen, 2016; Hansen et al., 2016; von Essen and Hansen, 2015). Applied in certain contexts, such as in wildlife conflicts like the wolf case, one can even argue that the “stakeholder” approach often reproduces and exacerbates the very problem it is supposed to solve by preventing any deliberative progress based on the commons to take place.

Contrary to the “stakeholder approach”, the critical-utopian dialogue approach encourages participants to feel empowered to accept their agency potential and act accordingly. Instead of marginalising people by inviting them as fragmented subjects “into” the agenda and rationality already defined by others, they are, as citizens, encouraged to take on a common responsibility (Habermas, 1992a). However, in order to take responsibility as citizens, they have to be “empowered,” that is to reclaim their positions as citizens and to be recognised as legitimate political “equals” (Honneth and Anderson, 1995). Only then, are they able to take on responsibility for society as a whole as agents of change.

The Wolf Dialogue Project

With a few exceptions all workshops were held in the evening and always started with dinner. The purpose of the dinner was twofold. On the practical level, starting with dinner made it easier for most of the participants to participate. The majority of the participants had regular working hours and by serving dinner they did not have to bother with dinner at home before heading out for the workshop. The second purpose was to establish an informal space for socialisation before the workshop making the transition from the informal pre-workshop situation to the more formal workshop easier. The dinner created a social space for small talk and the exchange of more informal information on everyday topics about participants’ family situations, work life, local events, personal experiences and the like.

On a practical level, each workshop always started by asking the participants whether they found the following three ground rules justified:

- We do not interrupt one another
- No personal attacks
- We make short comments

The three ground rules were used as the simple tool applied to enforce a discourse ethic for the deliberative space we tried to create (Habermas, 1992b). The rules became self-enforced by asking participants for their explicit support.

During the workshop all comments and reflections made by participants and occasional invited guests, were documented by facilitators on wallposters visible to all participants. This gave participants the opportunity to correct misunderstandings and to ensure that the documentation of the workshops was a common and transparent process. After each workshop the poster documentation was transformed into a document and emailed to each participant.

Following the principles of the critical-utopian action research methodology the dialogue process was divided into different stages (Egmose et al., 2000; Nielsen and Nielsen, 2006; Nielsen and Nielsen, 2016; Tofteng and Bladt 2020). The first stage included two brainstorming sessions. In the initial session people were asked only to express their critique of the present situation including their concerns and whatever problems they associate with the issue. All concerns and expressed problems were recorded as short sentences or keywords on the wall posters. Following the first brainstorming session, each participant was then asked to prioritise two or three keywords, illustrating which concerns or problems were most important on a collective level. In the second brainstorming session, participants were asked to imagine the ideal future scenario in relation to the theme of the project. Just like in the critique session, participants were then asked to prioritise the two or three most important future scenarios. Guided by the facilitators, participants went through all prioritised scenarios dividing them into various sub-themes and each participant was asked to pick a theme to work with. Based on each participant's choice of theme several working groups were formed.

In the second stage the working groups developed their sub-themes even further before they gradually started to discuss how their particular vision for the future could be implemented, acknowledging the need for support from the outside in terms of knowledge, resources and/or the change of certain determining factors such as rules and practices. This stage included a number of so-called "research workshops" for which relevant experts were invited to answer questions raised by the participating citizens and to engage in dialogue.

Critical-utopian dialogue processes are always centred around common matters/problems, of relevance to a broader public. Participants were therefore encouraged to present their visions and gathered knowledge and plans to a broader public and/or policymakers and governmental agencies during the final stage. Presenting the outcome of the critique, visions and joint fact-finding process to the public was referred to as "the public stage". In the WDP, the public stage was combined with the development of a "participants' report," expressing the situation and findings, not from the point of view of the facilitators and research team, but from the perspective of the participating citizens.

Altogether the duration of the WDP was two and half years and consisted of 14 workshops, divided into two subsequent loops described in the following (see **Table 1**). The first loop was guided by the headline: "The impact on our community," and the second process was guided by the headline: "Our proposal for a new wolf management plan". Our description of the two loops is based on written documentation, primarily workshop reports from meetings, but also the participants' reports and other reports, documents or papers/books referring to the project.[2]

Loop One—"The Impact on Our Community"

The research team from AU launched the project by contacting the local village council of the two parishes Idom and Råsted on the outskirts of the forest and heathland area of Stråsø, to ask whether the council would be interested in co-hosting a local dialogue experiment. The village council accepted the invitation and through the council an invitation was sent out to local citizens in the area to participate in an information meeting on the 17th of August 2017.

Fifty two people attended the meeting, the majority locals. The research team from AU presented the dialogue experiment idea, including the applied method. It was emphasised by the AU team that they did not represent any pro or anti wolf positions, nor any formal authority or governmental agency, but only a research interest in conflicts about common matters. Based on that interest the AU team offered participants 1) the establishment of a safe space for people to express their concerns on common matters, as well as their common visions for the future guided by four simple ground rules (described below), 2) a process of joint fact-finding based on the participants' questions, and 3) the support to make the voices of the locals heard by the public. The research teams only stated four ground-rules for the process: 1) everyone should agree to participate as citizens, not stakeholders, 2) no interruptions while someone else was speaking, 3) no personal verbal attacks were allowed, and 4) in order to give everybody a chance to speak during plenary sessions, everyone should express themselves briefly.

After having presented the idea of the experiment, and outlined the promises and rules, participants were asked to discuss two prepared questions in smaller groups during the coffee break: 1) "How does the wolf conflict impact the local community?" and 2) "Are you interested in participating in such an experiment?". Following the talk during the coffee break several participants stressed that the conflict had had a negative impact on the community and that–as expressed by

[2]Unfortunately, the majority of documentation from the work is in Danish. The main recordings of the process are workshop reports recorded at each workshop, and later transferred into electronic reports shared with all participants of the Wolf Dialogue Project.

TABLE 1 | List of activities from the Wolf Dialogue Project 2017–2020.

Activities and timeline of the project
The Wolf Dialogue Project phase I, 2017–2018
Info-meeting, Aug. 2017
"Future-creating workshop". September 2017
Meeting, October 2017
Research-workshop I, November 2017
Research-workshop II, November 2017
Conclusions and documentation, meeting, February 2018
Local, public meeting, March 2018
Meeting with authorities, April 2018
Activities between phases
"Next step"-meeting, May 2018
Excursion and meeting, August 2018
The Wolf Dialogue Project phase II, 2019–2020
Meeting, June 2019
Meeting, Aug. 2019
Meeting, September 2019
Meeting, November 2019
Meeting with authorities, February 2020

one participant - "*. . ..some people do not talk to each other in the grocery store anymore . . .* " Several participants also expressed that they felt excluded from the public debate about wolves and wolf management because of the heavily polarised, hard and personal nature of the debate and by the fact that they did not want to be associated with the hard and often vulgare rhetoric of either side of the debate. Based on what was communicated about this experiment, some expressed that they felt it offered a space for those who experience mixed feelings about the situation. Out of the 52 participants at the information meeting, 41 signed up for the WDP.

The actual dialogue project started with a workshop a few weeks after the introduction meeting. The workshop focused on formulating critiques and concerns (see **Table 2**), followed by a session of working with visions for the future (see **Table 3**). The stage that followed comprised of a total of four meetings, the "research-stage," where the participants first identified existing "knowledge-gaps" and on that basis formulated questions that they needed answered in order to qualify their visions for the future. During two meetings experts were invited to answer a total of 43 various raised questions and join the dialogue with the participants on wolves and wolf management (see **Table 4**). The purpose of the final meeting of this stage was to document and integrate the knowledge from the other meetings.

The experts invited included the biologist responsible for the Danish wolf monitoring program, a wolf researcher, a zoo director with experience in wolves' behaviour in relation to humans, a law professor and a wildlife manager from the regional state forest district responsible for documentation of wolf attacks on livestock. The process and the knowledge gathered was documented and integrated into the work of the participants, and ultimately into the first participants' report (Maarbjerg et al., 2018). Having a diverse group of citizens with varying backgrounds, the majority of whom are unfamiliar with writing and/or reading academic texts, it was tricky to develop an approach that ensured a process that did not exclude or disadvantage anyone. The AU research team made a first draft based on the produced workshop reports and asked for volunteers to read and comment on the draft. As a part of a planned workshop, all comments were presented to all participants and discussed prior to a revision of the first draft, again to be discussed with participants. Gradually a final report

TABLE 2 | List of prioritized critiques and concerns, as formulated by the participants in the start-up phase of the WDP, in 2017.

List of prioritized critiques from the start-up phase of the wolf dialogue project	
Insecurity and lack of knowledge causes fear (16)	Affects normal behavior (negatively) (2)
It is no longer safe to be in the forest/in nature (10)	Fear for the safety of children (2)
The wolf preys on livestock (8)	Concern that the authorities are dishonest when it comes to number of wolves (1)
Concern/fear for slow/poor management (8)	No trust in DNA-analysis (1)
Concerns/fears become negatively self-reinforcing (6)	Difficult to assess what information can be trusted (1)
Causes dispute on both local and national level (4)	Expenses for farmers (1)
EU decides too much (3)	

TABLE 3 | List of prioritized visions for an ideal future wolf management, as formulated by the participants in the WDP start-up phase, 2017.

List of prioritized visions for future wolf management	
The wolf can be regulated/culled (16)	People before wolves—proportions in relation to e.g. punishment for shooting wolves, as compared to crimes against people. (2)
Locally focused management (10)	Respect for different positions/viewpoints on wolf (1)
More research on wolves in a Denmark (8)	Export of wolves to other countries + wolf zones in the EU (1)
The wolf is harmless (5)	Faster response from authorities and more efficient DNA-analysis (1)
No wolves in Denmark (4)	The wolf as local pride and brand—"our wolf forest" (1)
More national influence on management—less EU influence (3)	An integral part of the ecosystem (1)
Reliable and accessible knowledge about the wolf (3)	Fenced gardens (1)
More vigilantism (2)	

TABLE 4 | Types of questions raised during the two research workshops of the first loop of the WDP, 2017.

Main topics and sub-themes from project part 1- research-phase
Topic 1: Wolves, monitoring, and research in Denmark
On the first of two research-workshops in part one of the project, the participants asked questions to researchers. The questions evolved around three main categories
Questions about monitoring and research on wolves in Denmark
Questions related to wolf behavior/biology and expected population trends
Questions related to human-wolf co-existence and experience from abroad
Topic 2: "The future management of wolves in Denmark and the potential for the community level to influence it"
On the second research workshop, law-experts and researchers assisted local participants in answering questions related to two main themes
Questions related to the EU Habitats directive and the wolf
Questions related to the potential for local-scale nature management

was finalised and printed. All participants were invited to be listed as authors.

In spring 2018, the project culminated in two meetings in which the participants presented their work to a broader audience. During the first of the two meetings, participants invited all interested fellow citizens from the two parishes to a public meeting. In preparation for the meeting, a working group was organised to develop a program for the meeting and decide who would chair and present. Members of the research team facilitated the talks and served as secretaries for the working group, writing minutes and coordination meetings and follow-up activities. A total of 99 local citizens joined the meeting held on 5 March 2018. After the participants from the WDP had presented the results everyone in the audience was given the opportunity to ask participants of the WDP and two invited "experts," namely the biologist responsible for the Danish wolf monitoring program, Dr. Kent Olsen and a wolf researcher, Professor Peter Sunde, both from AU, questions. The two experts had throughout the project been available for any questions raised by the participants. Strikingly, the questions were for the most part identical to the ones that had been raised in the early "research-stage" of the project. The public meeting caught the interest of several local as well as national newspapers, radio and television stations, broadcasting live from the meeting and several local participants and members of the research team was interviewed.

After the local public meeting, the WDP participants prepared a meeting for the members of the working group appointed under the Danish Wildlife Council (DWC)[3] to revise the existing national wolf management, as well as for officials from the Danish Environmental Protection Agency (DEPA) and the Danish Nature Agency (DNA). The point of this meeting was to present the outcome of the WDP and to have a dialogue. The invitation was initially met with silence and reluctance by the governmental agencies, but eventually both agencies, as well as the working group from the DWC accepted the invitation, and the meeting was held on 3 April 2018.

Both of these meetings were considered by the participating citizens of the WDP, to be very successful. The fact that both meetings offered the participants in the WDP a possibility to take responsibility for their own common situation, across internal differences, was likely the primary reason for the experienced success. Likewise, the invited representatives of the DWC and the officials representing the DEPA and the DNA were pleasantly surprised by the commitment of the locals, and at the meeting they expressed a strong admiration for the work done by the locals. The officials and the representatives from the DWC promised to take the local perspectives into consideration in the future wolf management and the DWC chairman expressed an interest in continuing the dialogue with the local participants in the years to come.

The meeting with representatives of the DWC, the DEPA and the DNA, and the completion of the participant report (Maarbjerg et al., 2018) concluded the first loop of the WDP.

In Between Loop One and Two—"What to do Next?"

When the first loop of the project had officially come to an end, approximately 20 participants expressed their interest in continuing the work in some form. Between the end of the first part of the project, and the beginning of the second loop, there was a gap of approximately 13 months. The timespan reflects uncertainties about the exact purpose of a second project part. A few meetings were held, including an excursion to the campus of the project team from AU[4] and the nearby Kalø castle ruin from 1313. The meetings attempted to clarify the possible content and ambition of a second loop, including discussions of whether to open the group to new participants or not. The question of opening up the project to new participants however was met with resistance amongst several participants, who were afraid that the trust established amongst the existing participant group would be compromised, if new participants joined. There was also a concern, that inviting new participants

[3]The Danish Wildlife Council is an advisory board to the government on issues related to wildlife management. The members of the council are representatives from some of the most significant interest groups in Denmark, including farmers, forest owners, hunters, nature conservationists, bird watchers, animal rights actors.

[4]The project team is located at the historical research campus at Kalø from where wildlife research has been made since the late 1940ties. The place is well known especially by hunters.

into the project would mean starting all over again, repeating much of the work already done in the first loop.

The opening for jumpstarting part two came, when in March 2019 it was announced, that the work on a revised national wolf management plan had been discarded altogether. The reason was that the working group on wolf management under the DWC, were unable to find common ground on the matter. As a final attempt, the chairman of the DWC, decided to appoint a new working group, with the mandate, not to revise the existing plan, but to develop a completely new management plan for the wolf. The remaining participants from the WDP now had a tangible goal. The goal was to inform and influence the new working group under the DWC on this new management plan. It was agreed that this opportunity should not be wasted, but exactly how to make an inclusive process took a while to figure out.

Loop Two—"Our Proposal for a New Wolf Management Plan"

Initially, a meeting was held to discuss how to proceed. Participants agreed to allow a few new participants to join the process and that the objective was to create a catalogue of more specific suggestions and reflections as a contribution to the work taking place at the national level. By recommendation of the AU project team, participants decided to approach the process following the template of an adaptive wolf management plan developed by a group of biology master students from AU during a course project in the spring semester of 2019. Since the student report was initially based on input from the WDP including conversations between students and locals the AU team figured it would be a good point of departure. Two students from the beforementioned project group volunteered to help the locals apply their own ideas and reflections to the template.

During three workshops held between June 2019 and November 2019 the participants and students worked together to develop goals and objectives to be incorporated into a future adaptive management plan. The three workshops followed the same procedures of facilitation, dialogue, and documentation as described in the first part of the WDP. Each workshop started with a summary of the previous meeting, before participants were divided into smaller groups to develop the one, two or three fundamental objectives that they considered important to address in a new management plan. At the end of each workshop each group presented the outcome of their discussions, including agreements as well as disagreements, and received feedback from the other participants.

During the first workshop the groups discussed the theme "Mitigate resource conflicts," at the second workshop the themes "Minimise fear" and "Increase safety" were discussed and at the last workshop participants discussed the themes "Improve knowledge," "Improve/increase international collaboration" and "Wolves in Jutland". In cases where participants were not able to attend a workshop, they were encouraged to call or email their ideas and reflections to the AU project team. A few participants took advantage of this opportunity, although attendance was largely stable between 15 and 18 participants.

Based on the records from all the meetings, a comprehensive document was prepared in a second participant report, with information about the process, suggestions, and reflections, including internal differences (Frøjk et al., 2020) (see **Table 5**). Hence, it was possible to ensure accuracy as well as transparency. Like the first participant report it was important to ensure that the document would reflect the participants' perceptions and not the facilitators', hence the report drafted by the AU research team was revised twice by the participants. At first, the draft was shared online before a follow-up meeting in which the document was discussed section by section. Citizens who had not participated in the second loop but had been part of the first one also got the opportunity to meet and share their thoughts and comments. The second time, the final report was sent out to all participants, and everyone was asked to actively respond to whether they would endorse the report or not. In that way it was possible to ensure the document's legitimacy.

Once the report had reached its final form, the task was to find out how best to present it and thus complete the project. A working group was set up to invite the DWC's new working group to a meeting on 6 February 2020. At the meeting all eight members of the working group of the DWC attended. Additionally, two representatives from the DEPA and three representatives from the DNA joined the meeting. At the meeting the chairman of the wolf working group under the DWC,[5] presented the status of the working group and the plan for the future process. Afterwards the locals presented their recent work in general terms, including their overall reflections and ideas regarding a new wolf management plan. After the plenary session locals divided themselves into three groups, each responsible for a particular objective. The national wolf working group and the officials from the DEPA were also divided into groups each joining a group of locals. Here, the locals presented their ideas on their specific objectives. Every 20 min the representatives from the national wolf working group and the officials would rotate to the next group of locals representing a different objective and so on.

RESULTS

The WDP generated some public attention. Quite a large number of local and national newspaper articles, radio and television stations frequently reported on the project while it was ongoing and interviewed citizens participating in the project. The national radio and television broadcasting network, DR, went one step further, and–since they were not allowed to broadcast live from the WDP workshops–based on consultations with the project leader, made a full evening live television broadcast of their own dialogue workshop with locals living in or nearby the wolf territory, invited experts and representatives of interest groups. Several participants from the WDP were also invited to for the DR workshop.

[5]The chair of the wolf working group, Jan Eriksen, was also the chairman of the Danish Wildlife Council.

TABLE 5 | An overview of input from the participants WDP to the expected new national wolf management.

Mitigate resourse conflicts	Minimise fear	Increase safety	Improve knowledge	Improve/increase international collaboration	Wolves in Jutland
Minimize/optimize use of livestock for nature management (of heathland) in wolf territory	Better access to updated information and knowledge about the wolves in specific areas	Increase the access to updated information about wolves and make a guide, describing how to act, if one encounter a wolf	Do more research on the sensitivity of wolves towards human beings	Strengthen international collaboration on wolf and wolf management	No restriction of local citizens access to nature in wolf protection zones
Wild deers/burning as an alternative to livestock (sheep) for nature management of heathland	Provide information on the behavior of wolves during different live stages (e.g., pups)/times of year, so people know what to expect as "normal wolf behavior"	Evaluate different types of deterrence	Evaluate different strategies to moderate wolf-behavior—e.g., means of deterrence	Establish wolf-zones on an European level	Make studies of how human activity is affected by wolf-zones
Cover costs to secure sheep if the state wants to continue using sheep	Include a plan of action under various, potential scenarios involving wolves, livestock or people	Make a more clear definition of a "problem wolf"	Document the effect of wolves on game, especially red deer	Establish an international network for reporting wolf-observations and sharing information, like the Danish www.ulveatlas.dk	Make guidelines for wolves-tourists how to behave on private land/forest in wolf territories
Animal husbandries should have access to advisers/support free of charge, when experiencing wolf attacks on livestock	Clarify existing legal means on deterrence and their efficiency	Make the results of DNA-samples from attacked livestock public. That will make it easier to decide if it is a "problem wolf	Distribute information and news about wolves in communities near wolf-areas		
Provide more information and financial support for sheep farmers on various protective means (sheep dogs, fences etc.)	Ensure the wolf management plan to be based on factual knowledge and experiences from a Danish context	Make guidelines for the visual identification of DNA-verified "problem wolves," so that they can be culled as quickly as possible	Reoccurring dialogue- and information meetings with authorities and researcher, for interested locals in wolf areas		
More clear guidelines for governmental institutions on possible actions to implement in relation to mitigate wolf conflicts related to wolves—e.g., safe transportation of children to school	Establish reoccurring dialogue- and information meetings with authorities and researcher, for locals living in wolf territories	A wolf defined as a "problem wolf" in Germany should also be defined as "problem wolf" in Denmark	Establish an online wolf-platform for locals, researchers and others		
Map if the occurrence wolves affect the value of real-estate		Define a maximum limit of wolves in locally and nationally	Establish a center for dialogue and distribution of knowledge		
Estimated max wolf capacity in terms of human/societal tolerance, and effect on other wildlife species		Minimize risk of habituation of wolves by the use of scaring techniques—e.g., the use of rubber-ammunition)	Increase access to support and information, e.g., *via* a hotline and/or libraries in wolf zones		
Set a maximum of one wolf pack pr. "wolf area" (5–8 wolves) and define when culling is needed		If a wolf is to be culled, it should be done in vicinity of other wolves in order to increase fear for human beings	More integrated collaboration amongst all actors working with wolf/ monitoring in Denmark		
There is an ethical dilemma between the protection/ care for livestock and the legal status/protection of wolves					

Several theses related to the project have been published by students from various universities (Mikkelsen, 2018; Schrøder, 2018; Steinvig et al., 2019; Fox, 2020). Internationally three publications have described the WDP (Ripley 2021a; Ripley, 2021b; Cirino, 2018). However, this paper is the first scientific publication reporting the general results from the concluded project. The scope of our presentation of results and our discussion will be the same as the general scope of the entire experiment, the possibilities to develop a productive alternative to the systematically distorted communication that characterises the Danish wolf management situation, applying a critical-utopian dialogue approach based on a Habermasian discourse ethic and joint fact-finding process. The ambition of the project was through empowerment to encourage the participants to take responsibility as citizens in respect to the needs of their community and society as a whole. Simply put, we have divided our presentation of results into impact on the local level and impact on national level.

Impact Local Level

Over time participants accepted and adopted the discourse ethic required by the tools and methods applied. Several times during the process and after the conclusion of the project, participants pointed out the three simple ground rules as critical for what they saw as the success of the entire process and dialogue. Whenever someone got carried away violating the ground rules, other participants would kindly remind that person about the agreed upon rules. We also witnessed how the process gradually evoked a kind of social responsibility at the individual level, even by some of the more rebellious participants. One example occurred during the planning of the local public meeting during loop one. The appointed working group responsible for planning the local public meeting had six members and included "Jamie".[6] At workshops and during personal conversations "Jamie" was often difficult to interpret due to their ironic jokes, sarcastic and sometimes provocative and conspiratorial comments. One task of the working group was to decide who should chair the public meeting. "Jamie" offered themself as the chair and since no one else volunteered, the group accepted "Jamie" as the chair, although with some hesitation. At the actual event "Jamie's" ironic jokes, sarcastic and sometimes provocative comments, were replaced with a well-prepared and serious chairmanship and strong loyalty to what was agreed upon.

The discourse ethic enforced by a few simple ground rules and the facilitators, served as the platform for advocating the participants' own perspectives, concerns, and a platform for the development of their suggestions in relation to wolf management. Hence, we observed a movement away from being a project initially driven by the AU research team, to a process gradually being driven by the locals themselves. Only on two occasions did the discussions get so much out of hand that the ground rules were violated, both times during the second loop. The second loop was characterised by a smaller and more polarised group of participants and for a relatively long period of time uncertainty about the objectives of the second loop.

The first occasion was at a workshop after a full day excursion into wolf territory co-organised by participants from the WDP, for locals as well for a group of students from Roskilde University. After the excursion a workshop was planned for the locals and one of the participants had invited the entire group to his/her house for the workshop. The spouse of the host joined the workshop, and gradually took over the agenda advocating for all wolves in the area to be removed and arguing the WDP to be a hoax initiated by "wolf lovers". The second occasion was at another workshop towards the end of loop two during a period when local, national, and social media were occupied by the question about why wolves disappeared. The project leader, who apart from researching wildlife conflicts also researches illegal hunting, was interviewed several times by newspapers, radio and television, to comment on the subject. At the particular workshop three participants expressed a strong dissatisfaction with the fact that the project leader in public had pointed out illegal killing to be a likely explanation for why wild wolves apparently disappeared in Denmark. Both incidents were critical in the sense that they could have put a stop to the WDP, and both times the research team considered whether they should end the project but decided both times to continue.

The project formally ended with the meeting with the national wolf management working group during loop two, in January 2020. Despite the project having officially ended several of the participating citizens are still engaged in the implementation of ideas developed during the two loops. Several participants have continued developing the idea of a local centre for knowledge and dialogue on nature and wildlife and recently received a grant of 860000 Danish Kronor, equivalent to 130,000 USD to make a plan for its implementation and funding (see also "New Conflicts Emerge"). Potentially such a centre will be able to deal with most of the issues raised during both loops of the WDP (see **Tables 3**, **4**, **5**).

The contact between former participants and members of the research team has also been maintained. From time-to-time participants phone or email researchers to catch up on the wolf management situation, to ask various questions or to share some reflections. Likewise, members of the AU research team occasionally call or email former participants, either to catch up on the local wildlife situation or to ask them to present to students about local perspectives on wildlife conflicts. In addition, local participants have, during and after the WDP, been invited to share their experiences with wolves and with the project, by organisations and other communities.

In terms of what has changed in relation to the local management of wolves, several participants have reported that the situation is less heated than before. This is not solely a result of WDP but also because there are currently fewer wolves in the area and that locals over time have probably become more used to the situation. But the fact that the WDP has procured some valuable knowledge locally, addressing some of the existing concerns, has likely also contributed to a less heated situation.

On a more practical level the WDP indirectly contributed to the solution of a specific problem. In the early stages of the project the younger child of one of the WDP participants who lives inside the wolf territory experienced being followed by a wolf walking

[6]This is not the real name of the participant refereed to.

home from the school bus. The family asked the local municipality for help but was initially rejected. However partly supported by the WDP the incident got quite a lot of attention by local and national media (BT 2018). Eventually the municipality invited the family to a meeting, and the municipality decided to change the placement of the bus stop to reduce the distance for the child to walk which solved the problem for the family. In terms of the changes on the national level the locals are still waiting for the new wolf management plan to be implemented (see Impact National level).

New Conflicts Emerge

As mentioned previously local citizens have continued to develop the idea of a local centre for knowledge and dialogue on nature and wildlife. Presented to the working group of the DWC, representatives from the DEPA and representatives from the DNA at the last workshop, and later to the municipal director of the local municipality, the idea has gained a lot of support. A centre could potentially be an institutionalisation of the dialogue and joint fact-finding space established by the WDP, representing local common problems, and giving locals a voice in nature and wildlife management.

A few months after the WDP concluded at the beginning of 2020 with the meeting with the DWC and DEPA officials, the citizen initially presenting the idea of a centre, invited some former members of the WDP, representatives from various organisations, officials from the local municipality, officials from the local state forest district and members of the AU research team, to join a meeting. The purpose of the meeting was to discuss how the idea of a centre could be developed and eventually implemented. Members of the AU team offered to serve as a kind of secretary for the workgroups, documenting meetings. Several meetings took place during 2020 and 2021 and gradually a written description of the centre and its purpose was made.

Early in the process the working group meetings revealed local tensions and gradually the process reflected a more traditional strategic decision-making process. After approximately a year the tensions cased a second group to be formed and the external representatives from various organisations, officials from the local municipality, officials from the local state forest district and the AU research team pulled out. The new working group, rooted in the village council that initially co-hosted the WDP, applied for–and recently received–a grant to hire a professional to make a plan for the implementation and funding of a Knowledge- and Dialogue Centre for Wildlife and Nature (our translation).[7]

Impact National Level

As previously mentioned, the WDP managed to attract the attention of the DWC and various governmental agencies. In both loops, council members and officials from the DEPA were invited to come to Idom-Råsted to listen and to engage in a dialogue with the locals. In the first loop the governmental agencies were suspicious of the entire project, but eventually they accepted the invitation.

The two meetings, and the two participant reports made during the WDP obviously functioned as an inspiration for DWC's work with initially the attempt to revise the existing wolf management plan from 2014, and later for an entirely new wolf management plan to replace the first one. From the proposed new management plan, it is evident that many of the inputs from the WDP have been incorporated as central goals, such as fear, safety, communication, and involvement (Danish Wildlife Council, 2020). The new wolf management plan displays a greater appreciation of the need to incorporate the human dimensions of wolf management for its long-term success and legitimacy.

The contribution of the WDP to the development of the new wolf management is credited in the introduction of the final proposal for a new wolf management plan to the government. The plan has not yet been accepted by the government, but the Minister of Environment has announced in a press release on 14 October 2021 (Miljøstyrelsen, 2021) that more resources will be designated to local dialogue meetings.

DISCUSSION

Wolf management conflicts may seem to be unsolvable "High conflicts", and traditional governance methods often fall short (Gieser and von Essen, 2021; Niemiec et al., 2021). However, this should not dissuade attempts to address such conflicts. On the contrary, taking the described consequences of the wolf management conflict into consideration, we argue that we as scholars hold a strong responsibility to deconstruct the conflicts and carefully examine potential solutions. Doing nothing does not seem to be a viable alternative, but we as scholars are also restricted by the limits of our own interpretations of the world, why we sometimes are forced leave our comfort zone and engage ourselves in the conflict. Like the late German-American psychologist Kurt Lewin once said: *"If you want truly to understand something, try to change it."* This was what we tried to do in the WDP.

Before entering our discussion, we want to stress two points. First and foremost, we want to avoid any deliberate "glorification" or exaggeration of the outcome of WDP. We do not claim the critical utopian dialogue approach to be "the solution" to all wildlife conflicts, in fact, this particular method should just be seen as a "vehicle" to test a Habermasian discourse ethic in a practical deliberative process in a real empirical setting. Additionally, the WDP was a small experiment including only a small number of citizens and based on a low budget. Together with the fact that the experiment was made in one of the most safe and political calm parts of the world, a Scandinavian welfare society, an important question to raise is the relevance of this experiment for other places in and outside Denmark. At the end of our

[7] In Danish: "Udvikling og afprøvning af Viden-og dialogcenter for vild natur og mennesker."

discussion, we will get back to the question of whether there are any universal lessons or experiences one can take form the project.

Secondly, we want to emphasise that it was not the purpose of the experiment to transform critics of wolves or wolf management into wolf supporters or visa-versa but, as previously stated, through the critical-utopian dialogue approach to create a shared and more productive responsibility for the common amongst the participating citizens. Guided by the initial header, "The impact on our community," the ambition of the WDP was to create a space for people, living in close proximity to wolf territory, in which to deal with existing concerns and identified problems, to develop solutions and to give the local citizens' a voice.

We will not discuss the content of the WDP and the various issues raised and explored by the participants, but will instead focus on, to what extent, and how, the project might have created a better understanding of the possibilities for developing a more productive alternative to the systematically distorted communication that characterises wolf management, creating responsibility by empowering citizens instead of stakeholders, using a critical-utopian dialogue approach.

Two Fundamental Differences

The WDP offered two fundamentally different takes on the wolf conflict, compared to more traditional governance approaches. Firstly, the WDP was not driven by any other strategic interests, than the curiosity of the research team to explore the potential of the dialogue approach described, within this specific context. Often researchers and/or facilitators are driven by certain governmental interests, or certain NGO interests and thereby, consciously or subconsciously, commit to specific values or predetermined goals or outcomes (von Essen and Hansen, 2015). In the case of the WDP, the research team chose to take a step back, focusing on the democratic deliberative process, and not on the promotion of certain conservation values, but instead trusting the ability of the participants to evaluate the situation and to make justified and responsible decisions.

Secondly the WDP differed fundamentally from traditional governance approaches, by not focusing directly on the wolves, but instead on the broader impact of the wolf conflict on the participants themselves and their community. By this shift of perspective, the WDP opened a totally different arena, and thereby broke with the dichotomy and deadlock created by strategic predetermined interests that dominate the public agenda. Based on the media coverage of wildlife conflicts, nuances are often lost in how public and social media portray the situation as very polarised. The WDP revealed that reality is much more complex, and that the participants' experiences and values are much more ambiguous and nuanced.

Building Trust and Evoking a Common Goal

Early in the process participants acknowledged the impact of the wolf conflict to be a common issue, and that there was no other alternative than to collaborate despite differences in opinion, in order to deal with the specific problems experienced. However, in order to reach a point, from which participants could communicate their experiences, values, and the knowledge they collectively created, including their ambiguities, it was necessary to establish trust between the participants themselves, trust towards the AU research team, as well as trust towards invited experts and officials.

The trust towards the AU research team facilitating the WDP developed relatively fast even though a general mistrust towards AU were expressed by several participants and the motives of the AU research team were questioned in the initial phase. The expression of mistrust towards the university deceased during the project but it required the attention of the AU research team throughout the entire project. Although only a fraction of the community participated in the process, local people started to use the slang-expression, "attending wolf" when talking about the WDP, and at the local community centre the workshops of the WDP became an integrated reoccurring event. We do not know how WDP is perceived among non-participating community members, but WDP participants reported that many conversations took place locally, and similar to the spouse at the WDP meeting in the private home, participants also reported that several community members were suspicious of the whole process. Like the expressed mistrust towards the university many participants also shared a mistrust towards authorities and questioned the real motives of wildlife managers and wildlife officials.

In the initial phase of the WDP participants expressed that they often shied away from uttering their concerns, especially to people living in nearby cities, as they would sometimes experience being ridiculed for them. During the first couple of meetings the project team thoroughly documented the concerns and fears of the local citizens. It was evident, that many of the local participants experienced that their concerns about living in close proximity to wolf territory were acknowledged by the WDP. This recognition of concerns had a positive and immediate effect on the polarisation among the participating citizens. This is not to say that the more radical positions disappeared, but we witnessed an almost instant movement towards much more nuanced reflections and away from the more "radical" expressions and exaggerations of viewpoints.

Apart from being the primary documentation for the AU research team of the process, the instant documentation of reflections, comments, inputs etc. on the walls during meetings, served as a physical common output from each meeting. Everyone had a shared ownership of these workshop reports which is why the facilitating team on several occasions had to turn down journalists, who wished to attend a meeting. To secure the safe space, nothing from the WDP was communicated to the broader public before the participants felt prepared to present something to the public themselves.

The main purpose of the "research stage" was to create an integrated platform of knowledge and learning in order to identify the real problems and possible solutions. The encounter with "experts" provided answers to the raised questions, but also offered the participants an insight into the nature of research including all its uncertainties. Further, meeting the researchers face-to-face gave the participants the opportunity to see them as subjects with various competences and holding different values, and not just as distant objects that occur in newspapers and on television, or who are demonised in social media. Participants hereby gradually developed a nuanced perspective on the quality of data but also a kind of respect for the willingness of researchers to visit their community and engage in–sometimes difficult–dialogue.

From being doubtful about the chance to have a say, and even more to make a difference, participants gradually saw the opportunity to have an impact. Gradually participants took on the responsibility to formulate their own experiences, visions for the future and ideas for solutions to specific problems. This collective responsibility culminated with the public meeting with their fellow local citizens and with the two dialogue meetings with officials and the DWC visiting the community. Especially the first meeting with officials and the DWC made several participants euphoric and–some–even quite emotional. It was also evident, that both the collective effort put forward by the participants, and especially the everyday-perspectives, concerns, and experiences of the group, made an impression on the officials and representatives of the DWC.

"Slow Impact Syndrome"

During the WDP "time" proved to be a critical factor in two ways. Building trust internally and externally required time, while participants at the same time were rather impatient with the pace. Especially when it came to the governmental processes and the existing bureaucracy of governmental institutions, it was hard for many of the participants to accept that it was not possible to implement obviously "good" ideas immediately. As one of the participants stated "*. . ..most people living in the countryside are used to acting immediately, when it is needed. We cannot understand why governmental institutions cannot do the same . . .* " This point is reenforced by the fact that 4 years after the start of the WDP, and 1 year after the DWC proposed an adaptive wolf management plan (The Danish Wildlife Council, 2021), the plan has still not been transformed into a new governmental wolf management plan, although elements from the recommendation have recently been adapted by the government.

The frustrations with the slow pace of changes caused some participants to withdraw during the WDP. Despite the slow impact, and exhausting meetings continuing late into the evenings, most of the initial participants during loop one attended workshops regularly. During loop two, less than half of the original participants participated, believing that they somehow could have an impact on the new wolf management plan. WDP has undeniably had a significant impact on the officials, as well as the members of the DWC, who visited the local participants. This is reflected in references made to the WDP by DWC members and officials in various settings, including DWC meeting minutes and in the suggested new wolf management plan. As such, the WDP managed to impact the agenda of future management more than most people would have expected. However, it is still a work in progress, and on a local level some still find that there is nothing or little to "show for it" yet.

This leads to the question to what extent have participants actually influenced wolf management? Obviously, the formal power structures related to wolf management have not been changed but are still embedded in the representative political structures exercised by representatives of governmental bodies such as the DWC and DEPA. However, considering that power is not just reflected by formal structures, the participating citizens have had a considerable impact. The longer-term impact made by the participants of the WDP, formally and informally, remains to be seen and will be the focus of follow-up studies.

Balancing Minority and Majority Needs

For the duration of the project, both loops one and two, facilitators had to balance the amount of time each participant was allowed to speak during meetings. Some participants would utter the same critiques and complaints time and time again. It took time away from the meetings and became a source of frustration for some of the other participants. This posed a dilemma to facilitators, as they both wanted to give the minority the space and time to express their frustrations, while also recognising the tiering effect it had on the majority of participants. However, balancing minority and majority needs was important to maintain the broad spectrum of voices, otherwise the WDP could be reduced to an echo-chamber in which the same arguments would have been repeated over and over again. It was vital to the AU research team to maintain the diversity of the group for as long as possible as it contributed to the dialectic dynamic.

Throughout the WFP, there were situations when participants temporarily relapsed into old narratives and beliefs contradicted by facts or science. One explanation is once again the time-factor combined with impact. It takes time to internalise new knowledge and replace previous beliefs with new ones. At the same time participants are impacted by the social control of their fellow citizens within and outside the WDP group, who question the credibility of experts and officials. Nevertheless, conversations with participants long after the WDP ended, have confirmed that the reflection process has continued, also among some of the more reluctant participants.

Twice the AU team experienced such setbacks and losses of control, that it was discussed by the team whether the WDP should stop. During the first incident it was evident that the choice of a non-neutral venue–the private home of one of the participants–at the time of the incident, lack of a clear purpose of the second loop, and a lack of a sufficient critical mass, were significant drivers of the "crisis". Although the second incident was not as critical as the first one, both incidents demonstrated how frustrations and distrust can easily reappear. Following both situations, the project leader decided to continue, and the critical incidents proved not to be as critical for the process as anticipated but revealed a kind of "WDP-resilience" that was able to overcome the setback. That said the "WDP-resilience" was not strong enough to avoid the post-WDP conflict between locals competing for the ownership of the Knowledge- and Dialogue for Wildlife Centre. While it seemed possible to create a rather strong unity, and a significant impact during the WDP, local participants were not able to maintain the unity after the AU team pulled out as facilitators. This indicate that the adaptation of the communicative processes applied in the WDP, might work as long as they are facilitated by professionals, but will require more time and practice in order to be internalised on a community level.

An Alternative?

To evaluate to what extent the WDP offered a productive alternative to the systematically distorted communication that characterises current wolf management, two questions can be raised: 1) did the WDP succeed in creating a safe and equal space for the participants to transcend their private interest and to exercise their responsibility for the commons? 2) To what extent has the WDP had a positive impact on the existing deadlock characterising the wolf management conflict? And for the relevance of the readers of this outlet a third question must be raised: Are any of the lessons from the WDP transferable to other political and cultural settings?

Based on the documentation from the workshop reports, participant reports, and personal notes, it seems that the WDP did create a relatively safe space of deliberation and recognition for most participants. As we recognise that power differences and expressions of power can be subtle and are embedded in social, political, cultural, and communicative structures, it would be naive to believe that the space created by the WDP has made all participants equal. Asymmetric power relations and conflicts exist within and between individuals and groups everywhere and are as such unavoidable. The question is how we work our way around these power relations and conflicts. Based on the relatively long duration of the project, and the desire of several participants to continue with a second loop, it is evident that the approach offered by WDP had something to offer in relation to the impact of the wolf management conflict on their everyday life. The fact that the participants managed, supported by the AU research team, to develop two catalogues of concerns, reflections, ideas, and solutions for the future wolf management, and collectively to communicate these concerns, reflections, ideas, and solutions to national authorities and the DWC, is a strong indication that the participants developed social and political responsibility for the commons as citizens.

In regard to the second question, the participating citizens did inspire the national authorities and the DWC and officials from the DEPA. And through the evoked interest from the media, the WDP and the participating citizens brought new perspectives into the media, and also raised an awareness about the nature and consequences of the way the wolf management conflict was portrayed and reproduced in the public. It is difficult not to perceive this as a positive impact on the deadlock of the wolf management conflict. Nevertheless, it is harder still to determine how strong this impact has been.

On the third and final question about whether any of the lessons from the WDP are transferable to other political and cultural settings, less homogeneous and more unequal than Denmark one might look at similar types of dialogue and joint fact-finding experiments, or processes guided by the same type of discourse ethic and ambition to create social and political responsibility through recognition and empowerment. Experiences from a range of other political and cultural settings, including Sweden, Mozambique, Nicaragua, and Colombia, indicate that it is possible in different social, political, and cultural settings to create spaces for dialogue on the commons guided by a common discourse ethic, making the participants–at least for a period of time–equal as citizens, as an alternative to strategically distorted communication (Dalsgaard, 2009; Sriskandarajah et al., 2016). In a world where populism and fake news threatens our ability to govern, there is an urgent need to explore the potential for similar approaches in different political and cultural contexts and on different scales, in order to test its applicability.

CONCLUSION

The WDP proved that it was possible, *via* dialogue and joint fact-finding, and based on the commons and simple rules of communication and recognition, to create a more constructive take on the wolf management conflict. The WDP managed to gather local participants, external experts and governmental institutions in an integrated learning process that explores visions and solutions for the future. Both on the local level and on the national level the project made a significant impact on the wolf management agenda.

The results from the WDP are promising and indicate that a dialogue approach, guided by a Habermasian discourse ethic, can be a useful "tool" in unchaining "High" wildlife conflict. The outcome of the WDP could inspire further studies on ways to empower and engage local citizens as a resource in the resolution of wildlife management conflicts.`

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent to participate in the study was not obtained as we obtained verbal informed consent.

AUTHOR CONTRIBUTIONS

HP, CD, GF, and AJ have been a part of the research project described and have all contributed to the manuscript. Being the project leader of the research project HH developed the theoretical framework of the paper. HH, CD, and AJ developed the outline. HH and CD drafted the first version of the manuscript. HH completed the manuscript for submission. GF proofread, edited and commented on two drafts and on the final submitted manuscript. The distribution of work required for the manuscript has been approximately like this in order of authors: 50%-30%-10%–10%.

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Wolf Responses to Experimental Human Approaches Using High-Resolution Positioning Data

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Humans pose a major mortality risk to wolves. Hence, similar to how prey respond to predators, wolves can be expected to show anti-predator responses to humans. When exposed to a threat, animals may show a fight, flight, freeze or hide response. The type of response and the circumstances (e.g., distance and speed) at which the animal flees are useful parameters to describe the responses of wild animals to approaching humans. Increasing knowledge about behavioral responses of wolves toward humans might improve appropriate management and decrease conflicts related to fear of wolves. We did a pilot study by conducting 21 approach trials on seven GPS-collared wolves in four territories to investigate their responses to experimental human approaches. We found that wolves predominantly showed a flight response (N = 18), in a few cases the wolf did not flee (N = 3), but no wolves were seen or heard during trials. When wolves were downwind of the observer the flight initiation distance was significantly larger than when upwind, consistent with the hypothesis that conditions facilitating early detection would result in an earlier flight. Our hypothesis that early detection would result in less intense flights was not supported, as we found no correlation between flight initiation distances and speed, distance or straightness of the flight. Wolves in more concealed habitat had a shorter flight initiation distance or did not flee at all, suggesting that perceived risk might have been affected by horizontal visibility. Contrary to our expectation, resettling positions were less concealed (larger horizontal visibility) than the wolves' initial site. Although our small number of study animals and trials does not allow for generalizations, this pilot study illustrates how standardized human approach trials with high-resolution GPS-data can be used to describe wolf responses at a local scale. In continuation, this method can be applied at larger spatial scales to compare wolf flight responses within and between populations and across anthropogenic gradients, thus increasing the knowledge of wolf behavior toward humans, and potentially improving coexistence with wolves across their range.

Keywords: experimental human disturbances, flight responses, *Canis lupus*, animal behavior, flight initiation distance

INTRODUCTION

In predator-prey systems, prey show anti-predator behaviors such as vigilance and altered foraging behavior to reduce the risk of being preyed upon (Ydenberg and Dill, 1986; Cooper and Frederick, 2007; Laundre et al., 2010). Detection is the first step in prey's response to a predator (Bednekoff and Lima, 1998). Predation risk vary in time and space and vigilant behavior likely corresponds with the risk perception (Lima and Bednekoff, 1999; Gaynor et al., 2019). In low risk situations animals might spend less time on vigilant behavior and increase time feeding or resting (Lima and Bednekoff, 1999). In resting situation animals might select for protective cover, but potentially with an overview to detect any risks (Lazarus and Symonds, 1992).

Once a prey has detected a predator, it has four basic response options: flight, fight, hide, or freeze (Lima and Dill, 1990; Rupia et al., 2016; Roelofs, 2017). Different responses come with different energetic costs, which together with the perceived severity of risk (Cooper and Frederick, 2007) affects the response. Optimally, when the potential risk of staying exceeds the costs of fleeing, the animal should flee (Ydenberg and Dill, 1986; Lima and Dill, 1990; Cooper and Frederick, 2007). Additionally, the response in a given interaction can be affected by the animal's personality and previous experience (Beale, 2007; Rupia et al., 2016; Found and Clair, 2018; Carricondo-Sanchez et al., 2020). Various disturbance intensities may affect the intensity and duration of the animal's response (Beckmann et al., 2004; Ordiz et al., 2013; Petracca et al., 2019; Suraci et al., 2019).

Anti-predator behaviors are not limited to prey species. Even top predators might display similar behaviors to avoid intra-guild aggression (Holt and Polis, 1997; Swenson et al., 2001; Frid and Dill, 2002; Mech and Boitani, 2003; Wikenros et al., 2017) and as a response to human-induced disturbances (Gill et al., 1996; Frid and Dill, 2002; Moen et al., 2012). For wolves (*Canis lupus*), encountering humans is still not without risk. Lethal control, poaching, and traffic collisions are main sources of wolf mortality (Colino-Rabanal et al., 2011; Liberg et al., 2012, 2020; Recio et al., 2018), and human-related mortality currently limits the population growth of wolves in Europe (Kuijper et al., 2019; Liberg et al., 2020; Sunde et al., 2021). Hence, human-caused disturbances are expected to result in anti-predator behavior due to a potentially lethal risk for the wolf (Frid and Dill, 2002; Ordiz et al., 2011). In fact, even though wolves and other predators are known to make use of human-made structures (e.g., roads and bridges) (Blanco et al., 2005; Zimmermann et al., 2014; Dickie et al., 2017; Bojarska et al., 2020), they tend to avoid human activities, resulting in spatiotemporal segregation between wolf and human activities (Lesmerises et al., 2012; Milleret et al., 2019; Carricondo-Sanchez et al., 2020). The avoidance of human activity may have been shaped by the century-long history of wolf persecution by humans, as suggested for the brown bear (*Ursus arctos)* in Europe (Zedrosser et al., 2011).

Responses to approaching humans have been studied previously in wolves using information from VHF-collars (Karlsson et al., 2007; Wam et al., 2012, 2014), and more recently in brown bears using high-frequency GPS data (Moen et al., 2012, 2018; Ordiz et al., 2019). In wolves, flight initiation distance (FID, i.e., the distance at which an animal flees from an approaching threat) was affected by wind conditions, with shorter FID when the wind was blowing away from the wolf, but not by horizontal visibility at the wolf's location (Karlsson et al., 2007). In contrast, reduced horizontal visibility at brown bear resting sites resulted in shorter FIDs when approached by humans (Moen et al., 2012). This indicates that the bear either made the decision to wait longer before fleeing (Beale, 2007; Cooper and Frederick, 2007), or it did not detect the observer (Moen et al., 2012), illustrating that the time of flight initiation does not necessarily equal the time of detection. After being disturbed by a human, VHF-collared wolves selected more concealed locations with lower horizontal visibility (Wam et al., 2012), and a recent study found that wolves select for more concealed resting sites during the day in response to increased human disturbances (Bojarska et al., 2021). Horizontal cover may benefit wolves more in terms of concealment more than it hampers their vigilance. Wolves have well developed auditory and olfactory systems, which may be more important in detection of threats over longer distances than visual detection (Mech, 1970; Harrington and Asa, 2003).

With this paper, we aimed to describe the flight response of seven wild GPS-collared wolves in Norway and Sweden by conducting experimental human approach trials. This is, to our knowledge, the first study assessing wolf flight responses toward humans with the use of high-resolution GPS data, which gives much more detailed and accurate information about flight intensity and flight patterns compared to VHF studies (Moen et al., 2012, 2018; Ordiz et al., 2019). High resolution GPS data makes it possible to re-construct details of the flight path without the need of snow tracking (Moen et al., 2012; Wam et al., 2012, 2014). With this advancement, fine-scaled studies of wolf flight responses no longer rely on snow cover, although supplementary snow-tracking may still have the potential to give additional behavioral information of importance.

Based on previous studies on wolves and bears (Karlsson et al., 2007; Moen et al., 2012) we hypothesized that wolves would avoid approaching humans (H1). Therefore, we predicted that during approach trials, wolves would show predominantly flight responses (P1) and flee before the observer would pass the wolf's initial location (P2). If seen by the observer, we predicted that the wolves would retreat without signs of aggression (P3).

We hypothesized that wolves likelihood to flee would depend on the detectability of the approaching humans (H2). Previous studies have shown that FID during experimental human approaches can be affected by the number of observers for brown bears (Moen et al., 2012), and the wind condition for wolves (Karlsson et al., 2007). We predict larger FID with increasing number of observers (P4), observers walking though noisy vegetation (e.g., forest with dense regrowth of trees) (P5) and wind direction from observer to wolf (P6).

The wolf's decision of whether and when to flee after detecting an observer may depend on the horizontal visibility at the individual's location (i.e., wolf's perception of risk) (H3). Previous study on bears found that individuals in more concealed resting site had shorter FIDs (Moen et al., 2012). We predicted that wolves resting at a more concealed location would wait for longer before fleeing (shorter FID) (P7) and have a higher occurrence of no flight (P8) compared to wolves at less concealed locations.

A higher response intensity is related to increased perceived risk (Ydenberg and Dill, 1986; Frid and Dill, 2002; Cooper and Frederick, 2007). Therefore, we hypothesized that an early retreat enabled by early detection would result in a lower perceived risk and thus a less intense flight (H4). From this hypothesis we predicted that larger FID would be associated with shorter (P9) and less straight (P10) flights at lower speed (P11).

Following the results from Wam et al. (2012), we hypothesized that after a flight, wolves will seek a more concealed resting location (H5). Therefore, we predicted that the wolf end position will have a shorter horizontal visibility than the wolf starting position (P12).

MATERIALS AND METHODS

Study Area and Animals

The study area is located along the Scandinavian border between Norway and Sweden. It included three wolf territories south of Trysil (Norway) (61°02′N, 12°18′E), and one wolf territory near Charlottenberg (Sweden) (59°55′N, 12°11′E). The study area is mainly dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and a lower abundance of birch (*Betula* spp.) and aspen (*Populous tremula*). The forests are intensively managed consisting of a mosaic of age classes and an extensive network of forest roads (Sand et al., 2008; Zimmermann et al., 2014). The human population density within the study area varied from 2 to 10 inhabitants per km^2 (Statistisk Sentralbyrå, 2020). The main prey of wolves in the study area is moose (*Alces alces*) (Sand et al., 2008; Zimmermann et al., 2015).

Seven wolves (five males, two females) were captured and equipped with VERTEX Plus GPS collars from VECTRONIC Aerospace GmbH. All wolves were scent-marking, territorial adults, and all were confirmed breeders, reproducing prior to or after the trial(s) (see **Table 1** for the overview of all approach trials). The captures followed the ethically approved procedures as described by Arnemo and Evans (2017). The captures and experimental human approach trials were approved by the Norwegian Food Safety Authority (FOTS ID 15370) and the Animal Welfare Ethics Committee of Uppsala, Sweden (ref. 5.8.18-13246/2019). The GPS data were collected using GSM and Iridium communication into the Wireless Remote Animal Monitoring database system for data validation and management (Dettki et al., 2013).

Experimental Approach Trials

For the approach trials we followed the standardized protocols for collar schedule, approach method, field data collection and GPS data extraction[1]. Trials were conducted between mid-August and April in order to avoid disturbance during the denning and pup rearing period. We used minimum 14 days between

[1]Eriksen, A., Versluijs, E., Fuchs, B., Zimmermann, B., Wabakken, P., Ordiz, A. (2022). A standardized method for experimental human approach trials on wild wolves. *Front. Ecol. Evol.*

TABLE 1 | Approach trials by humans toward seven territorial scent-marking, GPS-collared wolves along the Swedish-Norwegian border, 2018–2021.

Approach date	Obs (N)	Territory (country)	Focal wolf ID (Sex)	Partner GPS-ID	Social status	Together in trial
2018-09-13	2	Juvberget (N/S)	M18-12 (M)	M18-13	Pair	Together
2018-09-20	2	Varåa (N/S)	M18-17 (F)	M17-08	Pair	Separate
2018-09-27	1	Juvberget (N/S)	M18-12 (M)	M18-13	Pair	Together
2018-10-04	1	Varåa (N/S)	M17-08 (M)	M18-17	Pair	Together
2018-10-25	1	Juvberget (N/S)	M18-12 (M)	M18-13	Pair	Separate
2018-11-01	1	Varåa (N/S)	M18-17 (F)	M17-08	Pair	Together
2018-11-15	1	Varåa (N/S)	M18-17 (F)	M17-08	Pair	Together
2018-11-29	1	Varåa (N/S)	M18-17 (F)	M17-08	Pair	Together
2019-08-27	2	Varåa (N/S)	M17-08 (M)	M18-17	Pack	Separate
2019-10-29	1	Juvberget (N/S)	M18-13 (F)	M19-02	Pair	Together
2019-11-21	2	Varåa (N/S)	M18-17 (F)	M17-08	Pack	Separate
2019-12-13	1	Varåa (N/S)	M18-17 (F)	M17-08	Pack	Together
2019-12-30	2	Juvberget (N/S)	M19-02 (M)	M18-13	Pair	Together
2020-01-30	2	Juvberget (N/S)	M18-13 (F)	M19-02	Pair	Together
2020-09-16	2	Juvberget (N/S)	M19-02 (M)	M18-13	Pack	Separate
2020-12-18	2	Juvberget (N/S)	M19-02 (M)	M18-13	Pack	Together
2019-09-01	1	Magnor (N/S)	M18-11 (M)	–	Pack	–*
2019-10-19	2	Magnor (N/S)	M18-11 (M)	–	Pack	–*
2019-11-22	2	Magnor (N/S)	M18-11 (M)	–	Pack	–*
2021-04-16	2	Skärsjön (S)	M21-02 (M)	–	Pack	–*
2021-09-03	1	Skärsjön (S)	M21-02 (M)	–	Pack	–*

*Date of each approach trial, the number of human observers (Obs), name and country of the four wolf territories (N = Norway, S = Sweden), identity and sex of every focal wolf for approach, identity of GPS-collared partner-wolves, social status (scent-marking pair or pair with pups, i.e., pack), and whether the GPS-collared pair was together or not during the approach trial. *Only one of the adults GPS-collared.*

consecutive trials on the same individuals (**Table 1**). Approach trials were only conducted when wolves were stationary at a resting site, which was determined based on their GPS positions before the trial started. We used a 4 h preparation period with 10-min positioning intervals to define the approach route. The observer(s) would start approaching the wolf from a minimum distance of 1,000 m from the wolf start position (WSP, last received GPS position before the trial), pass at a passing position (PP) 50 m from WSP, and continue walking for at least another 500 m. The approach route was as straight as possible and did not follow existing roads or paths. The actual passing distance might not have been exactly 50 m due to GPS error and small wolf movement after the last received GPS position.

We used 1-min GPS positioning intervals during the approach period (12:00–14:00 local time), which allowed us to extract the flight initiation at high precision, and provided fine-scale data for the initial flight response. The observer position was logged every second using a handheld GPS unit. In order to collect consistently a minimum of 10 min of flight data at 1-min resolution, all approach trials were started in time to reach the PP at least 10 min before the approach period ended.

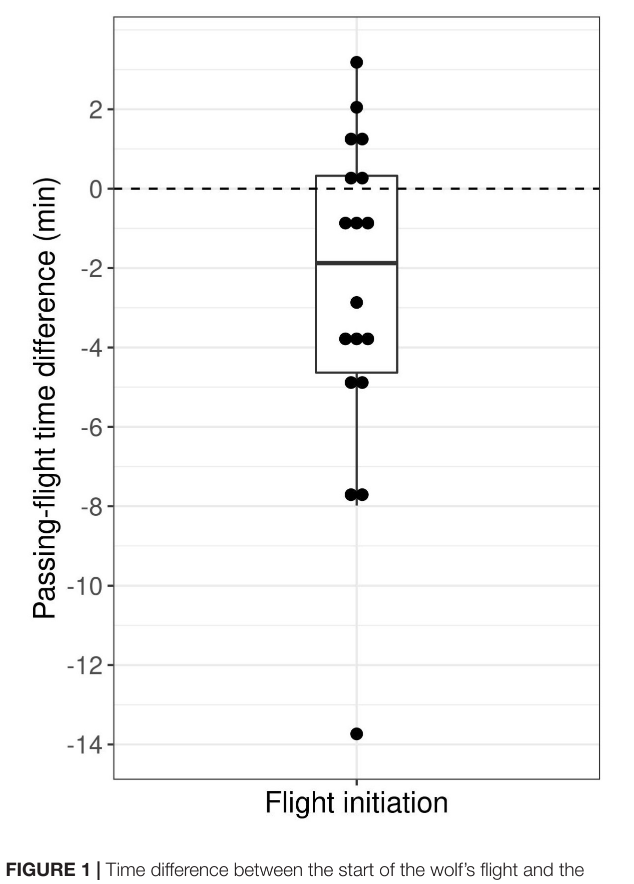

FIGURE 1 | Time difference between the start of the wolf's flight and the observer passing the passing position (PP) of wolves during experimental approach trials by humans in south-central Scandinavia, 2018–2021 (N = 18), where a negative time difference indicates a flight started before the observer passed the PP.

During single-observer trials, the observer did not make an effort to be quiet but was not talking. During two-observer trials, the observers would talk to each other. In total 17 different observers (seven males and ten females) conducted the approach trials, in different combinations and avoiding the same observer(s) conducting consecutive trials on the same individual. The observer would register wind direction relative to a clock, where 12:00 o'clock related to the observer's orientation toward the end of the approach route. Wind direction was later converged to head wind (wind from the wolf toward observer) when the wind came from 9:00 to 3:00 o'clock and tail wind (wind from observer toward the wolf) when the wind came from 3:00 to 9:00 o'clock. Furthermore, the observer estimated the noise made by walking through the vegetation at three levels: silent (e.g., mossy/peaty soil with no bushes), medium (e.g., crackling sound from leaves, some bushes scratching on observers clothes), and noisy (e.g., young forest with dense regrowth of trees). The level silent only occurred twice, therefore we pooled this level with medium and used two levels, noisy and not noisy, for further analyses.

We used 10-min positioning intervals during the post-disturbance period (14:00–17:00 local time) to capture the entire flight and to identify resettling. Post-trial we measured the horizontal visibility at the wolf's initial location and at the resettling position by placing a cylinder (brightly colored with a length of 60 cm and diameter of 30 cm) at the coordinates of the positions. We measured the distance at which the cylinder was still visible in the four cardinal directions and calculated the average distance as a proxy for concealment, using the method described by Ordiz et al. (2009).

Data Analyses

We used the software R, version 4.1.1 (R Core Team, 2021) for all data handling and analyses. When two GPS collared wolves were together during an approach trial (i.e., the adult territorial pair), only one was included in the analyses, as their responses could not be assumed to be independent of one another. If a flight was detected, we selected the wolf that moved first. In trials without detected flights, we chose the wolf which was passed closest by the observer.

For each trial the wolf and observer data were joined based on the timestamp, and the observer positions (originally 1-s intervals) were filtered to retain only those positions that matched the timestamps of the wolf positions (1-min intervals). The wolf moving speed was calculated as meters per minute by dividing the step length by the time difference between consecutive positions. The flight initiation was extracted by applying changepoint analysis for both change in mean and variance of the wolf speed at 1-min resolution using an MBIC (Modified Bayes Information System) penalty (Killick et al., 2016). In two cases in which no flight was detected with the MBIC penalty but visual inspection suggested that the wolf fled, the flight initiation was identified by rerunning changepoint analysis with the AIC penalty (see text footnote 1). We considered a flight when we detected the flight initiation within the 1-min resolution data. Additionally, we visually checked the wolf positions until the observer reached the end of the approach route. For 15 wolf flights, we identified the

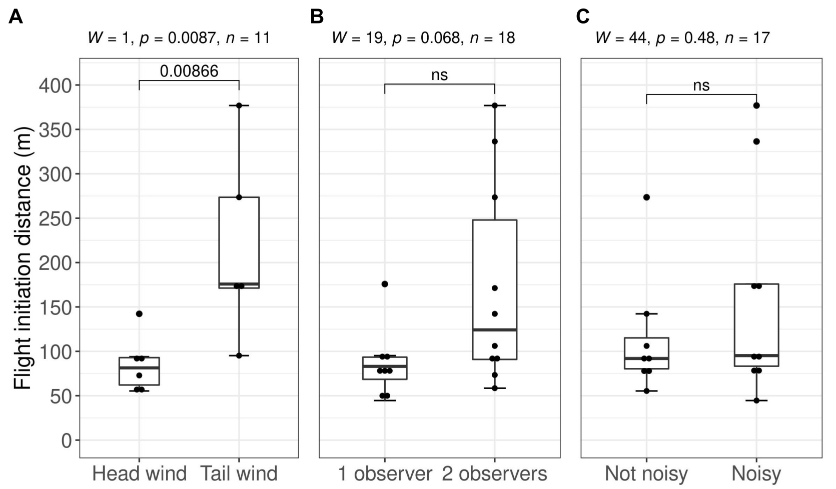

FIGURE 2 | Distribution of flight initiation distances (meters) with **(A)** head wind (wind from the wolf toward observer, *N* = 6) vs. tail wind (wind from observer toward the wolf, *N* = 5), **(B)** single-observer approach (*N* = 8) vs. double-observer approach (*N* = 10), and **(C)** not noisy (*N* = 8) vs. noisy sounds (*N* = 9) by walking through the vegetation. Using the non-parametric Wilcoxon rank-sum test based on experimental approach trials by humans on wolves in south-central Scandinavia, 2018–2021.

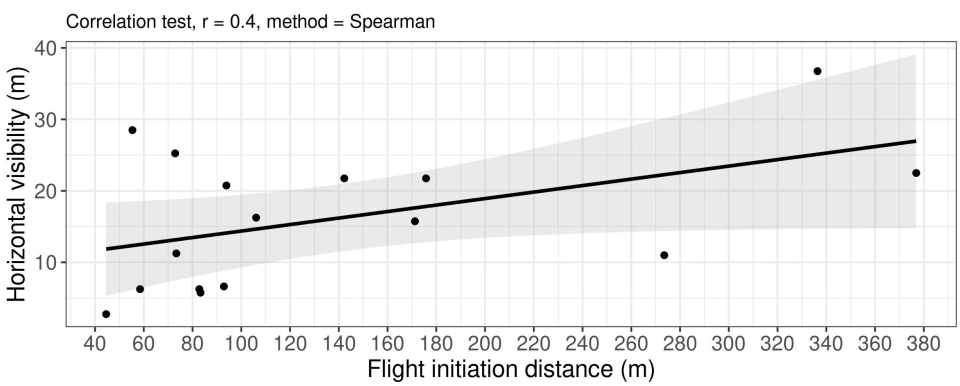

FIGURE 3 | The relation between flight initiation distances (*N* = 16) and the horizontal visibility (both in meters). Using the non-parametric Spearman's rank-order correlation test based on experimental approach trials by humans on wolves in south-central Scandinavia, 2018–2021. Wolves that did not fled are excluded (*N* = 3).

resettling position by applying changepoint analysis as described for flight initiation, but using GPS data at 10-min resolution.

Based on the obtained flight initiation and resettling positions, we extracted 11 variables to describe the wolf flight response for every interaction separately: We classified the wolf response as either *Flight* when flight initiation was identified, or *No flight* when no flight initiation was identified and the wolf remained stationary (1). Based on the 1-min positioning intervals, we calculated the *Minimum wolf-observer distance* as the minimum distance between simultaneous wolf and observer positions (2), *FID* as the wolf-observer distance at flight initiation (3), and *Passing-flight time difference* as the time difference between flight initiation and the observer passing the passing position (4). For the first 10 min after flight initiation and at 1-min resolution, we calculated *Initial speed* as the average speed (5) and *Initial straightness* as the sum of the step lengths divided by the linear displacement (6). We calculated *Flight duration* (7) and *Flight displacement* (8) as the time and distance from flight initiation to resettling, respectively. For the total flight (from flight initiation to resettling) and at 10-min resolution, we calculated *Total distance traveled* as the sum of the step lengths (9), *Overall speed* as the average speed (10), and *Overall straightness* as the average straightness index across the flight based on the straightness between every three consecutive positions (11) (see text footnote 1).

We did not test for consistent territory differences due to the small sample size. None of the variables showed visual differences between the territories (**Supplementary Figure 1**). Due to the small sample size and non-normality of the data we could not run multiple regression models. We used non-parametric tests to look at differences in the median of the response variables between categories (number of observers, noise level and wind direction, H2), we used the non-parametric Wilcoxon rank-sum test. We looked at the relationship between FID and horizontal visibility

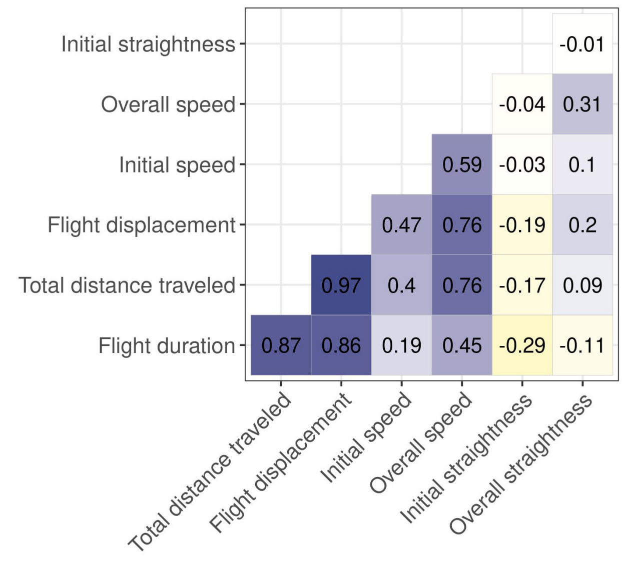

FIGURE 4 | Correlation matrix with correlation coefficients showing relations between the variables, using non-parametric Spearman's rank-order correlation test based on experimental approach trials by humans on wolves in south-central Scandinavia, 2018–2021.

(H3), and between the different flight variables (H4) by using non-parametric Spearman's rank-order correlation tests. Finally, we used Wilcoxon signed rank tests to compare concealment at flight initiation and resettling (H5). We visualized the results using the *ggplot2* package (Wickham, 2009) and the *ggcorplot* package (Kassambara, 2019).

RESULTS

We performed 21 successful experimental wolf approaches over the course of 4 years (8 in 2018, 8 in 2019, 3 in 2020, and 2 in 2021). Individual wolves were approached on average 4 times (range: 2–7, **Table 1**). Wolves fled in 18 out of 21 interactions, and did not initiate a flight in the other three interactions (P1). In two thirds (N = 12) of the cases, the flight initiation occurred before the observer(s) passed the passing position, and in one third (N = 6) shortly after the observer(s) passed (**Figure 1**, P2). Observers did not see or hear the wolves during any of the approach trials (P3).

The flight initiation distance was significantly different between trials conducted with head wind and tail wind (Wilcoxon rank-sum test: W = 1, n = 11, p = 0.009, **Figure 2**, P6). However, the FID did not differ significantly between one or two observers present (Wilcoxon rank-sum test: W = 19, n = 18, p = 0.068, P4) or between noisy and not noisy conditions (Wilcoxon rank-sum test: W = 44, n = 17, p = 0.481, P5).

Flight initiation distance and horizontal visibility were positively correlated (r_s = 0.4), i.e., the FID increased when the wolf was less concealed (**Figure 3**, P7). Additionally, the horizontal visibility for three interactions where the wolf did not flee was low, with a mean visibility of 4, 6, and 14 m, respectively (P8), while the median horizontal visibility of the resting sites for fleeing wolves was 16 m (quartiles 7; 22 m).

We found that flight duration, total distance traveled, and flight displacement were positively correlated ($r_s > 0.6$, **Figure 4** and **Table 2**). Therefore, we only analyzed the total distance traveled. Together with initial speed, initial straightness and overall straightness we considered those variables as a proxy representing flight intensity. We found no correlation between the FID and the total distance traveled (r_s = 0.1, P9), initial straightness (r_s = –0.12) and overall straightness (r_s = –0.24) (P10), and initial speed (r_s = 0.18, P11).

The horizontal visibility showed a significant increase between the wolf start position and the wolf end position (Wilcoxon signed-ranked test: V = 78, p = 0.025, N = 13, **Figure 5**, P12).

DISCUSSION

Most wolves that were approached in this pilot study showed what we interpret as an avoidance response, consistent with our first hypothesis (H1). In the majority of trials, the wolf left its initial resting site before the observer(s) passed the passing position (PP). During the remaining trials, the wolf fled shortly after the observer passed, or did not flee at all. No wolves were seen or heard during the approach trials, even when the observer(s) passed the wolf at less than 50 m. Kuijper et al. (2019) described getting closer than 100 m to wolves as "risk-enhancing human behavior". However, similar to previous studies on wolves as well as brown bears (Karlsson et al., 2007; Moen et al., 2012; Wam et al., 2014; Ordiz et al., 2019), the wolves did not show any aggressive response to our approach trials.

A wolf's decision to flee from an approaching human is contingent on the human being detected by the wolf. Despite their acute senses, Karlsson et al. (2007) demonstrated that it is possible to walk up to a resting wolf undetected. Hence, we hypothesized that FID would be larger under conditions that increase the detectability of humans (H2). Olfactory and auditory cues are important for a wolf's ability for communication, tracking prey, and social interactions (Mech, 1970; Harrington and Asa, 2003). Therefore, it is likely that sound and smell might be important for detecting threats as well. Karlsson et al. (2007) found that a combination of wind direction and wind speed affected wolf FID during earlier approach trials and hypothesized that noise made by the observer likely affected the wolf's FID. We found a significant difference between tail wind and head wind, where tail wind resulted in larger flight initiation distances. Unfortunately, we did not have sufficient observations of wind speed to make a similar comparison. The FID did not vary significantly with number of observers or the level of noise. Potentially, the noise made by the observer may have been masked by noise created by the wind. Exploring, this and other interactions between the explanatory variables will require a larger sample size and multiple regression analysis.

Once a wolf has detected an approaching human, the decision to flee should reflect the perception of risk (Ydenberg and Dill, 1986; Cooper and Frederick, 2007). We found a weak positive

TABLE 2 | Overview of the flight variables with the mean, standard deviation (SD), median, min, max, and number of observations (N).

Variable	Mean	*SD*	Median	Min	Max	N
Initial speed (m/min)	49.47	22.49	48.53	22.75	96.56	18
Initial straightness	0.75	0.23	0.84	0.15	0.96	18
Flight duration (min)	74.7	31.37	68.88	28.85	130.73	15
Total distance traveled (m)	2335.09	1761.81	1753.51	319.05	5789.82	15
Flight displacement (m)	1932.44	1382.09	1514.42	315.1	5172.16	15
Overall speed (m/min)	31.48	11.17	32.39	15.00	49.01	15
Overall straightness	0.87	0.12	0.92	0.56	0.99	15

The initial speed and initial straightness are based on 1-min resolution, the other variables are based on 10-min resolution.

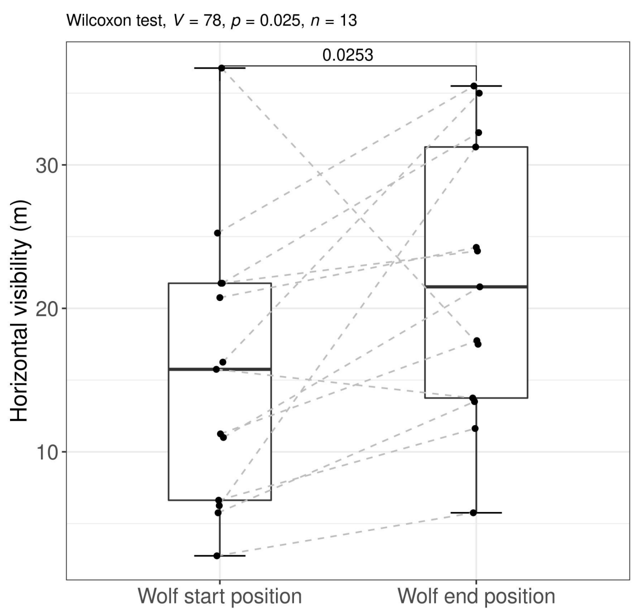

FIGURE 5 | Distribution of the horizontal visibility (in meters) at the wolf start position (WSP) and the wolf end position. The difference in horizontal visibility tested by a non-parametric Wilcoxon signed rank tests. The gray dashed lines indicate paired observations. Observations are based on experimental approach trials by humans on wolves in south-central Scandinavia, 2018–2021.

correlation between FID and the horizontal visibility at the wolf start position (H3). Furthermore, during three interactions without a flight, the horizontal visibility was low (<15 m). This is partly consistent with our hypothesis that wolves would perceive the risk as lower when they were more concealed, and allow the human to get closer before fleeing, or choose to not flee at all. However, GPS data alone does not allow us to identify the moment of detection, but rather shows the moment when the wolf responds spatially by dislocation. Hence, we cannot conclude whether the shorter FID or no flight at lower visibility was due to the wolf's perception of being less detectable by the observer (i.e., lower perceived risk) or because the wolf did not detect the observer. This was also described by Moen et al. (2012) who found that the FID for brown bears increased as the horizontal vegetation structure became less dense. Potentially, the wolf's social status, season, and habituation to human presence might affect the decision to flee, though the effect of habituation were found to be minor (Wam et al., 2014). Fine-scale accelerometer data or heart rate data from the wolves could provide additional information to distinguish between detection and risk perception by potentially measuring changes in heart rate, posture or fine-scale movement before the wolf flees (Græsli et al., 2020; Williams et al., 2020).

We expected that a shorter FID would be related with a more intense flight (larger distance traveled, higher speeds) due to a flush effect if the observer was not detected, or not perceived as a threat, until it was close by (H4). This could result in an energetically more costly flight (Ydenberg and Dill, 1986; Cooper and Frederick, 2007). However, we did not find a correlation between FID and the different flight variables. Other variables, such as landscape composition, road density and human population density might also have an effect on the initiation and path of the flight (Moen et al., 2018), but were not included in our study due to low sample size.

Wam et al. (2012) showed that wolves can adjust their strategy in choosing a resting site in a more concealed location after being disturbed. After centuries of persecution wolves might choose hiding and therefore sacrificing visual vigilance for better concealment to avoid human encounters (Wam et al., 2012). Similar strategies are found in lynx (*Lynx lynx*) and brown bear (Sunde et al., 1998; Ordiz et al., 2011). Therefore, we hypothesized that wolves would select for a more concealed (i.e., shorter horizontal visibility) resting site after being approached by a human (H5). Interestingly, we found the opposite effect where wolves chose resettling locations which were slightly more open and less concealed compared to their resting sites prior to the disturbance. It is likely that resting site selection after a disturbance might lead wolves to select places with a better overview on approaching humans, so they can initiate a new flight earlier. This would follow earlier results from a study on vigilance and protective cover on birds (Lazarus and Symonds, 1992). Additionally, concealed areas are available throughout the wolf's territory, and there is no lack of available sites. An increased sample size would give the possibility to explore whether this pattern is consistent and to what degree other factors (e.g., elevation and vegetation types) affect the resettling site selection.

The sample size in this study was small and we could not account for individual differences between wolves, but we are aware that individual choices may exist (Beale, 2007). However, we did not perceive visually obvious differences in response variables between wolf territories. Such potential differences should be considered, and for future studies with larger sample size, we would advise considering the effects of individuals and territories, together with variables as e.g., social status and sex.

Moreover, the small sample size does not allow us to generalize the results across the Scandinavian wolf population, let alone to wolves in general. This first study rather serves to illustrate the application of standardized human approach trials with high-resolution GPS-data for describing wolf responses at a local scale. In continuation, the protocol (see text footnote 1) can be applied at larger spatial scales to compare wolf flight responses within and between populations and across anthropogenic gradients. Potential applications are to establish the range of responses by wolves in a given area, allowing the identification of individual wolves that show atypical response patterns, or to identify consistent differences between wolves inhabiting different habitat types in different parts of their range. This may lead a better understanding of how wolves can be expected to behave toward humans, and thus improve the potential for wolf-human coexistence across their range. If future research confirms what the current and previous studies suggest (Karlsson et al., 2007), i.e., that wolves generally avoid approaching humans, and that increased detectability increases the likelihood of an early flight by the wolf, people who wish to avoid a wolf encounter when walking in wolf areas should maximize their possibility of being detected.

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 the Norwegian Food Safety Authority (FOTS ID 15370) and the Animal Welfare Ethics Committee of Uppsala, Sweden (ref. 5.8.18-13246/2019).

AUTHOR CONTRIBUTIONS

PW, BZ, AE, and EV conceived the study. AE, PW, BF, CW, HS, and BZ secured the funding. EV, BF, AE, BZ, and PW conducted field trials. EV conducted the analyses and drafted the manuscript. All authors contributed ideas and edits to the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.792916/full#supplementary-material

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Ojibwe Perspectives Toward Proper Wolf Stewardship and Wisconsin's February 2021 Wolf Hunting Season

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In February 2021, the Wisconsin DNR implemented a wolf season in which > 20% of the population was killed in 63 h. Wisconsin's Ojibwe tribes had a visceral reaction to this killing. This paper provides a perspective for this reaction by reviewing the Ojibwe relationship with Ma'iingan. This relationship maintains that Ma'iingan and Ojibwe are to be considered relatives whose fates are intertwined. Ma'iingan and Ojibwe have lived parallel histories, suffering from the effects of colonization, the decimation of wolf populations and decline of tribal culture. The Ojibwe tribes ceded vast territories in treaties with the United States while retaining common use rights, including the right to hunt and fish. These rights were reaffirmed just as wolves were reestablishing themselves in Wisconsin. The tribes continue to strengthen their culture, while wolf populations continue to recover. By examining these comparative histories, it becomes apparent that "whatever happens to one happens to the other." Unfortunately, Ma'iingan were not adjudicated during the Wisconsin treaty case, creating uncertainty over how the relationship between the Ojibwe and Ma'iingan is to be respected by the state. The tribes believe their treaty right includes protection for wolves, so that wolves can fulfill their cultural and ecological purposes. Tribes maintain that Ma'iingan should determine their own population levels, in order to provide ecological and cultural benefits. A respectful and appreciative relationship with Ma'iingan should be maintained so that the future well-being of both Ma'iingan and the Ojibwe will be assured.

Keywords: Ma'iingan, Ojibwe, stewardship, treaty rights, wolves, Wisconsin

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INTRODUCTION

At 12:00 AM, February 22, 2021, just 50 days after wolves (*Canis lupus*) were removed from the protections of the Untied States Endangered Species Act, Wisconsin's first hunting season in over 6 years began. It ended just 63 h later. The Ojibwe tribes in the upper Midwest, including all 11 member tribes of the Great Lakes Indian Fish and Wildlife Commission (GLIFWC, **Figure 1**) had a visceral reaction to this killing. We explain the reasons for this reaction and provide some insights on the perspectives of the Ojibwe toward *Ma'iingan*, (the wolf) in hopes of increasing cross-cultural understanding and improving the human/wolf relationship.

With more permits sold (1,548 Johnson and Schneider, 2021) than wolves in the woods (1,091 Price Tack et al., 2021), the slaughter (a word intentionally selected to reflect the Ojibwe perspective) was swift – with a wolf being killed, on average, every 17 min, day and night. With hunters equipped with firearms and replaceable packs of dogs, (86% of the wolves were killed with the aid of hounds), the state's quota of 119 animals was rapidly achieved. The tribes' effort to protect their portion of the quota (81 animals) so they could provide ecological and cultural benefits critical to the tribal community, was fruitless. Before the season could be closed, 99 additional animals were killed. The reported harvest of 218 animals (Johnson and Schneider, 2021) equaled 20% of the state's wolf population; the number of unrecovered crippling loss or animals intentionally left unretrieved is unknown. Only later was it discovered that a computing error existed in the application of the harvest model (Adams et al., 2008) that the Wisconsin Department of Natural Resources (WDNR) used to inform the quota setting process (D. MacFarland per. com). GLIFWC calculates this computing error may have resulted in the quota being set about 16% higher than intended.

While the hunting season was brief, it took place during the breeding season, ensuring that its impact would not be limited to the current generation. Among the small sample of wolves necropsied after the season (n = 22) were not only animals showing the hemorrhaging and bite marks of having interacted with hounds that pursed them, but females with fetuses (GLIFWC unpublished data). On the basis of studies such as Brainerd et al. (2008) which examined the impacts of breeder loss, Wisconsin's Green Fire estimated that 24–40% of recruitment was likely lost (Wisconsin's Green Fire, 2021). While harvest models such as Fuller et al. (2003) and Adams et al. (2008) suggest the population could recover to pre-hunt levels in 2–3 years if no further harvest were to take place, the WDNR was forced to begin preparing for a fall season to comply with Wisconsin Act 169, legislation that requires an annual season whenever wolves are not on the Wisconsin or Federal endangered species list. However, the fall 2021 season was halted by a stay issued in State court (Great Lakes Wildlife Alliance et al.; v. Wisconsin Natural Resources Board et al., Circuit Court, Dane County, WI, 2021 CVoo2103).

While some in the hunting community celebrated the wolf kill (intentional phrasing), regional Ojibwe tribes mourned the unnecessary slaughter of brother wolf and the trampling of their treaty-reserved rights. Herein we elaborate on the Ojibwe perspectives toward proper human relationship with Ma'iingan.

MY BROTHER

The relationship between Ma'iingan and the Anishinaabe (Ojibwe) extends all the way back to the Anishinaabe creation story. In that story, Ma'iingan was provided by the Creator to be a companion to the Original Man. As a result of this and other teachings, Anishinaabe people consider the wolf their relative. This concept of relatedness to another species is difficult for many Western-educated thinkers to comprehend because it contradicts the principles and values of western science and Judeo-Christian society held by some people. But to the Anishinaabe, the wolf is an integral part of identity and kinship. Through stories, clan membership and culture, the wolf is woven into the spirit and identity of Anishinaabe people (other Indigenous Nations have their own, and sometimes different relationship with the wolf). When Anishinaabe people are asked to put population goals or harvest quotas on Ma'iingan, they see it as analogous to putting goals and quotas on their relatives – something unthinkable if we were talking of human relatives.

In the creation story, the Creator indicates that Ma'iingan and Original Man will always be considered as relatives and their fates would be intertwined (Benton-Benai, 2010). Thus the well-being of the wolf reflects the well-being of Anishinaabe society, a relationship that is captured in the Anishinaabe teaching: "What happens to the wolf will happen to the Anishinaabe. And, what happens to the Anishinaabe will happen to the wolf." This narrative, which has been passed down through many generations, reflects their paralleled histories.

Prior to European colonists coming into the Anishinaabe territory the Ojibwe people had a well-developed society with a governance structure, division of responsibilities passed on *via* the clan system, and a seasonally nomadic lifestyle. Ma'iingan existed across the Ojibwe territory, fulfilling their role within the upper Great Lakes ecosystems. Both Anishinaabe and Ma'iingan lived healthy lives.

When European immigrants settled along the east coast and encountered both wolves and Indigenous peoples, they responded to both similarly. Both the wolf and the Native peoples were despised and persecuted by many in the newly forming colonies.

These parallel attitudes moved west with settlers crossing the continent, as efforts to eradicate both wolves and Native Americans from the landscape continued. In the upper Midwest, four land cession treaties (**Figure 1**) were entered into in which the Ojibwe tribes ceded vast areas to the United States. The influx of European settlers coincided with the beginning of the planned extermination of wolves from that region.

While settlers put pressure on the government to eradicate wolves *via* bounties and other unlimited killing, the United States Congress was passing laws to remove Ojibwe tribes and eradicate treaty claims in direct contrast to the terms of the recently enacted treaties. Wolves proved relatively easy to kill, and eventually they were eliminated from the lower 48 states with the exception of an area of Ojibwe territory in northern Minnesota. Concurrently, the population of American Indians fell as low as 250,000 (Thornton, 1977). The 1940–1950s is known as the Termination Era when the federal government eradicated many federally recognized tribes and dissolved their reservations.

As wolves were declining so too was the free practice of the Ojibwe culture. Children were taken from Ojibwe households and sent to boarding schools where they were not allowed to practice their language or ceremony. The combination of treaty-making and treaty-breaking, termination, removal and assimilation had severe consequences for the Ojibwe culture and language.

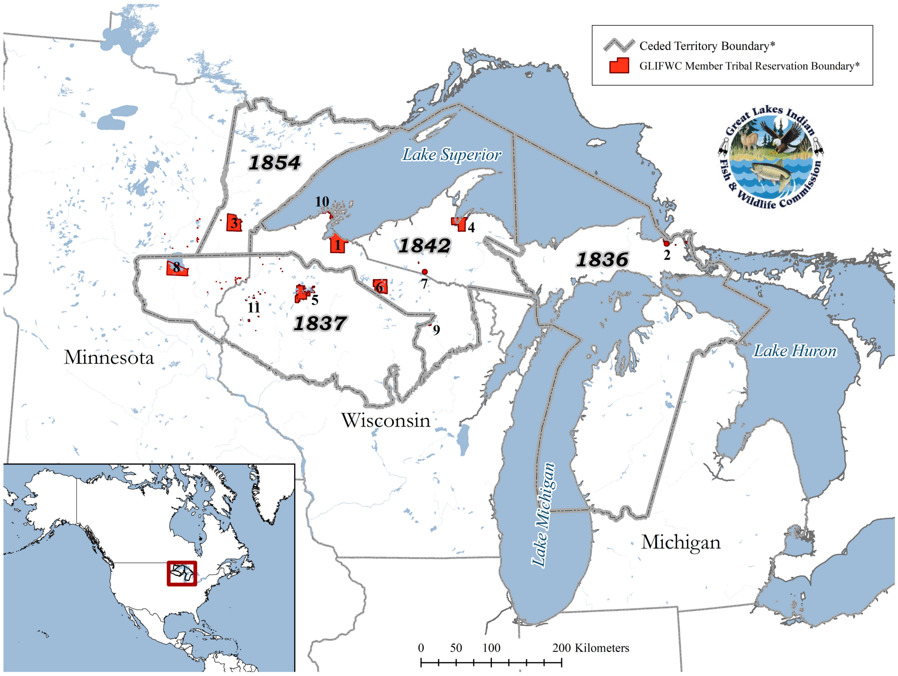

FIGURE 1 | Territories ceded to the United States in the Treaties of 1836, 1837, 1842, and 1854 in which Ojibwe tribes ceded the outlined lands and reserved the rights to hunt, fish, and gather to maintain their lifeway. GLIFWC member tribes are in red [(1) Bad River, (2) Bay Mills, (3) Fond du Lac, (4) Keweenaw Bay, (5) Lac Courte Oreilles, (6) Lac du Flambeau, (7) Lac Vieux Desert, (8) Mille Lacs, (9) Mole Lake, (10) Red Cliff, and (11) St. Croix]. *The ceded territory and reservation boundaries are representations and may not be the legally binding boundary. Map created using Ceded Territories Boundary Version 2.1.

In the 1960s, the fates of both Ma'iingan and the Ojibwe improved. The publication of Rachel Carson's *Silent Spring*, and the passage of the Civil Rights Act, allowed a new consciousness to emerge relative to ecology and equality. Additionally, the Indian Civil Rights Act was passed (1968), the Indian Education Act (1972); the American Indian Self-determination and Educational Assistance Act (1975), and the American Indian Religious Freedom Act (1978). This period also marked the passing of the Endangered Species Act (1973), and the following year, wolves finally had federal protection.

THE REAFFIRMATION OF TREATY RIGHTS

While most people think that the treaties between the tribes and the United States government granted rights to the tribes, the truth is that the treaties granted rights to the United States, and any rights that the tribes held and did not specifically cede were retained, including the rights to make their living by hunting, fishing and gathering. The Ojibwe tribes in the upper Midwest ceded large areas of what is now known as Michigan, Minnesota, and Wisconsin to the United States (**Figure 1**). In these treaties the signatory tribes reserved the right to remain in the ceded territories and to continue to live as they always had by fishing, hunting, and gathering. They relied on these activities to meet their needs for foods, medicines, materials for clothing and housing, and other utilitarian, spiritual and ceremonial purposes. Nevertheless, over time tribal members exercising these treaty-reserved rights were often arrested and charged under state laws.

In the mid-1980s the Ojibwe tribes in Wisconsin sued the state contending that their treaty rights continued to be valid and that tribes should have the sovereign prerogative to set their own natural resource regulations. As this treaty case unfolded, wolves from the Minnesota population began to reestablish themselves in Wisconsin. As in colonial times, many in the non-Indian community viewed both of these events as threats (David, 2009).

The tribes ultimately prevailed in this and related suits [see *Lac Courte Oreilles Band of Lake Superior Chippewa Indians v. Wisconsin, 775 F. Supp. 321 (W.D. Wis. 1991*) and *Minnesota v. Mille Lacs Band of Chippewa Indians, 526 U.S. 172, 176–177 (1999)*]. In these cases, it was found that the signatory tribes retained the right to harvest up to 50% of the harvestable surplus of fish and wildlife under their own set of rules and regulations, enjoining the states from enforcing state rules. Thus began the implementation of the tribes long-withheld exercise of treaty rights.

Subsequent to reaffirmation of the treaty rights, the tribes continued to reassert their sovereignty in a variety of venues including language revitalization and the reemergence of spiritual practices. Simultaneous with this cultural recovery, Wisconsin's tenuous Ma'iingan population grew in numbers and range.

Except during recent periods marked by recreational wolf killing, both the assertion of tribal sovereignty and the health of the Ma'iingan population have been greater than at any time in recent history.

By examining these comparative histories, it becomes apparent (or is an arguable logical perspective) that "What happens to the wolf will happen to the Anishinaabe, and what happens to the Anishinaabe will happen to the wolf." After the controversial February 2021 Wisconsin wolf hunt, many Anishinaabe people were traumatized and outraged. The wolf hunt was perceived by many as an assault on family members, and many felt – and continue to feel - compelled to protect their family. The Ojibwe mourned not only the loss of wolves, but the loss of Mokaan-giizis, Migizi dodem (Joe Rose Sr., Eagle Clan), a deeply respected elder of the Mashkiziibii (Bad River) Tribe and lifelong wolf advocate, who walked on in the midst of this short, brutal season. Many Ojibwe and non-Ojibwe people contended he went to help killed Ma'iingan journey to the afterlife.

TREATY RIGHTS AND MA'IINGAN

Existing treaty cases do not define the full extent of treaty-reserved rights. Notably, at the time of the final judgment in the Wisconsin case, Ma'iingan was classified as a federally endangered species and the state had little legal authority over wolves. In an update to the Wisconsin judgment [*Second Amendment of the Stipulations Incorporated in the Final Judgment, Lac Courte Oreilles Band of Lake Superior Chippewa Indians v. Wisconsin, Case No. 74-C-313-C, at 41–43 (March 15, 2011)*] the tribes and the state agreed that tribes should be required members of any wolf committee the state establishes. The state and the tribes agreed that consultation should take place and all attempts at consensus should be made in any wolf management action taken by the state.

The fact that Ma'iingan were not adjudicated during the Wisconsin trial or in any subsequent action creates uncertainty over how the unique relationship that exists between the Anishinaabe and Ma'iingan is to be recognized and respected by the state. Unlike other species litigated in the Wisconsin suit, Ojibwe people generally object to the recreational harvest of wolves. The tribes believe that their treaty right includes the right to protect wolves, so that living wolves can fulfill their cultural and ecological purposes.

In the instance of the 2021 February season the WDNR did not conduct the government-to-government consultation and attempts at reaching consensus with treaty tribes that is required by the federal treaty lawsuit case. Nevertheless, the WDNR pledged to honor the tribal declaration (of half of the quota attributed to ceded lands) while understanding that the tribes' intent was to protect those Ma'iingan from harvest. However, a lack of adequate harvest control mechanisms resulted in the 83% quota exceedance (218 harvested of a 119 quota) discussed above, rendering the state's pledge moot.

The Ojibwe contend that this gross overharvest is not only culturally abhorrent but threatens resources the tribes depend upon.

ECOLOGICAL AND CULTURAL SERVICES PROVIDED BY MA'IINGAN

The Anishinaabek relationship with Ma'iingan led them not to exterminate wolves, but to learn from, understand and accept them. In recent years western science added to this understanding, as it documents the ecological and social services wolves provide. What follows is not intended to be a thorough and comprehensive review of these ecosystem services, but some examples to illustrate the role of wolves in healthy ecosystems.

Historically, wolf reintroduction has resulted in increased biodiversity and ecological productivity in regions such as Yellowstone, where wolves were reintroduced in the late 20th century (Ripple and Beschta, 2012; Martin et al., 2020). The presence of wolves on a landscape can trigger a top-down trophic cascade, where a carnivore limits herbivore populations by direct predation, thereby allowing understory native plant species to regenerate (Ripple and Beschta, 2012; Ripple et al., 2014). These trophic effects have been seen to increase carbon storage capacity in boreal ecosystems, mitigating the effects of climate change (Ripple et al., 2014; Schmitz et al., 2014).

While not yet as extensively studied as the Yellowstone area, Ma'iingan affect landscapes in the Midwest as well. Wolf presence simultaneously supports the regeneration of herbaceous and woody plant species preferred by deer such as maple, hemlock, pine, spruce, and understory forbs (Flagel et al., 2016; Russell et al., 2017; Waller and Reo, 2018). In north-central Wisconsin, wolf presence was directly correlated with higher percentage cover and species richness of forb species in white cedar wetlands (Callan et al., 2013). These effects often have direct significance to Anishinaabe; plant species that benefit from these trophic cascades often have important medicinal, ceremonial, and utilitarian uses.

Ma'iingan prey upon the wild ungulate species that they co-evolved with, historically contributing to the health of white-tailed deer populations in the Great Lakes region since pre-European settlement (David, 2009). Ma'iingan likely help regulate the spread of contagious diseases such as Chronic Wasting Disease (CWD), a highly contagious, neurodegenerative prion-caused disease infecting four North American cervid species, including white-tailed deer (Wild et al., 2011; Oliveira-Santos et al., 2021). CWD is prevalent across the Midwest states, particularly in Wisconsin where 32 counties have reported CWD cases in free-ranging cervids (Centers for Disease Control and Prevention [CDC], 2021). The most effective control methods are still unclear, but studies have shown that top predators like the gray wolf can selectively predate on infected deer before human hunters are able to identify symptomatic individuals – which in turn likely reduces the spread and persistence of CWD in a system and potentially stops CWD emergence in new systems (Wild et al., 2011; Uehlinger et al., 2016).

Additionally, a recent study showed a significant reduction in CWD prions in the excrement of mountain lions fed CWD-infected meat, suggesting that the digestion system of top predators can be an effective mechanism for reducing environmental CWD contamination (Baune et al., 2021).

Deer are an important protein source for the Ojibwe tribes, and Ma'iingan are seen as a crucial element of defense against the spread of CWD in the ceded territory. Currently, exercise of the treaty right is limited to public lands in the ceded territory. Eighty percent of the February wolf kill in the ceded territory came from public lands, which make up only 28% of the area (GLIFWC, unpublished data). Thus, the very lands the tribes depend upon for providing venison and other harvested resources are the same lands which disproportionately lose the ecological benefits Ma'iingan provides.

Finally, humans benefit from wolves in non-ecological ways as well. For example, a recent study found a significant reduction in deer-vehicle collisions in Wisconsin, primarily as a result of wolves' influence on deer behavior, saving up to $8 million per year statewide (Raynor et al., 2021).

DISCUSSION

One of the seven primary teachings of the Ojibwe, humility (along with love, respect, courage, honesty, wisdom, truth), applies here as a reminder that our understanding of wolves is far from complete. Just as we understand wolf ecology much more now than we did 20 years ago, we will understand much more 20 years from now. Embracing humility from an ecological perspective suggests we are wise to assume that Ma'iingan – a being which occupied this region for thousands of years before being extirpated – has functions and benefits of which we are still ignorant. In the lack of perfect understanding, we maintain it is both arrogant and ecologically foolish to reduce or eliminate wolves from large parts of the landscape that wolves themselves find appropriate.

Looking forward, it is unclear if or how state and tribal wolf objectives can be meshed, particularly as long as the WDNR remains under the direction of, or are most responsive to, traditional resource harvesting interests.

While many in the non-Indian community disparage the application of Ojibwe cultural perspectives in wolf stewardship (a term more aligned with the Ojibwe world view than "management"), they often overlook the cultural underpinnings of wolf management in the non-tribal community. While traditional Ojibwe teachings may seem outdated to some, they can directly inform appropriate Ma'iingan stewardship today. And they suggest a pathway based on embracing ecological principals, sound science, and human responsibility for co-existence.

In this view, Ma'iingan are allowed to determine their own range and population levels, so that they can provide ecological benefits in all areas of suitable habitat. In addition, wolves are not killed without sound and significant justification – as should be the case for any species. And a respectful and appreciative relationship is maintained.

While simple and straightforward, this approach is radically different from most wolf management traditionally embraced by state and federal natural resource agencies. However, we contend that the agencies that do so will find a large tribal and non-tribal public already eager to embrace an ecologically defensible and scientifically sound approach. In this way tribal perspectives can be incorporated into state's approach to Ma'iingan stewardship.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

JG and PD shared equally in writing the manuscript and shared first authorship. MP contributed to partial writing of manuscript and edited manuscript from TEK perspective. JO contributed to partial writing of manuscript, especially ecological perspectives, and edited manuscript. All authors contributed to the article and approved the submitted version.

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The Role of Wolves in Regulating a Chronic Non-communicable Disease, Osteoarthritis, in Prey Populations

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It is widely accepted that predators disproportionately prey on individuals that are old, weak, diseased or injured. By selectively removing individuals with diseases, predators may play an important role in regulating the overall health of prey populations. However, that idea is seldom tested empirically. Here we assess the extent that wolves (*Canis lupus*) select adult moose (*Alces alces*) in Isle Royale National Park on the basis of age-class and osteoarthritis, a chronic, non-communicable disease. We also assess how temporal variation in kill rates (on moose by wolves) were associated with the subsequent incidence of osteoarthritis in the moose population over a 33-year period (1975–2007). Wolves showed strong selection for senescent moose and tended to avoid prime-aged adults. However, the presence of severe osteoarthritis, but not mild or moderate osteoarthritis, appeared to increase the vulnerability of prime-aged moose to predation. There was weak evidence to suggest that senescent moose with osteoarthritis maybe more vulnerable to wolves, compared to senescent moose without the disease. The incidence of osteoarthritis declined following years with higher kill rates–which is plausibly due to the selective removal of individuals with osteoarthritis. Together those results suggest that selective predation plays an important role in regulating the health of prey populations. Additionally, because osteoarthritis is influenced by genetic factors, these results highlight how wolf predation may act as a selective force against genes associated with developing severe osteoarthritis as a prime-aged adult. Our findings highlight one benefits of allowing predators to naturally regulate prey populations. The evidence we present for predation's influence on the health of prey populations is also relevant for policy-related arguments about refraining from intensively hunting wolf populations.

Keywords: bone disease, senescent related pathology, chronic pathology, selective predation, resource selection, disease dynamics, ungulates, carnivores

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INTRODUCTION

Selective predation occurs when a particular type of prey occurs more frequently in the predator's diet than is expected based on the prey types frequency in the environment. Selective predation is believed to be common for coursing predators, such as wolves (Peterson, 1977; Wright et al., 2006; Hoy et al., 2021), and may also be common among stalking predators (Krumm et al., 2010;

Heurich et al., 2016). Selection tends to be for individuals that are in some way easier or less risky for predators to capture because of differences in age, conspicuousness, behaviors or body size and condition (Temple, 1987; Magnhagen, 1991; Pierce et al., 2000; Berger-Tal et al., 2009). For example, senescent prey, and prey with diseases or parasites are thought to be easier for predators to catch because they are in substandard condition (Hudson et al., 1992; Krumm et al., 2010; Hoy et al., 2015, 2021).

Age-based selection can have important, if not readily anticipated, impacts on prey population dynamics. For example, prey population growth rates tend to be less impacted by predation when predators exhibit selection for juveniles and senescent adults because those age-classes have lower reproductive values than prime-aged adults (Wright et al., 2006; Gervasi et al., 2012; Hoy et al., 2015). Other effects of age-based selection are not so easily anticipated, such as sometimes making prey populations less resilient, reducing prey equilibrium values or having a destabilizing effect on predator-prey dynamics (Hoy et al., 2021).

Less well understood – but commonly speculated – is the notion that selection for prey with infectious or communicable diseases and parasites can result in healthier prey populations. For example, mathematical models predict that selection for infected individuals may reduce the prevalence and transmission rates of diseases or parasites under certain circumstances (Packer et al., 2003; Wild et al., 2011), but empirical assessments have been less forthcoming (Tanner et al., 2019). Even less well understood is whether the health of prey populations is affected by selective predation for non-communicable diseases with a genetic basis.

Here we assess the extent that wolves (*Canis lupus*) select adult moose (*Alces alces*) in Isle Royale National Park (IRNP) on the basis of both age-class and osteoarthritis, which is a chronic, non-communicable disease that is strongly influenced by genetic factors (Fernández-Moreno et al., 2008; Valdes and Spector, 2008). Osteoarthritis is a progressively crippling disease caused by degeneration of cartilage in the articulating surfaces of moveable joints. Osteoarthritis often becomes painful and limits mobility, which could increase vulnerability to wolf predation.

This analysis uses a database of necropsies, which includes information about the year-of-death, age-at-death, cause-of-death, and incidence of osteoarthritis for 1,571 moose dying over a 47-year period (1959–2007). We also assessed the extent that temporal variation in per capita kill rates (prey killed, per predator, per unit of time) was associated with the subsequent incidence of osteoarthritis in the moose population over a 33-year period (1975–2007).

Assessments of the extent that wolves selectively prey on individuals with osteoarthritis and the impact of selective predation on the incidence of osteoarthritis would contribute to better understanding of the ecological importance of wolves for maintaining healthy prey populations and the breath of ecosystem services that predators provide. Additionally, because osteoarthritis is a senescent-related disease, these assessments allow for disentangling the extent to which the basis for selective predation in this population is some generic consequences of senescence or more specifically osteoarthritis.

MATERIALS AND METHODS

Study System

Isle Royale National Park is an archipelago in Lake Superior, North America (47°50′N, 89°00′W), comprised of a large island (544 km^2) and dozens of smaller islets (most of which are$<$ 2 km^2). Isle Royale is also known as Minong by local indigenous communities and is under the stewardship of the Grand Portage Anishinaabe and U.S. National Park Service. Populations of wolves and moose have been continuously studied in IRNP since 1959 (Peterson et al., 2014). Moose are the primary prey for wolves, comprising$\sim$90% of their kills, and wolves are the only predator of moose (Peterson et al., 1998). Neither the forest nor moose have been harvested for over a century, and wolves have been unaffected by human-caused mortality since their arrival in the mid-20th century.

Osteoarthritis is a senescent-related disease and its incidence increases with age (Peterson et al., 2010; **Figure 1**). Older individuals are also more likely to have severe forms of the disease (**Figure 1**). However, osteoarthritis can sometimes result from trauma or injury to joints (Lacourt et al., 2012; Rickey et al., 2012; Boyce et al., 2013; Jiménez et al., 2018). In humans and horses, the rate at which osteoarthritis progresses can vary greatly among individuals: in some cases, it may take several years before individuals develop severe forms of the disease; in other cases, rapid deterioration may occur in less than a year (Pivec et al., 2013; Driban et al., 2014; McCoy et al., 2020). The rate at which osteoarthritis progresses in moose may be similarly variable.

Data Collection

Each year between 1959–2007, we conducted intensive aerial surveys in winter (January–February) and ground surveys in summer (May–September) to locate the carcasses of moose that died during the previous year (Montgomery et al., 2014;

FIGURE 1 | The proportion of moose exhibiting any sign of osteoarthritis (black circles) and severe osteoarthritis (white triangles) at the time of death increases with age in a population of moose in Isle Royale National Park. Dataset is based on necropsies of 1,571 moose that died between 1959–2007.

Hoy et al., 2021). We necropsied carcasses to determine the individual's cause-of-death, age-at-death and whether that individual had osteoarthritis. Moose died from various causes, primarily predation, starvation and accidents. We observed various types of accidental deaths including: moose falling on or through ice, falling down cliffs or abandoned mine-shafts, injuries sustained during the rut. We used field sign, such as blood on trees, signs of a chase as indicated by tracks, hair and blood in the snow and signs of struggle including broken branches to infer the cause-of-death as predation (Metz et al., 2012; Montgomery et al., 2014). If predation was not determined to be the cause of death, we used the condition of bone marrow in the femur to assess whether starvation/malnutrition was a likely cause of death (Peterson, 1977; Mech and Delgiudices, 1985). We estimated the age-at-death for yearlings through tooth eruption patterns and for adults by counting cementum lines of teeth (Peterson, 1977; Haagenrud, 1978; Rolandsen et al., 2008). We excluded calves from this analysis as previous studies have assessed wolf selection for calves (Wright et al., 2006; Hoy et al., 2021). Moreover, in most cases the carcasses of calves are too badly damaged to assess whether individuals had skeletal abnormalities or defects.

We searched for the presence of osteoarthritis throughout each skeleton. Osteoarthritis was most commonly observed in the lowest vertebrae (fifth lumbar and first sacral) and pelvic (coxofemoral) joint (Peterson et al., 2010). We classified instances of osteoarthritis as being slight, moderate, or severe. Specimens were classed as slight if we observed small osteophytes on vertebral edges or if the acetabular fossa of the pelvis was largely open but exhibited bone ingrowths. Specimens were classed as moderate if osteophytes had started to bridge gaps between vertebra or if bone growth had entirely closed the acetabular fossa and small areas of cartilage loss (sclerosis) were observed, but no other modifications of the acetabular joints were observed. Lastly, specimens were classed as severe if we observed any of these conditions: osteophytes extending over vertebral joints, vertebrae starting to fuse together, significant remodeling of joints in the pelvis, such as sclerosis, subchondral lesions (cavities) and osteophytes growing around the entire coxofemoral joint or dorsal migration of the joint. **Figure 1** in Peterson et al. (2010) provides images which show the progressive deterioration of the coxofemoral joint associated with osteoarthritis. To ensure that individuals were assessed for osteoarthritis in a consistent manner, the severity of osteoarthritis was determined by the same observer (ROP) throughout the entire study period. It was not possible to determine how long individuals might have had osteoarthritis prior to death because the rate at which osteoarthritis progresses is known to be highly variable (Pivec et al., 2013; Driban et al., 2014; McCoy et al., 2020).

Statistical Analyses

All analyses were performed in Program-R version 4.0.5 (R Core Team, 2021). First, we assessed whether wolves selectively preyed on moose with osteoarthritis whilst also taking into consideration whether prey were prime-aged (aged 1–9 years old) or senescent (>10 years old). It is plausible that an individual's vulnerability to predators may vary with the severity of the osteoarthritis, e.g., moose with more severe osteoarthritis may have more limited mobility than individuals with slight osteoarthritis. Therefore, we considered eight types of moose: prime-absent (n = 639), prime-slight (n = 33), prime-moderate (n = 30), prime-severe (n = 39), senescent-absent (n = 374), senescent-slight (n = 102), senescent-moderate (n = 194), and senescent-severe (n = 264).

Following Hoy et al. (2021), we estimated the strength of wolves' selection for each of the eight moosetypes using the Manly-Chesson selection index, denoted α (Manly, 1974; Chesson, 1978, 1983). The Manly-Chesson index is a relative measure of selection and commonly used to assess wolf predation (Ståhlberg et al., 2017; Torretta et al., 2017; Hoy et al., 2021). It is calculated as:

$$\alpha_i = \frac{r_i \ / \ e_i}{\sum_{i=1}^{m} r_i \ / \ e_i} \tag{1}$$

where r_i is the proportion of prey item i in the diet (i.e., *dietary frequency*), e_i is the proportion of prey item i in the environment (*environmental frequency*), and m represents the number of prey types in the environment, where m = 8 in our case. Values of α_i range from 0 (complete avoidance) to 1 (strongest possible selection). If predators exhibit no selection, then frequency in the diet matches the frequency in the environment and $\alpha_i = 1/m$. In a formal sense, α is proportional to the probability that a predator attacks a prey type given an encounter. Additionally, α is also related to the attack rate in the functional response of a consumer-resource model (Chesson, 1978).

We estimated the *environmental frequency* of osteoarthritis by multiplying estimates of the age-specific incidence of moderate to severe osteoarthritis (**Figure 1**) by estimates of the average age-structure of the moose population between 1959–2007. The average age structure of the moose population was estimated from annual estimates of age-structure between 1959–2007, which were produced as part of an earlier study (Hoy et al., 2020, 2021). We do not assess whether selection for moose with osteoarthritis differed for bulls and cows because sex-specific estimates of age-structure are not available for this population. To estimate *dietary frequency*, we filtered our necropsy database to include only moose killed by wolves between 1959–2007 (same period as age-structure estimates) and then estimated the proportion of all wolf-killed moose belonging to each of the eight prey types.

Second, we assessed whether cause-specific mortality differed with the severity of osteoarthritis. To do so, we used generalized linear models (GLMs), with a binomial error structure, where the response variable was 1 or 0 depending on whether moose died from wolf predation or from other causes (i.e., starvation, accidents) respectively. If an individual's cause of death could not be determined (due to inconclusive field evidence) we excluded it from this analysis. The predictor variable indicated whether osteoarthritis was absent, slight, moderate or severe. We assessed cause-specific mortality separately for prime-aged and senescent moose because wolves are known to show strong selection for senescent moose(Hoy et al., 2021).

Lastly, we used GLMs with a binomial error structure to assess the extent that interannual variation in per capita kill rate subsequently influenced the proportion of moose dying with osteoarthritis. To account for interannual variability in the number of individuals dying we carried out a weighted regression (annual sample sizes used as weights) where the response variable was the proportion of moose dying with osteoarthritis. For this analysis, we considered only two types of moose (those with and without osteoarthritis) because annual sample size was not large enough to support an analysis that takes account of the severity of osteoarthritis. We built models allowing for the possibility that kill rate's effect on the incidence of osteoarthritis occurs after some time lag (up to 3 years). Time lags are a common feature of ecological interactions, including predation and disease (MacDonald, 1978). We estimated per capita kill rate from aerial surveys each surveys in Jan-Feb each year (Gasaway et al., 1986; Peterson and Page, 1988). We excluded data prior to 1975 because estimates of per capita kill rate (with 3-year lag) are not available for earlier years. Because the incidence of osteoarthritis is also likely influenced by fluctuations in the age structure of the moose population, we included an index of age structure (proportion of adults that were senescent, > 9 years old) as a predictor variable (Hoy et al., 2020).

To check assumptions of heteroskedasticity and normally distributed errors we visually inspected plots of model residuals and we formally tested for heteroskedasticity using Breusch-Pagan tests. We also checked for overdispersion and refitted models with a quasibinomial error structure if the dispersion factor was greater than 1.3. We estimated Cook's distance to check whether any observations had unduly large leverage. Lastly, we estimated variance inflation factors (VIF) to check whether multicollinearity was a concern for each model.

RESULTS

Osteoarthritis was detected in 38.3% of the 1,571 skeletons of moose that we examined whose age-at-death could be determined. Senescent moose accounted for 35.4% of individuals dying with no signs of osteoarthritis (n = 970), 74.0% of individuals dying with slight osteoarthritis (n = 127), 86.4% of individuals with moderate osteoarthritis (n = 214), and 86.9% of individuals with severe osteoarthritis (n = 260). Wolf predation accounted for 58.0% of the 1,416 dead moose whose cause-of-death could be determined, with prime-aged individuals accounting for 42.9% of moose killed by wolves.

Wolves showed strong selection for senescent moose, and avoidance of prime-aged adults. However, wolves showed weaker avoidance of prime-age moose with severe osteoarthritis (α = 0.08) compared to prime-aged moose without osteoarthritis or with only slight or moderate osteoarthritis (α = 0.04, **Figure 2**). Moreover, wolves exhibited weaker selection for senescent moose without osteoarthritis (α = 0.16) compared to senescent moose with slight, moderate or severe osteoarthritis (α = 0.21, α = 0.22, α = 0.20, respectively, **Figure 2**). For additional context, we would expect α = 0.13 if wolves exhibited no selection or no avoidance for a prey class (i.e., they killed prey types in proportion to their relative abundance).

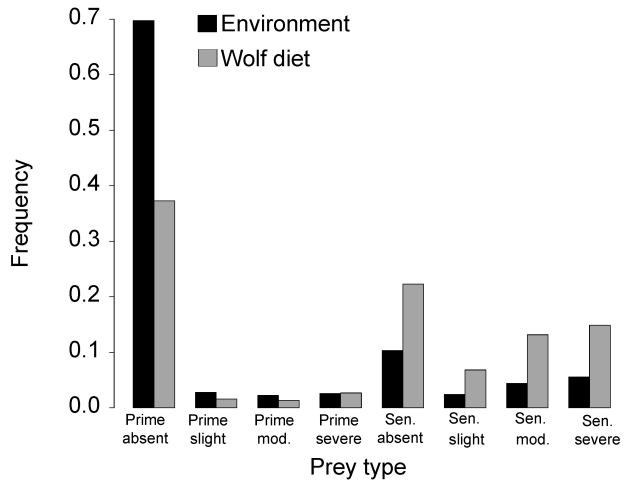

FIGURE 2 | Frequency of different types of moose in the environment and in wolf diets in Isle Royale National Park, 1959–2007. Moose were grouped according to age [prime-aged (1–9 years old) or senescent (>9 years old, abbreviated "Sen")] and severity of OA [absent, mild, moderate (abbreviated to mod.), severe]. Black bars indicate environmental frequency, averaged across years. Gray bars indicate dietary frequency, averaged across years.

Cause-specific mortality differed with the severity of osteoarthritis for prime-aged moose (see **Figure 3A**). More precisely, the probability of being killed by wolves was significantly higher for prime-aged moose with severe osteoarthritis compared to prime-aged moose with slight, moderate or no sign of osteoarthritis (p = 0.02). There was weak evidence to suggest that senescent moose without osteoarthritis were less likely to be killed by wolves than moose with slight, moderate or severe osteoarthritis; but the difference was not statistically significant (**Figure 3B**, p = 0.08).

The incidence of osteoarthritis among dead moose was negatively correlated with kill rates following a 2–3-year lag (**Table 1** and **Figure 4**) with the correlation being strongest for a 3-year lag. By contrast, temporal variation in the incidence of osteoarthritis among dead moose was not strongly correlated with the indicator of population age-structure (proportion of adults in the population that were senescent, **Table 1**).

DISCUSSION

Wolves showed strong selection for senescent moose and tended to avoid prime-aged adults, which is consistent with previous research (Hoy et al., 2021). However, this research goes further by showing that selection for age-classes of moose may also be influenced by a chronic disease, osteoarthritis. More precisely, our results suggest that the presence of severe, but not mild or moderate osteoarthritis, increases the vulnerability of prime-aged moose to predation by wolves. Two results point to this conclusion. First, wolf predation was more likely the cause of death for prime-aged moose with severe osteoarthritis than for prime-aged moose without osteoarthritis or with mild or moderate osteoarthritis (**Figure 3A**). Second, wolves avoided

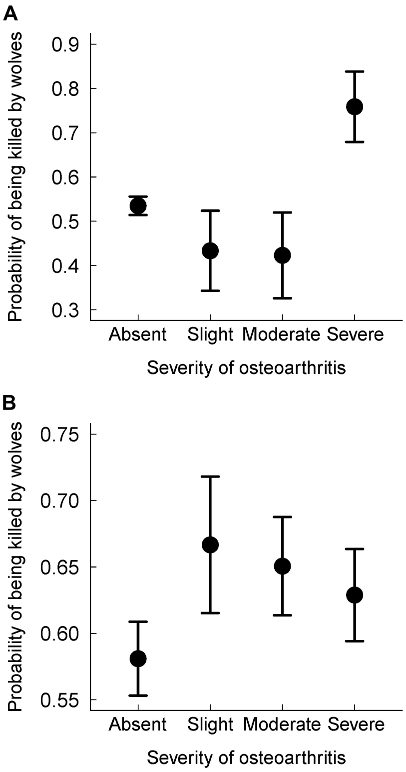

FIGURE 3 | Proportion of moose killed by wolves (as opposed to dying from other causes, i.e., starvation or accidents) varies with the severity of osteoarthritis for prime-aged moose **(A)** but not for senescent moose **(B)**. Moose were considered to be in their "prime" if they died between 1–9 years old or senescent if they died> 9 years old. Bars represent standard errors. Analysis is based on necropsies of 1,416 moose in Isle Royale National Park between 1959–2007 and for whom age-at-death, cause-of-death, and osteoarthritis status could be determined.

prime-aged moose with severe osteoarthritis less intensely (α = 0.08) than prime-aged moose without the disease or with mild and moderate cases of osteoarthritis (α = 0.04, **Figure 2**).

There was weak evidence to suggest that senescent moose without osteoarthritis were less vulnerable to wolves, compared to senescent moose with the disease. Specifically, the estimated value of α for senescentmoose without osteoarthritis (α = 0.16) was close to the value that corresponds to no selection for a given prey type (α = 0.13). There was also some evidence to suggest that the probability of being killed by wolves is lower for senescent moose with no signs of osteoarthritis (**Figure 3B**), but that result was not statistically significant. Therefore, this study offers limited support for the idea that osteoarthritis is a more important basis for selection, rather than some other aspect(s) of being senescent.

Senescent adults may be more vulnerable to coursing predators, irrespective of whether they have osteoarthritis, due to some combination of the following factors. First, senescent mammals may be less able to detect nearby predators because of age-related declines in hearing, visual acuity, and cognition (Spear et al., 1994; Chapagain et al., 2018; Jayakody et al., 2018). Second, older adults tend to become more sedentary (Ingram, 2000; Froy et al., 2018) because of declines in muscle mass and strength, aerobic capacity or spatial memory (Barnes, 1988; Doherty, 2003; Short et al., 2005; Tanaka and Seals, 2008). Third, sedentariness may be accompanied by a tendency to spend more time in habitats where forage availability is high (Froy et al., 2018), even if doing so increases the likelihood of encountering predators. This pattern has been observed on Isle Royale, where senescent moose were more likely than prime-aged moose to be killed closer to the shorelines where forage availability is thought to be higher and where wolves tend to be more active (Montgomery et al., 2013). Thus, age-related changes in behaviors, such as habitat selection, in addition to physiological declines, may contribute to senescent moose being more vulnerable to predation, irrespective of whether they have osteoarthritis. For these reasons, age should also be an important consideration when evaluating the effect of disease on prey vulnerability.

The incidence of osteoarthritis tended to be higher following years with lower kill rates (**Figure 4** and **Table 1**). Because predation is a major cause of mortality in this moose population (Vucetich et al., 2011; **Figure 3**), its plausible that arthritic individuals may live longer during periods when kill rates are low, leading to an increase in osteoarthritis in the population. Conversely, the incidence of osteoarthritis may lower following years with high kill rates because of the selective removal of moose with severe osteoarthritis. Because osteoarthritis is

TABLE 1 | Coefficients from bivariate models predicting temporal variation in the incidence of OA among dead moose over a 33-year period (1975–2007) from the proportion of adults in the populations that were senescent (Prop.sen, an indicator of population age structure) and kill rate by wolves (the number of moose killed, per wolf, each year) lagged up to 3 years.

Model number	Predictor variables	Coefficients (Standard errors)	*P*-values	Dispersion factor	VIF
1.	Prop.sen (t)	–0.11 (0.68)	0.87	1.67	1.05
	Kill rate (t-1)	–0.61 (0.33)	0.07		
2.	Prop.sen (t)	0.05 (0.66)	0.94	1.59	1.01
	Kill rate (t-2)	–0.69 (0.31)	0.03*		
3.	Prop.sen (t)	0.09 (0.63)	0.89	1.49	1.00
	Kill rate (t-3)	–0.78 (0.29)	0.01*		

We removed one observation (data from 1996) because it had high leverage (Cooks distance> 3). Models were fitted with a quasibinomial error structure to account for overdispersion (see fourth column). VIF is variance inflation factor. Asterisks are used to highlight predictor variables that were statistically significant.

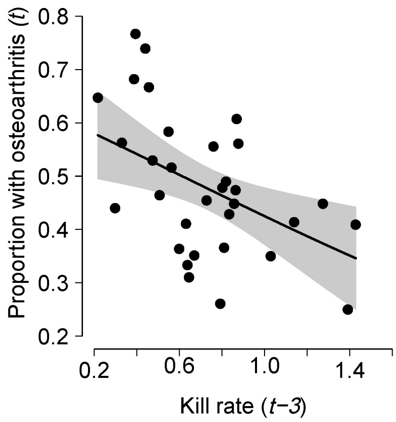

FIGURE 4 | Proportion of moose exhibiting osteoarthritis that died (from all causes) in year *t* in relationship to the per capita kill rate by wolves in year *t*–3. Each point represents a year (*t*) between 1979–2010. The line indicates a predicted value from a generalized linear model with two predictor variables, kill rate (*t-3*) and proportion of senescent moose in the population (*t*), where the proportion of senescent moose was fixed at the median value observed during the 33-year study period. Gray areas indicate 95% confidence intervals. The relationship with the proportion of moose exhibiting osteoarthritis and kill rates (*t-2*) is similar to the one shown above.

importantly influenced by genetic factors (Fernández-Moreno et al., 2008; Valdes and Spector, 2008) our results highlight the potential for wolf predation to act as an important selective force against genes that predispose individuals to developing severe osteoarthritis at a relatively young age. Wolves may also play an important role in regulating other chronic, non-communicable diseases in prey populations given that osteoarthritis is linked to (and may be an important risk factor for) other serious health conditions–at least in humans (Wang et al., 2016; Hawker and King, 2021). Therefore, we suggest that future studies assess how selective predation by wolves is influenced by prey having osteoarthritis as well as other chronic health conditions. Valuable insights might also be gained by future studies comparing how the incidence of osteoarthritis varies among prey populations that are subject to different levels of predation by wolves.

Temporal fluctuations in the incidence of osteoarthritis could also be caused by several other processes, in addition to wolf predation. First, the incidence of osteoarthritis may be related to processes which affect gene frequencies, such as genetic drift or inbreeding given that osteoarthritis is importantly influenced by genetic factors (Fernández-Moreno et al., 2008; Valdes and Spector, 2008). Any such effects of genetic drift and inbreeding on osteoarthritis may be more pronounced in Isle Royale moose than in mainland moose populations because the Isle Royale population is a relatively small and isolated. Second, the incidence of osteoarthritis has also been linked to fluctuations in nutritional condition for moose. Specifically, previous research suggests that moose which experienced poor nutritional conditions in early life are more likely to develop osteoarthritis in later life (Peterson et al., 2010). The nutritional condition of moose is importantly determined by interannual variation in weather [summer temperatures and snow depth, (Hoy et al., 2022)] because weather can affect physiological and energetic costs for moose, moose foraging behavior, the abundance of important parasites for moose, and the growth and quality of important forage species for moose. Nutritional conditions for moose may also fluctuate over time in response to changes in the level of intraspecific competition for food. However, there is no strong evidence linking fluctuations in nutritional condition to moose abundance (a common indicator of intraspecific competition) in this study system (Hoy et al., 2022). More importantly, fluctuations in moose abundance are largely driven by wolf predation in IRNP (Vucetich et al., 2011). Thus, even if changes in moose abundance have an important influence on nutrition and the incidence of osteoarthritis, then any such fluctuations are likely to ultimately trace back to changes in predation pressure. That observation highlights the complex interrelationships among processes influencing the incidence of osteoarthritis. We suggest future research focus on assessing the top-down and bottom-up processes causing temporal fluctuations in the incidence of osteoarthritis.

Management Implications

This research adds significant evidence for how selective predation may regulate the health of prey populations (Packer et al., 2003; Barber-Meyer et al., 2007; Wild et al., 2011; Tanner et al., 2019), which has implications for two management issues. First, the management of population health for ungulates has typically focused on the use of culls or recreational hunting to reduce the incidence of disease or parasites of concern (Mysterud et al., 2019; Debow et al., 2021). However, culls and harvests tend to be less selective for old and diseased individuals than predation (Wright et al., 2006; Krumm et al., 2010). Furthermore, killing healthy prime-aged adults is likely to be less effective at controlling diseases and may reduce ungulate populations to unnecessarily low densities. Indeed, previously published simulation analyses have indicated that selective predation is more effective at reducing disease prevalence and causes smaller declines in prey populations compared to a similar rate of culling or harvest that is non-selective (Wild et al., 2011). This strongly suggests that predation is largely compensatory to overall mortality, whereas culling and hunting is largely additive to overall mortality. Moreover, field evidence suggests that recreational hunting is typically not effective for limiting the incidence of disease in ungulate populations, even when regulations are designed to increase the efficacy of recreational hunters (Mysterud et al., 2019). Although culling can limit diseases more effectively than recreational hunting, culls tend to be highly controversial among hunters and the general public (Mysterud et al., 2019). Our work supports the view that natural predator populations represent a valuable alternative approach toward disease management (Tanner et al., 2019; Escobar et al., 2020).

Second, the evidence we present for predation's influence on the health of prey populations is also relevant for policy arguments about hunting wolf populations. More precisely, a common policy-related argument is that reasons offered for intensive wolf hunting (i.e., to mitigate threats to human safety, livestock loss, opportunities to hunt ungulates) do not outweigh the reasons to refrain from intensive wolf hunting (Vucetich et al., 2017). Those reasons for refraining include moral considerations (Vucetich et al., 2015), ecological consequences of allowing wolves to naturally regulate prey populations (Ripple et al., 2014), evolutionary consequences of allowing wolves to naturally regulate prey populations (Coltman et al., 2003; Festa-Bianchet, 2013). Our work contributes to better understanding the robustness of that argument by providing evidence for how unharvested wolf populations may influence the incidence ofosteoarthritis, a genetically based non-communicable disease.

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 the Institutional Animal Care and Use Committee (IACUC) at Michigan Technological University (protocol number L0093R).

AUTHOR CONTRIBUTIONS

SH, JV, and RP conceived the ideas for the study. RP and JV led data collection. SH carried out the analysis and led the writing of the manuscript. All authors contributed to editing drafts and gave final approval for publication.

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METHODS
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A Standardized Method for Experimental Human Approach Trials on Wild Wolves

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As wolves recolonize areas of Europe ranging from moderate to high anthropogenic impact, fear of wolves is a recurring source of conflict. Shared tools for evaluating wolf responses to humans, and comparing such responses across their range, can be valuable. Experiments in which humans approach wild wolves can increase our understanding of how wolves respond to humans, facilitating human-wolf coexistence. We have developed the first standardized protocol for evaluating wolf responses to approaching humans using high-resolution GPS data, and tested it on wild wolves. We present a field protocol for experimentally approaching GPS-collared wolves, a descriptive comparison of two statistical methods for detecting a measurable flight response, a tutorial for identifying wolf flight initiation and resettling positions, and an evaluation of the method when reducing GPS positioning frequency. The field protocol, a data collection form, and the tutorial with R code for extracting flight parameters are provided. This protocol will facilitate studies of wolf responses to approaching humans, applicable at a local, national, and international level. Data compiled in a standardized way from multiple study areas can be used to quantify the variation in wolf responses to humans within and between populations, and in relation to predictors such as social status, landscape factors, or human population density, and to establish a baseline distribution of wolf response patterns given a number of known predictors. The variation in wolf responses can be used to assess the degree to which results can be generalized to areas where GPS studies are not feasible, e.g., for predicting the range of likely wolf behaviors, assessing the likelihood of wolf-human encounters, and complementing existing tools for evaluating reports of bold wolves. Showing how wolves respond to human encounters should help demystify the behavior of wild wolves toward humans in their shared habitat.

Keywords: carnivores, *Canis lupus*, changepoint analysis, field experiments, flight initiation distance (FID), upper control limit (UCL), wildlife-human interaction

INTRODUCTION

After centuries of decline and subsequent legal protection, large carnivores are recolonizing parts of their historical European range (Trouwborst, 2010; Chapron et al., 2014). The multifunctional patchwork landscapes to which they are returning vary from moderate to high anthropogenic impact, and across Europe, large carnivores are settling in managed forests (Wabakken et al., 2001; Gurarie et al., 2011), forest-farmland mosaics (Sunde and Olsen, 2018), agro-ecosystems (Blanco and Cortés, 2007), and sometimes near human settlements (Carricondo-Sanchez et al., 2020) and urban areas (Basille et al., 2009; Bateman and Fleming, 2012; López-Bao et al., 2013). The distribution ranges of large carnivores are still increasing, and ecological niche models indicate that European human-dominated landscapes still provide ample space for further range expansions (Milanesi et al., 2017). Hence, although wilderness areas may be essential to keep favorable trends in the long term (Gilroy et al., 2015), the idea that large carnivores can only survive in remote or protected wilderness areas does not apply to today's Europe (Chapron et al., 2014).

Among the European large carnivores, wolves (*Canis lupus*) have adapted to the most populated areas, with a mean human density of 36.7 inhabitants/km^2 (range = 0–3,050) in areas of permanent wolf presence in Europe (Chapron et al., 2014). For instance, Europe hosts more wolves than the United States, despite being half the size and more than twice as densely populated (Chapron et al., 2014; Boitani, 2018). This land sharing between wolves and humans gives increased potential for direct wolf-human interactions (Bateman and Fleming, 2012).

The prospect of encountering wolves is a factor that can affect human attitudes toward the species (Bath, 2000; Røskaft et al., 2007). Fear of wolves is a recurring source of conflict, and has been associated with a lack of knowledge about the species (Bath, 2000; Bath and Majic, 2001), a perception that wolves are dangerous and unpredictable (Johansson et al., 2012), and a fear of the unknown (Zimmermann et al., 2001). Some people living in areas recolonized by wolves report that a concern for their own or their family's safety results in diminished quality of life (Røskaft et al., 2007). In modern times, non-rabid wolf attacks on humans are very rare, and documented cases are usually linked to habituation to anthropogenic food sources (Linnell and Alleau, 2016; Reinhardt et al., 2020; Linnell et al., 2021; Nowak et al., 2021). In developed countries, recent focus has been on wolves developing fearless behavior, and on human behaviors that may enhance the risk of attacks (Linnell and Alleau, 2016; Penteriani et al., 2016; LCIE, 2019; Reinhardt et al., 2020). However, there is a lack of research to understand the processes that may lead to risky situations (Löe and Röskaft, 2004; Linnell and Alleau, 2016). Knowledge about wolf behavior toward humans should help mitigate fear and thus facilitate wolf-human coexistence.

Because fear of wolves is a common challenge across their recolonized European range (e.g., Bath, 2000; Bath and Majic, 2001; Røskaft et al., 2007; Johansson et al., 2012; Reinhardt et al., 2020), shared tools for evaluating wolf responses to humans, and comparing such responses across their range, can be valuable. Experiments in which human observers approach marked wolves can increase the knowledge about how wolves can be expected to respond to interactions with humans (Karlsson et al., 2007). Experimental human approaches have been done previously on species such as common buzzards (*Buteo buteo*) (Sunde et al., 2009a), reindeer (*Rangifer tarandus*) (Colman et al., 2012), red deer (*Cervus elaphus*) (Sunde et al., 2009b), moose (*Alces alces*) (Viljanen, 2019), polar bears (*Ursus maritimus*) (Andersen and Aars, 2008), brown bears (*Ursus arctos*) (Moen et al., 2012, 2018; Ordiz et al., 2013, 2019), lynx (*Lynx lynx*) (Sunde et al., 1998), and wolves (Karlsson et al., 2007; Wam et al., 2012, 2014). However, previous studies on wolves used VHF collars (Karlsson et al., 2007; Wam et al., 2012, 2014), limiting the level of detail at which the wolf response could be recorded without subsequent snow tracking (Karlsson et al., 2007). Today's GPS collars provide movement data at much higher temporal resolution and spatial precision and accuracy, without the need for snow cover. Additionally, a standardized protocol will allow comparative studies across different study areas, e.g., comparing responses within and between populations, and among areas of varying human density. Hence, a baseline distribution of wolf response patterns can be established given a number of known predictors. Such knowledge about likely wolf responses to humans may increase predictability of wolf behavior to people living in wolf areas.

Large carnivores can show physiological and behavioral antipredator responses to humans (Ordiz et al., 2011; Støen et al., 2015), and may show a proactive fight or flight, or a reactive freeze or hide response (Koolhaas et al., 1999; Roelofs, 2017). The presence or absence of a flight response, and the distance from the disturbance at which the animal flees (flight initiation distance, hereafter FID), are therefore useful parameters to describe the responses of wild animals to human disturbance (for examples, see Colman et al., 2012; Moen et al., 2012; Ordiz et al., 2019; Viljanen, 2019). As shown in brown bears, extensive experimental approaches on GPS collared animals make it possible to compare flight initiation distances between individuals and demographic groups, and to study potential habituation and lasting behavior when approached repeatedly (Ordiz et al., 2013, 2019; Sahlen et al., 2015). For detecting flight initiation during human approaches, two statistical methods have been used previously, i.e., Upper Control Limit (UCL; Moen et al., 2012; Sahlen et al., 2015; Ordiz et al., 2019) and changepoint analyses (Killick et al., 2012; Viljanen, 2019; Græsli et al., 2020). However, it is not known if the methods differ in results for FID calculations.

In this paper, we present (1) a standardized field protocol for experimentally approaching GPS-collared wolves to assess their responses to encounters with humans, controlling for factors such as habitat parameters and number of approaching humans; (2) a descriptive comparison of two statistical methods (changepoint analysis and UCL) to detect the presence or absence of a measurable flight response, and to identify the time and location of both flight initiation and resettling; (3) a tutorial for using changepoint analyses to identify wolf flight initiation and resettling positions as a basis for extracting a number of flight parameters; and (4) a quantitative assessment of the effects on success rate and precision when extracting flight parameters from wolf GPS data at reduced temporal resolution. Lowering the GPS positioning frequency for the approach trials can be an alternative to increase collar battery life. The field protocol, a field data collection form, and a tutorial with the R code for extracting the time and coordinates for flight initiation and resettling are provided as **Supplementary Presentations 1–3**. This standardized protocol will facilitate studies of wolf responses to direct interactions with humans, and it is applicable at local, national, and international levels.

EQUIPMENT

The protocol requires wolves equipped with GPS collars with positioning frequency programmable down to 1-min intervals, and with two-way wireless radio or satellite communication allowing remote re-programming of positioning schedule and data transmission after a set number of acquired positions. The field trials require a handheld GPS unit that can record a track log with 1-s positioning intervals, and an anemometer for measuring wind speed and direction (optional). The post-trial visibility measurements require a brightly colored cylinder (60 cm tall and 30 cm diameter) as described by Ordiz et al. (2009), or an equivalent structure.

MATERIALS AND METHODS

Wolves, Captures and Study Areas

Wolf captures were carried out in Scandinavia (Norway and Sweden), and Germany, and experimental human approaches were carried out in Scandinavia, Germany and Poland. These are areas where wolf populations have been recolonizing former grounds in recent decades (e.g., Chapron et al., 2014).

All wolves were chemically immobilized using tiletamine-zolazepam (Zoletil forte®, Virbac, Carros, France) and equipped with VERTEX GPS PLUS collars (Vectronics aerospace GmbH, Berlin Germany). The collars had two-way wireless communication (GSM or Iridium), enabling remote re-programming of GPS positioning schedule down to 1-min intervals and transmission of data batches after a set number of acquired GPS positions.

In central Scandinavia, a total of 11 wolves in six different territories were immobilized by darting from a helicopter during the winters of 2017–2021. The captures were conducted by the Scandinavian Wolf Research Project (SKANDULV), and the technique is described in detail by Sand et al. (2006), and followed the ethically approved procedures described by Arnemo and Evans (2017). Captures and experimental human approach trials were approved by the Norwegian Food Safety Authority (FOTS ID 15370) and the Animal Welfare Ethics Committee of Uppsala, Sweden (ref. 5.8.18–13246/2019). At the time of the approach trials, all of the collared wolves were territory-marking adults.

In eastern Germany, three wolves were captured and collared during the winters of 2019–2021 as part of the projects "Interspecific interaction behavior of wolves and red deer" and "Interaction behavior of wolves and mega herbivores (Konik horses and Heck cattle) on a large year-round grazing area." The wolves were captured with foothold-traps (equipped with trap transmitters from MinkPolice or VECTRONIC Aerospace GmbH, Berlin Germany) and immobilized within 30 min after capture using a blowpipe. One of the wolves (ID4) dispersed across the border to western Poland, close to the river Oder, where it was a non-territorial single wolf at the time of the trials. The other two were still in Germany at the time of the trials, one as a territory-marking adult (ID5) and one as a yearling (ID6) which, based on the GPS data, was not fully included in the natal pack anymore, but still tolerated close by.

The Norwegian/Swedish study area is mainly dominated by coniferous forest, with a lower abundance of deciduous species. The intensively managed forests consist of a mosaic of stands with different age classes, with an extensive network of forest roads (Sand et al., 2008). The human population density in the area ranges from two to ten inhabitants per km^2 (Statistisk Sentralbyrå, 2020,[1]). Moose is the most important prey for wolves and is found throughout the study area (Zimmermann, 2014; Zimmermann et al., 2015; Sand et al., 2016).

The study area in eastern Germany is dominated by mixed forests and agriculture areas, as well as moorland and open grassland with scattered villages. The area provides numerous hiking trails and forest roads, providing easy access to the public. The average human population density is around 80 inhabitants per square kilometer, but in the wolf territories less than 10 inhabitants per square kilometer. The main prey species for wolves in summer are roe deer (*Capreolus capreolus*), red deer, and wild boar (*Sus scrofa*) (Ansorge et al., 2006).

The Polish study area (with the GPS collared German immigrant wolf) is an end moraine region dominated by beech and mixed forests, as well as wetland habitats, agricultural land, and floodplains. The human density and infrastructure in this area is very low. Roe deer, fallow deer (*Dama dama*), and wild boar are prey species for the wolves in the area.

Field Trials

The field protocol was first developed and tested in two Scandinavian wolf territories in 2018. Subsequent fine-tuning and testing of the protocol took place in 2019–2021 in Scandinavia, Germany and Poland. Trials were not conducted in the period of May to mid-August to avoid disturbance in the denning and early pup rearing period, and we allowed on average 38 days (min = 14, max = 98) between consecutive trials on the same individuals within the same trial year (Aug-April).

GPS Scheduling

The GPS collars were programmed to a baseline positioning frequency of one position every 4 h, optimized for longer-term research projects. Collars were programmed to send positions in batches of seven using GSM or Iridium communication, i.e., every 28 h at 100% GPS success and adequate conditions for data transmission. The two-way communication also allowed for remote re-programming of the positioning schedule. A new schedule could be sent at any time and would be received next time the collar would connect to transmit acquired positions.

[1] https://www.scb.se/

Hence, when planning an approach trial, the positioning schedule had to be sent in time for the collar to receive the programming.

As a trade-off between collar battery usage and allowing sufficient time to carry out the trial and register the wolf response, we decided on a 2-h approach period at 1-min positioning frequency. This would give high-resolution raw data, which could then be down-sampled to evaluate the effects of lower positioning frequency. We scheduled a preparation period with 10-min positioning intervals prior to the approach period to locate the wolf. In 2018 we used a preparation period of 2 h. However, to increase the chances of receiving updated positions in time to start the trial, we increased the preparation period to 4 h from 2019. We scheduled a post-disturbance period with 10-min positioning intervals immediately following the approach period to capture the flight of the wolf until it resettled. In 2018 we used a post-disturbance period of 1 h, but changed it to 3 h from 2019 to increase the likelihood of capturing the entire flight until resettling.

Based on published data on wolf circadian activity patterns (Merrill and Mech, 2003; Theuerkauf, 2009; Eriksen et al., 2011) and similar approach studies on brown bears (e.g., Moen et al., 2012), we scheduled the approach period to start at noon local time (13:00 during Daylight Savings Time DST) to maximize the likelihood of the wolf being at a day bed. Hence, on the day of an approach trial, the GPS collar was programmed for 10-min positions during 08:00–12:00, 1-min positions during 12:00–14:00, and 10-min positions from 14:00–17:00 (1 h later for all three periods during DST). With this schedule, the wolf collar was programmed to take a total of 163 positions during one 9-h trial period (08:00–17:00). For considerations of battery life trade-offs, this corresponds to 27 days of four-hourly positions.

Field Methods

Following our standardized approach route (AR, **Figure 1**), the observer would walk in a straight line from a starting distance (SD) of at least one km from the wolf start position (WSP), pass the passing position (PP) at a passing distance (PD) of 50 m from the WSP, and continue walking for another 500 m to the observer end position (OEP) before walking back in an arc away from the WSP to the observer start position (OSP).

On approach days, we used incoming GPS positions during the preparation period to determine the location of the wolf. Centered on the last acquired wolf position (assumed WSP), we plotted a circle with a 1 km radius, and selected a suitable OSP on or outside this circle. Then, centered on the assumed WSP, we plotted another circle with a 50 m radius, and plotted the AR as a straight line starting at OSP, tangent to the 50 m circle, and continuing for another 500 m. The tangent point between the line (AR) and the 50 m circle defined the PP, and the end point defined the OEP. We selected an AR that facilitated walking in a straight line, preferably from an OSP that was accessible from a forest road, and with no ridges between AR and WSP that might potentially obstruct detection. Before starting the trial, we made the final corrections to the AR based on the last wolf position available, when possible, after receiving the first batch of 1-min positions. For some trials, wolf positions were monitored and AR was determined in the field. In most cases however, this was done more conveniently at the office and communicated to the field team.

The trials were conducted by either one or two human observers. Once the final AR was set, the observers would initiate track log with a handheld GPS unit and start walking at a regular hiking pace from OSP along AR in as straight a line as possible. The handheld GPS unit was set to log one position per second to facilitate matching with simultaneous wolf positions. In order for the trials to represent relevant and realistic scenarios of human hikers, observers did not try to be quiet, and pairs of observers would talk with each other while walking. Observers would leave the OSP in time to pass the PP at least 10 min before the end of the approach period to ensure at least 10 min of 1-min positions from the wolf after the observer passed the PP.

During the trial, environmental variables were recorded in a field form (**Supplementary Presentation 2**), including air temperature, wind strength and direction relative to AR, precipitation, humidity, vegetation cover, noise level from moving through the vegetation, and habitat type, following instructions for data registration given in the form (**Supplementary Presentation 2**).

As long as no wolf was seen, observers would follow the "standard approach protocol" as described above and outlined in **Figure 2A**, walking from OSP to OEP. However, in the case of a direct encounter with a wolf, observers were instructed to switch to the "direct encounter approach protocol" outlined in **Figure 2B**. We defined a direct encounter as: (1) visual observation of a wolf ahead of the observer when facing OEP, (2) observer would have noticed the wolf in a non-trial situation, (3) wolf being aware of observer, and (4) wolf not leaving immediately. All four criteria would need to be met, but the observer was not required to verify that the wolf was wearing a collar, before moving from the standard protocol to the direct encounter protocol. The direct encounter protocol consisted of a sequence of actions of increasing intensity: (1) stopping and waiting for 1 min, (2) counting to ten loudly, (3) waving arms and shouting loudly. Whenever the wolf would leave, the sequence would be terminated and the observers would resume the trial, walking toward OEP. If the wolf would not leave after completing the sequence, the observer would turn around and walk back to OSP. Direct encounters would be registered in the field form (**Supplementary Presentation 2**).

Post-trial Data Sampling

After the trial we identified the locations of flight initiation and resettling using the methods described under Data analyses and in **Supplementary Presentation 3**, and/or through visual inspection of the wolf positions. After the focal wolf had moved at least one km from the flight initiation and resettling position, we measured the visibility at these two locations as a measure of the concealment provided by vegetation. Following the description by Ordiz et al. (2009), we used a brightly colored cylinder (60 cm tall and 30 cm diameter), placed the cylinder at the coordinate of flight initiation/resettling, and measured the maximum distance in the four cardinal directions at which the cylinder could be seen.

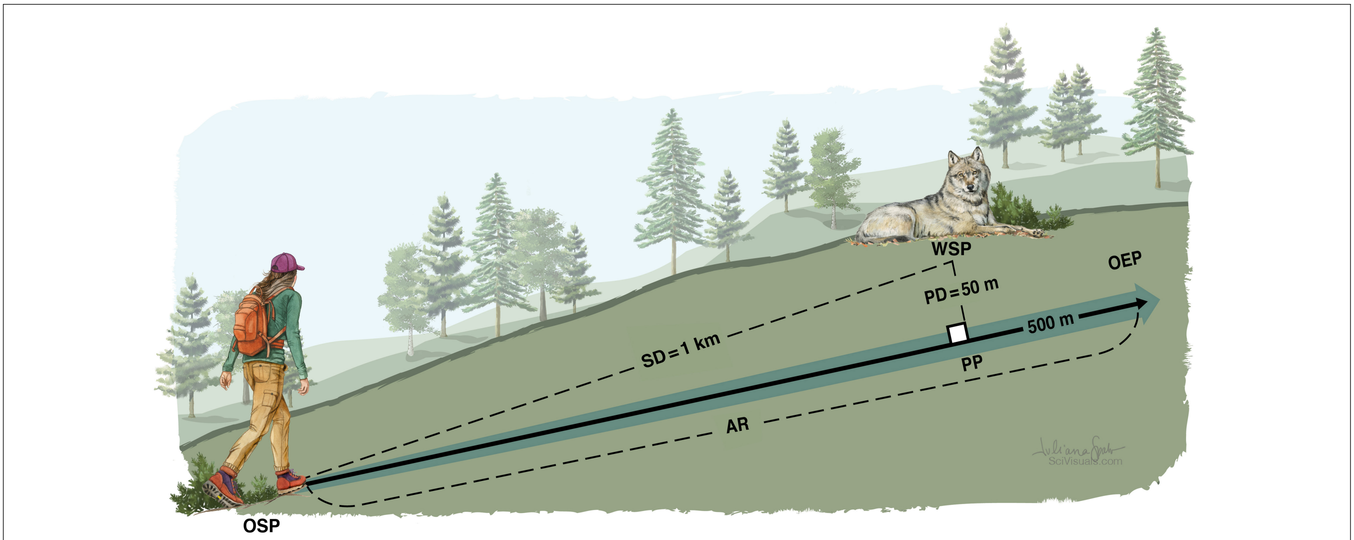

FIGURE 1 | Spatial arrangement of a standardized experimental human approach trial on wild wolves. OSP, observer start position; WSP, wolf start position; SD, starting distance; AR, approach route; PP, passing position; PD, passing distance; OEP, observer end position. Note that the graphic is not drawn to scale. Illustration: Juliana Spahr.

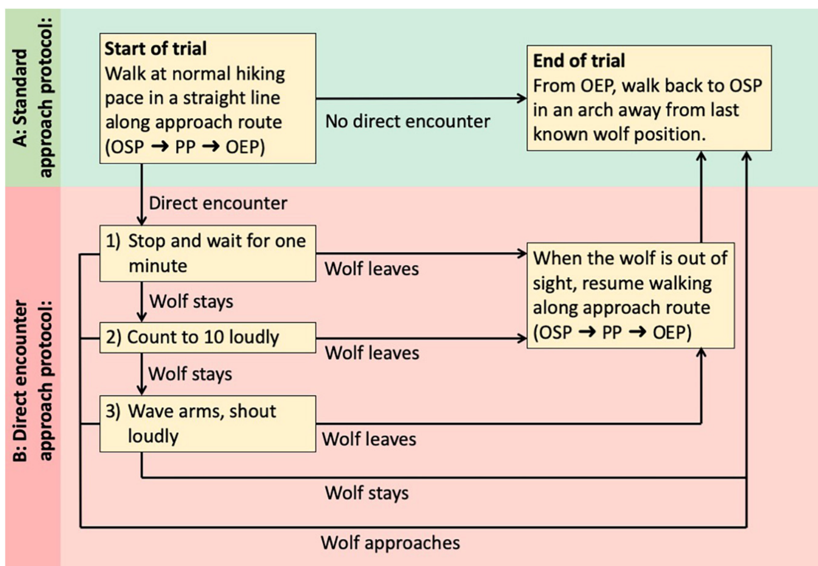

FIGURE 2 | Sequence of a standardized experimental human approach trial on wild wolves. Observer will switch from standard protocol **(A)** to direct encounter protocol **(B)** if all the following criteria for direct encounter are met: (1) visual observation of a wolf ahead of the observer when observer is facing OEP, (2) observer would have noticed the wolf in a non-trial situation, (3) wolf is aware of observer, and (4) wolf does not leave immediately. OSP, observer start position; PP, passing position; OEP, observer end position (defined in **Figure 1**).

A comprehensive field protocol for conducting the trials and the field form for data registration are provided in **Supplementary Presentations 1, 2**, respectively.

Data Analyses

Data Preparation

We used the R environment (R Core Team, 2019) within the interface of R-Studio (RStudio Team, 2016) for data preparation and analyses. Time and date formats were handled with the *lubridate* package (Grolemund and Wickham, 2011). Time was corrected to time zone GMT + 01:00, as approach trials during daylight saving time were in GMT + 02:00. The data from wolves and observers were extracted and trimmed to a period from 12:00 to 17:00 of the approach day. We visually assessed the data by plotting and animating individual approach trials with the *ggplot2* package (Wickham, 2016) and the *MoveVis* package (Schwalb-Willmann, 2019). We calculated step lengths as the Euclidean distance between consecutive wolf positions. The speed was calculated as meters per minute by dividing the step length by the difference in time.

We used the *sp* package (Bivand et al., 2013) to transform the coordinates from the observer data to a projected coordinate system (WGS84/UTM zone 33N). We joined the observer data with the wolf data based on the date and time using the *dplyr* package (Wickham et al., 2019). If the observer data was lacking positions, we used the *data.table* package (Dowle and Srinivasan, 2019) to select the observer position that was the closest in time to the wolf position. We then calculated the Euclidean distance between simultaneous wolf and observer positions. Final coordinates for the WSP (to replace the assumed WSP used when setting up the AR prior to the trial) was defined as the first wolf position after the observer started walking from OSP.

Extracting Wolf Response Variables

We used changepoint analysis of wolf speed at 1-min resolution to identify flight initiation. For this purpose, we adjusted the wolf speed to a gamma distribution by changing values of 0 m/min to 0.01 m/min based on the assumption that a speed of exactly zero will be nearly impossible, due to GPS measurement error. We then applied a pruned exact linear time (PELT) algorithm with a gamma distribution on both mean and variance of the wolf speed with MBIC (Modified Bayes Information System) penalty on 95% CI using the function *cpt.meanvar* from the *ChangePoint* package (Killick et al., 2016). We chose the MBIC penalty, as the AIC and BIC penalties are prone to overestimating changepoints (Lavielle, 2005). The flight initiation was defined as the first changepoint after the observer started the approach trial (**Figure 3**).

For comparison, we also extracted flight initiation using a different statistical method, estimating an Upper Control Limit (UCL), i.e., a defined threshold for the movement speed to distinguish between stationary and non-stationary wolf behavior (Montgomery, 2007; Moen et al., 2012; Ordiz et al., 2019). As opposed to changepoint analyses, UCL calculations rely on control data representing the baseline condition, which in this case was GPS data from stationary wolves. As control, we used 1099 positions from days when wolf collars were programmed for an approach trial, but no trial was carried out, and from wolf GPS data from successful trials during which the wolves did not move. We only used control data for which visual inspection of the GPS positions indicated no movement, and the time difference between positions was between 30 and 90 s. The movement speed from this dataset was assumed to primarily represent GPS error. This gave us a UCL of 23 m/min. We defined the flight initiation as the last position before the movement speed exceeded the UCL for at least two consecutive intervals.

For all trials for which flight initiation was identified, we used 10-min positioning intervals to identify the position where the wolf resettled after the flight. We down-sampled the data to 10-min intervals for the period 12:00 to 17:00 using the *data.table* package (Dowle and Srinivasan, 2019), and applied changepoint analysis as described for flight initiation. We defined resettling as the first position after the first changepoint after flight initiation, i.e., the start of a stationary period (**Figure 3**).

We extracted the following variables to describe the wolf flight response (**Table 1**): We classified the wolf response as either *Flight* when flight initiation was identified, or *No flight* when no flight initiation was identified and the wolf remained stationary. Based on the 1-min positioning intervals, we calculated the *Minimum wolf-observer distance* as the minimum distance between simultaneous wolf and observer positions, *Flight initiation distance* (*FID*) as the wolf-observer distance at flight initiation, and *Passing-flight time difference* as the time difference between flight initiation and the observer passing the passing position. For the first 10 min after flight initiation and at 1-min resolution, we calculated *Initial speed* as the average speed and *Initial straightness* as the sum of the step lengths divided by the linear displacement. We calculated *Flight duration* and *Flight displacement* as the time and the distance from flight initiation to resettling, respectively. For the total flight (from flight initiation to resettling) and at 10-min resolution, we calculated *Total distance travelled* as the sum of the step lengths, *Overall speed* as the average speed, and *Overall straightness* as

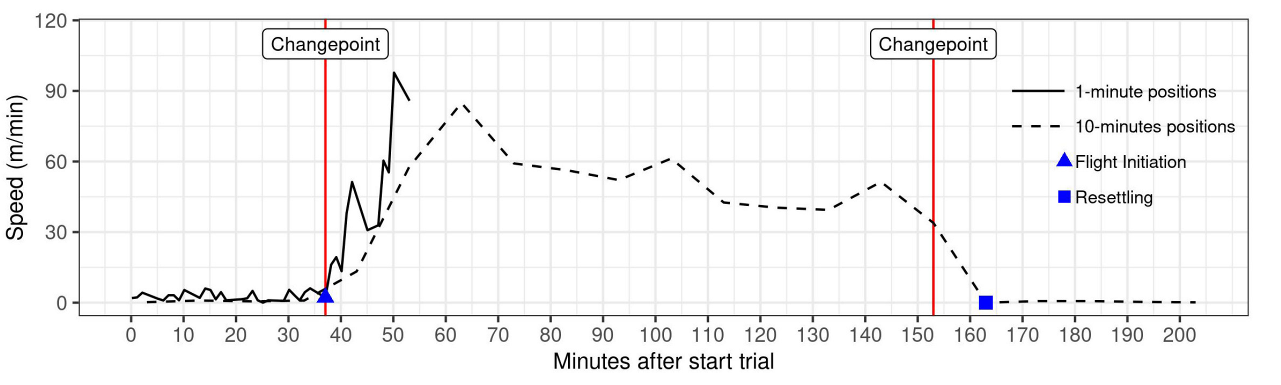

FIGURE 3 | Visualization of the detection of flight initiation and resettling positions of a wolf during experimental human approach trials. For detection, we used changepoint analysis with change in mean and variance of wolf movement speed using the MBIC penalty. The first changepoint indicates the moment of flight initiation based on 1-min GPS positioning intervals (solid line). Resettling location is defined as the first position after the first changepoint after flight initiation, based on 10-min positioning intervals (dashed line).

TABLE 1 | Description, temporal resolution and time period of the extracted variables used to describe the responses of wild wolves when approached by humans.

Variable name	Description	GPS frequency	Time period
Flight / No flight	Binary variable indicating whether or not a flight was identified using changepoint analyses.	1 min	-
Minimum wolf-observer distance	Shortest distance between simultaneous wolf and observer positions	1 min	-
Flight initiation distance (FID)	Distance between wolf and observer at flight initiation	1 min	-
Passing-flight time difference	Time between flight initiation and observer passing the passing position (PP). Negative if wolf fled before, and positive if wolf fled after observer passed PP.	1 min	-
Initial speed	Average speed	1 min	First 10 min after flight initiation
Initial straightness	Sum of step lengths divided by linear displacement	1 min	
Flight duration	Time difference	10 min	From flight initiation to resettling
Total distance traveled	Sum of the step lengths	10 min	
Flight displacement	Linear displacement	10 min	
Overall speed	Average speed	10 min	
Overall straightness	Straightness index across the flight calculated as the average straightness between every three consecutive positions	10 min	

Flight initiation and resettling were identified using GPS data at 1 and 10-min resolution, respectively.

the average straightness index across the flight based on the straightness between every three consecutive positions (**Table 1**).

An instruction manual with R code for identifying flight initiation and resettling using changepoint analysis with MBIC penalty, and for calculating the flight response variables listed in **Table 1**, is provided in **Supplementary Presentation 3**.

Down-Sampling of GPS Positioning Intervals

To quantify the effects of reduced GPS positioning frequency on the calculation of wolf response variables for studies that need to preserve collar battery, we down-sampled the original data from 1-min to 2-, 3-, and 5-min resolution for calculating flight initiation, and from 10- to 20-min resolution for calculating resettling. Down-sampling was done by creating a new data frame with the intended time stamps, and then adding GPS positions from the original data set to the new data frame by using *roll = "nearest"* from the *data.table* package (Dowle and Srinivasan, 2019). We then removed double observations resulting from the same position being the nearest to more than one time stamp (in cases of gaps in the data), and we used the original time stamp of the data. This created a time series including gaps, as would be expected in a real-life situation. With these down-sampled datasets, we identified flight initiation and resettling and calculated the flight response variables as described above. To compare the down-sampled data to the original temporal 1- and 10-min resolutions of GPS positions, we used generalized linear mixed models (GLMMs) from the *lme4* package (Bates et al., 2015) for each of the flight response variables. For all models, GPS interval was the single fixed-effects variable with the original 1- and 10-min intervals as the reference (intercept), and trial ID as a random effect. To meet the assumption of normally distributed residuals, minimum wolf-observer distance was transformed by $\sqrt{x}$, flight initiation distance by $\sqrt{log(x+1)}$, and overall straightness by log(1-x). We considered results from the down-sampled data significantly different when their 95% confidence intervals (CIs) did not overlap with the predicted value for the original data (i.e., the intercept). This coincided with an alpha level of 0.05.

RESULTS

Overview of Approach Trials

Between September 2018 and September 2021, experimental approach trials were attempted in eleven wolf territories/home ranges in Scandinavia, Germany and Poland, resulting in 25 successful trials in seven different territories/home ranges (**Table 2**). On eleven occasions, wolf collars were programmed for an approach trial, but the trial was unsuccessful because the wolf did not settle at a day bed, but kept moving throughout the approach period (n = 5), the wolf collars did not send positions in time to start the trial (n = 4), the wolf moved to an area where we did not have an ethical permit at the time (n = 1), we could not reach the start position in time due to inaccessible roads (n = 1). Notably, after increasing the preparation period with 10-min positioning intervals from 2 to 4 h, we did not miss any trials due to not receiving positions in time. In one last case in Germany in 2019, the approach schedule was not picked up by the collar but the approach was conducted anyway. This was the only case in which the observers saw the wolves (seven individuals including the collared wolf), but the wolves moved away from the observers before the direct encounter protocol was initiated. The trial was considered unsuccessful due to the lack of wolf GPS positions. On a few additional occasions, an approach schedule was sent but not picked up by the wolf collar, and therefore no approach trial was attempted.

GPS Data

When two collared wolves were together during a single approach trial, we used data from the interactions between the observer and each individual wolf, although the behavior of the two wolves would not be independent of each other in such cases. However, the objective at this stage was to test the method

TABLE 2 | Overview of successful and unsuccessful experimental human approach trials on wild wolves in Norway (N), Sweden (S), Poland (P), and Germany (G) during 2018–2021.

Territory/home range (country)	Year	Wolf ID (sex)	Communication	Successful trials	Unsuccessful trials
Varåa (N/S)	2018	M18-17 (F)	GSM	5	1
		M17-08 (M)	Iridium		
	2019	M18-17 (F)	GSM	3	0
		M17-08 (M)	GSM		
Juvberget (N/S)	2018	M18-13 (F)	GSM	3	3
		M18-12 (M1)	Iridium		
	2019	M18-13 (F)	GSM	2	1
		M19-02 (M2)	Iridium		
	2020	M18-13 (F)	GSM	3	0
		M19-02 (M2)	GSM		
Bograngen (N/S)	2019	M19-01 (F)	GSM	0	2
		M19-04 (M)	GSM		
Magnor (N/S)	2019	M18-11 (M)	GSM	3	1
Norrsjö (S)	2019	M18-14 (M)	GSM	0	2
Ulvåa (N/S)	2020	M20-02 (F)	GSM	0	1
Skärsjön (S)	2021	M21-02 (M)	Iridium	2	0
Oranienbaumer Heide (G)	2019	WolfID4 (M)	Iridium	0	1
Oder (P)	2019	WolfID4 (M)	Iridium	1	0
	2020	WolfID4 (M)	Iridium	1	0
Dübener Heide (G)	2020	WolfID5 (M)	Iridium	1	0
Glücksburger Heide (G)	2021	WolfID6 (F)	Iridium	1	0
Total				25	12

TABLE 3 | Variation in interval duration (seconds), GPS success rate (max–min), and number of flights detected using changepoint analysis with MBIC penalty, for different positioning frequencies down-sampled from original 1-min resolution wolf GPS data from experimental human approach trials.

	Interval duration (seconds)						
Interval	Mean	sd	Median	min	max	GPS success rate	# Detected flights
1-min	75.4	54.9	60	6	590	78% (52–99)	29
2-min	125.2	58.7	120	8	590	97% (76–99)	29
3-min	183.1	61.1	180	14	590	98% (83–100)	29
5-min	299.4	65.2	300	14	715	99% (90–100)	28

rather than to interpret the wolf behavior. This resulted in a total of 35 individual wolf-human interactions (hereafter called interactions) involving nine different wolves, from which we could test the extraction of response variables.

At 1-min intervals, the GPS success rate of the wolf collars was 78% (range = 52–99, **Table 3**). The gaps encompassed on average 3 ± 1.4 missing positions, whereas the 10-min interval data did not show any gaps.

For 14 interactions, the observer data lacked positions, e.g., if the GPS track log was not programmed correctly. For those cases, we selected the nearest observer position in time relative to the wolf position. Average time difference between wolf and observer positions that were matched using this method was 6 s (range = 0–78 s), and maximum time difference in gaps that encompassed the flight initiation was 41 s.

Detecting Flight Initiation

Visual inspection of the GPS positions indicated that the wolf fled in 29 out of 35 interactions (**Supplementary Presentation 4**). Changepoint analysis with MBIC penalty detected a flight for 27 interactions and the UCL detected a flight for 29 interactions, all of which matched the flights detected by visual inspection. Neither method detected flights that were not identified by visual inspection. There was no significant difference between flight initiation distances based on changepoint analysis and UCL (Wilcoxon signed-rank test: V = 41, p = 0.9, **Figure 4**). In two interactions, the changepoint analysis failed to detect a flight that was identified by both visual inspection and UCL analysis. For these interactions, we reran the changepoints analysis using the AIC penalty instead of the MBIC penalty, resulting in changepoints corresponding with the flights detected by visual inspection and UCL (**Supplementary Presentation 4**, Panel 5).

To assess whether AIC might be generally preferable over MBIC for detecting flight initiation, we reran the changepoint analysis for all interactions using the AIC penalty. This resulted in 31 interactions for which the first changepoint after the start of the trial did not correspond to flight initiation identified using MBIC penalty, UCL or visual inspection. Among the 29 flight initiations detected with the MBIC penalty, 26 were also identified as changepoints when using the AIC penalty. However, AIC found on average 2.8 ± 2.3 additional changepoints per interaction, which did not represent flight initiation detected using the other methods. A full overview of the flight initiations identified for all interactions with all methods can be found in **Supplementary Presentation 4**.

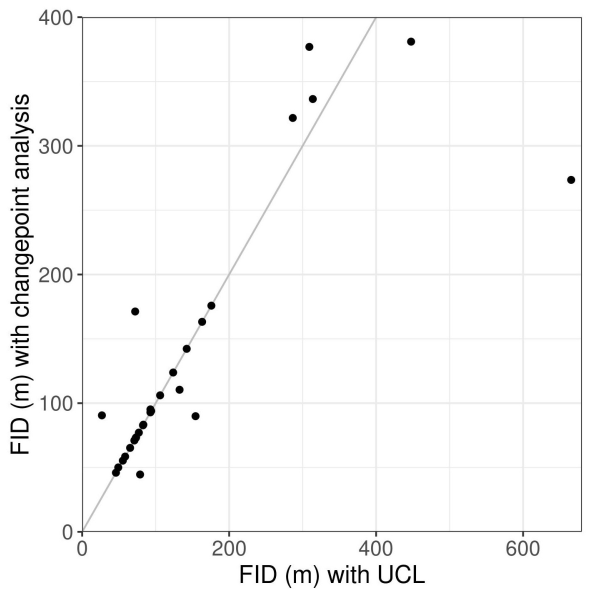

FIGURE 4 | Comparison of values for flight initiation distances (FID) of wolves when approached by humans, obtained using the two alternative methods changepoint analysis and upper control limit (UCL). Each dot represents one wolf-human interaction. Dots on the gray line indicate interactions in which the two methods gave identical FID values.

Detecting Resettling

The time and location of resettling were identified as changepoints for 26 out of the 29 interactions for which we identified a flight. In two interactions, the total flight, as observed visually, lasted for less than 20 min. As the temporal resolution of the GPS positions used to identify resettling was 10 min, a flight of 20 min was too short to be detected with the changepoint analysis. For another interaction, visual inspection as well as changepoint analysis indicated no resettling within the post-disturbance period of 3 h.

Down-Sampled Positioning Intervals

Down-sampling the original 1-min interval data to longer GPS intervals (2-, 3- and 5-min intervals) resulted in datasets in which gaps and missing data were replicated (**Table 3**). We consider this to be representative for data originally sampled at these temporal resolutions. Re-running the changepoint analyses at 2- and 3-min resolution did not reduce the number of detected flights, however, one flight was missed when running the analyses at 5-min resolution (**Table 3**). The down-sampling did affect the values of the flight variables (**Table 4** and **Figure 5**). Minimum wolf-observer distance and flight initiation distance increased with the longer sampling intervals, and became significantly larger at $\geq$ 3-min intervals compared to the original 1-min intervals (**Table 4** and **Figures 5A,B**). Passing-flight time difference and initial straightness became significantly different at 5-min intervals (**Table 4** and **Figures 5C,E**), whereas the initial speed decreased significantly with each successively longer interval, as none of the 95% CIs overlapped (**Table 4** and **Figure 5D**).

Down-sampling the original 10-min GPS data to 20-min intervals did not result in loss of detection of resettling. However, at 20-min intervals, calculated flight duration increased, total distance travelled decreased, and flight displacement decreased (**Table 5** and **Figures 6A–C**). Overall speed did not differ significantly between different temporal resolutions (**Table 5** and **Figure 6D**), but overall paths became straighter (**Table 5** and **Figure 6E**).

DISCUSSION

We developed and successfully tested a standardized protocol for experimental human approach trials on wild, GPS-collared wolves. The wolves generally avoided the observers, as described in detail by Versluijs et al. (2022). The purpose of the experimental set-up was to create a realistic but standardized representation of human off-trail hikers in wolf habitat, to assess the wolf flight response at high temporal resolution. The protocol can be expanded, e.g., to involve observers that are jogging, skiing, or accompanied by a dog. Similarly, the purpose of the direct encounter criteria and the actions outlined in the direct encounter protocol, was to mimic the likely response of a hiker when meeting a wolf outside of an experimental setting. It provides information about potential wolf responses while leaving the opportunity for the wolf to retreat rather than provoking an aggressive response. In a non-trial situation, hikers may not detect a wolf that is not obviously visible ahead of them (criterion 2). Once seeing a wolf, we believe that most hikers would stop rather than continue walking toward it. In the presumably rare event that criterion 2 is met, but the wolf does not appear to have detected the observer (criterion 3 not met), we propose walking until detected, so that the wolf detects the observer approaching rather than suddenly counting out loud. The stepwise intensification of the actions in the direct encounter protocol provides the wolf the opportunity to assess and react upon increasing levels of human-induced stress, and its response can be scored accordingly. Notably, we were not able to test our direct encounter protocol as none of the trials fulfilled the direct encounter criteria.

Each approach trial is a large investment in terms of time as well as collar battery life. In the following, we discuss factors that can affect the likelihood of successful trials and the quality of the acquired data, weighed against collar battery usage. Our recommendations are summarized in **Table 2** of the field protocol (**Supplementary Presentation 1**).

Consistent with previous studies of wolf circadian activity patterns in Scandinavia (Eriksen et al., 2011) and elsewhere (Merrill and Mech, 2003; Theuerkauf, 2009), most of the wolves approached in this study were mainly stationary in the middle of the day when the approach trials were initiated. Similar timing has been used in studies approaching brown bears, which have a similar circadian rhythm (e.g., Moen et al., 2012). In two wolf territories however, we were unable to conduct any successful trials due to wolves moving throughout the approach period. Prior to the first approach trial on an individual wolf, it is advisable to inspect the GPS data of the specific wolf. If the wolf

TABLE 4 | Generalized linear mixed models (GLMMs) comparing initial wolf flight responses calculated from GPS data at varying sampling intervals during experimental human approach trials on wild wolves (first 10 min after flight initiation).

Response	GPS interval	Estimate (95% CI)	T	df	p
Min. wolf-observer distance	1 min (intercept)	9.44 (8.40–10.47)	17.79	36	<0.001
	2 min	0.21 (−0.39–0.81)	0.68	83	0.498
	3 min	0.98 (0.37–1.58)	3.16	83	0.002
	5 min	1.95 (1.34–2.56)	6.42	83	<0.001
Flight initiation distance	1 min (intercept)	2.16 (2.11–2.22)	77.50	48	<0.001
	2 min	0.04 (−0.01–0.08)	1.62	83	0.108
	3 min	0.05 (0.00–0.09)	2.02	83	0.047
	5 min	0.09 (0.05–0.14)	4.07	83	<0.001
Passing-flight time difference	1 min (intercept)	−2.36 (−3.94–−0.78)	−2.93	40	<0.001
	2 min	−0.98 (−2.05–0.09)	−0.98	83	0.077
	3 min	−1.01 (−2.08–0.07)	−1.01	83	0.070
	5 min	−2.63 (−3.72–−1.54)	−2.63	83	<0.001
Initial speed	1 min (intercept)	46.77 (39.63–53.91)	12.84	36	<0.001
	2 min	−7.01 (−11.17–−2.86)	−3.31	82	0.001
	3 min	−14.71 (−18.87 −−10.55)	−6.94	82	<0.001
	5 min	−25.62 (−29.83–−21.83)	−11.94	83	<0.001
Initial straightness	1 min (intercept)	0.79 (0.72–0.85)	23.22	72	<0.001
	2 min	0.05 (−0.02–0.12)	1.30	81	0.197
	3 min	0.07 (−0.00–0.14)	1.92	81	0.058
	5 min	0.13 (0.06–0.21)	3.56	81	<0.001

*Datasets with different sampling intervals were obtained by down-sampling the original 1-min data. In all models, GPS interval was the single fixed effect, and trial ID was included as a random effect. Response variables were minimum wolf-observer distance, flight initiation distance, passing-flight time difference, initial speed, and initial straightness (see **Table 1** for variable descriptions). To meet the assumption of normally distributed residuals, minimum wolf-observer distance was transformed by* $\sqrt{x}$*, and flight initiation distance by* $\sqrt{log(x+1)}$.

shows consistently high activity during the day, the trial can be scheduled for the time of day when the wolf tends to be the least active. Any variation in the time of day of the trials will need to be considered when interpreting the results.

Depending on the collar's mode of communication, poor coverage can result in a lack of updated positions during the preparation period. The duration and positioning frequency of the preparation period, and the data transmission frequency, can be adjusted to suit each project or study area. Increasing any of these will increase the number of times at which the collar tries to send positions and hence the chances of receiving updated positions in time to start the trial, albeit at battery cost. After we increased the preparation period from 2 h in 2018 to 4 h in 2019–2021, we did not miss any trials due to not receiving updated positions in time. Poor coverage can also result in the collar needing multiple attempts before picking up the approach schedule. This should be considered when planning a trial, making sure to send the programming long enough in advance. In areas with poor GSM coverage, other communication options can be considered. In the case of our study, the four trials that failed due to collars not sending positions were all conducted in territories where one wolf had Iridium and one had GSM communication. Hence, neither of these two communication methods is a guarantee against this problem.

The challenge of reaching the start position in time will depend on accessibility, territory size, and wolf activity during the preparation period, i.e., whether the start position needs to be changed due to the wolves moving. In our Scandinavian study area, the high road density ranging from 0.5 to 1.1 km/km^2 allowed us to access the start position by car for most of the trials, although access was sometimes restricted by gated or snow-covered roads. Reaching the start position may be a bigger challenge in more remote study areas.

We expected a starting distance of one kilometer to be far enough that the wolves would not immediately respond to our presence, as previous studies have reported average FIDs of 106 m (Karlsson et al., 2007) and 248 m (Wam et al., 2014), and average alert distances of 293 m (Wam et al., 2014). In our trials, flight initiation distance never exceeded 400 m, hence we believe that a 1 km starting distance will be sufficient in most cases. A shorter starting distance can be considered in areas of high human impact, where it is not feasible to find a starting position at 1 km without other sources of disturbance (e.g., roads) between the wolf and the observer. However, given the range in FIDs and alert distances, the starting distance should not be less than 500 m. We used a passing distance of 50 m rather than walking straight toward the wolf to give the wolf an opportunity to either stay or flee. A 50 m passing distance has also been used during human approaches on Scandinavian brown bears (Ordiz et al., 2013). Even when planning a passing distance of 50 m, the real passing distance will vary due to GPS error, wolves moving between the last acquired wolf position and the passing time, and the difficulty of walking in a perfectly straight line in rugged terrain. However, keeping the passing distance as standardized as possible within and between studies is important

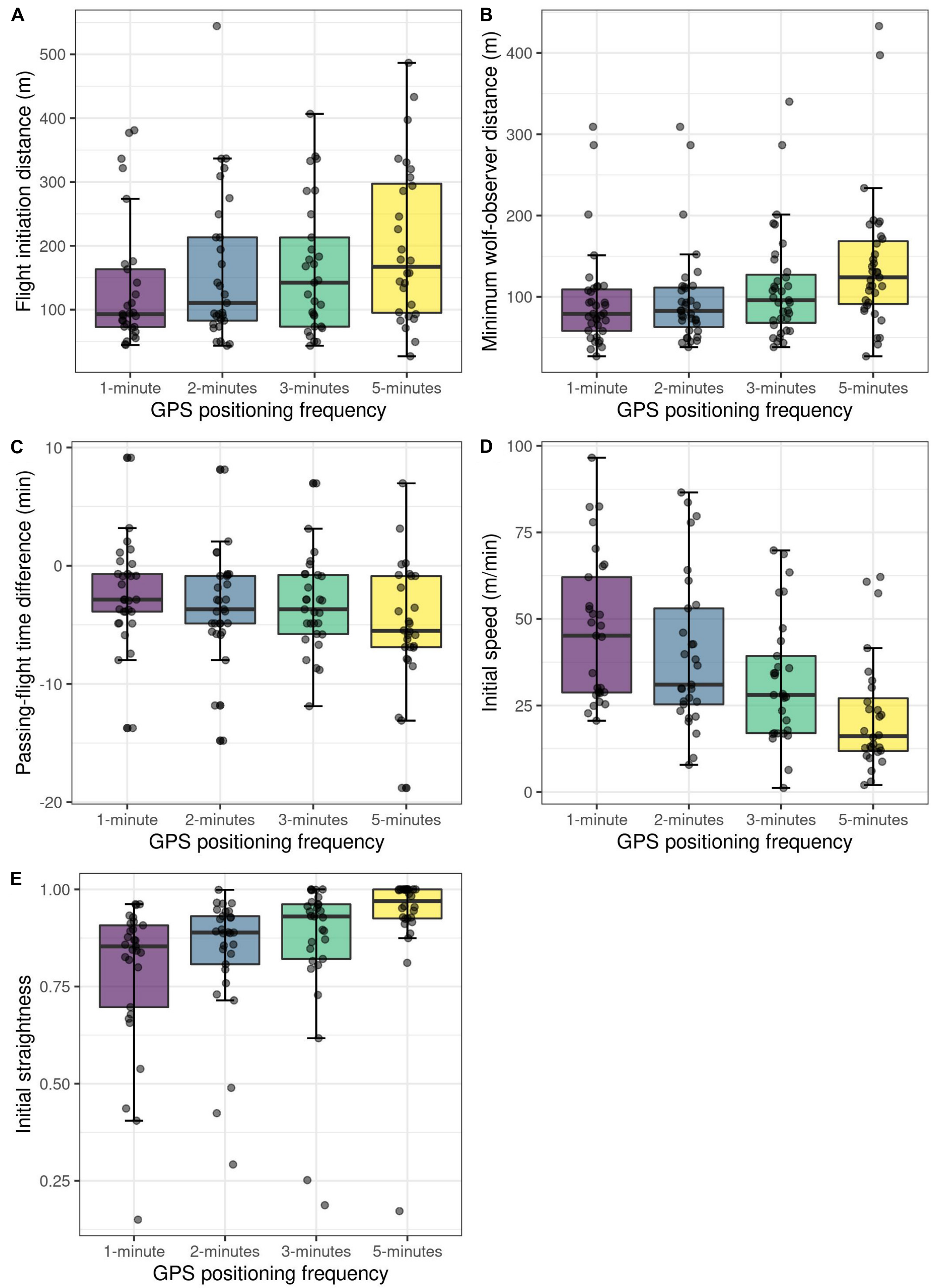

FIGURE 5 | Comparison of five different wolf response variables **(A–E)** from experimental human approach trials, calculated with varying GPS positioning frequency. Variables were calculated from data from the first 10 min after flight initiation.

for comparing the tendency for the wolves to stay or flee, as it is reasonable to assume that wolves are less likely to stay when passing distances are shorter.

The somewhat arbitrary choice of analyzing the first 10 min of the flight at 1-min resolution ("initial flight") does not reflect an observed change in flight parameters after 10 min of fleeing

TABLE 5 | Generalized linear mixed models (GLMMs) comparing overall wolf flight responses calculated from GPS data at varying sampling intervals during experimental human approach trials on wild wolves (from flight initiation to resettling).

Response	GPS interval	Estimate (95% CI)	t	df	*p*
Duration	10 min (intercept)	70.85 (60.22–81.47)	13.07	25	<0.001
	20 min	12.69 (9.91–15.48)	8.94	25	<0.001
Total distance traveled	10 min (intercept)	1 987.95 (1 405.80–2 570.09)	6.69	25	<0.001
	20 min	−370.48 (−491.93–−249.02)	−5.98	25	<0.001
Displacement	10 min (intercept)	1640.55 (1145.52–2135.58)	−6.50	25	<0.001
	20 min	−223.02 (−328.11–−117.92)	−4.16	25	<0.001
Overall speed	10 min (intercept)	28.18 (23.05–33.31)	10.77	26	<0.001
	20 min	0.99 (−0.77–2.76)	1.11	25	0.280
Overall straightness	10 min (intercept)	−2.74 (−3.26–−2.22)	−10.35	44	<0.001
	20 min	−0.79 (−1.38–−0.19)	−2.59	25	0.016

The dataset with 20-min sampling intervals was obtained by down-sampling the original 10-min data. In all models, GPS interval was the single fixed effect, and trial ID was included as a random effect. Response variables were flight duration, displacement, total distance traveled, overall speed, and overall straightness (see ***Table 1*** *for variable descriptions). To meet the assumption of normally distributed residuals, overall straightness was transformed by log(1-x).*

(**Supplementary Figure 1**). However, considering the battery cost of the high positioning frequency, we allocated 2 h of 1-min positioning to each approach. This was assumed to be enough to confirm the wolves being stationary, walk the approach route and have a minimum of ten 1-min positions for analysis. The duration of the post-disturbance positioning (10-min intervals) is set to 3 h in this protocol, but most importantly, it should be long enough to include the entire flight period as defined in the instruction manual for data analyses (**Supplementary Presentation 3**).

In the vast majority of trials with a detected flight, it seemed convincing from visual inspection that the wolf movement was in fact a response to the approaching human. Only one case was unclear, as visual inspection of the GPS positions revealed two movements, the first of which was detected as the flight initiation by the changepoint analysis (**Supplementary Presentation 4**, Panel 3D). Importantly, in any given trial and regardless of the definition criteria, one can never exclude the possibility that what we interpret as a flight response is just coincidental movement. Nevertheless, without ever being able to unequivocally identify a flight response, we believe that the frequency of incorrectly inferred flights will be low enough to justify general inference about wolf flight response using our protocol.

The collars were programmed to transmit the maximum available batch size of seven positions. During data transmission the GPS is turned off, and in areas of low network coverage, transmission might exceed 1 min resulting in data gaps on high-frequency schedules. This will result in an earlier detected flight initiation if the flight starts during a gap, since the flight initiation will be the last position before the gap. Excluding approach trials with missing data around the time of the suspected flight initiation is a way to avoid a bias in FID (Moen et al., 2012). However, the potential bias should be weighed against the reduction of the sample size if such gaps are frequent. Imputation as an alternative method to account for gaps is inappropriate in this case, as it is usually based on an assumption of constant speed. Furthermore, different imputation techniques can differ in results (Moritz et al., 2015).

To increase collar battery life, it may be desirable to conduct the trials using GPS data at lower temporal resolution. Furthermore, reducing the positioning frequency may allow enough time for data transmission between fixes, thus reducing the number of gaps. In this study, 23% of the positions on a 1-min schedule were missing versus 4% for 2-min schedule. Calculating flight initiation from GPS data at 2- and 3-min resolution did not reduce the number of detected flights compared to the 1-min positioning data. With the exception of initial speed, we did not detect significant differences in the response variables calculated at 2-min resolution. However, at 3-min intervals, the calculated minimum wolf-observer distance, flight initiation distance, as well as initial speed, differed significantly from those calculated from the original 1-min positioning data. At 5-min resolution, all initial flight variables differed significantly from those calculated from the original 1-min data. Notably, with a larger sample size, significant differences may also be found at 2-min intervals, as the same tendency was observed for all variables also at this resolution. Similarly, down-sampling from 10- to 20-min intervals did not result in loss of detection of resettling, but it did result in increased flight duration and overall straightness, and reduced flight displacement and total distance travelled. Reducing the GPS positioning frequency can be considered in future wolf approach trials to increase collar battery life. However, flight parameters cannot be directly compared across datasets collected at different temporal resolution, and consequently, comparative studies will need to down-sample all data sets to match the one with the lowest resolution. Additionally, with a reduced positioning frequency, it may not be feasible to wait for the first batch of positions from the approach period before making the final corrections to the approach route and starting the trial, increasing the risk of unsuccessful trials. All things considered, when possible, we recommend keeping the 1- and 10-min positioning frequency for the approach period and post-disturbance period, respectively. Nevertheless, our results show that the protocol can generate useful data also at lower temporal resolution.

Changepoint analyses require data point segments of a certain length to detect a change in mean and variance. Hence it is important to have enough data before and after the change (Killick et al., 2012). If the flight happens too early or too late

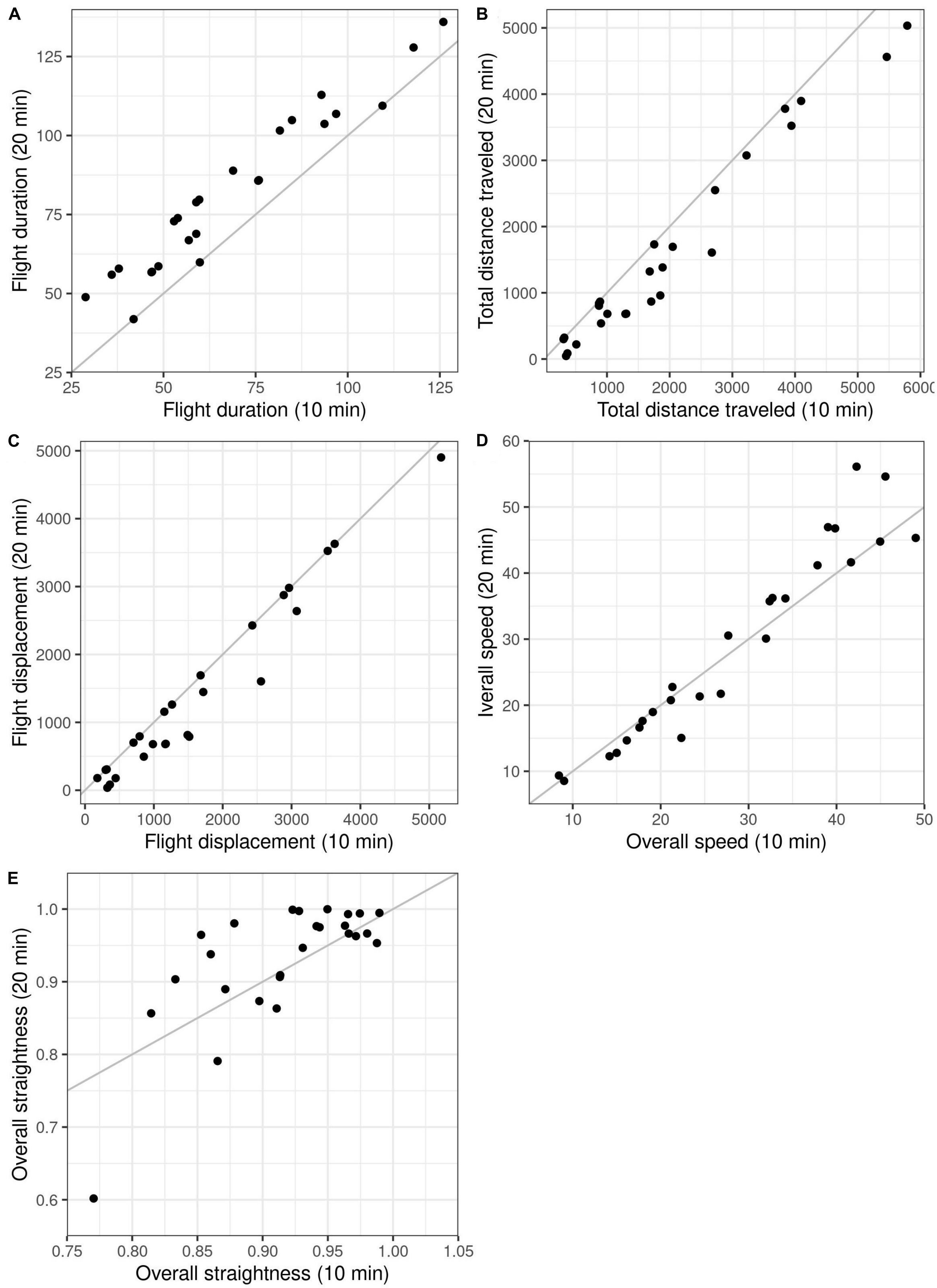

FIGURE 6 | Comparison of five different wolf response variables **(A–E)** from experimental human approach trials, calculated from GPS data at 10- and 20-min resolution. Variables were calculated for the duration of the flight, i.e., from flight initiation to resettling. Each dot represents one wolf-human interaction. Dots on the gray lines indicate interactions in which the temporal resolutions gave identical values.

within the 2-h timeslot of 1-min positions, there is a chance that none or inaccurate changepoints are found. As a rule, we intended to reach the passing position (PP) minimum 10 min before the end of the approach period to ensure fine-resolution data for the first 10 min of the flight. However, since gaps in the data exist with an average length of 3 ± 1.4 positions per gap, we rather recommend reaching the passing position (PP) at least 15 min before the end of the approach period. Using 15 min as a buffer will likely create a minimum of ten 1-min positions after flight initiation, which is unlikely to create problems with the changepoint analyses.

Changepoint analysis uses a penalty structure to test the likelihood of a change happening. Different penalty methods are available, and in certain cases it is known which penalty gives the most accurate results in changepoint location (Killick et al., 2012; Truong et al., 2020). The AIC penalty is prone to overestimation as it increases the probability of detecting changepoints (Lavielle, 2005). However, in approach trials with a short flight duration, changepoint analyses with MBIC penalty may not be able to detect changepoints. When visual inspection shows a flight that is not detected using MBIC penalty, AIC penalty may be used, as changepoint analyses are done independently for every individual interaction. However, flight initiations identified with this method should always be checked visually.

In most cases, changepoint analysis detected the resettling with 10-min positioning intervals. Exceptions were if the resettling did not take place within the post-disturbance period or when the flight was too short. Both exceptions can be detected by visual inspection of the data. When the flight is short, detecting the resettling with the 1-min positions might be considered.

The obtained UCL of 23 m/min is comparable to the UCL found in brown bears approached by humans (15.1 m/min, Ordiz et al., 2019). With this UCL, flight initiation could be identified for all interactions where a flight was confirmed by visual inspection. However, filtering the control data on intervals between 30 and 90 s was necessary to calculate the UCL. As the UCL was used as a defined threshold between stationary and non-stationary behavior, a high UCL resulted in the inability to identify flight initiation. Therefore, omitting the deviating time intervals resulted in a better estimate for the UCL, as we were interested in the baseline speed that is detected due to GPS measurement error even when wolves are not moving. As described by Montgomery (2007), a process is out-of-control when exceeding the UCL, which in this case means that the wolf exceeds the speed at which it can be considered stationary. In the brown bear approach studies, the UCL was set and checked visually before defining the FID (Moen et al., 2012; Ordiz et al., 2019). Occasionally the UCL was exceeded with only one position, and visual inspection showed no spatial movement when this occurred. Therefore, we added the condition that the UCL is exceeded for more than one position.

Overall, both changepoint analysis and UCL performed similarly well for detecting flight initiation. Hence, as previous studies have shown, both can be used successfully to detect flight initiation (Moen et al., 2012, 2018; Ordiz et al., 2019; Viljanen, 2019). However, both methods have limitations, and neither performed flawlessly in our study. It might be necessary to calculate the UCL separately for different areas as GPS measurement error can vary between collar type, location and environmental factors. Additionally, UCL calculations rely on control data. Using control data from when the wolves were not moving, based on visual inspection, can result in interpretation errors. In this study, UCL detected all flights which were also confirmed by visual inspection. However, Moen et al. (2012, 2018) reported cases in which visual inspection indicated a flight, but speed did not exceed the UCL. Changepoint analysis does not require control data, and it requires less data preparation, as it can handle various data distributions. However, limitations such as the bias toward the start and the end of the time series, and the probability that a short flight might not result in a changepoint, should be considered. Furthermore, changepoint analyses can be done in various ways, with a broad palette of possible requirements. This makes it customizable to many types of data (Killick et al., 2012, 2016; Truong et al., 2020). However, there is a risk of adjusting changepoint analyses to a desired result. (Le Corre et al., 2014; Edelhoff et al., 2016; Gurarie et al., 2016; Barry et al., 2020). We used visual inspection of the GPS data to confirm the flight initiations detected using automated methods, which we recommend doing given that future studies of this kind will have a limited sample size.

We suggest using changepoint analysis in combination with visual inspection for studying the flight response of wolves during experimental human approaches, as it increases reproducibility and comparability for this type of studies, does not need control data, and can be used in a variety of situations. This is consistent with the objective of the protocol, which is to provide a standardized method which increases reproducibility and is applicable across different study areas.

Although we found that speed alone is a simple and suitable variable for flight detection, other, more spatially explicit tools (such as First Passage Time) have been explored for identifying changes in animal movement patterns (McKenzie et al., 2009; Le Corre et al., 2014; Edelhoff et al., 2016; Gurarie et al., 2016; Barry et al., 2020), and could also be considered.

The standardized protocol developed in this study (**Supplementary Presentations 1–3**) will facilitate studies of wolf behavioral responses to direct interactions with humans, applicable at a local, national, and international level. From a scientific perspective, data compiled in a standardized way from multiple study areas can be used to quantify the variation in wolf responses to humans within and between populations, and in relation to predictors such as social or reproductive status of the wolves, landscape factors, human population density, and proxies of anthropogenic impact. Once standardized data with a sufficient range in the above-mentioned predictors have been collected, the variation in wolf responses can be used to quantify the degree to which results can be generalized for comparable areas and circumstances. This is of particular importance, as a likely limitation for the extensive application of this protocol is the cost associated with equipping wolves with programmable GPS collars. Hence, from a management perspective, results might be used to establish a baseline distribution of wolf response patterns given a number of known predictors. This information can contribute to the knowledge base for management authorities also in areas where GPS studies are not feasible, e.g., for predicting the range of likely wolf behaviors, assessing the likelihood of wolf-human encounters, and complementing existing tools for evaluating reports of wolves that are perceived as bold (Karlsson et al., 2006; LCIE, 2019; Reinhardt et al., 2020). From a dissemination perspective, showing how wolves in general, as well as in specific cases, respond to human encounters, should help demystify the behavior of wild wolves toward humans in their shared habitat. In fact, to date, neither brown bears nor wolves have shown any aggressive reaction to standardized approach trials in Scandinavia (Karlsson et al., 2007; Wam et al., 2012, 2014; Ordiz et al., 2019; Versluijs et al., 2022), which is by itself an important message for managers and the general public. Fine-scale GPS data from experimental approach trials gives ample opportunities for displaying the results graphically, e.g., in videos or animations. However, finding effective ways of disseminating such information to the general public is a challenge, as the scientific literature reports mixed results from efforts to use dissemination to reduce fear of carnivores (Johansson et al., 2016a). Some studies propose animal or habitat exposure to increase predictability of animal behavior (Johansson et al., 2016a), and in Scandinavia, bringing people along for guided brown bear approach trials resulted in reduced self-reported feelings of fear among the participants (Johansson et al., 2016b). However, Johansson et al. (2016a) points out that any intervention aimed at reducing fear toward large carnivores should be accompanied by thorough evaluations of the effects of the intervention, preferably as part of an adaptive management scheme. From a conservation perspective, human approach trials generate important information on the behavioral reactions of large carnivores inhabiting human-dominated landscapes, such as the time it takes to resume their regular circadian activity patterns after being disturbed. Altering the time budgets from more profitable activities (foraging, resting) to increased vigilance after disturbance may have fitness costs (Ordiz et al., 2013). Therefore, quantifying how human activities can affect carnivore behavior, and the potential implications for energy budgets (e.g., Bryce et al., 2022), can elucidate the role of wilderness areas for large carnivore conservation (Gilroy et al., 2015).

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 the Norwegian Food Safety Authority (FOTS ID 15370) and the Animal Welfare Ethics Committee of Uppsala, Sweden (ref. 5.8.18-13246/2019).

AUTHOR CONTRIBUTIONS

PW, BZ, PS, AE, and LG conceived the study. AE, LG, PS, PW, BF, BZ, AO, DC-S, FM, BG, and SR secured the funding. AE, EV, PS, BF, BZ, PW, AO, KN, DC-S, CW, HS, FM, and BG developed the field protocol. EV, BF, AE, FM, BG, KN, BZ, and PW conducted the field trials. EV, AO, and KN developed the analytical methods. EV conducted the analyses. AE and EV drafted the manuscript. All authors contributed to the ideas and edits to the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.793307/full#supplementary-material

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Potential Futures for Coastal Wolves and Their Ecosystem Services in Alaska, With Implications for Management of a Social-Ecological System

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Carnivores across much of the world are declining, leading to loss of biodiversity as well as the ecosystem services carnivores provide. In 2020, the Alexander Archipelago (AA) wolf was petitioned for protection under the U.S. Endangered Species Act (ESA) for the third time in 30 years. Concerns included habitat alteration from industrial timber harvest and subsequent declines in prey (deer), human-caused mortality, climate change, and genetic inbreeding. However, the underlying biogeography and ecology of these wolves continues to suggest resiliency across the subspecies' range, even though local populations may go extinct. If local wolf populations go extinct, it will result in loss of their ecosystem services (e.g., interactions of wolves with their prey, which prevents over-browsing and protects carbon sequestration in soils and trees), which will likely have major consequences for the local social-ecological system. Here, we updated a model we constructed for the last ESA listing process (2015) to examine the dynamics of wolf and deer populations on Prince of Wales Island (the primary geographic focus of all three petitions) in response to future environmental and management scenarios developed with stakeholders. Further, we considered how changes in deer abundance impact predation services (prevention of over-browsing by deer). We found that wolf populations generally persisted over 30 years, but dropped below an effective population size of 50 wolves in 10–98% of years simulated. Low wolf abundance resulted in higher deer abundance, which increased hunting opportunity, but also browsing damages (e.g., 19% of areas would be over-browsed if wolf harvest caps are removed, and >30% of areas would be over-browsed if wolves go extinct). Human harvest of wildlife was a key regulator of abundance and ecosystem services within the coastal rainforest social-ecological system; wolf abundance was most affected by wolf harvest regulations; and deer harvest restrictions increased wolf and deer abundances, but also greatly increased browsing impacts (>70% of areas heavily browsed if hunting ceased). Our findings support an integrated approach to management of this social-ecological system, such that social and ecological sciences are both used to monitor important components of the system (e.g., measuring public sentiment and likelihood of poaching, alongside wolf and deer numbers). Integration and adaptive approaches are needed to ensure that the many ecosystem services humans depend on are valued, conserved, and restored, including the cryptic predation services wolves have historically provided to the timber industry via reduced browsing pressure by deer.

Keywords: Tongass National Forest, Alaska (United States), ecosystem service (ES) values, predator-prey interactions, social-ecological systems (SES), Endangered Species Act, hunting, *Canis lupus ligoni*

INTRODUCTION

Most top carnivore species around the world are in decline (Ripple et al., 2014), with corresponding losses not only of biodiversity but also of "predation services" that regulate the abundance and behavior of prey species that have net negative effects on people and ecosystems (Braczkowski et al., 2018; O'Bryan et al., 2018; Gilbert et al., 2021a). However, in many parts of Europe and North America, large carnivore populations are making a comeback due to increased legal protection, and in some cases increasing tolerance, for predatory wildlife (Treves et al., 2013; Dressel et al., 2015; Manfredo et al., 2021b), leading to heated debate about whether carnivores should be lethally managed to reduce damages, enjoy continued protection under laws such as the U.S. Endangered Species Act (ESA), or be actively re-introduced to new areas (Manfredo et al., 2021a). These divergent desires regarding carnivore recovery are likely due in part to the fact that those who experience or perceive negative effects of predation (e.g., some ranchers and hunters) are not the same people that experience or perceive the positive services of predation (e.g., environmentalists, wildlife viewers, range and forest land managers; Gilbert et al., 2021a; Manfredo et al., 2021a).

In contrast to trends on the mainland of North America, wolves in some portions of the coastal temperate rainforests of Alaska (*Canis lupus ligoni*) have declined from historical levels due to many of the same factors that are driving global carnivore declines: reductions in prey base following habitat, alteration and human harvest (Person and Brinkman, 2013; Gilbert et al., 2015). As a result, the Alexander Archipelago (AA) wolf has been petitioned for listing under the ESA three times in the past 30 years, including a recent petition filed in 2020 that is currently under 12-month review (U.S. Fish and Wildlife Service [USFWS], 2020), with concerns focused on the population of wolves living on Prince of Wales Island. Over the past century, timber harvest and associated development has dramatically altered coastal temperate rainforests of the Pacific Northwest of North America (DellaSala et al., 2011), a highly productive region that provides many ecosystem services (Brandt et al., 2014). As a result, the coastal temperate rainforest has become a focus of controversy for both the timber industry and conservation interests, with AA wolves one of the most contentious species. As is common with many wolf populations (Musiani and Paquet, 2004), public perceptions of AA wolves range widely, from wolves being undesirable due to negative cultural stereotypes and real and perceived competition with deer hunters (Brinkman et al., 2007; Liberg et al., 2012; Person and Brinkman, 2013; Pohja-Mykrä and Kurki, 2014; Bradley et al., 2015), to high conservation concern for the persistence of AA wolves in the face of various impacts, including a reduction in prey (Person and Brinkman, 2013) and potential genetic inbreeding following heavy human harvest (Center for Biological Diversity, Alaska Rainforest Defenders, and Defenders of Wildlife 2020).

While the causes of AA wolf declines are varied, most pathways directly or indirectly lead back to human actions driven by timber harvest. The impacts to deer habitat have manifested through large scale old-growth logging and subsequent forest succession. Massive old-growth logging in the last decades of the twentieth century and subsequent forest succession to lower-productivity, older second-growth stages (Alaback, 1982) has reduced the habitat carrying capacity for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), the primary food source for AA wolves. Timber harvest also increases the density of road networks, providing greater access for wolf hunting and trapping (Person and Russell, 2008; Person and Logan, 2012; **Figure 1**). In addition, industrial logging compacts soils, which can reduce seedling recruitment and forage quality by disrupting plant-soil-microbe feedbacks. Given strong links to deer and wolf populations, high levels of timber harvest likely reduce the long-term viability of wolf populations, the stability of predator-prey dynamics, and ecosystem resiliency in Southeast Alaska (Person et al., 1996; Person and Brinkman, 2013; Roffler et al., 2018).

Prince of Wales (POW) and adjacent outlying islands support a significant percentage of the wolves in Southeast Alaska (Person et al., 1996), and the POW population has declined sharply in recent years (U.S. Fish and Wildlife Service [USFWS], 1997; Alaska Department of Fish and Game [ADFG], 2015a; Alaska Department of Fish and Game [ADFG], 2017). In 1993, a petition was filed for protection of the AA wolf under the ESA, but ultimately the U.S. Fish and Wildlife Service (USFWS) determined that listing was not warranted because declines would stop within an acceptable level (U.S. Fish and Wildlife Service [USFWS], 1997). In 2011, another ESA petition was filed, citing the same primary threats but adding climate change and inadequate harvest regulatory mechanisms as additional pressures (Center for Biological Diversity and Greenpeace, 2011; U.S. Fish and Wildlife Service [USFWS], 2014).

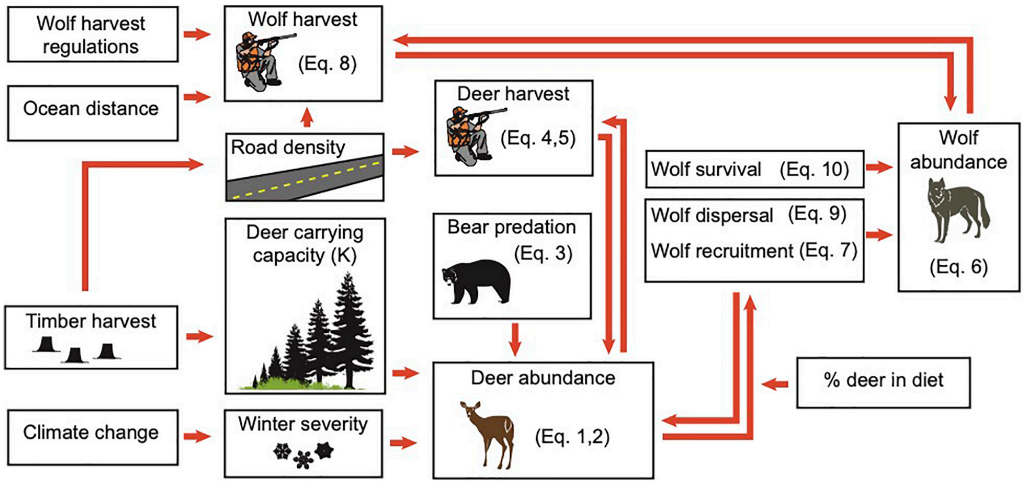

FIGURE 1 | Relationship among primary model components, based on connections among major environmental drivers of wolf abundance in the coastal temperate rainforest of Southeast Alaska. Equation (Eq.) numbers reference **Supplementary Appendix A**.

At the request of the USFWS, we created a population model in 2014–2015 for wolves on POW and the surrounding islands to inform the listing decision (U.S. Fish and Wildlife Service [USFWS], 2014; Gilbert et al., 2015). The purpose of our analysis was to develop a model best representing our current understanding of predator-prey dynamics on POW, then assess the effects of major stressors on future wolf abundance. We evaluated six possible scenarios spanning a range of likely conditions for future timber harvest, silvicultural treatments that affect forest succession, deer abundance, road building and closures, and wolf harvest regulations. We also conducted sensitivity analyses to measure the relative influence of these factors on wolf and deer abundances. While our model identified a number of scenarios in which wolves on POW could decline to low levels in the future, the USFWS declined to list AA wolves in their 12-month finding (2015), because the AA wolf was not deemed threatened through all or a portion of its range (all of Southeast Alaska and northern British Columbia), and the POW population was not deemed ecologically or genetically unique enough to qualify as a distinct population segment under the ESA (U.S. Fish and Wildlife Service [USFWS], 2015). The current petition, rather than focusing on the POW population, requests that AA wolves throughout Southeast Alaska be listed as a threatened, distinct population segment within the broader sub-species range in coastal Canada and Alaska. However, POW's wolves are again at the heart of the petition, in part because recent intensive harvests wolf harvest in recent years may have led to inbreeding depression (Zarn, 2019).

Regardless of the outcome of the current ESA listing decision, wolves on POW may go functionally or completely extinct, with potential for profound but poorly recognized impacts to the social-ecological system (the ESA does not require consideration of economic impacts, even if the wolves were listed). What would a "world without wolves" look like on POW? AA wolves clearly are valued by some residents and non-residents, and provide a number of "predation services and disservices" via their consumption of deer, the only significant ungulate herbivore in the ecosystem.

Fortunately, a wolf-free comparison is available for consideration on Haida Gwaii, the large island complex just south of POW in British Columbia. Sitka black-tailed deer are not native to Haida Gwaii, but were introduced to the northern portion of the archipelago ~100 years ago, after which they spread rapidly across much of the archipelago. They currently sustain densities of ~15–35 deer/km^2(or almost 40 deer/square mile). Despite having drastically depleted understory biomass and impacted soils (Gaston et al., 2006; Le Saout et al., 2014), deer remain at high densities and continue to suppress plant recruitment and growth, potentially by consuming lichens that blow down from old-growth forest canopies in fall and winter, when deer would otherwise be nutritionally limited by terrestrial plant biomass (Le Saout et al., 2014). Palatable plants, such as huckleberry, and commercial and culturally important tree species, such as western red cedar (*Thuja plicata*), have been almost entirely removed by browsing where deer are present. Even less palatable conifer species, such as Sitka spruce (*Picea sitchensis*) exhibit stunted growth by up to two decades by browsing pressure compared to deer-free areas, until they are finally able to reach a height where they "escape" browsing (Bachand et al., 2014).

Browsing disservices not only damage the forestry industry by delaying timber rotations for high-value cedar and other conifers, but also impact Haida and Tlingit tribal members living on POW who value cedar and huckleberry for their traditional uses (Norton, 1981; Moss, 2004; Benner et al., 2021). Over-browsing can negatively impact habitat availability, the biodiversity of plants, birds, and invertebrates (Maillard et al., 2021), and ecosystem resiliency. Preferential consumption of higher-quality plant lower (lower C to nitrogen) by deer may also reduce microbial productivity and the delivery of critical nutrients, such as nitrogen, to the soil (Maillard et al., 2021).

Forest carbon sequestration could decline if nutrient limitation stimulates microbial respiration, although abundant deer may offset carbon losses through greater soil compaction. In addition to ecosystem services, deer are a regionally prized game species for both sport and subsistence hunters (Brinkman et al., 2009; Colson et al., 2013), and more abundant deer provide more hunting opportunities. As a result, wolves exert both a predation disservice, by reducing hunting opportunities, and a predation service, by increasing the abundance of desirable conifer species and provisioning other ecosystem benefits that are difficult to quantify and often overlooked (Martin et al., 2020; Maillard et al., 2021). Critically, wolves prey on deer wherever they co-occur within the remote, rugged landscapes of the temperate rainforest, whereas human hunters have a strong preference for landscapes with easy boat and road access and high sightability (Brinkman et al., 2009). Therefore, even if deer hunting regulations were drastically loosened or the number of hunters increased greatly, it is unlikely that human hunting could provide an equivalent deer regulatory service over the entirety of the study area. For example, despite extremely generous hunting regulations on wolf-free Haida Gwaii (>15 deer per hunter per year), hunters are unable to regulate deer numbers and negative impacts of deer persist. Indeed, the Canadian government recently spent millions of dollars hiring professional hunters from New Zealand to remove deer from several small islands that are part of the Haida Gwaii archipelago to produce deer-free biodiversity refuges (Anthony, 2019).

Here, we update our 2015 model to consider loss of predation services, via increased browsing pressure, and discuss the implications for AA wolf conservation and social-ecological feedbacks on POW and elsewhere.

MATERIALS AND METHODS

Study Area

We focus on the POW region (**Figure 2**) because it has historically supported a large, and relatively isolated (Weckworth et al., 2005; Breed, 2007; Cronin et al., 2015; Zarn, 2019) portion of the AA wolf population in Southeast Alaska (Person et al., 1996) and has a high concentration of stressors that could lead to local extinction, including intensive timber harvest, road density, and easy boat access (Person, 2001). This study region was also a focal area in the status assessment conducted in 2015 by the USFWS for consideration of listing of AA wolves under the Endangered Species Act (Gilbert et al., 2015). The POW region (**Figure 2**) has a mean annual precipitation of > 300 cm which produces a diversity of temperate rainforest habitats including old-growth forest types, alpine and subalpine vegetation above ∼400 m, and muskeg heaths (Farmer and Kirchhoff, 2007; Alaback and Saunders, 2013). Industrial timber harvest has dramatically altered old-growth forests and removed disproportionate amounts of commercially valuable forest from the study area relative to the region as a whole (Albert and Schoen, 2013). Albert and Schoen (2007) estimate that 40% of the productive forest land on North POW and 9% on South POW has been logged.

The diet of POW wolves is diverse compared to their continental counterparts, and includes a greater marine component, although deer remain the most important prey item (Szepanski et al., 1999). The primary drivers of deer population dynamics in Southeast Alaska include winter severity, habitat quality, predation by wild carnivores, and harvest by humans (**Figure 1**). During winter, deep snow impacts deer by increasing the cost of movement (Parker et al., 1984), burying forage (Parker et al., 1999; White et al., 2009), reducing landscape connectivity, foraging efficiency, and by habitat carrying capacity (Kirchhoff, 1994; Parker et al., 1999; Hanley et al., 2012; Gilbert et al., 2017). Consequently, deer populations can decline sharply in or following severe winters (Farmer et al., 2006; Person et al., 2009; Brinkman et al., 2011; Gilbert et al., 2020).

Industrial timber harvest has diminished habitat quality for deer by converting structurally diverse old-growth forests to even-aged stands throughout much of Southeast Alaska, and especially in the southern portions of the Alexander Archipelago, including POW. Young and old second-growth has been associated with increased mortality risk for deer due to increased hunting and malnutrition (Farmer et al., 2006; Person et al., 2009) and old second-growth landscapes the lowest deer densities after consecutive severe winters (Brinkman et al., 2011). Landscapes dominated by second-growth habitats are likely to have lower deer populations, which in turn negatively affects wolf densities.

In addition to acting as primary prey of wolves, deer are also an important resource for both humans and bears (**Figure 1**). Much of the deer harvest in Southeast Alaska is concentrated on POW due to the ease of access on the widespread road system created by timber harvest, relatively high deer densities, and liberal harvest regulations (Brinkman et al., 2009). In addition to human harvest, deer populations experience mortality due to predation on fawns occasionally by eagles (Gilbert, 2016) and more frequently by black bears (*Ursus americanus*; Gilbert, 2015).

Modeling Approach

We based our model on a pre-existing population model for wolves on POW and surrounding small islands. This model was originally created by Person and Bowyer (1997), refined in 2001 (Person, 2001) henceforth the "2001 model"), and updated via changes to some model parameters to evaluate new scenarios in 2015 (Gilbert et al., 2015). Here, we further update the 2001 model, making our code, data, and approach fully public and reproducible for the first time. Our 2015 efforts were not published in a peer-reviewed journal, although the USFWS did send the model to outside experts for peer review. Therefore, this analysis is in many ways the same as our 2015 efforts, but with parameter improvements based on current best available science and the 2015 outside reviewers' comments. We also expand the scenarios considered, and include ecosystem service considerations.

The 2001 model used data specific to wolves in the study area when available, as well as data and relationships from studies of wolves and deer in other ecosystems when data specific to POW were not available. The 2001 model exhibited good performance for describing population dynamics when validated on other systems with more complete data, such as deer at the George

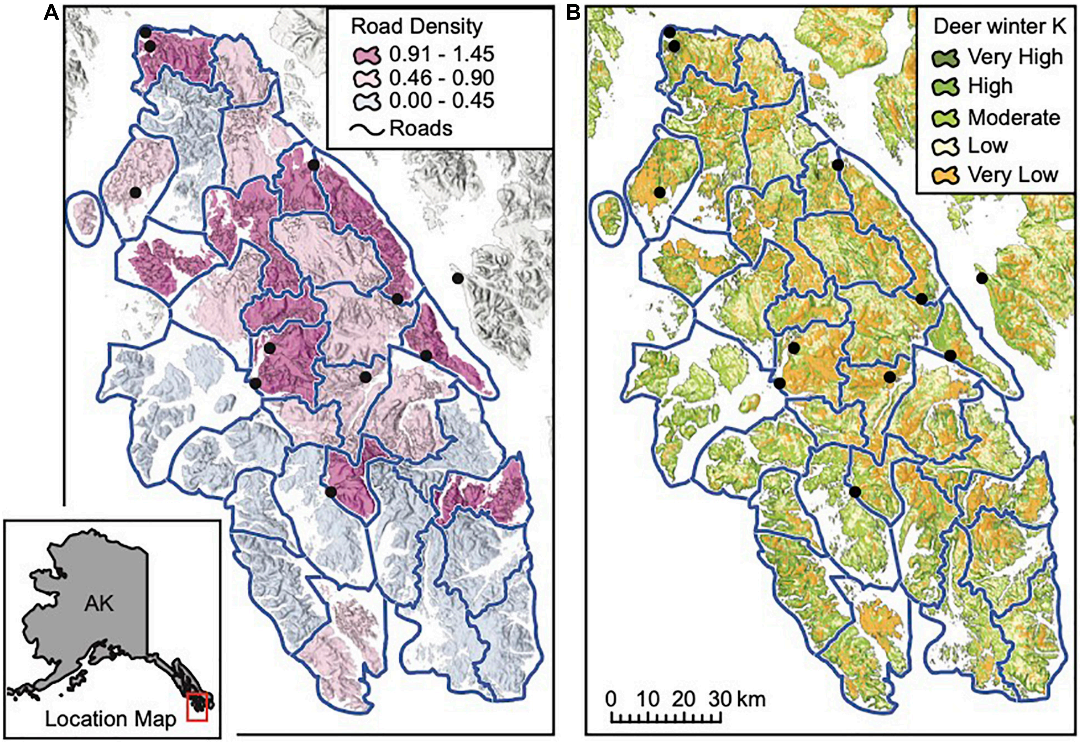

FIGURE 2 | The study area, located on Prince of Wales and outlying islands in Southeast Alaska; pack areas in the wolf population model are outlined in blue and towns are shown as black circles. Maps display **(A)** road density in km per km^2 in each pack area, and **(B)** deer winter carrying capacity (K) based on the interagency deer habitat suitability index, which ranges from very high (76–130 deer per mi^2), to high (43–75 deer per mi^2), moderate (23–42 deer per mi^2), low (7.1–22 deer per mi^2), and very low (0–7 deer per mi^2).

Reserve, wolves on Coronation Island, and wolves and moose at Isle Royale (Person et al., 2001). We updated the 2001 model using new data from Southeast Alaska to better parameterize variables (**Supplementary Table 1**).

Using our updated model, we simulated the effects of a range of plausible environmental changes on wolf abundance. The basic structure of the model includes the major factors expected to influence future wolf abundance: changes to deer carrying capacity, projections of winter severity, and harvest rates of wolves by humans. Secondary drivers are considerably more complex (**Figure 1**), resulting in relationships that are either one-way, or involve density-dependent feedback loops. We describe in detail the equations used to structure the wolf population model, as well as updates made to the model's parameters in **Supplementary Appendix A**, and list new data sources in **Supplementary Table A1**. Below, we describe the basic model structures.

We modeled wolf population dynamics as a cumulative sum of dynamics of 31 hypothetical, spatially explicit, contiguous wolf "packs" (**Figure 2**). Each pack's home-range was represented by a polygon with a mean size of 303 km^2 (SD = 87), which is in line with empirical estimates of wolf home-range sizes, ranging from 260 km^2 (SE = 48; Person, 2001) to 535 km^2 (Alaska Department of Fish and Game [ADFG], 2015b). Although we use the term "packs" to describe wolves in each polygon, wolves in a polygon do not have to be organized into a single pack, although the dynamics of all packs in a given polygon are linked. We recognize that wolf pack territories and home ranges are dynamic and our pack areas are modeled as static. We used the same pack polygon boundaries established by Person (2001) and assumed a closed population of wolves in the study area, although we allowed wolves to disperse among all pack polygons without geographic restrictions. Dispersal of wolves among packs allowed packs to be more realistically dynamic in terms of recovery from local extinction, because new wolves could colonize from other packs. Demographic rates for wolves in our model, particularly recruitment and mortality, are regulated by the ratio of deer to wolf abundance in pack areas. In addition, those demographic rates are given wide distributions such that they can accommodate hypothetical changes in numbers of packs within pack areas. For example, if the ratio of deer to wolves is high, recruitment to wolves also can be high. In this example, our model would accommodate either a single pack with a large litter of pups, or a situation in which a second breeding pair establish a territory within the pack area, although such social dynamics are not modeled explicitly. We allow a 2-year time lag for the effects of deer/wolf ratios to be fully manifested within a pack to account for asynchrony between deer and wolves. A limitation of our model is it does not model the distribution of those resources at a finer resolution than the pack area. For example, if high quality habitat for deer is concentrated along a border between pack areas, a small change in area boundaries could have a large effect on which group sequesters those deer. Consequently, our model likely underestimates the potential variation in the ratio of prey to wolves and in wolf-deer predator-prey dynamics.

Model Structure

Within each wolf pack area *i*, annual wolf numbers at time *t* are described using the formula:

$$P_{t+1(i)} = P_{t(i)} + R_{Pt(i)} - T_{t(i)} - D_{t(i)} - M_{t(i)} + I_{t(i)}$$

where $P_{t(i)}$ is the size of the wolf pack prior to parturition in pack area *i*, $R_{t(i)}$ is recruitment, $T_{t(i)}$ is wolves harvested, $D_{t(i)}$ is dispersal, $M_{t(i)}$ is natural mortality, and $I_{t(i)}$ is immigration from other packs. Recruitment, natural mortality, and dispersal probability were modeled as density dependent, based on the ratio of deer available to deer consumed for each wolf pack (**Supplementary Appendix A**, Equations A.7, A.9, and A.10). We considered natural mortality and dispersal to be compensatory with mortality from human harvest (i.e., human harvest reduces rates of natural mortality and dispersal; Person and Bowyer, 1997). Human harvest of wolves for each pack was determined based on road density and distance via ocean from the nearest human settlement (Person and Russell, 2008; **Supplementary Appendix A**, Equation A.8). Individual wolf packs affect overall wolf pack dynamics by contributing dispersing wolves to a population wide "dispersal pool" in a density-dependent manner. Wolves that enter the dispersal pool could colonize vacant pack areas. We modified the 2001 model so that if wolves in the dispersal pool did not colonize a vacant pack area in year *t*, individuals in this pool had an annual survival probability of 0.34 (*SE* = 0.17) (Person and Russell, 2008).

The deer sub-model is a component of the wolf population model that represents prey resource dynamics in the pack areas (details in **Supplementary Appendix A**). The deer population ($U_{t(i)}$) at time *t* was calculated as:

$$U_{t+1(i)} = U_{t(i)} + R_{ut(i)} - BA_{t(i)} - CP_{at(i)} - H_{t(i)}$$

Where $R_{ut(i)}$ is recruitment into the deer population in pack area *i*, $BA_{t(i)}$ is predation mortality of adult deer by black bears, $CP_{at(i)}$ is predation mortality of deer by wolves, and $H_{t(i)}$ is harvest mortality from human hunting. *C*, the per-capita wolf predation rate (15 deer/wolf/year) was based on a wolf diet estimate for POW from a stable isotope analysis (Szepanski et al., 1999) and thus represents a conservative minimum number of deer killed, given that wolves do not necessarily consume the entire deer carcass. $P_{at(i)}$ is the average of spring and fall population sizes of wolves in year *t*. Similar to the wolf model, the deer model was density-dependent. Recruitment scaled with proximity of the deer population in pack area *i* to the carrying capacity of deer in that pack area (**Supplementary Material 1**, Equation 2), and was assumed to have failed completely if a severe winter occurred, as severe winters impact fawns far more than adults (Gilbert et al., 2021a,b). Predation of fawns by black bears was also modeled as density-dependent, with the percentage of compensatory mortality increasing as the deer population approached carrying capacity, *K* (**Supplementary Material 1**, Equation 3). We predicted deer carrying capacity in each pack area from the deer habitat capability index (deer HCI; originally developed by Suring et al., 1993, and updated by an interagency deer team intermittently), which estimates the maximum number of deer that can be nutritionally supported during winter in a specified area (United States Forest Service, 2008). We treated adult deer mortality due to hunting, and predation by black bears and wolves as completely additive. Hunting mortality on deer was a function of road length, based on a published regression relationship between road length and reported harvest (Person and Bowyer, 1997; **Supplementary Material 1**, Equation 5), although importantly this equation is not sex or age specific, and specifies no maximum capacity for hunting in terms of demand or number of total hunters and their effort, other than the total population of deer available in a WAA. Person and Bowyer (1997) found no difference in performance of more complex sex- and age-structured models vs. an unstructured model, so we retained their equation. Potential biases produced by this equation are over-estimation of deer hunters' ability to harvest deer and resulting hunting services and wolf disservices, as real-world harvest is heavily male-biased.

Predation services and disservices via deer reductions were based on impacts to cedar recruitment and delays in conifer regrowth on Haida Gwaii, and predicted levels of hunting (see above for potential biases in hunting). However, because the deer HCI model generally predicts relatively low deer densities, well below the 30 deer/km^2 density at which severe browse impacts to conifers were observed on Haida Gwaii, and is a predictor of habitat value to deer rather than absolute deer densities, we instead assumed that deer browse impacts would occur if deer density exceeded 90% of carrying capacity (K).

Scenario Development

We developed six scenarios for analysis that spanned a range of possible future conditions on POW. The conditions for each scenario were based on proposed or planned land use and resource management actions, as well as on future climate possibilities for the region, downscaled from global climate models (i.e., winter severity frequency, **Supplementary Material 1**). We developed the scenarios during a technical model review workshop (Anchorage, AK, March 18–19, 2015) that included participants from key management agencies, along with technical experts in population modeling, spatial analysis, and wolf ecology.

Scenarios included likely future changes to timber harvest, road building or closures (i.e., decommissioning), effects of climate change on frequency of severe winters, and wolf harvest regulations. We considered changes to vegetation based on five potential timber harvest conditions: (1) no future timber harvest after 2014 (i.e., forest successional change only); (2) a transition to harvest of second-growth forest on Tongass National Forest lands (i.e., the young growth transition currently in planning by the U.S. Forest Service); (3) continued harvest of old-growth at the rates observed from 2000 to 2014; (4) increased harvest of old-growth forest at the rates observed from 1995 to 2000; and (5) maximum harvest of old-growth forest allowable under the

2008 Tongass Land Management Plan. We also varied the rate of future timber harvest assumed to occur on non-federal lands among these alternatives. Details and assumptions associated with these possible future vegetation conditions are included in **Supplementary Material 2**.

We considered five alternative conditions for road construction and decommission: (1) no change in total road length from 2014 levels; (2) road decommissioning at levels in current management plan (i.e., –2.2% total road length, implemented during 2015–2025; United States Forest Service, 2009); (3) road decommissioning at increased levels (i.e., –28.7% total road length, implemented during 2015–2025); (4) road decommissioning at maximum levels (i.e., –232% total road length, implemented during 2015–2025); and (5) road construction necessary to access new old-growth harvest areas if the maximum old-growth harvest scenario takes place (i.e., 30% increase in total road length). We calculated road construction necessary to access new old-growth based on a regression relationship between existing total road length and acres of timber harvest in the wolf pack areas (United States Forest Service, 2008). We used the resulting slope (i.e., regression coefficient, $\beta = 0.0385$, $SE = 0.0026$, $R^2 = 0.88$), which specifies 0.0385 km of road construction per hectare of new logging.

Wolf harvest regulations included in the scenarios ranged from complete closure of regulated harvest (0% reported harvest) to closure of harvest within a harvest season if reported harvest exceeded a fixed percentage (20 and 30%) of the previous fall population (i.e., a harvest "cap"). In addition, Person and Russell (2008) found that 13 of 31 (42%) wolves harvested by humans were not reported. As a result, we use regression relationships to predict reported harvest based on road density and distance to nearest town via ocean (see **Supplementary Material 1**, equation 8), then multiplied the result by an unreported harvest scalar of 1.72, equivalent to total harvest ($n = 31$) divided by reported harvest ($n = 18$), then applied a harvest cap to the reported portion of the predicted harvest for each pack if the cap threshold for a scenario was exceeded at the population level.

Combining these factors, along with possible future frequencies of severe winters (**Supplementary Material 1**), we created six scenarios with input from workshop participants for evaluation (**Table 1**). Across scenarios, we hypothesized that Scenario A would be most favorable for wolf abundance and resilience of the predator-prey community, Scenario B would be the most likely under current agency policy, Scenario E would be least favorable for wolf abundance, and Scenarios C and D are intermediates between A and E in terms of favorability for wolves. We also included a No New Action scenario, which represented ongoing changes in forest succession and habitat values from past logging, with no additional change or management action in the future (**Table 1**). We chose a 30-year timeframe (2015–2045) for model simulations because it encompassed enough years for the population dynamics of long-lived animals such as deer and wolves to stabilize and respond to environmental change but was short enough to minimize uncertainty associated with future management, climate, and socioeconomics. For each scenario, we conducted 1,000, 30-year simulations of the wolf-deer model.

Sensitivity Analysis

To isolate how scenarios are affected by changes to vegetation, road length, frequency of severe winters, and wolf harvest regulations, we perturbed each of these variables separately across the range of values found in the scenarios, while holding all other variables at Scenario B values. As with the primary scenarios analysis, for each parameter perturbation, we conducted 1,000, 30-year simulations of the wolf-deer model. We also tested model sensitivity to wolf diet composition, examining wolf diets comprised of 15 deer/wolf/year used in scenarios (i.e., 45% deer in the diet) vs. 9.5 deer/wolf/year (i.e., 28% deer in the diet), 20.5 deer/wolf/year (i.e., 60% deer in the diet), or 26 deer/wolf/year (i.e., 77% deer in the diet; the value used by Person, 1996). Finally, we explored the effects of changing deer harvest in the study area, by considering the most extreme alternative: no deer harvest. We included this condition because the model could not realistically quantify the effects of different levels of deer harvest in its current form (i.e., a model with a single sex and adult age class). We included a wolf harvest perturbation of no cap on harvest (i.e., harvest depends on environmental predictors only), because ADFG shifted harvest regulations to a non-capped system in recent years, resulting in high harvest rates (Alaska Department of Fish and Game [ADFG], 2021). As with scenario results, we present results of sensitivity analysis as a percent change in abundance over 30 years from 2014 levels (i.e., total change by 2045) and base interpretation on relative comparisons.

Quasi-Extinction Calculations

We investigated effects of six possible scenarios on the probability that wolf abundance would fall below a quasi-extinction (QE) threshold (i.e., abundance that is so low that the population is at significant risk of extinction). The 50–500 rule is commonly used in conservation genetics to determine the QE threshold

TABLE 1 | Description of scenarios evaluated using the wolf population model.

Scenario	Vegetation	Roads	Wolf harvest	Predicted frequency of severe winter
No New Action	Natural succession only	No change	20% harvest cap	Average
Scenario A	Natural succession only	Planned decommission	No legal harvest	Low
Scenario B	Young growth transition	Planned decommission	20% harvest cap	Average
Scenario C	Continued harvest of old growth	No change	20% harvest cap	Average
Scenario D	Maximum harvest of old growth	Road construction	30% harvest cap	High
Scenario E	Increased harvest of old growth	No change	30% harvest cap	High

(Franklin, 1980). This rule suggests that an effective population size (N_e; number of animals contributing genes to the next generation) of at least 50 is needed for short-term population viability, whereas an N_e of 500 or more is needed to ensure long-term viability (Laikre et al., 2016). Among wolves, only a fraction of the population breeds, so that N_e is lower than total abundance, N (Aspi et al., 2006; Laikre et al., 2016). We therefore assume a ratio of N_e/N of 0.42 (i.e., only 42% of wolves pass on genes to the next generation), as has been recorded for Finnish wolves, an analogously small and isolated population (Aspi et al., 2006; Laikre et al., 2016). Using this ratio, we calculated that to achieve N_e = 50, an N = 119 was needed, whereas to achieve N_e = 500, N must equal 1,190 wolves, far beyond likely historical wolf abundance on POW. We calculated the percentage of years under each scenario that wolf abundance will drop below 119 wolves to assess how frequently the POW wolf population would drop below the QE threshold. We chose this approach, rather than simply counting number of population realizations where N < QE, because the low initial starting size of the population (i.e., 89 wolves) ensures that almost all populations start below the QE threshold.

RESULTS

Scenario Development

Between 1995 and 2015, the composition of forests logged in the study area shifted from primarily young growth to primarily old second-growth, despite continued but slowed harvest of remaining old-growth forests (**Supplementary Table 3**). These changes represent a decline of approximately 13% in carrying capacity (K) for deer from 1995 to 2015. By 2045, we project that 100, 86, 89, 90, and 93% of cut forests will have transitioned to old second-growth in No New Action, Scenario A, Scenario B, Scenario C, Scenario D, and Scenario E, respectively (**Supplementary Table 3**). Under the "No New Action" scenario and Scenario A, we estimated an additional decline of 6% in deer K by 2045, with larger projected declines under Scenario B (–9%), Scenario C (–11%), Scenario D (–14%), and Scenario E (–17%).

Scenario Outcomes

From the low, empirically estimated starting abundance of 89 wolves in fall of 2014 (95% CI = 50, 159; (Alaska Department of Fish and Game [ADFG], 2015a), the projected wolf population in 2045 increased in four scenarios and decreased in two (range: –35 to 284%) and deer abundance declined across all scenarios (range: –9 to –36%; **Table 2** and **Figures 3**, **4**). Across scenarios, wolf abundance dropped below an effective population size of 50 wolves in 10–98% of years simulated. Deer browsing damage to conifers varied across scenarios and through time, with 0–16% of wolf home ranges impacted by heavy browsing by 2045, whereas deer hunting opportunity declined across scenarios from 19 to 60% (**Table 2**), although only some of this loss is attributable to wolves (see sensitivity analysis, below), because deer abundance declined in general due to dwindling habitat carrying capacity.

Scenario A resulted in the largest increase in wolf abundance (284%, 95% CI = 222, 342), which included no further timber harvest (i.e., natural succession only from 2015 onward), planned decommission of roads, a low future frequency of severe winters, and no reported wolf harvest (although unreported wolf harvest continued). Scenario A also produced the lowest percentage of pack areas unoccupied (0% unoccupied by 2045), and lowest percentage of years in which the wolf population dropped below N_e = 50 (10% of years, 95% CI = 0, 32%; **Figure 3**). Despite less frequent severe winters, Scenario A also resulted in the largest decrease in deer population (–36%, 95% CI = –51, –22) and deer hunting opportunity (–60%, 95% CI = –78, –43) among the scenarios, because wolf numbers were high while deer carrying capacity continued to diminish due to post-logging forest succession, wolf predation, and deer hunting pressure. In contrast, Scenario E resulted in the largest declines in wolf abundance (–35%, 95% CI = –89, –21), which included increased harvest of old growth forest, no change in road density, a 30% cap on wolf harvest, and a high future frequency of severe winters. Old forest logging paired with road access, severe winters, and a high cap on wolf hunting and trapping resulted in the lowest rates of pack occupancy and the highest percentage of years dropping below N_e = 50 (98%, 95% CI = 81, 100). Deer hunting opportunity was the highest across all scenarios (–19%, 95% CI = –37, –14).

Scenario B, which we considered the most likely scenario, resulted in a median increase of 63% in wolf abundance (95% CI = –42, 122), median rate of pack area vacancy of 25% (95% CI = 0, 74), 52% of years with populations below the QE threshold N_e = 50 (95% CI = 0, 100; **Figure 3**), and a median decline of 11%

TABLE 2 | Modeled changes from 2015 to 2045 in spring abundance of wolves, deer, and predation services (percentage of wolf pack areas exposed to heavy browsing in 2045) and disservices (change in hunting opportunities for deer) under future scenarios.

Scenario	Median wolf abundance	Median% change wolf	Median% change deer	Median% change hunt	Percent wolf ranges browsed
No New Action	134 (48, 184)	65 (–41, 127)	–10 (–25, –1)	–30 (–45, –14)	6 (0, 22)
Scenario A	311 (261, 358)	284 (222, 342)	–36 (–51, –22)	–6 (–8, –4)	0 (0, 0)
Scenario B	132 (47, 180)	63 (–42, 122)	–11 (–25, –2)	–30 (–5, –17)	10 (0, 23)
Scenario C	132 (46, 180)	64 (–43, 125)	–12 (–26, –4)	–31 (–46, –20)	10 (0, 23)
Scenario D	58 (8, 109)	–28 (–90, 35)	–9 (–22, –5)	–27 (–41, –21)	16 (3, 29)
Scenario E	53 (9, 98)	–35 (–89, 21)	–17 (–30, –14)	–19 (–37, –14)	13 (3, 23)

Populations with fewer than 119 wolves drop below the quasi-extinction (QE) threshold. Estimates are shown with 95% confidence intervals.

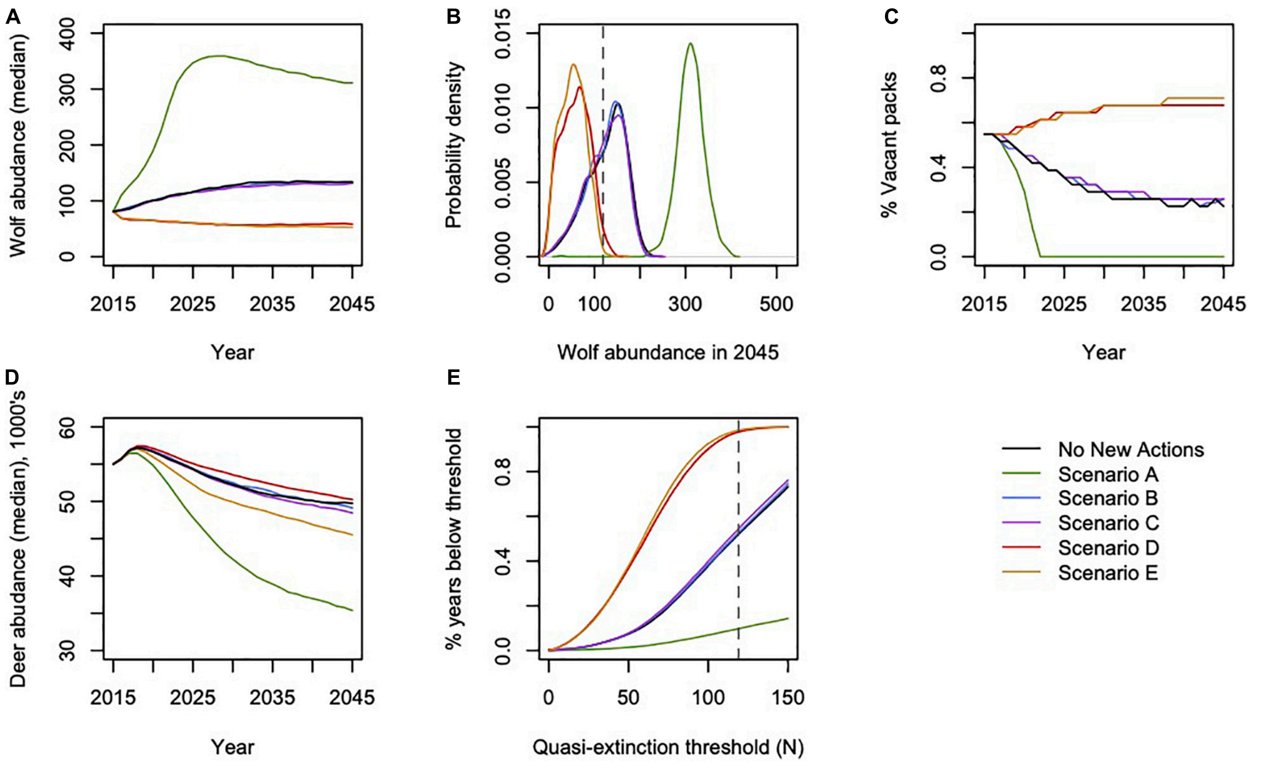

FIGURE 3 | Projected effects of modeled scenarios on **(A)** annual wolf abundance; **(B)** distribution of final wolf abundance in 2045; **(C)** percent of pack areas vacant annually; **(D)** annual deer abundance; and **(E)** percentage of years during which wolf abundance dropped below a range of quasi-extinction thresholds. Dashed horizontal lines in **(B,E)** indicate the quasi-extinction threshold of N = 119 wolves, the abundance needed to ensure an effective population size (N_e) of 50 wolves.

in deer abundance (95% CI = −25, −2). The resulting predation services included browsing impacts in a median of 10% of pack ranges by 2045 (95% CI = 0, 23), a reduction from starting median values of 19% (95% CI = 9, 30).

Sensitivity Analysis

Deer abundance declined in 22 of the 26 sensitivity models because of ongoing changes in post-logging forest succession; however, wolf abundance increased across all of the sensitivity models, except for wolf harvest regulations with a 30% legal cap or no cap, in part because the starting value for the models was low based on the ADFG empirical estimate of wolf abundance (**Supplementary Figure 1**). Changes in wolf abundance due to changes in harvest regulations ranged from an increase of 200% (95% CI = 148, 266) if there was no legal or illegal wolf harvest, to a decrease of −30% (95% CI = 30, −90) if there was no cap on harvest. The second most influential variable on wolf abundance was the percentage of deer in wolf diets, which increased by 31–52%. These sensitivity results allow us to evaluate the influence of a variable across a reasonable range of values, but does not allow us to compare the absolute influence among variables on a per-unit basis.

Eliminating deer harvest entirely had a positive effect on both wolf and deer abundance compared to 2015 levels, increasing wolf abundance by 75% (95% CI = −38, 145) and deer abundance by 12%, (95% CI = 5, 16; **Supplementary Table 4** and **Supplementary Figure 1**). Although an extreme and unrealistic perturbation, these results suggest wolves and humans are competing for deer in some watersheds and in some years. Imposing moderate deer harvest regulations could increase wolf and deer abundance, although hunting restrictions would reduce ecosystem services of hunting (i.e., protein provisioning to humans, cultural and recreational values).

The ecosystem disservices of severe deer browsing (deer at 90% of carrying capacity or more within a wolf pack's home range) were most strongly influenced by wolf harvest regulations and deer hunting (**Supplementary Table 5** and **Supplementary Figure 2**). Starting conditions for the simulation, which represent the lowest estimate of wolf abundance on record, showed that 19% of pack ranges (95% CI = 10, 32) were impacted by severe browsing. When wolf harvest was comprised only of illegal harvest or absent entirely, no pack ranges were heavily browsed by 2045. However, if a 30% cap or no cap on wolf harvest were implemented, 16% (95% CI = 3, 29) of pack ranges were heavily browsed. Without any deer hunting, 71% of pack ranges were heavily browsed (95% CI = 39, 90) compared to only 10% (95% CI = 0, 22) if hunting continued.

Ecosystem services provided by deer hunting were most strongly influenced by wolf harvest regulations and the percentage of deer in wolf diets, whereas disservices created by severe deer browsing were most strongly influenced by

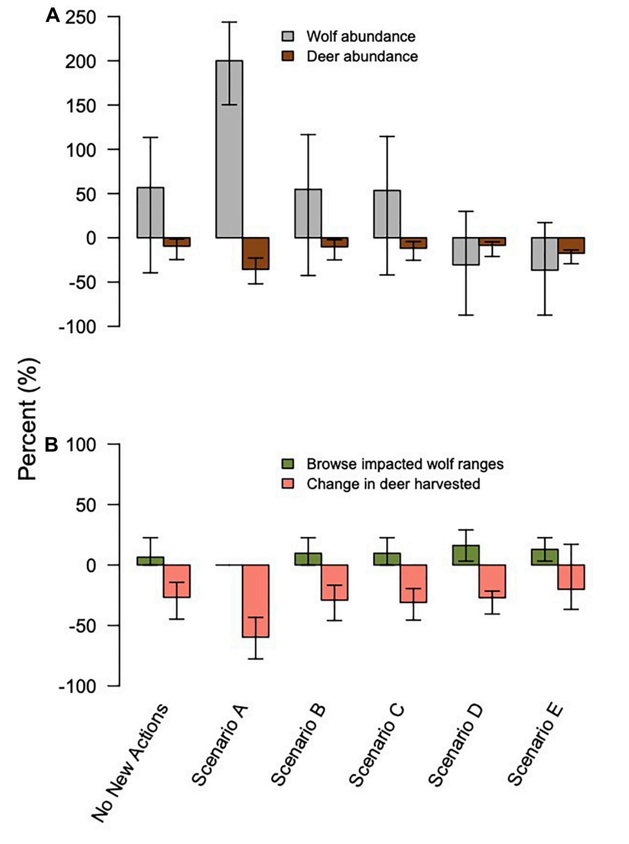

FIGURE 4 | Change from 2014–2045 in **(A)** percent change of wolf (gray) and deer (brown) abundance, and **(B)** ecosystem services and disservices across model scenarios, with 95% confidence interval bars. Services and disservices include the % change in deer harvested by hunters and the percentage of pack areas exposed to intensive deer browsing on conifers by 2045.

trapping regulations and deer hunting (**Supplementary Table 5** and **Supplementary Figure 2**). When no wolf harvest occurred, deer hunting services declined drastically (–80%, 95% CI = –87, –66), but so did browsing disservices (0% pack ranges browsed, 95% CI = 0, 0). Conversely, if wolves went extinct, deer hunting services declined moderately (–18% CI = –29, –14) but browsing disservices rose (29% pack ranges browsed, 95% CI = 10, 32). Wolf diets showed similar, expected inverse relationships between services and disservices: when wolves ate 9.5 deer/year, deer browsing disservices were higher (16% pack ranges browsed, 95% CI = 3, 26), and hunting services declined less (–24%, 95% CI = –38, –16). When wolves ate the maximum of 26 deer/year, browsing disservices were almost eliminated (3% of pack ranges browsed, 95% CI = 0, 16), but hunting services declined considerably (–44%, 95% CI = –63, 23).

DISCUSSION

Our model indicated that wolf populations would likely increase from our initial spring 2015 population for the "No New Action" scenario and scenarios A–C. This prediction was broadly supported by recent population estimates using a DNA-based capture-mark-recapture technique (n = 316 wolves estimated for fall 2019; **Supplementary Figure 3**), although there is considerable uncertainty around these empirical estimates (Alaska Department of Fish and Game [ADFG], 2017). However, recent wolf harvests have been record-breaking (n = 165 harvested winter 2019–2020; Alaska Department of Fish and Game [ADFG], 2017), and all scenarios except scenario A resulted in predicted negative population growth in a portion of the simulations, indicating some degree of risk of future decline regardless of scenario. Wolf populations fell below the quasi-extinction threshold of $N_e = 50$ in 10% of years under scenario A, in > 50% of the years simulated for scenarios No New Action, B and C, and by at least 97% of years in scenarios D and E. While our results suggest the potential for modest population growth under current and proposed conditions, wolf recovery likely will be well below historical levels and the potential for inbreeding and resulting population declines will likely remain. Moreover, about 70% of pack areas would be vacant in scenarios D and E and resulting potential for ecosystem disservices via deer browse impacts to conifer regeneration are probable in some areas. Our pack areas were static entities that in reality can be fluid and, as we stated previously, we likely underestimated the variation in predator-prey dynamics that would actually occur. Therefore, our simulation results are likely optimistic.

Mortality of wolves from legal and illegal harvest had the greatest influence on wolf abundance, (Santiago-Ávila et al., 2020; Louchouarn et al., 2021; Musto et al., 2021; Nowak et al., 2021) and also strongly affected deer services (hunting) and disservices (browsing impacts to conifers). Many studies of wolf population dynamics identify human exploitation as a primary driver of population change (Fuller et al., 2003) and the sensitivity of wolf population in our model to harvest is consistent with those studies. The effect of roads on wolves within our study area is also strongly linked to rates of mortality from harvest (Person et al., 1996; Person, 2001; Person and Russell, 2008; Person and Logan, 2012); however, our simulations show little effect of new road construction on future wolf population because the simulated increase in road density was small relative to the existing road extent. Similarly, the effects of forest succession on wolf and deer numbers did not vary much between scenarios because all scenarios included the successional transition to stem exclusion in large areas of second-growth that were harvested prior to 2015. Likewise, the influence of new clearcuts transitioning to old second-growth during the 30-year period covered by our simulations minimizes that same influence from new clearcuts because productive forest sites take 25–40 years to fully transition to low-nutrition old second growth (Alaback, 1982). Overall, the changes in forest conditions and roads that we included are a small fraction of the changes that have already occurred to those components between the initiation of industrial-scale logging in the mid-1950s and 2015.

Number of deer killed/year/wolf also exerted a strong influence on wolf and deer numbers, reducing both as predation rates increased. Person (2001) modeled the predator-prey system on Prince of Wales Island using a simpler version of our model with a higher per capita rate of predation. He estimated mean and variance of predation rate on deer from incidence of occurrence data in scats collected during all seasons (Person et al., 1996; Kohira and Rexstad, 1997), whereas we employed a lower rate of per capita predation based on stable isotope analyses (Szepanski et al., 1999). Both methods likely underestimate actual predation rates because diet composition cannot be easily converted to number of prey killed, particularly when predators such as wolves do not always consume entire carcasses. Severe winters can substantially reduce deer numbers (Brinkman et al., 2011) and increase the ratio of wolves to deer, which may result in wolves suppressing deer population to low levels for multiple years (Ballard et al., 2001; Bowyer et al., 2005). Our simulations failed to express that dynamic, likely because we used low rates of predation and initial population size of wolves. In contrast, model simulations by Person (2001) for conditions similar to our scenarios B and C, showed that severe winter events reduced deer populations below 50% of K in 39% of individual model runs, and that 16% of those remained below that threshold for $\geq$10 years (Person, 2001). The direct consequence for wolves of suppressed deer populations is not immediate food stress because other prey, particularly salmon and beaver, can be temporarily substituted (Darimont et al., 2008). Rather, the belief that wolves are competing for fewer deer will motivate hunters and trappers to kill more wolves legally and illegally (Person and Brinkman, 2013).

Our focus was constrained mostly to wolves because ESA decisions are species centric. Nonetheless, to sustain a resilient population of wolves, deer and other prey are required in sufficient numbers to also sustain other predators like black bears and satisfy deer hunters. Predation by black bears had little influence on changes in predator-prey dynamics between wolves and deer, but hunter harvest of deer reduced both deer and wolf numbers. If wolves had been listed as threatened, scenario “A” likely best represents the resulting conditions in which wolf harvest is curtailed and a significant percentage of roads closed to vehicular use. However, deer harvest likely would plunge 43–78% to levels well below current harvests (Harper and McCarthy, 2015) and result in a strong backlash against protecting wolves from subsistence and recreational deer hunters. This could introduce substantial instability to the wolf-deer-people system. Most scenarios indicate deer harvests will decline by 20–30% from 2015 levels, raising the risk that retaliatory legal and illegal wolf harvest will increase and suppress wolf populations below our predicted levels.

The results of our analyses suggest that radical changes in system dynamics on POW are possible and highlight the challenge of conserving predator-prey systems, as well as the potential for considerable changes to predation services and disservices. We argue that large mammalian predators are inevitably dependent on complex social-ecological communities and must be considered within the context of a system rather than an individual species population. Ultimately, loss of deer habitat will drive the systemic decline of deer over the coming decades. The proximate threat to wolf viability will likely still be risk of unsustainable legal and illegal wolf harvest rather than prey scarcity. The motivation for hunters and trappers to kill wolves will be driven by their perception of deer abundance, which is influenced not only by relative abundance of deer and wolves but also by landscape changes (Brinkman et al., 2009). As areas dominated by clearcuts transition to thick, even-aged second growth, deer hunters can no longer see or hunt deer in those landscapes and their perception of competition with wolves and other hunters for deer on dwindling lands suitable for hunting will continue to grow.

As deer carrying capacity and resulting deer abundance declines, deer will also likely continue to cause browsing disservices by reducing or eliminating red and yellow cedar and slowing regeneration rates of conifers in young clearcuts, especially if populations are regulated by nutrition rather than predation. As we demonstrate here, wolves are likely providing a predation service to the forestry industry by reducing browsing damage, but this service is currently overlooked, despite its potential high value. In our analysis of potential wolf extinction effects, browsing impacts to conifer occurred in 30% of pack ranges by 2045; this percentage could be much higher if hunting does not keep pace with the deer population, and areas with poor access or sightability for hunters are especially likely to show such effects in the absence of wolves. For example, if deer hunting is absent from the system, over 70% of pack ranges would be impacted by severe conifer browsing, even with continued wolf predation. Long timber rotations are one of the limiting factors affecting the competitiveness of the Southeast Alaskan second-growth timber economy, and the potential for 20 years of delayed regeneration or complete loss of commercially valuable species, as has been documented on wolf-free neighboring Haida Gwaii (where hunters are unable to regulate the deer population in the absence of wolves) could make this marginal industry unfeasible. Given the simplistic and optimistic way that hunting is included in our models, we are likely over-estimating deer harvest and hunters’ abilities to reduce deer browsing. For example, we included no sex structure in our models, implying both sexes are hunted equally, whereas in reality availability of male deer limits hunting opportunity; likewise, we included no habitat limitations to hunting, while in reality older successional forest stages are very difficult habitats in which to spot and successfully hunt deer.

Importantly, deer can provide other important ecosystem services (such as wildlife viewing and existence values) and disservices (such as suppression of berry bushes, reduction of bird and invertebrate biodiversity, and reduction of carbon sequestration) that we do not attempt to estimate (Côté et al., 2004; Martin et al., 2020). While explicitly representing these feedbacks is beyond the scope of our analysis, the effects of predator-prey interactions on ecosystem function are important to consider, especially as worldwide interest in carbon sequestration and biodiversity conservation accelerates (Schmitz et al., 2018). For example, moderate browsing may increase soil organic carbon (SOC) storage by increasing soil bulk density through trampling and compaction and increase plant biodiversity by influencing plant competitiveness and assembly rules (Nishizawa et al., 2016). However, heavy browsing may reduce forest net primary productivity (NPP) and carbon (C) sequestration by removing aboveground biomass, delaying seedling recruitment, and degrading soil structure (Harada et al., 2020). Preferential browsing can also reduce litter quality by removing palatable species (e.g., cedar and huckleberries) and inducing plants to invest in antiherbivore defense compounds and structural tissues (Côté et al., 2004), although high egestion rates could bypass the litter decomposition pathway (Bardgett and Wardle, 2003). Reducing the quality of litter entering the soil ecosystem alters microbial functional traits (Shao et al., 2019), increases SOC mineralization, and decelerates soil nutrient and litter cycling (Harrison and Bardgett, 2004). If microbial communities attack existing stocks to access nutrients (a phenomenon known as priming; Kuzyakov et al., 2000), conversion of SOC to CO_2 could flip heavily browed forests from a regional C sink to source.

Wolf predation could help mitigate, or reverse, SOC loss by inducing trophic cascades that release plants from intense browsing pressures (Kirchhoff and Person, 2008; Callaghan et al., 2013; Flagel et al., 2016; Schmitz et al., 2018). As recovering plants allocate C belowground, they gain access to limiting nutrients (including from decomposing carcasses that are not exported from the forest by hunters; Daufresne, 2021). This belowground carbon allocation can in turn stimulate rhizosphere microbial communities (Bardgett et al., 1998). Resulting increases in forage quality could not only help stabilize deer and wolf populations, but may also promote efficient microbial biomass production (Wardle et al., 2002; Liang et al., 2017). The retention of microbial byproducts on soil minerals is now thought to be a primary driver of SOC formation and persistence (Lehmann et al., 2020) and could be especially important in Coastal Alaska where more than 60% of total forest C is held in mineral pools (Yatskov et al., 2019). Wolf-regulated increases in microbial efficiency could thus reinforce the forest C sink. The effects of growing pressure on the soil ecosystem is complex and could exert a positive feedback on SOC (Conant and Paustian, 2002), by increasing microbial metabolic efficiency and the formation of new SOC, or a negative feedback, by increasing priming and SOC loss as CO_2. Browsing and predator-prey interactions modulate the balance between litter inputs and heterotrophic respiration, which is difficult to predict but has large consequences for the forest C balance (Pugh et al., 2019). Explicitly incorporating predator-prey dynamics could improve the predictive capacity of ecosystem models and may reveal additional ecosystem services provided by wolves and deer (Schmitz et al., 2018).

In closing, we argue for a new, integrated approach to forest and wildlife management in Southeast Alaska and beyond, in which the "multi-use" mandate of the US Forest Service grows to encompass the wide variety of valuable ecosystem services provided by forests. From providing incredible beauty for tourists and residents, to sequestering carbon, sheltering biodiversity, and providing livelihoods, food, and cultural values to indigenous and rural residents, this multitude of services should be considered and valued in management planning. Clearly, herbivory can strongly affect above- and below-ground carbon stores, and predators can regulate the numbers and behavior of their prey; there should be a corresponding, concerted effort by USFS to quantify and incorporate these dynamics into their research program and management decisions. We also recommend several specific management actions. First, we recommend that state and federal agencies more rigorously monitor wolf and deer and require accurate and timely reporting of wolf and deer harvests, as well as implement parallel rigorous social science to understand people's attitudes and behaviors in relation to deer and wolves. We also suggest that a cautious approach to management of wolf hunting and trapping within the Prince of Wales Island archipelago is necessary, given the potentially large downsides of wolf extinction for forest regeneration and carbon dynamics, and that explicit inclusion of social science into management planning would be enormously helpful for managing this social-ecological system. For example, if deer harvest is insufficient to meet people's expectations and subsistence needs, simply tightening wolf harvest will probably not be sufficient to prevent retaliatory killings of wolves if people perceive wolves, rather than habitat, as limiting their deer harvest opportunity. In addition, we urge the U.S. Forest Service to implement existing plans to close roads while preserving access to popular deer hunting areas, and to adopt application of methods to maintain and reestablish understory vegetation in both young and old second-growth stands, such as canopy gaps and small clearcuts (Wolf Technical Committee, 2017). New harvest of second-growth forest should be configured to maximize a broad range of ecosystem services across the landscape, not only board-feet of merchantable timber. Restoration treatments should be well distributed within hunter accessible watersheds as well as those closed to vehicular use, ensuring that hunters can harvest deer and that conifers can re-generate in deer-suppressed areas. Finally, a collaborative approach that includes consideration of all stakeholders' values, notably traditional values, offers the best strategy to ensure compliance with harvest regulations, meet needs of all stakeholders, and help maintain the long-term stability of this social-ecological system.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/sophielgilbert/alexander-archipelago-wolf.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because we used only existing data from past studies of animals.

AUTHOR CONTRIBUTIONS

SG, TH, ML, MK, DA, and DP contributed to the analysis. All co-authors contributed to the ideas and framing, writing, and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.809371/full#supplementary-material

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On the Multiple Identities of Stakeholders in Wolf Management in Minnesota, United States

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Social identity theory offers a means to understand attitudes about wolves, with consequences for management support. Using data from a mail survey about wolves, we explored relationships among seven identities (i.e., wolf advocate, hunter, environmentalist, nature enthusiast, farmer, trapper, conservationist) using multidimensional scaling (MDS) and principal components analysis (PCA). We examined how identities correlated with political ideology, trust in a wildlife management agency, wildlife value orientations (WVOs) and attitudes about wolves, and we evaluated whether WVOs mediated the relationship between identities and attitudes. PCA suggested two factors in identifying relationships among stakeholders, while MDS and correlations found diversity among stakeholders beyond these factors. Hunter identity was most strongly associated with a domination WVO and conservative political ideology. Farmer identity was most strongly associated with agency distrust and negative wolf attitudes. Wolf advocate was most strongly associated with a mutualism WVO (i.e., beliefs that humans are meant to coexist in harmonious relationships with wildlife), agency trust, and positive wolf attitudes. Conservationist identity was positively correlated with all other identities. WVOs partially mediated the relationship between identities and attitudes.

Keywords: social identity theory, wolf management, human dimensions, conservation social science, wildlife value orientations, ideology

INTRODUCTION

There are numerous and competing constellations of human actors in nearly every wildlife conservation issue, and sometimes this diversity results in conflict over management decisions (Marshall et al., 2007). The issue of wolf (*Canis lupus*) management is particularly ripe for conflict given high interest among many stakeholders with heterogeneous experiences with wolves, wildlife values, and ideologies, among other individual and group differences (Lute and Gore, 2014; Carlson et al., 2020). Understanding the patterns of policy preference among parties affected by decisions related to wolf management is an important part of responsive wildlife governance (Decker et al., 2015). Identity, defined both as the meanings individuals ascribe to the self (Stryker and Burke, 2000) and the roles and categories they occupy in society (Tajfel, 1982), has emerged as a means to understand heterogeneity in wolf stakeholders' values, beliefs, attitudes and behaviors (Lute et al., 2014; Carlson et al., 2020; van Eeden et al., 2020a,b). Although recent studies have documented the relationship between constituents' identities and their higher order cognitions related to wolves and wolf management (Schroeder et al., 2021), there is much to learn about identity processes in governance. Individuals, for instance, can identify with many categories or labels, each with varying degrees of prominence, salience, and commitment in a given context (Burke and Stets, 2009). Identities may be similar or dissimilar to one another, and there may be similar or dissimilar relationships between different identities and values, beliefs, and attitudes toward wolves and wolf management issues. Different groups of wolf stakeholders may make competing claims to the same identities, complicating normative narratives about stakeholders' positions. Developing an understanding of the inter-relationships among the embodied self-meanings of constituents can aid in mapping the broad array of perspectives on a given topic, and clarify the relative sources of those perspectives. In this study, we used multidimensional scaling (MDS) to explore the relationships among seven putative identities held by stakeholders in wolf management in Minnesota, United States: (a) wolf advocate, (b) hunter, (c) environmentalist, (d) nature enthusiast, (e) farmer, (f) trapper, and (g) conservationist. We then tested the relationships between these identities and individuals' wildlife value orientations, political ideology, trust in the state wildlife management agency (SWMA), and general attitudes toward wolves, to contextualize observed differences. Our analysis contributes to the literature by describing similarities and differences in the identities of wolf stakeholders and situating theses identities within the broader nomological network of cognitions pertinent to evaluations of wolves and wolf management. Past studies have shown relationships between social categories like hunter and farmer as determined by *a priori* sampling using survey methods and individuals' attitudes toward wolves, but studies have not examined the relationships between the strength of ones' identification with social identities and other important elements of the hierarchy of cognitions contributing to individuals' evaluations of wolves and wolf policy. This study occurred in the context of the state's effort to update its species management plan. Although the topic is limited to single species in a single state, the broader issue of stakeholder identity is one that transcends many natural resource governance contexts.

Theoretical Framework

Social Identity Theory

Social identity theory provides a foundation to understand differences in stakeholders' attitudes toward wildlife and wildlife management. Social identity theory began as a theory of intergroup relationships (Tajfel and Turner, 1979), but has expanded to examine the role of self and identity related to in-groups and out-groups (Turner et al., 1987). Self-categorization theory (Turner et al., 1987) clarified how people make binary categorizations between the groups they identify with (i.e., in-groups) and groups they do not identify with (i.e., out-groups). Group prototypes are idealized members of a group. The group prototypes are both descriptive and prescriptive in that they model role expectations, and suggest ways that group members should think, feel, and act (Hornsey, 2008).

Social identities guide peoples' values, ideologies, attitudes, and beliefs (Tajfel and Turner, 1986; Turner et al., 1994; Onorato and Turner, 2004; Mayer and O'Connor Shelley, 2018). Social identity and self-categorization offer theoretically plausible explanations for observed differences in attitudes among individuals who identify with different groups (Unsworth and Fielding, 2014). Research has demonstrated a relationship between stakeholder groups, and their attitudes about wolf management (Lute and Gore, 2014; von Essen and Hansen, 2015; Landon et al., 2018). With some exceptions (e.g., Bruskotter et al., 2019; van Eeden et al., 2019) many previous studies related to wolves have compared the attitudes of stakeholder categories targeted in sample designs (e.g., livestock producers, licensed deer hunters), rather than examine the strength of individuals reported identification with a given role, similarities and differences among different identities, and how those identities influence attitudes toward wildlife and wildlife management (Tucker and Pletscher, 1989; Ericsson and Heberlein, 2003; Landon et al., 2018). Studies examining attitudes and consensus about management of carnivores have also documented high levels of disagreement within stakeholder groups (Metcalf et al., 2017), suggesting that further research is needed to understand both individual and group level identities. Looking at self-reported strengths of various identities among individuals, rather than *a priori* stakeholder group membership, may enhance understanding of the diversity of perspectives on wolf management and their relative sources.

Research in the European context has also found evidence for the role of identity in shaping individuals' positions on wolves and wolf management, sometimes with conflicting results. Bongi et al. (2022) found that among residents in northwest Italy, conservationists and hunters held much more positive views of wolves than did farmers, and this relationship held irrespective of exposure. Skogen and colleagues (Skogen and Krange, 2003; Skogen et al., 2008), described how negative perceptions toward wolves may be shaped by social processes in rural Norway and France. Similarly, Heberlein and Ericsson (2005) demonstrated place effects on Swedes' attitudes toward wolves. Interestingly, and in contradiction to findings in the United States (Williams et al., 2002), Heberlein and Ericsson (2005) found that urban residents that lacked a tie to the countryside held the least positive attitudes toward wolves compared to rural or urban residents that engaged in nature-based recreation. While not identity per se, one's place of residence correlates with values and ideologies reflective of heterogeneous identities (Creswell, 1996). The positions of Swedish stakeholders have not remained static overtime. Hunters were supporters of wolves in Scandinavia during the early part of reintroduction, but support has declined the longer hunters have coexisted with wolves (Ericsson and Heberlein, 2003; Dressel et al., 2014). Numerous studies on wolves in Europe highlight the complex social dynamics of living with wolves. Nilsson et al. (2020) highlight the dynamic nature of coalitions of wolf advocates and opponents in Sweden.

These authors examined an alternate conceptualization of coalitions of humans drawing on both social identity theory and the advocacy coalition framework, to show that belief-based coalitions may offer greater explanatory power regarding stakeholder perspectives on wolves than identities per se. These results suggest some overlap in the beliefs of groups of humans defined by role identities, but that identities and beliefs are mutually constitutive elements of one's self-concept. von Essen and Hansen (2015) further demonstrate how stakeholder dynamics, especially as it relates to classifications of individuals into groups, potentially serve to reify existing conflict and exacerbate identity-based evaluations of management problems and solutions.

Wildlife Value Orientation

Wildlife value orientations (WVO) are basic beliefs that characterize individuals' and groups' convictions about humans' relationship with wildlife. A long-term research program (Fulton et al., 1996; Manfredo et al., 2009, 2020) has operationalized WVOs along two dimensions referred to as domination and mutualism (Teel and Manfredo, 2009; Manfredo et al., 2017). Domination reflects beliefs that humans have mastery over wildlife, human well-being has priority over that of wildlife, and that wildlife exists to benefit humans. Mutualism represents beliefs that humans are meant to coexist in harmonious relationships with wildlife, and that wildlife have rights similar to humans. The strength of individuals' agreement with measures of mutualism and domination have been found to correlate with wildlife-related attitudes and behaviors (Teel and Manfredo, 2009). Previous research findings also indicate cultural level patterns of variance in WVOs, stemming from predictions of modernization theory (Manfredo et al., 2020; Jacobs et al., 2022).

Several recent studies have incorporated both social identity theory and WVOs to examine how personal values and group identity affect attitudes about wildlife management (Heeren et al., 2017; Landon et al., 2018; Bruskotter et al., 2019). Bruskotter et al. (2019) found identification with groups (i.e., farmer, environmentalist, hunter, gun rights advocate, animal rights advocate) correlated with WVOs. Heeren et al. (2017) found identity and WVO influenced attitudes among wildlife professionals. Landon et al. (2018) found stakeholder group (i.e., public versus agricultural producer) and WVOs predicted attitudes about recolonization of predators in Illinois, United States. Individuals with utilitarian beliefs about wildlife (traditionalist orientation) and agricultural producers were found to exhibit the most negative attitudes, while individuals who believed that wildlife have intrinsic rights (mutualist orientation) and members of the general public had more positive attitudes (Landon et al., 2018). This research suggests that group identity and WVOs correlate, but additional work could clarify the relationships between identity, WVOs, and attitudes about wildlife and wolves specifically. This paper will extend correlation analyses with mediation analysis to examine whether WVOs mediate relationships between identity and attitudes toward wolves. Mediation analysis provides a means to understand the process that underlies observed relationships between independent (i.e., predictor) and dependent (i.e., criterion) variables via the inclusion of a third mediator variable (Baron and Kenny, 1986; MacKinnon, 2011).

Political Ideology

The terms liberal and conservative arguably are motivated social cognitions that characterize political ideology across cultures (Jost et al., 2003). Jost (2006) and Jost et al. (2003) identified core dimensions differentiating liberals and conservatives: (a) attitudes toward inequality, and (b) attitudes toward social change versus tradition. The concept of political ideology is often captured with liberal-conservative or left-right scales in quantitative analysis (Mayer and O'Connor Shelley, 2018). This study examines political ideological identification along the scale ranging from liberal to conservative (Petrocik, 2009). Our use of the terms "liberal" and "conservative" is consistent with the operationalization of political ideology in the United States, and our results are specific to that national context. Researchers examining these issues in other cultural contexts may consider how members of those cultures interpret political ideology. We measured identification with these labels—or as middle of the road—rather than specifically examining attitudes about positions or values associated with liberals or conservatives (Mason, 2018), or affiliation with a political party. Our analysis explores correlations between identities and political ideology to understand differences among seven identities that may be associated with attitudes about wolves. Recent research (Schroeder et al., 2021) has documented relationships between political ideology and stakeholder groups, and between political ideology and WVOs. Yet, gaps remain in understanding how political ideology relates to stakeholders' identification with roles pertinent to wolves and wolf management.

Agency Trust

Institutional trust reflects the willingness to rely on those with formal responsibility for decision-making and management of public resources and risks (Siegrist et al., 2000), and often represents the trust relationship between stakeholders and an institution (Winter and Cvetkovich, 2010; Zajac et al., 2012; Smith et al., 2013). In an attempt to understand the origins of trust, researchers have tested numerous antecedents of trust (Needham and Vaske, 2008; Schroeder and Fulton, 2017; Riley et al., 2018). One hypothesis regarding the source of trust is salient values similarity (Siegrist et al., 2000). Several studies about constituents' trust in natural resource management institutions has operationalized institutional trust as shared values between constituents and an agency (Cvetkovich and Winter, 2003; Winter and Cvetkovich, 2010). Shared goals, values, and opinions (i.e., perceived similarity) are hypothesized foundations of institutional trust (Siegrist et al., 2000; Cvetkovich and Winter, 2003; Needham and Vaske, 2008). Beyond shared values, research has demonstrated the influence of process, outcomes, and technical competence on institutional trust (Poortinga and Pidgeon, 2003; Van Ryzin, 2011), and these concepts are examined in the trust literature related to natural resource management (Schroeder and Fulton, 2017; Riley et al., 2018).

Numerous researchers have explored the role of trust in the management of large carnivores, including wolves. Söjlander-Linquist et al. (2015) conceptualize the legitimacy of aspects of governance as a function of myriad individual and collective responses embedded in dynamic bio-physical, socio-cultural, and institutional contexts. These authors suggest that trust is "crucial for large carnivore management" (p. 180), and that a lack of trust can further exacerbate individual appraisals of risk and fear, and shape attitudes toward management (Johansson et al., 2012, 2016). Skogen and Krange (2020) argue that a mistrust of environmental institutions underpinned Norwegian hunters' acceptance of illegal wolf killings, among other variables. Documenting the positive effects of trust, Ghasemi et al. (2021) demonstrated that trust in a wildlife management agency could reduce perceived risks from large carnivores including wolves, and increase support for their recovery in a landscape where viable populations of large carnivores do not exist currently. Similarly, Arbieu et al. (2019) found that individuals' trust in information sources about wolves had a positive effect on their attitudes toward wolves. These results suggest that trust can influence the cognitive evaluations of wolves among individuals that have not had direct experience with wolves.

Trust, however, is a function of both direct experience with individuals and groups whom bear responsibility for shared resources, and broad patterns of values consistent with social identity processes and other cultural dimensions. Krange et al. (2021) provide evidence for this assertion in their investigation of Norwegian stakeholders' beliefs about the anthropogenic cause of climate change. They found that trust influenced climate change beliefs directly, but that beliefs about nature in general and indicators of right wing populism including ant-elitism and beliefs about immigrants, partially mediated the effect. Other scholars have documented decline in social trust among Americans following value shift, with implications for collaborative governance of natural resources (Rahn and Transue, 2002).

Trust in government varies by political ideology, values, and stakeholder group, and, for this reason, examining trust may help clarify differences among identities associated with wolves. Political ideology consistently predicts trust of government in the United States, with conservatives more trusting of the private sector and liberals more trusting of government (Cacciatore et al., 2018). Research has also found stakeholder group, WVO, and political ideology to predict trust in a SWMA (Schroeder et al., 2021). Manfredo et al. (2017) examined relationships between WVOs and trust in SWMAs, finding that residents with domination values were less trusting of SWMAs. Similarly, Gigliotti et al. (2020) found utilitarian landowners less trusting of a SWMA. Our study examined similarities and differences in trust related to self-reported strengths of identities associated with wildlife management.

Scholars and wildlife managers have examined the role of several individual and group identities in wolf management. In this study, we limited our analysis to a subset of identities associated with individuals and groups engaged in discourse about wolves and wolf management including; wolf advocate, hunter, environmentalist, nature enthusiast, farmer, trapper, and conservationist.

Study Hypotheses

We offer the following hypotheses regarding the relationships between wolf stakeholders' identities, WVOs, and trust in the SWMA. We did not establish *a priori* hypotheses regarding the relationships between identity and political ideology.

H1. Identities will correlate with WVOs.

H2. Identities will correlate with attitudes about wolves. Farmer and hunter identities are expected to correlate with negative attitudes.

H3. Domination WVO will correlate with negative attitudes about wolves.

H4. Mutualism WVO will correlate with positive attitudes about wolves.

H5. Domination WVO will negatively correlate with trust in the SWMA.

H6. Mutualism WVO will positively correlate with trust in the SWMA.

MATERIALS AND METHODS

Study Context

Minnesota began revision to the state wolf plan in 2019 prior to recent federal wolf policy decisions. Regardless of the status of wolves under the U.S. Endangered Species Act (16 United States Code Sections 1531–1544), it is necessary to possess data regarding constituents' values, beliefs, attitudes and behaviors toward wolves. It is under this context that the Minnesota Department of Natural Resources (DNR) and the University of Minnesota (Twin Cities) collaborated to conduct a survey of Minnesota wolf stakeholders described in the section to follow. Since collection of the data presented in this study, wolves have since been removed from and placed back under protection afforded by the ESA. In November 2020—more than 45 years after they were first listed under the ESA—gray wolves were delisted (United States Fish and Wildlife Service [USFWS], 2020). Beginning in 2021, state and tribal wildlife managers resumed responsibility for management and protection of gray wolves, with monitoring by the U.S. Fish and Wildlife Service for 5 years to ensure the continued success of the species (United States Fish and Wildlife Service [USFWS], 2020). State and tribal authority was short lived, when a federal court ruling placed wolves back on the ESA in February 2022 (Defenders of Wildlife et al. v. U.S. Fish and Wildlife Service et al., 2022).

Sampling

The populations of interest in this study included (a) Minnesota residents, (b) Minnesota resident deer hunters, and (c) livestock producers (individuals who farm cattle and sheep) in the state's wolf range. In each case, samples were drawn of individuals

18 years and older. We purchased the sample of state residents from Marketing Systems Group who derived the sample from postal addresses. The sampling frame used to draw the sample of deer hunters was the Minnesota DNR's electronic licensing system. We obtained the sample of livestock producers from the state Board of Animal Health.[1] We distributed questionnaires to 5,250 residents, 2,000 deer hunters, and 2,500 livestock producers.

Data Collection, Response Rate, and Nonresponse Check

Data were collected by researchers at the University of Minnesota (Twin Cities) for the Minnesota DNR using mail-back questionnaires following a process outlined by Dillman et al. (2014) to enhance response rates. Personalized cover letters, surveys, and business-reply envelopes were mailed to potential study participants between September and December 2019. In order to examine nonresponse bias, we examined mailing wave differences in stakeholder identities and respondent age. This assessment of nonresponse bias reflects extrapolation methods, which are based on the assumption that subjects who respond less readily resemble non-respondents (Armstrong and Overton, 1977). We did not observe meaningful differences in identities or age by survey response wave [Effect size (Eta^2) of ANOVA by wave < 0.00].

Of the 9,750 total questionnaires mailed, 1,059 were undeliverable and an additional 170 were unusable (i.e., deceased, non-resident, etc.). Of the remaining 8,521 questionnaires, a total of 3,500 questionnaires were returned for a response rate of 41.1%. The effective response rates for the three research strata were: 46.6% for hunters, 32.8% for the general public, and 53.4% for livestock producers. In order to provide accurate population estimates for the resident sample, we compared our respondents to demographic information available through the U.S. Census Bureau (2010) and known rates of hunting participation derived from SWMA license records. The resident sample was drawn using a stratified random sample within SWMA management regions defining the study strata. Data were weighted to reflect the proportion of the population in the different regions within cells representing two categories of hunter status, two categories of gender, and five categories of age (18–39, 40–49, 50–59, 60–69, and 70+).

Measurement

Questions included in the analysis presented in this paper were a subset of those included in the study questionnaire. The analysis presented in this paper focused on respondents' self-reported identity, political ideology, WVOs, agency trust, and attitudes about wolves. Respondents rated how much they identified with seven labels including: (a) wolf advocate, (b) hunter, (c) environmentalist, (d) nature enthusiast, (e) farmer, (f) trapper, and (g) conservationist. Identity was rated on a 5-point scale ranging from 1 (not at all like me) to 5 (very much like me). Political ideology was rated on a 7-point scale ranging from very liberal to very conservative. We measured WVOs using 22 items and scales derived from Manfredo et al. (2009, 2017; **Appendix A**), and trust using 17 items and scales derived from Riley et al. (2018) and Schroeder et al. (2020; **Appendix B**). WVOs and agency trust were both measured using 7-point Likert scales ranging from strongly disagree to strongly agree. Attitudes were measured using four 7-point semantic differential scales anchored by the words dangerous-harmless, bad-good, harmful-beneficial, and negative-positive, which were used in an equal-weighed scale.

[1] https://www.bah.state.mn.us

Analysis

We conducted several analyses to examine respondent identity, and to look at how identity correlated with trust, WVOs, political ideology and attitudes toward wolves. First, we employed multidimensional scaling to visualize relationships among the seven identities. Next, we conducted an exploratory factor analysis (EFA) using principal components analysis with varimax rotation, and extraction based on eigenvalues greater than 1.0. Then, we conducted bivariate correlations between identities, political ideology, mutualism and domination WVOs, agency trust, and wolf attitudes. We interpret correlations using Cohen's (1988) definitions of small (0.10), medium (0.30), and large (0.50) effect sizes. Finally, we conducted mediation analysis using multiple regression analysis. Data were analyzed using the Statistical Program for the Social Sciences (SPSS 27) and Stata (StataCorp, 2019).

Multidimensional Scaling

MDS creates a map displaying the relative positions of a number of objects, given a table of the distances between them referred to as a proximity matrix (Davison and Sireci, 2000). The map may consist of one, two, three, or even more dimensions. MDS techniques prove useful in circumstances where the actual coordinates of objects are not known, but some type of distance matrix is available. This is especially the case in psychology where people may not be able to draw an overall picture of a group of objects, but they can express how different individual pairs of objects are (NCSS, 2021). Stress values provide measures of goodness of fit in MDS, with the following fit levels: 0.000 (perfect), 0.025 (excellent), 0.050 (good), 0.100 (fair), and 0.200 (poor; Kruskal, 1964). A scree plot of stress values is often used to determine the number of dimensions to include (Kruskal and Wish, 1978). If the addition of a dimension provides little improvement in the stress value, it is unlikely the additional dimension is needed (Davison and Sireci, 2000). The MDS map is the chief outcome of MDS analysis, and interpretation of results in the map is largely subjective although external data can be used to help interpret the solution (Davison and Sireci, 2000).

Mediation Analysis

We conducted mediation analysis based on the three-step process described by Baron and Kenny (1986): (1) regress the mediators on the predictor (i.e., independent) variable, (2) regress the criterion (i.e., dependent) variable on the independent variable, and (3) regress the dependent variable on both the predictor and the mediator. Therefore, in the mediation analysis examining wolf attitudes, the three steps were to: (1) regress WVOs on the identities, (2) regress attitudes about wolves on identities, and (3) regress attitudes about wolves on both identities and WVOs. Separate coefficients were estimated for each equation. Mediation is found when the following three conditions occur: (1) the predictor affects the mediator variable, (2) predictor affects the criterion variable, and (3) the mediator affects the criterion variable in the third equation. If these conditions all hold in the predicted direction, then the effect of the predictor on the criterion variable must be less in the third equation than in the second. Full mediation holds if the predictor variable has no effect on the criterion variable, and partial mediation occurs if the predictor variable has a reduced effect on the criterion variable. We provide results from the Sobel test for mediator variables in the final regression analyses. The Sobel test provides a method to test the statistical significance of the reduction in the effect of the independent variable on the dependent variable after including the mediator in the model (Baron and Kenny, 1986). We estimated regression models in Stata version 16 (StataCorp, 2019), and used to the rwolf package to derive Romano-Wolf stepped-down *p*-values for multiple comparisons in order to control for familywise error (Clarke, 2016).

RESULTS

First, we employed MDS to explore relationships among identities. We used a scree test to determine the number of dimensions. The stress level dropped from 0.102 for one dimension to 0.003 for two dimensions, which provided a parsimonious description of the data. MDS suggested similarities among environmentalists, conservationists, and nature enthusiasts, and diversity among the other identities (i.e., hunters, farmers, trappers and wolf advocates; **Figure 1**). EFA suggested a two-dimensional solution with identities suggestive of benefits from wild wolves (i.e., environmentalist, nature enthusiast, conservationist, and wolf advocate) on the first factor and identities suggestive of costs from wild wolves (i.e., hunters, farmers, and trappers) on the other (**Table 1**).

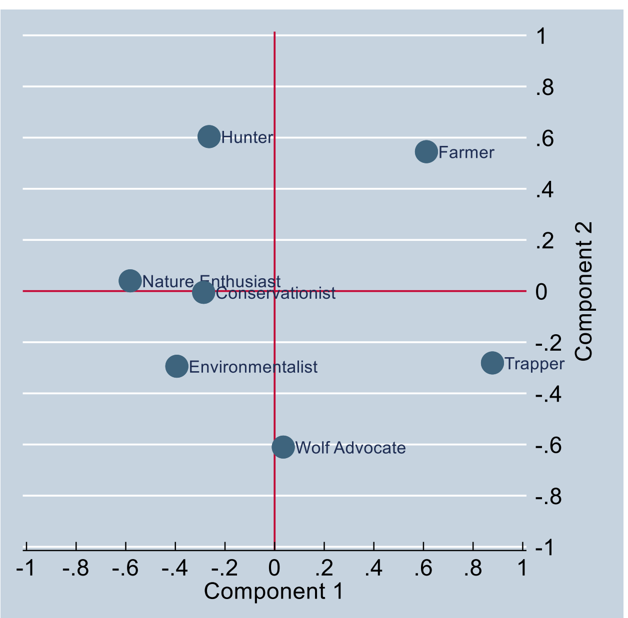

FIGURE 1 | Multidimensional scaling of putative identities of wolf stakeholders in Minnesota, United States.

Correlation analyses helped clarify the similarities and differences among identities. Bivariate correlations among the identities reinforce similarities among environmentalists, conservationists, and nature enthusiasts found in both the MDS and EFA (**Table 2**). Consistent with the EFA, identity as a wolf advocate was positively correlated with the environmentalist, conservationist, and nature enthusiast identities with medium to large effect sizes. Reflective of the MDS, environmentalist, conservationist, and nature enthusiast identities were correlated with large effect sizes. Also consistent with the MDS and EFA, we found hunter, farmer, and trapper identities were positively correlated with each other, with medium to large effect sizes. A conservationist identity was positively correlated with all six other identities; the effect size was large for environmentalists and nature enthusiasts, medium for wolf advocates, and small for hunters, farmers, and trappers.

Next, we looked at correlations between identities, with political ideology, trust in the SWMA, wildlife value orientations, and attitudes about wolves (**Table 3**). Environmentalists and wolf advocates reported the most liberal political ideologies with medium effect sizes, and hunters were the most conservative politically with a medium to large effect size. Conservationist identity was closest to neutral in political ideology, being slightly conservative with a small effect size. Wolf advocate identity was most strongly positively correlated with measures of trust in the SWMA, while farmer identity was most strongly negatively correlated with trust measures, with medium effect sizes. A wolf advocate identity was most positively correlated with mutualism and most negatively correlated with the domination wildlife value orientation, both with medium to large effect sizes. Hunter identity was most positively correlated with domination with a large effect size, and most negatively correlated with mutualism with a medium effect size. Wolf advocate was most strongly correlated with positive attitudes toward wolves with a large effect size, and farmer most strongly correlated with negative attitudes with a medium to

TABLE 1 | Principal component analysis of putative identity of wolf stakeholders in Minnesota, United States: Rotated component matrix (varimax rotation with Kaiser normalization).

	Component 1 "Pro-wolf"	Component 2 "Anti-wolf"
Wolf advocate	0.653	–0.384
Hunter	0.082	0.782
Environmentalist	0.875	–0.059
Nature enthusiast	0.845	0.002
Farmer	–0.101	0.741
Trapper	–0.008	0.808
Conservationist	0.823	0.231

large effect size. Conservationist identity was closest to neutral attitudes, but on the positive side with a small to medium effect size.

Results from mediation analysis found most identities and domination WVO influential on attitudes about wolves (**Tables 4**, **5**). Results suggested that domination partially mediated the relationships between five of seven identities and attitudes. Mutualism did not mediate the relationships between identity and attitudes (**Table 6**).

DISCUSSION

We found support for all of our hypotheses. These results reflect expected relationships between identities with WVOs and attitudes about wolves. They also support expected relationships between WVOs and attitudes about wolves and trust in the SWMA.

Understanding Identities That May Be Associated With Wolf Management

Our work helps distinguish among various identities to enhance understanding of diverse perspectives on wolves. Among identities that associated benefits with wild wolves, we found strong similarities among the identities of environmentalists, nature enthusiasts, and conservationists. The wolf advocate identity was also aligned with these three identities but differed from them by having more positive correlations with mutualism, trust in the SWMA, and attitudes about wolves. Results suggest that wolf advocates tend to be more liberal, more mutualists, and more trusting of the SWMA. This finding supports previous research documenting

TABLE 2 | Bivariate correlations among identities for wolf stakeholders in Minnesota, United States.

	Wolf advocate	Hunter	Environmentalist	Nature enthusiast	Farmer	Trapper	Conservationist
Wolf advocate	1						
Hunter	–0.220**	1					
Environmentalist	0.500**	–0.001	1				
Nature enthusiast	0.420**	0.103**	0.652**	1			
Farmer	–0.272**	0.355**	–0.107**	–0.119**	1		
Trapper	–0.197**	0.492**	–0.069**	–0.043*	0.441**	1	
Conservationist	0.355**	0.162**	0.629**	0.588**	0.091**	0.133**	1

***p < 0.001, *p < 0.05.*

TABLE 3 | Bivariate correlations of identities with political ideology and trust in the state wildlife management agency for wolf stakeholders in Minnesota, United States.

	Political ideology	Process	Outcomes	Trust	Social values similarity	Technical competence	Mutualism	Domination	Attitudes
Wolf advocate	–0.297	0.343	0.354	0.333	0.366	0.305	0.482	–0.412	0.623
Hunter	0.371	–0.251	–0.266	–0.241	–0.159	–0.177	–0.288	0.547	–0.382
Environmentalist	–0.300	0.205	0.218	0.210	0.254	0.229	0.376	–0.247	0.347
Nature enthusiast	0.136	0.168	0.175	0.178	0.242	0.199	0.292	–0.134	0.292
Farmer	0.280	–0.344	–0.325	–0.325	–0.298	–0.243	–0.159	0.337	–0.457
Trapper	0.251	–0.279	–0.285	–0.270	–0.232	–0.216	–0.194	0.351	–0.352
Conservationist	–0.088	0.093	0.093	0.093	0.172	0.146	0.277	–0.064	0.169

All correlations p < 0.001.

TABLE 4 | Bivariate correlations among political orientation, wildlife value orientations, and trust in the state wildlife management agency for wolf stakeholders in Minnesota, United States.

	Political ideology	Process	Outcomes	Trust	Social values similarity	Technical competence	Mutualism	Domination	Attitudes
Political ideology	1								
Process	–0.219	1							
Outcomes	–0.248	0.902	1						
Trust	–0.224	0.935	0.941	1					
Social values similarity	–0.211	0.796	0.803	0.812	1				
Technical competence	–0.199	0.710	0.749	0.742	0.682	1			
Mutualism	–0.350	0.213	0.216	0.200	0.248	0.208	1		
Domination	0.481	–0.210	–0.224	–0.199	–0.174	–0.159	–0.479	1	
Attitudes	–0.392	0.427	0.433	0.419	0.415	0.363	0.384	–0.493	1

All correlations p < 0.001.

TABLE 5 | Summary of regression mediation analyses examining of how identities and wildlife value orientations predict attitudes about wolves for wolf stakeholders in Minnesota, United States.

	B	SE B	β	T	Model *p*	Romano-Wolf *p*[4]
Regression 1: predictor and mediators[1]						
WA→DOM	–0.167	0.014	–0.212	–11.89	<0.001	0.001
HUNT→DOM	0.266	0.010	0.443	25.48	<0.001	0.001
ENV→DOM	–0.098	0.017	–0.125	–5.71	<0.001	0.001
NE→DOM	0.005	0.017	0.001	0.03	0.974	0.978
FARM→DOM	0.044	0.010	0.075	4.46	<0.001	0.002
TRAP→DOM	0.043	0.014	0.053	3.00	0.003	0.012
CONS→DOM	0.015	0.016	0.019	0.94	0.347	0.502
WA→MUT	0.308	0.019	0.307	16.17	<0.001	0.001
HUNT→MUT	–0.190	0.014	–0.249	–13.38	<0.001	0.001
ENV→MUT	0.131	0.023	0.138	5.58	<0.001	0.001
NE→MUT	0.067	0.024	0.062	2.84	0.005	0.068
FARM→MUT	0.036	0.014	0.048	2.64	0.008	0.028
TRAP→MUT	–0.037	0.019	–0.035	–1.87	0.061	0.105
CONS→MUT	0.092	0.022	0.091	4.13	<0.001	0.007
Regression 2: predictor and criterion[2]						
WA→ATTS	0.576	0.020	0.456	28.42	<0.001	0.001
HUNT→ATTS	–0.166	0.015	–0.174	–11.01	<0.001	0.001
ENV→ATTS	0.078	0.024	0.062	3.16	0.002	0.006
NE→ATTS	0.068	0.025	0.050	2.71	0.007	0.022
FARM→ATTS	–0.218	0.014	–0.232	–15.20	<0.001	0.001
TRAP→ATTS	–0.096	0.021	–0.073	–4.54	<0.001	0.001
CONS→ATTS	–0.011	0.023	–0.009	–0.48	0.630	0.686
Regression 3: predictor, mediators, criterion[3]						
WA→ATTS	0.529	0.021	0.420	24.14	<0.001	0.001
HUNT→ATTS	–0.116	0.017	–0.122	–6.78	<0.001	0.001
ENV→ATTS	0.057	0.026	0.045	2.19	0.028	0.061
NE→ATTS	0.079	0.026	0.059	3.06	0.002	0.010
FARM→ATTS	–0.209	0.015	–0.221	–14.02	<0.001	0.001
TRAP→ATTS	–0.080	0.022	–0.060	–3.69	<0.001	0.001
CONS→ATTS	–0.016	0.024	–0.013	–0.67	0.503	0.580
DOM→ATTS	–0.209	0.029	–0.132	–7.21	<0.001	0.001
MUT→ATTS	0.026	0.022	0.020	1.19	0.234	0.357

WA, wolf advocate; HUNT, hunter; ENV, environmentalist; NE, nature enthusiast; FARM, farmer; TRAP, trapper; CONS, conservationist; DOM, domination; MUT, mutualism; ATTS, attitudes about wolves.
[1]*Adj. R^2: 0.397 (DOM); 0.313 (MUT).*
[2]*Adj. R^2: 0.520.*
[3]*Adj. R^2: 0.540.*
[4]*Corrected p-values control for the family-wise error rate, using the rwolf package in Stata (Clarke, 2016). Bootstrapped with 1,000 draws.*

similar, close interrelationships among identity, values, political ideology, and trust in government (Bright et al., 2000; Manfredo et al., 2017; Cacciatore et al., 2018; Schroeder et al., 2021).

Although we identified similarities among environmentalists, nature enthusiasts, and conservationists, we found the conservationist identity to be more centrist in terms of their political ideology, WVOs, trust in the agency, and attitudes about wolves. This finding may reflect the association of the term conservationist with hunting and angling (Holsman, 2000; Snyder et al., 2021), and that Gifford Pinchot's definition of conservation suggested the "wise use of the earth and its resources for the lasting good of men" (United States Department of the Interior [USDOI], 2021). A conservationist identity may resonate with a broader constituency because of its roots in the progressive conservation movement at the end of the 19th century (Mertig, 2015). This movement was narrowly focused on conservation of local wildlife and scenic areas, rather than the broader concerns of the modern environmental movement, which incorporates concerns about pollution, biodiversity, and climate change (Mertig, 2015). It is somewhat surprising that the conservationist identity did not have a stronger correlation with trust in the SWMA in this study. However, our results suggest that some individuals may not perceive strong differences between conservationist and environmentalist identities suggesting the definition of conservationist may be shifting over time.

TABLE 6 | Sobel test results.

Mediator - predictor	Sobel test	P
DOM		
- WA	5.456	<0.001
- HUNT	6.039	<0.001
- ENV	4.502	<0.001
- NE	0.294	0.769
- FARM	3.755	<0.001
- TRAP	2.825	0.004
- CONS	0.929	0.353
MUT		
- WA	1.179	0.239
- HUNT	1.177	0.239
- ENV	1.157	0.247
- NE	1.089	0.276
- FARM	1.074	0.282
- TRAP	1.010	0.312
- CONS	1.141	0.254

WA, wolf advocate; HUNT, hunter; ENV, environmentalist; NE, nature enthusiast; FARM, farmer; TRAP, trapper; CONS, conservationist; DOM,domination; MUT,mutualism.

We found less similarity among the identities that associate costs with wild wolves. The hunting identity was more strongly correlated with a conservative political ideology and a domination WVO, while the farmer identity was more strongly correlated with distrust in the SWMA and negative attitudes about wolves. Although hunters, trappers, and farmers may on average share negative attitudes about wolves, they differ in their trust in the management agency, political ideology and WVOs. Perhaps farmers interact with the SWMA less than hunters and trappers or in more antagonistic ways (e.g., denied wildlife damage claims), which leads to reduced trust (Gigliotti et al., 2020). Hunters and trappers may have more interaction with SWMA staff, or perceived greater salient values similarity with the agency (Gigliotti et al., 2020). Despite similarities in trust in the SWMA between hunters and trappers, trappers reported lower levels of political conservatism and domination compared to hunters. Previous work has suggested that trappers may think of themselves as part of nature or as fulfilling a stewardship function by controlling nuisance or problem animals and controlling the spread of wildlife disease (Daigle et al., 1998), and this may provide some explanation for a somewhat unexpected result.

Identity and Values as Predictors of Attitudes About Wolves

Our analyses demonstrate the importance of the domination WVO as a predictor of attitudes about wolves. Domination was more strongly correlated with attitudes about wolves than mutualism, which is in contrast to other published studies (Bruskotter et al., 2017). In addition, domination—but not mutualism—partially mediated the relationship between identity and wolf attitudes. Previous studies have found both domination and mutualism to predict wildlife-related attitudes and behaviors (Teel and Manfredo, 2009). In the context of identities and attitudes about wolves, the influence of domination may reflect the symbolic nature of the animal and what wolves can represent (Wilson, 1997; Bruskotter and Fulton, 2012). Among hunters, ranchers, and other individuals, wolves may represent a threat to desired game species and livestock (Treves, 2009; Bruskotter and Wilson, 2014; Hogberg et al., 2015; Schroeder et al., 2018). Beyond this, the presence of wolves may reflect loss of social power, property rights, and a utilitarian landscape (Wilson, 1997) for some individuals (Skogen and Krange, 2003; Skogen et al., 2008).

This study provides a step in exploring how identities may relate to attitudes about wolves. Our work is somewhat limited by the fact that we derived our data from a study related to wolf management, and response to our survey measurement items addressing identity and other social psychological constructs was influenced by this context. Additional work could explore the similarities and differences of these identities, and how the identities correlate with attitudes, values, and trust, in the context of other topics. Future research could clarify conservationist, environmentalist, nature enthusiast, and animal advocate identities, and how these identities relate to WVOs, trust in government, and attitudes about wildlife management. Psychological constructs found to explain patterns of policy preference like social dominance orientation (Pratto et al., 1994; Ho et al., 2015) and right-wing authoritarianism (Altemeyer, 1981, 1996) may also relate to identities associated with wildlife management issues and may be worthy of further consideration (Sinn, 2019). In addition, inclusion of other cognitive measures such as perceptions of risks and benefits of wildlife species that might mediate the relationship between identity and WVOs could also help clarify relationships among constructs (Bruskotter and Wilson, 2014).

Despite study results showing that liberal political ideology and mutualist WVO correlated with increased trust in SWMAs, little published research exists on the actual values and WVOs of SWMA professionals (Muth et al., 2006; Gamborg et al., 2019). Very limited research on SWMA staff suggests that their values may align more closely with those of traditional stakeholder groups (Muth et al., 2006). However, a study of wildlife management students (pre-professional) found a majority were mutualists, which may reflect changes in WVOs observed in larger society (Manfredo et al., 2003). In addition, given the relative difference in the domination WVO observed between hunters and trappers, work might examine WVOs among different consumptive recreation participants including hunters and trappers targeting different species, as well as anglers. Future research could replicate our analysis to examine how domination versus mutualism mediate relationships between identities and attitudes or behaviors in other wildlife and natural resource management contexts. Our results underscored domination, rather than mutualism, as a correlate of attitudes about wolves, but research is needed to clarify how WVOs interact with identity related to other potentially less symbolic wildlife species. This finding is especially important for identities that a wider swath of society have internalized, like conservationist.

Our results provide some insight for managers when working with multiple stakeholders in wolf management. We found strong similarities among environmentalists, nature enthusiasts, and conservationists, but clarified that a conservationist identity was correlated with all identities, including hunter, trapper, and farmer identities. This finding suggests that management communications that emphasize a conservationist, rather than an environmentalist or sportsperson perspective may garner support from a broader constituency and encourage trust in agency actions. However, conflicting attitudes about wolves, and the importance of a domination WVO to attitudes, may present a challenge to building consensus on wolf management.

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 studies involving human participants were reviewed and approved by University of Minnesota Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

SS collected the data, conducted the analysis, and wrote portions of the manuscript. AL conceived the idea and wrote portions of the manuscript. DF edited the manuscript and provided support for the hypotheses. LM edited the manuscript and provided support for the hypotheses. All authors contributed to the article and approved the submitted version.

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APPENDIX A

TABLE A1 | Wildlife value orientation survey items adapted from Teel and Manfredo (2009)[1].

Factor - **Items**	**Cronbach's Alpha**
Domination value orientation	0.801
- Humans should manage fish and wildlife populations so that humans benefit.	
- The needs of humans should take priority over fish and wildlife protection.	
- It is acceptable for people to kill wildlife if they think it poses a threat to their life.	
- It is acceptable for people to kill wildlife if they think it poses a threat to their property.	
- It is acceptable to use fish and wildlife in research even if it may harm or kill some animals.	
- Fish and wildlife are on earth primarily for people to use.	
- We should strive for a world where there's an abundance of fish and wildlife for hunting and fishing.	
- Hunting is cruel and inhumane to the animals.[2]	
- Hunting does not respect the lives of animals.[2]	
- People who want to hunt should be provided the opportunity to do so.	
Mutualism value orientation	0.879
- We should strive for a world where humans and fish and wildlife can live side by side without fear.	
- I view all living things as part of one big family.	
- Animals should have rights similar to the rights of humans.	
- Wildlife are like my family and I want to protect them.	
- I care about animals as much as I do other people.	
- It would be more rewarding to me to help animals rather than people.	
- I take great comfort in the relationships I have with animals.	
- I feel a strong emotional bond with animals.	
- I value the sense of companionship I receive from animals.	

[1] *Items were measured on a scale ranging from 1 (strongly disagree) to 7 (strongly agree).*
[2] *Item was reverse-coded prior to analysis.*

APPENDIX B

TABLE B1 | Trust survey items adapted from Riley et al. (2018) and Schroeder et al. (2020)[1].

Factor - **Items**	**Cronbach's Alpha**
Process	0.926
- Is open and honest about things they do and say related to wildlife management.	
- Will make decisions about wildlife management in a way that is fair.	
- Listens to the concerns of citizens.	
Outcomes	0.931
- Does a good job of managing wildlife in Minnesota.	
- Spends public money effectively.	
- Adequately manages Minnesota's wildlife	
Trust	0.949
- Can be trusted to make decisions about that wildlife management are good for the resource.	
- Can be trusted to take responsibility for managing Minnesota's wildlife resources.	
- Is trustworthy.	
Social values similarity	0.971
- Shares similar values as me.	
- Shares similar opinions as me.	
- Thinks in a similar way as me.	
- Takes similar actions as I would.	
- Shares similar goals as me.	
Technical competence	0.955
- Has wildlife managers and biologists who are well-trained for their jobs.	
- Is operated by employees who are well-qualified	
- Is operated by employees who understand the work that needs to be done	

[1] *Items were measured on a scale ranging from 1 (strongly disagree) to 7 (strongly agree).*

ORIGINAL RESEARCH
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Recent Trends in Survival and Mortality of Wolves in Minnesota, United States

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Survival is a key determinant of population growth and persistence; computation and understanding of this metric is key to successful population management, especially for recovering populations of large carnivores such as wolves. Using a Bayesian frailty analytical approach, we evaluated information from 150 radio-tagged wolves over a 16-year time period to determine temporal trends and age- and sex-specific survival rates of wolves in Minnesota, United States. Based on our analyses, overall annual survival of wolves during the study was 0.67, with no clear evidence for age- or sex-specific differences in the population. Our model demonstrated statistical support for a temporal trend in annual survival; the highest survival was predicted at the beginning of the time series (0.87), with lowest survival (0.55) during 2018. We did not observe evidence that survival was markedly reduced during years when a regulated hunting and trapping season was implemented for wolves (years 2012–2014). However, cause-specific mortality analysis indicated that most mortality was human-caused. While the estimate for increasing human-caused mortality over time was positive, the evidence was not statistically significant. Anthropogenic causes resulted in ∼66% of known mortalities, including legal and illegal killing, and vehicular collisions. Trends in wolf survival in Minnesota may reflect an expanding distribution; wolf range has spread to areas with more human development during the study, presumably leading to increased hazard and reduced survival. Our results provide foundational information for evaluating and guiding future policy decisions pertaining to the Great Lakes wolf population.

Keywords: carnivore management, demography, Endangered Species Act, known-fate, long-term monitoring, radiotelemetry

INTRODUCTION

Human expansion and persecution have endangered terrestrial carnivores worldwide (Ripple et al., 2014). Some carnivore species or populations however, have recovered to varying degrees from past exploitation, expanding from "refuges" back into parts of their former range. As their populations expand or human populations encroach new areas, large carnivores compete with humans for space or wild prey and may kill or injure pets, livestock and humans, while humans often respond by removing individuals, groups or entire populations (Cardillo et al., 2004; Treves and Bruskotter, 2014). Carnivore conservation in the Anthropocene is thus a challenge, and characterization of key vital rates such as survival is crucial for aiding recovery and understanding population dynamics.

Although the ecological roles of carnivores in their respective ecosystems lack generalities and fuel discourse (reviewed in Ford and Goheen, 2015), large carnivores indisputably remain as flagbearers for conservation of large landscapes (Ritchie et al., 2012). For their conservation roles and their connection to the human psyche, restoration efforts continue to be implemented and evaluated, and have often resulted in optimistic recoveries of carnivore species such as the tiger *Panthera tigris* (Jhala et al., 2021), puma *Puma concolor* (Jansen and Logan, 2002), Asian lion *P. leo leo* (Jhala et al., 2019), brown bear *Ursus arctos* (Lamb et al., 2018), gray wolf *Canis lupus* (Wydeven et al., 2009; Mech and Boitani, 2010; Ripple and Beschta, 2012; Nowak and Mysłajek, 2016), African wild dog *Lyacon Pictus* (Gusset et al., 2010), and black-footed ferret *Mustela nigripes* (Jachowski et al., 2011).

However, the Anthropocene has disparately affected the persistence and distribution of carnivore populations (Ripple et al., 2014), rendering certain sub-populations more vulnerable than other populations of the same species (Bruskotter et al., 2014). Thus, it is imperative to prioritize management actions for effective conservation. An understanding of population dynamics is necessary for successful management (Caughley, 1994), whether for: (i) increased protection, (ii) supplementation, (iii) reintroduction, and/or (iv) population control. For example, wolf populations in Yellowstone and Isle Royale have been restored through reintroductions, recolonization, and supplementation (Ripple and Beschta, 2012; Hervey et al., 2021) and the Gir lions in India have increased from less than 50 animals to ∼700 in the past 100 years because of committed protection and conservation (Jhala et al., 2019). Some carnivore populations have also been controlled to maintain ecological carrying capacity and to reduce human-carnivore conflict (e.g., American black bears *Ursus americanus*, Garshelis et al., 2020).

Wolves are iconic predators across their extant range, but perhaps nowhere are their contemporary fates so entwined with human actions as they are in North America. Wolves evoke strong and polarizing reactions of support and persecution, and are thus involved in intense conservation conflicts. Such conflicts are often aggravated because people connect with wolves as symbols of pristine wilderness, reconciliation, invasion, disease, and government overreach. As a consequence, the status of wolves still ranges from complete to no legal protection, resulting in a mosaic of management emphasis across regional to national scales (Bruskotter, 2013). This was recently exemplified in the dialog around the delisting of wolves from the federal Endangered Species Act (ESA)[1] in the United States. Historically, the last remaining wolves in the "Lower 48 states" were protected in Minnesota and gradually expanded to repopulate northern Wisconsin and Michigan's upper peninsula[2]. Consequently, Minnesota has a long history of successful wolf management aided by scientific monitoring, including intense regional study (e.g., Olson, 1938; Van Ballenberghe et al., 1975; Fuller, 1991; Mech et al., 2000; Erb and Benson, 2004; Gable and Windels, 2018). However, wolves in Minnesota still face threats from habitat alteration, and mortalities from escalating linear infrastructure, roadkill, depredation management, and illegal killing[2].

Wolves in North America, with the exception of the Northern Rocky Mountain population, have been re-listed on the Endangered Species Act; the Minnesota population considered as 'threatened'[1]. It is therefore imperative to monitor the population for long-term viability. Annual survival rate is a key parameter that informs our understanding of the ecological dynamics and persistence potential of a population. Herein, we determine survival rates for wolves with data from 150 radio- or GPS-collared wolves spanning 16 years (2004–2019) across Minnesota. Although estimates of annual or seasonal survival rate can provide important information for management, awareness of any temporal trend in survival can be crucial for policy formulation. Such a temporal analysis of survival becomes even more necessary when populations are affected by environmental stochasticity, human impacts that vary over time, and socio-biological factors (such as territoriality, competition and density dependence), which often affect group-living carnivores (Cubaynes et al., 2014; O'Neil et al., 2017). Using long-term known-fate data on individuals, we estimate human versus natural mortality while testing for the effect of time on wolf survival with four major questions: (1) how does annual survival vary between years, (2) does survival show a trend over time, (3) is there a particular inflection point or period where survival rates or trends change, and (4) did recreational wolf hunting and trapping (years 2012–2014) affect survival rates of wolves in Minnesota.

MATERIALS AND METHODS

Study Area

We evaluated wolf survival and mortality within northern Minnesota, United States. Wolf distribution and abundance has expanded south and west within the state since the 1970s[2] (**Figure 1**). The study area was primarily characterized by mixed northern hardwood forest, bog, wetland, and agricultural land cover types (Erb and Sampson, 2013; Erb and Humpal, 2021). Human population and road densities were generally low (typically < 5 humans / km^2 and < 2 km of roads / km^2; MN DNR unpublished data), with primary land uses being recreation, logging, and some mining, with increasing agriculture in the south and west of wolf range. Prey and food sources for wolves included white-tailed deer (*Odocoileus virginianus*), beaver (*Castor canadensis*), moose (*Alces alces*), and sometimes fish and berries (Gable et al., 2016, 2018; Homkes et al., 2020).

After ESA protections were established in the 1970s, public harvest of wolves was prohibited until their delisting in 2012. However, lethal control of wolves in response to livestock

[1] https://www.fws.gov/home/wolfrecovery/

[2] https://www.dnr.state.mn.us/wolves/index.html

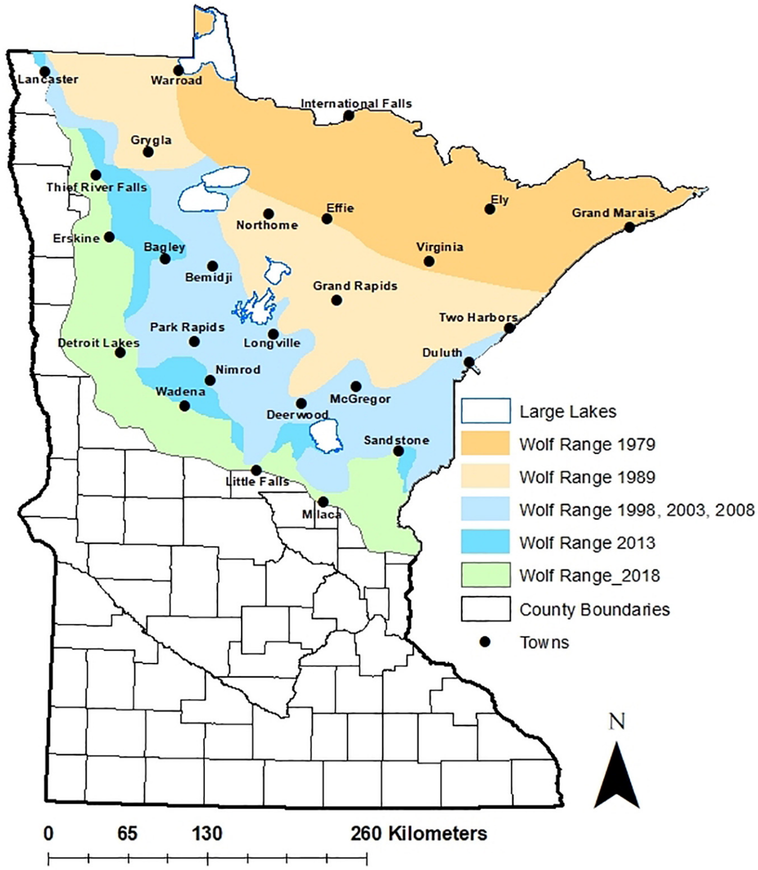

FIGURE 1 | Distribution and expansion of gray wolves (*Canis lupus*) in Minnesota, United States, from 1978 to 2018, from Minnesota Department of Natural Resources (https://www.dnr.state.mn.us/wolves).

depredation was permitted throughout the study period and region (available reporting indicates that the annual number of wolves killed ranged from 95 to 216 for 2011–2020). During 2012–2014, state law permitted a regulated, public harvest of wolves. These hunting and trapping seasons occurred in the late fall and early winter months, with a total of 915 wolves killed (Erb and Sampson, 2013). Federal (ESA) protection of wolves has varied during the period of our analysis, but public harvest has not been allowed since 2014[2].

Data Collection

For radiotelemetry, most wolves were captured using foothold traps (Erb and Humpal, 2021). Some wolves were also captured with the use of live-restraining neck snares (Gese et al., 2019), and a few by aerial darting from a helicopter. Wolves captured with foothold traps were captured between May-October and live-snared wolves were caught between December-March, however, winter live-snaring only started from 2013. Upon capture, each individual was weighed, sexed, and aged prior to release. Based on tooth- wear and color, coupled with appearance and behavior, individuals were aged into three categories: pups (<1 year), juveniles (1–2 years) and adults (>2 years). Post-mortem aging of some of the tagged wolves from tooth cross sections aligned with our initial assessments. Telemetry equipment ranged from VHF-only (20%) to VHF/GPS collars (remaining 80%). Most GPS radio-collars were programmed to take 3–6 locations per day, and wolves fitted with VHF-only radio-collars were relocated at approximately 7 to 10-day intervals throughout the year, and in some cases, primarily from early winter through spring (Erb and Humpal, 2021). All captures were done as per regulations and guidelines from the Minnesota Department of Natural Resources.

Statistical Analysis

We used a Bayesian shared frailty model (Halstead et al., 2012; Heisey, 2012) to capture variation in annual survival of wolves from 2004 to 2019, and as a function of sex and estimated age at capture. In addition, we partitioned the hazard rate from the frailty model into cause-specific mortality rates over the same time period (Heisey and Patterson, 2006). For each individual wolf, we created encounter histories that reflected the time period (number of days) between initial date of capture and date last known alive. Individuals that were characterized by "loss to follow-up" had undetermined fates and were right censored with an encounter history endpoint being the last alive date (DeCesare et al., 2016; Moore, 2016). Individual collars that were detected in mortality mode were located in the field, where fate was determined. The time period between last known alive and date confirmed dead was interval censored, such that date of death was considered unknown and was imputed by the frailty model (i.e., fate could have occurred any time between last date known alive and date confirmed death). Known fate mortality was classified as human (e.g., legally or illegally killed, vehicle collision), natural (e.g., disease, starvation, intraspecific strife), or unknown (cause undetermined). We generated time-varying covariates to estimate temporal effects and age. Specifically, we set the initial day of season, year, and age for each individual encounter history. As encounter histories progressed, the corresponding covariates for year and age were updated in alignment with each individual encounter history across time. Age was classified as either adult or non-adult (pup or juvenile) due to uncertainty in age estimation. As such, pups and juveniles graduated to adults after 2 and 1 years, respectively, with the date of graduation set to the 15th of April to correspond with the approximate wolf biological year.

We identified five *a priori* candidate models to test relative support for each of our research questions, specifically whether survival changed over time, whether a change in survival (e.g., an inflection point) was evident during the study, and whether years with legal hunting and trapping resulted in lower survival. The shared frailty model infers survival across a specified encounter history interval *via* a hazard function, expressed as

$$UH = \exp(\gamma_0 + \kappa + X\beta) \tag{1}$$

where UH represents the unit hazard, with the unit defined as length of interval (daily, weekly, monthly). In this model, γ_0 is the intercept, providing a constant baseline hazard that can be offset by any number of fixed covariates X, or random effects κ. We specified the following models to evaluate evidence for temporal and/or hunting effects on survival:

$$UH = \exp(\gamma_0 + \beta_1 x_{male} + \beta_2 x_{adult} + \beta_3 x_{time}) \tag{2}$$

$$UH = \exp(\gamma_0 + \beta_1 x_{male} + \beta_2 x_{adult} + \beta_3 x_{time} + \beta_4 {x_{time}}^2) \tag{3}$$

$$UH = \exp\left(\gamma_0 + \beta_1 x_{male} + \beta_2 x_{adult} + \beta_3 log\left(x_{time}\right)\right) \tag{4}$$

$$UH = \exp(\gamma_0 + \beta_1 x_{male} + \beta_2 x_{adult} + \beta_3 x_{hunt}) \tag{5}$$

$$UH = \exp(\gamma_0 + \beta_1 x_{male} + \beta_2 x_{adult} + \beta_3 x_{time} + \beta_4 x_{hunt}) \tag{6}$$

Each model represented a different hypothesis about the temporal trend in wolf survival, including a linear trend (Equation 2), a hyperbolic trend (survival rises and then falls, or falls and then rises; Equation 3), a log-linear threshold trend (Equation 4), a change in survival only during years of regulated public harvest (harvest effect; Equation 5), and a linear time trend as well as a harvest effect (Equation 6). For each model, time was treated as a continuous variable ($t = 1{:}16$ for years 2004–2019, respectively). For models including a harvest effect, the years associated with public harvest were represented by a binary indicator covariate for harvest ($x_{hunt} = 1$) vs. no harvest ($x_{hunt} = 0$). We included sex and age (time-varying) in all models, which were also treated as binary fixed covariates, where the respective coefficients, β_1 *and* β_2, modeled the influence of being male ($x_{male} = 1$) vs. female ($x_{male} = 0$), and adult ($x_{adult} = 1$) vs. pup or juvenile ($x_{adult} = 0$), respectively. We did not include a separate parameter for pups due to sample size, as very few pups with known fates were included in the dataset. We ranked models using the Bayesian widely applicable information criterion (WAIC; Vehtari et al., 2017). We also included results of leave-one-out (LOO) cross-validation and deviance information criterion (DIC) to check for consistency across evaluation metrics (Spiegelhalter et al., 2014; Vehtari et al., 2017).

Following identification of the top performing model, we refit the model with an additional parameter to capture residual variation across years (e.g., year effects are not assumed independent of one another) and added a component to evaluate competing mortality sources. For each known mortality, cause was assigned as $k \in \{1 = \text{human}, 2 = \text{natural}, 3 = \text{unknown}\}$, using a categorical distribution with cause probabilities (p_1, p_2, p_3), where $\sum_{k=1}^{K} p_k = 1$ (Cross et al., 2015; Stenglein et al., 2018). We tested evidence for the following mortality cause effects by relating covariates (α) to cause probabilities *via* the logit link function (Stenglein et al., 2018): first, human cause changes over time (relative to other causes), second, a difference in human vs. natural cause for adults relative to sub-adults, and third, a difference in unknown cause vs. other causes for adults relative to sub-adults.

Following estimation of the unit hazard, we calculated annual survival as

$$CH = \sum_{i=1}^{T=365} UH \tag{7}$$

$$S = e^{-CH} \tag{8}$$

where CH represents the annual, cumulative hazard and S represents the annual, cumulative survival rate.

For reporting, we derived estimates of annual hazard and survival from the final model under the condition that ratios of male to female and adult to non-adult were equivalent to those observed during the study. In addition, we derived estimates of annual survival for each of the four age and sex classes (adult-male, adult-female, juvenile-male, juvenile-female) assuming an average year during the study.

We specified uninformative Normal prior distributions ($\mu = 0$, $\tau = 1/\sigma^2 = 0.01$) for all fixed covariate effects, as

TABLE 1 | Model rankings for five Bayesian shared frailty models of gray wolf (*Canis lupus*) mortality and survival in Minnesota, United States, from 2004 to 2019.

Model rank	Model structure	DIC	WAIC	LOOIC
1	Age + sex + log(time)	684	686	686
2	Age + sex + time	685	687	688
3	Age + sex + time + time^2	686	689	689
4	Age + sex + hunt + time	687	690	690
5	Age + sex + hunt	687	692	692

All models included effects of age (adult vs. sub-adult), sex (male vs. female). Model information criterion (DIC, WAIC, LOOIC) were included to infer a top model based on temporal structure, including linear, log-linear, and quadratic forms representing a time trend (time), a recreational hunting effect (hunt) for years when wolves were subject to a legal hunt, and a random offset term capturing year-to-year variation from the overall trend. Models were ranked by WAIC.

TABLE 2 | Estimates of model parameters for a Bayesian shared frailty model of gray wolf (*Canis lupus*) mortality and survival in Minnesota, United States, 2004–2019.

Parameter	Interpretation	Mean	SD	2.50%	50%	97.50%
gamma.n	UH: Intercept	−7.885	0.61	−9.107	−7.869	−6.721
b.age	UH: age effect	−0.162	0.287	−0.71	−0.168	0.413
b.sex	UH: sex effect	−0.024	0.265	−0.549	−0.022	0.49
b.year	UH: log(year) effect	0.554	0.249	0.072	0.55	1.053
kappa.year[1]	UH: year[1] random offset	−0.014	0.244	−0.555	−0.002	0.479
kappa.year[2]	UH: year[2] random offset	−0.047	0.242	−0.638	−0.011	0.387
kappa.year[3]	UH: year[3] random offset	0.006	0.218	−0.462	0.001	0.49
kappa.year[4]	UH: year[4] random offset	0.069	0.217	−0.303	0.023	0.623
kappa.year[5]	UH: year[5] random offset	0.033	0.214	−0.385	0.009	0.55
kappa.year[6]	UH: year[6] random offset	−0.082	0.252	−0.734	−0.025	0.307
kappa.year[7]	UH: year[7] random offset	−0.04	0.215	−0.56	−0.011	0.367
kappa.year[8]	UH: year[8] random offset	−0.008	0.215	−0.486	−0.001	0.452
kappa.year[9]	UH: year[9] random offset	0.03	0.195	−0.356	0.008	0.491
kappa.year[10]	UH: year[10] random offset	0.062	0.212	−0.312	0.021	0.599
kappa.year[11]	UH: year[11] random offset	0.008	0.189	−0.395	0.001	0.439
kappa.year[12]	UH: year[12] random offset	−0.029	0.194	−0.484	−0.009	0.358
kappa.year[13]	UH: year[13] random offset	0.058	0.195	−0.292	0.021	0.544
kappa.year[14]	UH: year[14] random offset	−0.105	0.232	−0.717	−0.041	0.238
kappa.year[15]	UH: year[15] random offset	0.078	0.202	−0.254	0.031	0.597
kappa.year[16]	UH: year[16] random offset	−0.024	0.207	−0.51	−0.006	0.394
S0_avg[1]	Annual Survival year = 1	0.868	0.075	0.682	0.883	0.966
S0_avg[2]	Annual Survival year = 2	0.829	0.068	0.673	0.838	0.936
S0_avg[3]	Annual Survival year = 3	0.787	0.066	0.641	0.794	0.897
S0_avg[4]	Annual Survival year = 4	0.746	0.065	0.599	0.752	0.854
S0_avg[5]	Annual Survival year = 5	0.727	0.064	0.583	0.732	0.839
S0_avg[6]	Annual Survival year = 6	0.729	0.064	0.606	0.727	0.866
S0_avg[7]	Annual Survival year = 7	0.701	0.061	0.579	0.7	0.827
S0_avg[8]	Annual Survival year = 8	0.674	0.065	0.536	0.675	0.804
S0_avg[9]	Annual Survival year = 9	0.647	0.062	0.51	0.651	0.764
S0_avg[10]	Annual Survival year = 10	0.621	0.07	0.455	0.627	0.742
S0_avg[11]	Annual Survival year = 11	0.622	0.064	0.49	0.623	0.748
S0_avg[12]	Annual Survival year = 12	0.618	0.066	0.488	0.617	0.756
S0_avg[13]	Annual Survival year = 13	0.579	0.069	0.428	0.583	0.705
S0_avg[14]	Annual Survival year = 14	0.613	0.079	0.471	0.607	0.789
S0_avg[15]	Annual Survival year = 15	0.547	0.074	0.386	0.551	0.681
S0_avg[16]	Annual Survival year = 16	0.567	0.082	0.404	0.566	0.734
S0_AM_avg	Annual Survival Adult-Male	0.693	0.055	0.58	0.695	0.797
S0_AF_avg	Annual Survival Adult-Female	0.687	0.056	0.573	0.689	0.79
S0_JM_avg	Annual Survival Juvenile-Male	0.647	0.085	0.469	0.651	0.798
S0_JF_avg	Annual Survival Juvenile-Female	0.642	0.074	0.489	0.645	0.777
b[1]	Mortality cause intercept (not estimated)	0	0	0	0	0
b[2]	Mortality cause = Natural	−1.016	1.182	−3.396	−0.996	1.234
b[3]	Mortality cause = Unknown	−1.509	1.296	−4.169	−1.464	0.912
bc.age[1]	Adult vs. Juvenile intercept (not estimated)	0	0	0	0	0
bc.age[2]	Adult vs. Juvenile Natural cause	0.437	0.803	−1.052	0.404	2.101
bc.age[3]	Adult vs. Juvenile Other cause	−0.168	1.045	−2.109	−0.206	2.001
bc.year[1]	Time trend: Human cause	0.035	0.079	−0.122	0.035	0.189
bc.year[2]	Time trend: Natural cause (not estimated)	0	0	0	0	0
bc.year[3]	Time trend: Other cause (not estimated)	0	0	0	0	0
Deviance		783.843	4.675	776.46	783.239	794.733

Parameters were estimated with respect to the daily unit hazard (UH), and estimates were obtained from Gibbs MCMC sampling.

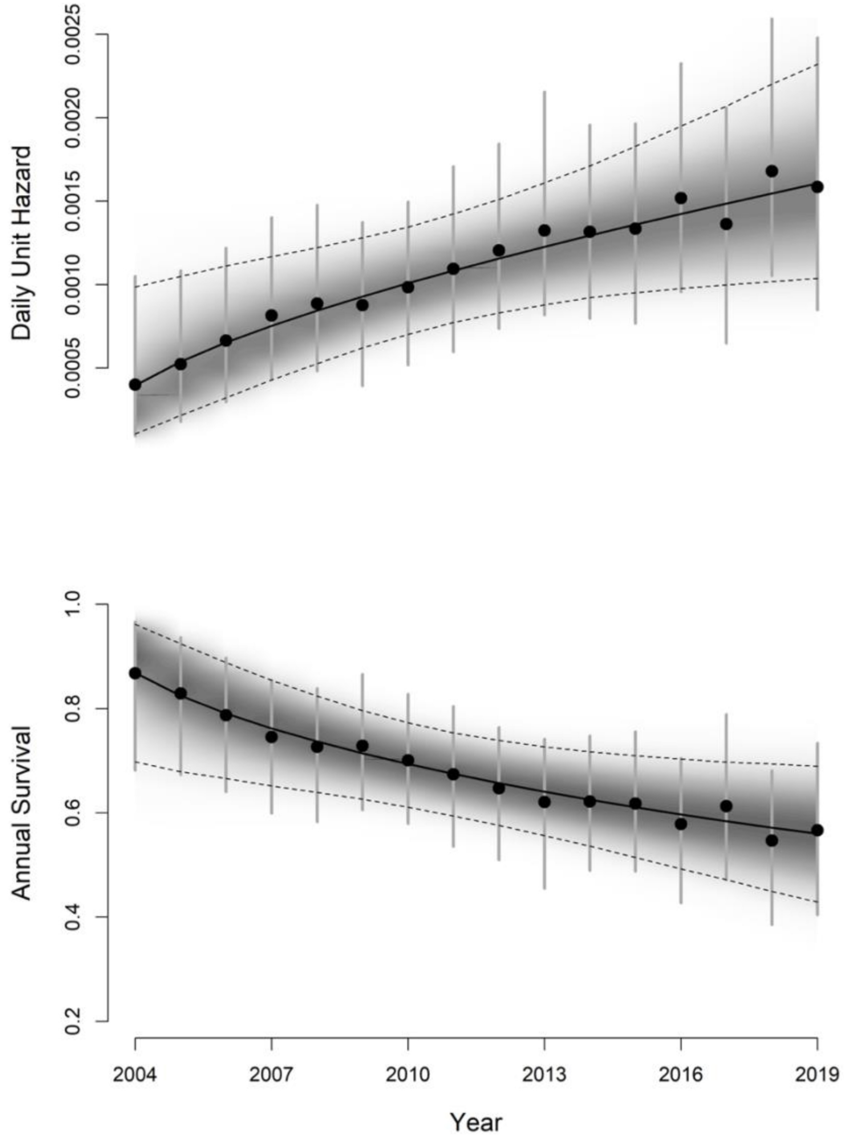

FIGURE 2 | Daily unit hazard (mortality risk) and annual survival estimates of gray wolves (Canis lupus) in Minnesota, United States, 2004–2019. Survival parameters were estimated with respect to the daily unit hazard (UH) from a selected Bayesian shared frailty and cause-specific model of wolf mortality and survival, and all estimates were obtained from Gibbs MCMC sampling. Year effects were based on the modeled time trend, and deviation away from the trend was represented by random normally distributed residual offsets. Annual means and upper and lower credible intervals are represented by black dots and vertical error bars respectively. The trend is represented by the black regression line with shaded distribution, and dotted lines indicating upper and lower 95% credible intervals.

well as the residual year effects. For the baseline hazard, we specified a weakly informative prior, $\gamma_0 \sim N(\mu, \sigma^2)$, based on a comprehensive literature review of wolf survival (annual estimates ranging from 0.24–0.91), and used moment matching to appropriately place the hyperparameters on the *UH* scale ($\mu = -7.47$, $\sigma = 1.12$). We estimated all model parameters for the frailty model using the Gibbs MCMC sampler in JAGS 4.2.0 (Plummer, 2003), by way of the *jagsUI* package (Kellner, 2019) implemented in R 4.0.3 (R Core Team, 2020). We ran three chains of 50,000 iterations and retained every 10th sample following a burn-in phase of 20,000. We calculated DIC using the *jagsUI* package and WAIC and LOOIC from the model's posterior predictive distribution using the *loo* package (Vehtari et al., 2020). We visually examined chains and calculated Gelman-Rubin statistics to verify chain convergence ($r < 1.05$). We report median values of posterior distributions and 95% credible intervals (CRI) for each parameter, unless otherwise stated.

RESULTS

We evaluated annual hazard and subsequent survival for 150 individual wolves during 2004–2019. Of these, 84 were females (56.0%) and 66 were males (44.0%). At the time of capture, 91

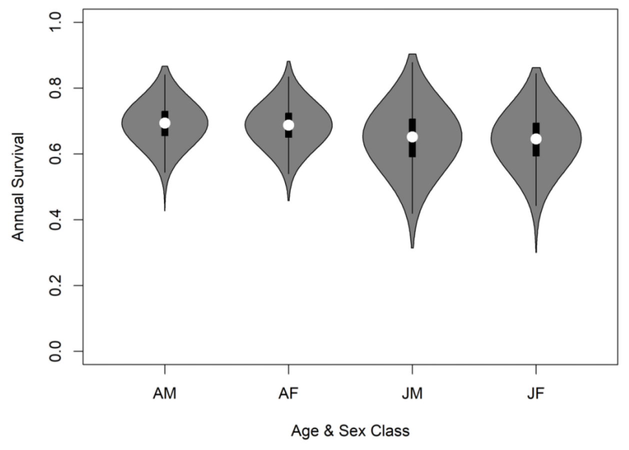

FIGURE 3 | Summary statistics of annual survival estimates of gray wolves (*Canis lupus*) in Minnesota, United States, 2004–2019, where wolves were categorized according to age class and sex (AM = adult-male, AF = adult-female, JM = pup/juvenile male, JF = pup/juvenile female). Open circle indicates median estimate from posterior distribution, thick line indicates interquartile range, thin line indicates 95% Credible Intervals, shaded area indicates kernel density estimation to show the distributional shape of the data.

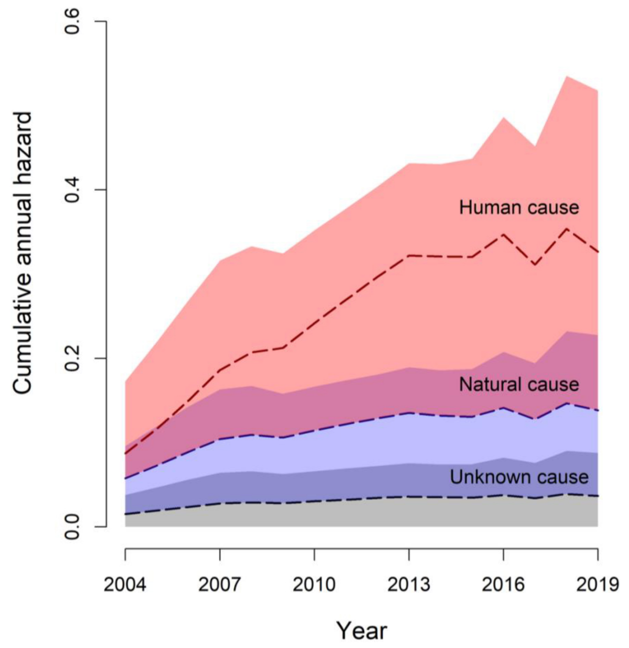

FIGURE 4 | Cumulative incidence function representing proportion of total annual gray wolf (*Canis lupus*) mortality (cumulative annual hazard) from unknown (gray shade), natural (lavender shade), and human (apricot shade) causes over 16 years in Minnesota, United States, 2004–2019. Overlapping shades represent uncertainty in mortality sources as well as the estimated cumulative annual hazard.

wolves were estimated to be adults (≥2 years; 60.6%), 44 were yearlings (∼1 year old; 29.3%), and 15 were pups (<1 year old; 10.0%). Mortality information (known fate) was obtained for 59 individuals. Of these mortalities, 39 were attributed to anthropogenic causes (66.1%), 14 were natural deaths (23.7%), and 6 had undetermined causes (10.2%).

Our top frailty model was based on Eq. 4, with temporal change in the hazard represented by a log-transformation on the continuous year variable. This model indicated a curvilinear relationship between the hazard and time (**Table 1** and **Figure 2**). The linear time trend model was also competitive (e.g., within 2 WAIC units of top model; **Table 1**), with less support for models representing an effect of regulated public harvest on the hazard rate. Our model demonstrated statistical support for a temporal trend in annual survival [$\beta_3 = 0.54$, 95% CRI = (0.07, 1.04), $p > 0 = 0.99$], with greatest survival generally occurring in the early years of the time series and lower survival during the later years (**Table 2** and **Figure 3**), though the rate of change slowed over time (**Figure 3**). The highest survival was predicted at the beginning of the time series [0.87, 95% CRI = (0.68,0.97)], with lowest survival during 2018 [0.55, 95% CRI = (0.39,0.68)]. From all Bayesian information criteria rankings, we did not observe evidence that survival was markedly reduced during years when a public harvest was allowed on wolves (years 2012–2014; **Table 1**).

Based on observed sex and age ratios and inference from our final model, overall annual survival during the study was estimated to be 0.67 (95% CRI: 0.54, 0.79). Our model did not indicate strong evidence that mortality varied by sex [$\beta_1 = -0.03$, 95% CRI = (−0.55, 0.49), $p < 0 = 0.54$], or that adults exhibited reduced mortality relative to non-adults [$\beta_1 = -0.16$, 95% CRI = (−0.71, 0.41), $p < 0 = 0.72$]. Thus, on average, our model predicted annual survival ranging from 0.65 (95% CRI = 0.49, 0.78) for non-adult females to 0.69 (95% CRI = 0.58, 0.80) for adult males (**Table 2** and **Figure 3**).

Cause-specific mortality analysis reflected the observed data, indicating that most mortality was human-caused. The estimate for increasing human-caused mortality over time was positive, but evidence was not clear, with 95% CRI's overlapping zero [$\alpha = 0.04$, 95% CRI = (−0.12, 0.189), **Figure 4**]. Similarly, the estimate for greater natural mortality in adults was positive, but evidence was unclear [$\alpha = 0.44$, 95% CRI = (−1.05, 2.10)]. Derived model estimates for mortality causes across age classes were $p_{1\,human\ causes} = 0.63$ (95% CRI = 0.45, 0.78), $p_{2\,natural\ mortality} = 0.27$ (95% CRI = 0.14, 0.43), and $p_{3\,unknown\ causes} = 0.10$ (95% CRI = 0.03, 0.21) for adults; and $p_1 = 0.68$ (95% CRI = 0.37, 0.88), $p_2 = 0.20$ (95% CRI = 0.14, 0.43), and $p_3 = 0.12$ (95% CRI = 0.02, 0.36) for sub-adults, respectively. The cumulative incidence function revealed the contributions of different mortality sources, as a proportion of total mortality, where the hazard increased over time according to our top model (**Figure 4**).

DISCUSSION

Survival is a key determinant of population growth and persistence, and computation and understanding of this metric is key to successful population management (e.g.,

TABLE 3 | Survival estimates of wolf populations from contemporary literature (not necessarily exhaustive).

Estimate	Study area	Authors
Overall 0.75 (95% CI = 0.70–0.80)	Upper Peninsula, Michigan	O'Neil et al., 2017
Overall 0.75	Wisconsin	Wydeven et al., 2009
Overall 0.76 (SD = 0.019)	Wisconsin	Stenglein et al., 2018
Overall 0.79	Central Brooks Range, AK	Adams et al., 2008
Overall 0.75	Greater Yellowstone Ecosystem	Smith et al., 2010
Adult = 0·82 ± 0·04 Juvenile = 0·24 ± 0·06	Western Alps	Marucco et al., 2009
Adult = 0.89 Juvenile = 0.81	Finlayson Study Area, Yukon	Hayes and Harestad, 2000
Residents = 0.65 ± 0·17 Dispersers = 0.34 ± 0·17	SE Alaska, United States	Person and Russell, 2008
Overall = 0.71 ± 0.16	Isle Royale, United States	Marucco et al., 2009
0.11–0.24 (high poaching scenario) to 0.43–0.60 (no poaching)	Finland	Suutarinen and Kojola, 2017
Overall: 0.64 ± 0·07	Papineau-Labelle reserve, Quebec	Potvin, 1988
Overall: 0.66–0.75	Italian Appenines	Caniglia et al., 2012
Dispersers = 0.76 ± 0·10, Breeders = 0.77 ± 0·14	Rocky Mountains	Boyd and Pletscher, 1999
Yearlings: 0·79 [0·72; 0·84] Adult age 2: 0·76 [0·69; 0·83] Adult age 3: 0·79 [0·71; 0·86] Adult age 4: 0·80 [0·70; 0·88] Adult age 5: 0·78 [0·66; 0·87] Adult age 6: 0·85 [0·71; 0·92] Old Adult age 7+: 0·63 [0·52; 0·74]	Yellowstone NP	Cubaynes et al., 2014
Annual Adult survival rate (0.80) Residents: 0.84 Dispersers: 0.66	NW Montana	Pletscher et al., 1997
Adult = 0.78 [95% (CI) = 0.76–0.81]	Minnesota	Barber-Meyer et al., 2021
Adult = 0.82 Summer pup = 0.39	Wisconsin	
Adult = 0.64 Summer pup = 0.48	Minnesota	Fuller, 1989
Adult = 0.56 Summer pup = 0.48	Southern Yukon	Hayes et al., 1991
Adult = 0.72 Summer pup = 0.57	Minnesota	Fritts and Mech, 1981
Adult = 0.86 Summer pup = 0.69	Northeastern Alberta	Fuller and Keith, 1980
Adult = 0.67 Summer pup = 0.76	Kenai Peninsula Alaska	Peterson et al., 1984
Adult = 0.59 Summer pup = 0.89	South-central Alaska	Ballard et al., 1987
Adult = 0.73 Summer pup = 0.91	Denali National Park	Mech et al., 1998

O'Neil et al., 2017) and understanding our relationship with wolves (Treves and Bruskotter, 2014). Foremost, our results indicate a gradual increase in hazard and associated decline in median annual wolf survival in Minnesota over 16 years (**Figure 2**). While our results likely hint toward lower overall survival in Minnesota's wolves during the study period than the contiguous populations in Wisconsin and Michigan (**Table 3**), populations in those two states over our study timeframe were growing rapidly as wolves recolonized and recovered (Stenglein et al., 2015a; O'Neil et al., 2020). In contrast, the Minnesota wolf population was not in a consistent growth phase during most of the period of our analysis. Carnivore species often show higher survival in years when the population expands into new range or is recovering, while the rate diminishes as it nears carrying capacity because of density dependent factors such as competition and territoriality (Banerjee and Jhala, 2012; Cubaynes et al., 2014; O'Neil et al., 2017). The temporal trajectory of our study possibly mirrors a similar trend where higher survival rates were documented in the earlier periods of the time series (first 8–9 years) than the later (last 6–7 years) (**Figure 2**). The higher mortality in the later part of the time series might be because of intra-specific competition for food and space, density dependent population regulation, as well as human-induced causes. Wolf survey counts indicate that the population in Minnesota increased until 2007–2008 to about 2,500–3,000 individuals, reaching relative stability thereafter (Erb and Humpal, 2021), potentially corroborating density dependence as a mechanism that likely dampened annual survival and population growth. In addition, this population has expanded its distribution into areas with greater human population density and development (**Figure 1**).

Although the most recent years when legal public harvest was allowed (2012–2014) were not characterized by significant alteration in survival rates, human-induced mortalities were the most common reason for wolf deaths in Minnesota, as was the case in adjoining populations in Michigan's Upper Peninsula (O'Neil et al., 2017) and Wisconsin (Stenglein et al., 2015a). Human-caused mortality also showed a positive temporal trend, but we recommend caution in interpreting this owing to the lack of statistical strength. Anthropogenic causes resulted in ~66% of known mortalities, which includes legal and illegal killing, and vehicular collisions. The road and highway network have expanded in Minnesota over the past 50 years and the state governance has committed to further increase this network till 2040 (Minnesota Transport Alliance, 2011). Vehicular collisions continue to cause wolf deaths in Minnesota, and they likely can increase because of increase in road networks.

Although we did not detect any significant age- or sex-specific differences in annual survival rates of wolves, wolf behavior suggests younger dispersing wolves are often more vulnerable to mortality (Mech and Boitani, 2010). Dispersal events often compel young wolves to navigate around or across risky unfamiliar wolf territories and human-dominated landscapes and roads, thereby reducing their survival chances (Barber-Meyer et al., 2021). More information from younger/dispersing wolves is necessary to confirm such patterns.

While we evaluated extensive and long-term data on collared wolves, we acknowledge that fate could only be confirmed for ~40% of the collared wolves. Data from the remaining individuals had to be censored owing to the lack of information following endpoints when either the collar failed or contact was lost. It is possible that censoring and mortality could be confounded in some cases, i.e., if censored wolves died and collars failed in such a way that the mortality went undetected (Liberg et al., 2012; Stenglein et al., 2018), but we found no evidence or reason to indicate that to be of concern here. First, the author team included those who work directly with collared wolves within the study area, with experiences indicating that known collar loss and failure has been extremely common among marked individuals. Further, there is little reason to believe that the circumstances (e.g., illegal killing followed by destruction of the transmitter) causing such misclassification are common in our study region; illegal kills are commonly detected as a mortality cause. Second, most prevailing literature from neighboring regions with similar socio-political environments suggests that the percentage of wolves with lost collars that may have confounded the detection of dead wolves has been quite low (< 1%, Stenglein et al., 2015b), thereby reducing any significant positive survival biases in our interpretations. Finally, in the Bayesian shared frailty model that we have used to analyze survival, the censored endpoint for a given wolf does not depend on a survival assumption beyond the endpoint. Instead, the assumption is that the wolf continues to exhibit the expected survival rate (given the model) beyond the point of censoring. While misclassification of a large number of dead wolves as censored could ultimately result in optimistic survival estimates, all indications suggest this type of error is rare. Having incorporated these checks and balances, we are confident in the survival estimates from our analysis.

Our results provide baseline information on the recent trend in annual survival rate of and cause specific mortality of wolves in Minnesota. These demographic parameters would be helpful to inform policy decisions for wolves in the Great Lakes population. Future research exploring site-specific variability in these demographic parameters can provide spatial contexts to the trends that we have reported here and augment our current understanding of the Great Lakes wolf population. Studies have revealed that spatially varying survival rates can be crucial for prioritizing management actions within a landscape, wherein certain areas can be "riskier" for carnivores (characterized by lower survival) and act as population sinks (Robinson et al., 2008; Stenglein et al., 2015a; O'Neil et al., 2017; Barber-Meyer et al., 2021). Identification of such source-sink dynamics through the characterization of area-specific variation in population parameters is important to successful monitoring and management, especially where the population is or has been increasing in number and distribution, and human-caused mortality is a significant contributor to annual survival. Such analyses would also provide fine-scale patterns of survival in protected and non-protected areas (e.g., Barber-Meyer et al., 2021), within core wolf areas versus expanding frontiers, and on tribal lands where cultural differences toward wolf recovery manifest. Additionally, an increase in number and distribution of wolves expands the human-wolf interface, thereby increasing risk of conflicts. Hence, we recommend continued monitoring of collared wolves to further investigate temporal and spatial patterns of mortality and survival amidst shifting management authority (e.g., state, federal, tribal), landscape conditions, and public attitudes.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

All research protocols were undertaken by the Minnesota Department of Natural Resources (MN DNR) as per their guidelines and regulations.

AUTHOR CONTRIBUTIONS

JE, SO, and JB conceptualized the study. SO and SC performed the analysis with guidance from JE, CH, and JB. SC prepared the manuscript with critical feedback from SO, JE, CH, and JB. All authors contributed to the article and approved the submitted version.

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REVIEW
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Overview of Current Research on Wolves in Russia

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This paper provides an overview of wolf research in Russia at the beginning of the 21st century. Wolf research covered various directions, including population density estimation, management methods and minimization of human-wildlife conflicts, general and behavioral ecology, behavior, wolf population genetics and morphology, paleontology, dog domestication, helminthology and the wolves' role in the rabies transmission. Some studies are performed with state-of-art methodology using molecular genetics, mathematical modeling, camera traps, and GPS telemetry.

Keywords: wolf, *Canis lupus*, Russia, population management, behavioral ecology, population genetic and morphology

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INTRODUCTION

Wolf research in Russia has a long history. One of the first wolf papers (Sabaneev, 1877) summarizes Leonid P. Sabaneev's wolf hunting experience to increase hunting efficiency. Sabaneev also provides relevant facts on wolves' biology. After Sabaneev's book, the main focus of wolf research was wolf hunting (Zvorykin, 1936; Manteuffel, 1949; Kozlov, 1966; Pavlov, 1982). At the same time, academic studies describing several aspects of wolf biology were published (Dinnik, 1914; Satunin, 1915; Naumov, 1967). In 1973, the Wolf Working Group (herein and after WWG) was created and chaired by Professor Dmitry I. Bibikov. WWG made a considerable contribution to wolf research. First, Wolf Working Group members studied consequences of disrupted population structure, in particular emergence of feral dog and wolf-dog hybrid populations (Ryabov, 1978, 1979). Second, wolf ontogenesis received thorough attention (Badridze, 1987, 2003) as well as population abundance in various regions (Bondarev, 2012a; Yudin, 2013). One of WWG's accomplishments was changing public opinion on wolves, in particular a ban on poisons, and a ban on wolves killing within protected areas. The WWG held debates about best wolf monitoring practices as a basis for management decisions (Bibikov et al., 1990). The results of WWG activity are summarized in the monograph *The Wolf. History, Systematics, Morphology, Ecology* (Bibikov, 1985).

Reviewing all the wolf research over the past two decades is beyond the scope of our work. Rather, we describe the main directions and overall trends. We emphasize that in the Soviet, and later, Russian society, the attitude toward wolves always has been very emotional. The overwhelming majority of hunters, game managers, and rural residents have a sharply negative attitude toward wolves. We analyzed the 2019 and 2020 editions of three hunting magazines popular in Russia: Hunting and hunting ground, Hunting and Fishing, and Okhotnik. In 2019, out of 17 articles on the wolf, 13 were strongly negative, 1 was positive, and 3 offered a science-based assessment approach. In 2020, 10 publications were negative, one was positive and 4 proposed a scientific-based approach.

Assessing the role of the species in ecosystems and its economic impact is a very difficult task that requires an integrated and objective approach and long-term consistent research. Unfortunately, this task is yet to be accomplished. However, the wolf in the USSR and Russia has always had a special attitude. Often, an oversight or simply theft of livestock was covered by the alleged wolf's predation. Unfortunately, recent evidence suggest that wolves remain "scape goats" (Zheleznov-Chukotsky, 2016).

WOLF DISTRIBUTION, NUMBER, AND POPULATION DENSITY

The most recent (2011–2015) wolf population estimate in Russia is 39.98 ± 1.20 thousand animals, and this large number is accounted to both wolf ecological plasticity and the lack of hunting pressure as a result of expensive hunting equipment (Kolesnikov et al., 2016). Below we, first, discuss historical changes of wolf population, second, report methods of abundance estimation, and then wolf dynamics in several Russian regions namely Komi, Dagestan, and Sakha Republics (northwest, southwest, and northeast of Russia, respectively) as well as local studies from Verkhne-Kondinsky (Khanty-Mansi Autonomous Okrug) and Lazo (Primorsky Krai) Nature Reserves.

Overall, wolf population number in Russia is tightly linked to Russian history. After World War I and Russian Civil War (1914–1923), wolf population increased dramatically. Then, it was brought down by intense population control. However, during World War II (1939–1945) wolf control was stopped and the population increased again. Afterward, bounties were paid to kill wolves, and the population declined (Bibikov, 1985). In 1990s, after the Soviet Union collapsed, population control stopped and the number of wolves skyrocketed (Bragina et al., 2015).

Wolf surveys are conducted in Russia with several methods: winter track counts (Bragina et al., 2015), home range mapping (Stepanova and Okhlopkov, 2020), and camera traps surveys (Zheltukhin and Ogurtsov, 2018; Volkov, 2020). For winter track counts, established transects are followed every year, and number of tracks crossing a transect is counted; second part includes following each species daily routes to estimate daily travel distance. Two numbers provide density estimation with Formozov's formula: number of track crossings and daily travel distance (Bragina et al., 2015). Second method requires mapping a territory of each pack and then estimating the number of animals in a pack. Latter method is labor-intensive but more precise; in fact, difference between two methods' assessments can be disagree by 2–3 times with winter track count providing inaccurate numbers (Stepanova and Okhlopkov, 2020; Volkov, 2020). Camera trap surveys provide abundance indices rather than population numbers, for example a number of animals per camera trap-days, and are expensive as they require camera traps arrays placed representatively in all habitat types. The most widely used index for camera-trapping data is the number of focal species captures per trap day (O'Brien, 2011), also often referred to as relative abundance index (RAI). As "capture" here is each series of photos or videos of the focal species made during a given time interval. Usually, camera traps are used within protected areas. For example, a wolf pack of 10–13 individuals was observed with camera traps in Kerzhensky Nature Reserve (Nizhny Novgorod Oblast; Volkov, 2020); similar wolf abundance was reported for Central Forest Nature Reserve (Tver Oblast, Central Russia; Zheltukhin and Ogurtsov, 2018).

The northeast of European Russia (Komi Republic) was inhabited by 2 wolf subspecies, arctic and taiga wolves, in 1930–1950s, which concentrated, respectively, in the northern and southern parts of Komi Republic. Wolf abundance in open habitats was significantly higher than in forested ones, and habitat type was the only abundance driver while hunter number and moose *Alces alces* density did not matter. In 1980s though two large clusters were formed: one included wolves in the northern and eastern parts while one—wolves in the central, western, and southern parts of Komi Republic. The most important driver of wolf abundance was moose and reindeer population density. Wolf penetration deep into the territory and its wide dispersal are associated with the landscape transformation by humans. Forest fragmentation, the growth of mosaicism, the emergence of large areas with young forests, and the road network development contributed to the wolf range expansion in Komi Republic (Korolev, 2016).

At the Northern Caucasus, the number and distribution of carnivores, including wolves, has been impacted by land use change: forest disturbance, agriculture development, melioration, and establishment of protective forest belts (Sukhomesova, 2013). For example, in Dagestan Republic (eastern Caucasus), wolf population is estimated at 2,750 individuals (Yarovenko, 2015). Hunters and fishermen are involved in the wolf population regulation within assigned hunting grounds. Despite the population control, there has been a slight tendency toward a number increase within those hunting grounds in 2013–2016, while throughout the whole Dagestan Republic the increase of wolf population has been even more significant (Yarovenko, 2015).

Survey of the huge Sakha Republic area, > 3,000,000 km^2, resulted into 0.01 wolves/1,000 ha (Stepanova and Okhlopkov, 2020). This density is 5 times lower than the desirable goal set by the Russian Ministry of Natural Resources. Nevertheless, the authors make a point that total number of wolves in Russia in 2019 is at least twice as large as it was 40 years ago, 55,000 vs. 25,000, while the annual harvest of wolves is two times lower, 23% vs. 55%. Wolf population has been increasing in Sakha Republic, though the highest number was observed in 2011–2012, then declined in 2013, increased until 2019, and declined again in 2020. An additional driver of the wolf population increase is so-called synanthropic wolves i.e., wolves feeding on livestock. Labutin (1950 cit. by Stepanova and Okhlopkov, 2020) identified three "types" of Yakutian wolves based on their feeding behavior: tundra wolves predominantly feeding on wild and domestic deer, central taiga wolves feeding on mountain hare *Lepus timidus*, and southern taiga wolves preferring moose and red deer *Cerphus elaphus* (Stepanova and Okhlopkov, 2020). Recently, the white hare population in Sakha Republic has decreased leading to increase of wolf attacks on domestic reindeer and free-grazing horses (Safronov, 2016). The authors conclude that wolf population number exceeds desirable by 2–3 times. A mass-media campaign was launched to fight the "wolf threat" in the Republic, resulting in more funding allocated to regulate wolf population.

Long-term dynamics of the game species density in the Verkhne-Kondinsky Nature Reserve (Khanty-Mansi Autonomous Okrug) provides data on wolf population density dynamics in 1970–2010 (Vorobiev, 2015). The average density was 0.05 individuals per 1,000 ha. Wolf population was surveyed in 1975, 1994, 2009. The maximum populations number was 30 individuals, the long-term average was 12 individuals. The wolf population growth was not always associated with its prey increase. For example, average wolf density was higher in 1990s than in 1980s, 0.07 vs. 0.02 individuals/1,000 ha while moose breeding in adjacent territories decreased significantly at the same time, probably forcing wolves to move toward high abundance of ungulates.

Interaction with a larger carnivore results into wolves being displaced by Amur tigers *Panthera tigris* (Miquelle et al., 2005), according to habitat suitability modeling for both species (Voloshina et al., 2014). Study period spans 1960–1989 and includes 566 wolf and 2,543 tiger locations within and around Lazo Nature Reserve, Russian Far East. In 1960s and 1970s, out of 19 WolrdClim variables (Hijmans et al., 2005) main environmental variables impacting wolf presence was annual precipitation and precipitation of wettest quarter; in 1980s, when wolf population declined, it was precipitation of coldest quarter. Amur tiger presence was mostly impacted by temperature metrics: maximum temperature of warmest month in 1960s and annual mean temperature in 1970s. Only in 1980s, annual precipitation started playing the most important role for tigers. Overall, habitat quality has been improving for tigers and declining for wolves across the study period.

WOLF MANAGEMENT

In spite of fundamental ecological and societal importance of wolf population dynamic and management, there is currently no strategy nor action plan for population management other than encouragement for wolf killing and bounties for wolf pelts. At the same time, killing wolves can exacerbate the situation instead of improving it, while other methods of population control are more effective (Bondarev and Kotlov, 2006, 2007, 2008; Suvorov and Kirienko, 2008; Bondarev, 2012a, 2013). Both A.Y. Bondarev and A.P. Suvorov, active members of WWG in the 1980s, embraced the ideas of population self-regulation within the system "ungulates—predators. Using buffer zone hypotesis (Mech, 1977, 1979)". Below, we discuss disadvantages of opportunistic killing and advantages of other methods.

First, we believe that an approach to wolf population control should be region- and habitat-specific. Intensive control is required in areas where wolves have a significant impact on livestock and game mammals e.g., in forest-steppe, regions of wild ungulates active exploitation, and remote livestock husbandry (Bondarev, 2012a). In other words, it is important to focus efforts on control of steppe synanthropic wolves. At the same time, mountain taiga wolves should not be controlled since they feed mainly on wild ungulates in slightly disturbed habitats (Suvorov and Kirienko, 2008). Also, the polar wolf of the Yenisei Territory (Central Siberia) should not be managed with aircrafts and snowmobiles, since this led to the total population extirpation in the past (Suvorov, 2016a). Similar concerns about complete extirpation of wolves with high-speed vehicles are raised in European Russia e.g., Belgorod Oblast (Chervonny and Gorbacheva, 2014).

In our opinion, the most effective strategy to control wolves is removing cubs from the dens because it reduces population number while maintaining the population structure at the same time. This way, a wolf population ages, and older wolves produce fewer cubs. In the south-western Altai Kray, this strategy successfully and cheaply prevents wolf immigration from numerous Kazakhstan population, excludes feral dogs from the wild, and, mostly important, significantly reduces wolf damage on livestock and wild ungulates maintaining the highest population density of roe deer and moose in the region (Bondarev, 2012a). If removing cubs is not possible, for example because of protected area regime or proximity to a state border, this procedure should be applied to adjacent areas while preserving breeding pairs. When a mating pair is killed, the boundaries of their home range and buffer zones are erased, the intrapopulation structure and spatial predator-prey relationships are disrupted. The destruction of wolf packs and consequent population size decrease facilitates wolf-dog hybridizations leading to a quick population recover. Therefore, such control does more harm than good for wild ungulates (Suvorov and Kirienko, 2008). Stable breeding pairs will prevent wolf immigration and reduce the damage from wolves, since the pairs need several times less food than large packs. This approach, in spite of being labor-intensive, keeps population spatial structure due to preserving adult breeding pairs as well as denning and territorial fidelity inherent to wolves (Bondarev and Kotlov, 2007).

Another popular approach for wolf population control is professional brigades of wolf hunters (Bondarev, 2013; Suvorov, 2016b). This idea was also discussed at the WWG meetings in the 1980s and was recognized as useful and cost-efficient as compared to the aviation use (Suvorov, 2016b).

In spite of proven and efficient management tools described above, there is a big hunting lobby promoting other approaches: increasing the hunting season length, bounties for wolf pelts, and use of currently prohibited foot traps and snares (Budlyansky and Sinilov, 2019). Advocates of this approach consider wolves a "pest species," and do not take into account wolves' population structure, social organization, and self-regulation mechanisms. According to this point of view, wolves should be hunted all year around instead of the current season of 5.5 months/year, and bounties of 10,000–20,000 rubles ($100–200) should be paid for each killed wolf from the federal budget. Currently, the main obstacle preventing evidence-based scientific approach to wolf management is a requirement #138 signed on April 30, 2010 directing to keep maximum wolf density in hunting grounds below 0.05 individuals/1,000 ha (Budlyansky and Sinilov, 2019)/While this document indicates the upper limit of wolf density, nothing is said about the lower one, leaving a loophole for hunting outside of the hunting period.

One of the hunting lobby's arguments is assumption that wolves have high impact on ungulates. For example, Bersenev et al. (2012) provide calculations of wolves' predation pressure: "Every year wolves kill about 34 thousand moose, 123 thousand roe deer, 20 thousand red deer, and 140 thousand reindeer. Lost profit for the hunting economy as a result of the annual feeding of one wolf is 0.6 moose + 2.5 reindeer (or another species replacing it) + 0.37 red deer + 1.85 roe deer + 0.7 wild boar + 49.7 hares + farm animals weighing 77.6 kg." They conclude that "at present, the necessity to control for wolf number in the Russian Federation is obvious. With a 50% reduction of the wolf population, the positive economic effect from the ungulate number increase alone will be at least 4,000,000,000 rubles ($40,000,000) annually." This calculation does not account for (1) compensatory as opposed additive impact of carnivore on ungulates and (2) species other than ungulates in wolf diet, especially important during summer time (Kolpashchikov, 2016; Suvorov, 2016a).

We should mention that in spite of the strong hunting lobby, some ecologists do recognize importance of wolves for ecosystems and promote wolf conservation (Suvorov, 2016a,b). For example, there are no more than 30 wolves in Samara region (53,600 km^2), and it is not clear how many of those belong to local population as opposed to migrants and hybrids with dogs. For such a large territory, this is an extremely small number. In the neighboring Orenburg region, there are 200 wolves, and it was suggested that wolves should be included in the local Red List (Rigina and Vinogradov, 2007a,b).

WOLF-UNGULATES RELATIONSHIP

Below we describe 3 studies of wolf-ungulate relationships. Neither study found that wolves limit ungulate density. First study was conducted in the ecosystem with multiple ungulate species while second one in a system where moose is wolves' exclusive prey, and the 3rd study was theoretical.

In Belgorod region, wolves prey on moose, red deer, wild boar, and roe deer (Chervonny and Gorbacheva, 2014). In 1964–2011, wolf number declined from 103 to 12 individuals, and then to 0 in 2013. The highest population density of > 100 animals was observed in 1964 and 1973, and also more than 70 wolves were observed in 1990s. For the rest of the study period, there were 25–30 individuals in 2–3 packs, and less than half suitable wolf habitats were occupied. Ratio of ungulate/wolf number varied from 20 to 285, with 20 ungulates per 1 wolf observed only at the beginning of the study period when it resulted in a sharp decline of wolves. For most of the study period, number of wolves was too low to impact ungulates. Local wolf extinction was caused by excessive hunting and increase of the snowmobiles use for hunting (Chervonny and Gorbacheva, 2014).

In Karelia Republic, at the Russian northwest, wolves predominantly hunt moose. In 1961–2020, wolf/moose ratio always was higher than 1–23, usually much higher (Danilov et al., 2020). Wolves did not consume more than 6–7% of the winter moose population and mostly ate calves and females. In winter, wolves killed 35–80% of the moose population while in the summer it was only 10–17%. The nature and efficiency of wolf hunting moose barely depended on a pack size (Danilov, 2017). In 2018, the highest number of wolves was killed in Karelia (250), and the total number of this carnivore in the region has recently decreased to 300–350 individuals (Danilov et al., 2020). The high wolf harvest rate results from cash bounties for wolf pelts and reduced payment to hunt ungulates.

Agent-based modeling of wolf-moose system with AnyLogic software also provided evidence for moose driving the wolf population, not wolves limited moose (Elufereva and Limanova, 2020). In spite of erroneous assumption that wolves breed twice as opposed to once a year (Mech, 1970; Packard, 2003), the author concluded that wolf number followed their prey density. The authors fitted a large number of models varying the wolf hunting parameters (in a pack or alone), food availability (moose density), temperature, human hunting pressure on wolf and moose as well as presence of infection (Elufereva and Limanova, 2020). At a low moose number, the wolf disappeared from suboptimal habitats without being pursued by hunters. When hunters were introduced into the model with a high probability of wolf extermination, the extinction of species occured. After introducing an infection into the model that killed 50% of any species, populations recovered in 2–3 years (Elufereva and Limanova, 2020).

WOLF DIET AND PREY PREFERENCES

Wolf diet was analyzed in European Russia, Kaluzhskiye Zaseki Nature Reserve, where wolf prey include red deer, wild boar, moose, European bison, and roe deer, and Russian Far East, in Bolshekhetskirsky and Sikhote-Alin Nature Reserves where prey species include red deer, wild boar, roe deer. The latter reserves protect an interesting ecosystem where wolves interact with Amur tigers. Prey species composition was calculated as occurrence rate of various species in feces identified based on hair cuticula characteristics (Teerink, 1991; Rozhnov et al., 2011). This method does not account for prey species body mass.

In forest habitats of Kaluzhskiye Zaseki Nature Reserve, wild board and roe deer are the main prey species for wolves (38.7% and 30.6%, respectively, N = 87) in spite of moose, European bison, and red deer also being available within a pack's home range. However, wolves prefer wild boar during the snowless period and roe deer in the snow period (Hernandez-Blanco and Litvinova, 2003).

In Bolshekhetskirsky Nature Reserve ungulates also provide the most of wolves' diet—92.5%. However, the most common species is red deer making 66.3% of wolf diet in the snow period and less in snowless period. In comparison with protected lands, livestock carrions (42–55%) and small- and medium-sized mammals (33–42%) dominate wolf diet on agricultural fields surrounding Bolshekhetskirsky Nature Reserve (Tkachenko, 2010). Interestingly, this study spans a period of 1989–2005, and since the mid-1990s, wolves were forced out of the reserve by Amur tigers and barely reappeared in some winter seasons.

Influence of wolves and tigers on other carnivores was also studied in the Sikhote-Alin mountains (Salkina and Eremin, 2017) by analysis of carnivore occurrences (more than 4,000 data points). Wolves negatively impacted domestic dogs, common raccoon dogs, European badgers, European lynx, and Amur leopard cats but did not affect red foxes. Amur tiger population increase correlated with the wolf population decrease. The authors suggest that in the absence of wolves, their niche can be occupied by feral dogs. Therefore, wolf control during low population density periods is not desired (Salkina and Eremin, 2017).

SPACE USE

In this section, we describe spatial structure of a pack's home range, habitat selection, individual movements, home range sizes and individual daily travel distances.

A wolf pack's home range in forested habitats of European Russia (Voronezh Nature Reserve), calculated as a minimal convex polygon, is 146–167 km^2 (Hernandez-Blanco et al., 2005). Average minimal convex polygon of individual wolf home ranges in steppe zone of Asian Russia (Daurian Nature Reserve) is much larger, 832 km^2, exceeding wolf home rages in European and North American forested habitats by 2–4 folds, perhaps due to low cost of moving through the snowless landscape (Kirilyuk et al., 2019). Large distances of movements from a place of birth were recorded for 2 year old wolves of both sexes (Kirilyuk et al., 2020). Interestingly, daily activity of 17 GPS-collared wolves in the Daurian steppe (Kirilyuk et al., 2021) revealed that during invasions of neighboring packs and, also, long-distance departure from the habitat, wolves move over long distances and for longer time. In summer, activity is higher than in winter.

A concept of wolf pack home range structure proposed by Hernandez-Blanco et al. (2003a,b, 2005) identifies 3 spatial subunits: home core, vital space, and spatial shell. Home core includes den sites and rendezvous-sites. Vital space is used by adult animals to hunt with their offspring. Spatial shell is a peripheral part of the home site usually used by yearlings from the rut season until the mid-summer. In case there are so-called buffer zones between neighboring packs, they are shaped by the spatial shells from the neighboring home sites. This structure of the space use by wolves also impacts ungulates' spatial distribution (Kazmin et al., 2001). Home ranges of neighboring packs are separated with so called buffer zones shaped by spatial shells. Continuation of the territory use through generations is provided through the replication effect when two females, an old and young one, breed at the same time within a pack's home range.

Wolf movement analysis reveals that wolves have strong preferences for using roads and moving along ravines and rivers as opposed to crossing them (Melnik et al., 2007). At the same time, terrain characteristics of a route depend on a route's type. Melnik et al. (2007) identify several route types: search-hunting, marking, search-social and linear. On search-hunting and search-social routes, wolves more often cross terrain isoclines, make turns, loops and temporarily separate from group members than on marking and linear routes. Among all habitat types, wolves choose those preferred by ungulates (Melnik et al., 2007).

EXPERIMENTAL RESEARCH ON WOLF BEHAVIOR

Yachmennikova et al. (2009) described so-called "Transformational" period in ontogenesis of wolf pups: a dramatic increase followed by a decrease in the number of behavioral pattern types between 75th and 115th day. Ontogenesis of wolf behavior (Yachmennikova and Poyarkov, 2010, 2011) was studied with software Theme 5.0 from Noldus designed specially to reveal hidden temporal patterns (Magnusson, 2000). The activity type of each animal was registered each minute with the time slice method. Eighteen types of activity were recorded. The sequential stream of activity of four animals was analyzed to find time patterns that are repetitive events not randomly following each other within the critical time interval. Often, pattern types including various activities were observed (1,300–13,500 types). Although most patterns consist of 2–3 elements, complex sequences of 15–16 behavioral acts are also noted. Over the linear sequence of initial events, a complex non-linear and clearly ordered organization of the other type is revealed.

Ontogenetic development of wolf pups was studied to identify conditions critical for successful reintroduction. Badridze (2017) found that foot massage of mother's mammary glands and opportunity to suck is dramatically important for small pups. If pups cannot exercise these behaviors, they become overstimulated, and development of their manipulative behavior is impeded leading to challenges after reintroduction. Reintroduction success also depends on food hiding behavior (Badridze, 2010b), hunting behavior (Badridze, 2010a), and avoiding of humans and livestock (Badridze et al., 1992). Successful reintroduction of 4 wolf groups led to establishing 4 wolf packs. In 3 years after the reintroduction, feral dogs disappeared from the area and roe deer travel distance increased. Wolf hunting success decreased during first 6 months after the reintroduction and then remain stable (Badridze, 2017).

MORPHOLOGY OF WOLVES

Morphological approach, and craniometric measurements in particular, represent an effective tool for studying the polymorphism and differentiation of mammal populations (Palmeirim, 1998; Gauthier et al., 2003). In Russia, the morphological research traditions are strong; therefore, the morphological variability of the gray wolf has always been the subject of a wide range of studies. The results of these studies performed up to the half of the 1980s were summarized in the monograph "The Wolf. History, Systematics, Morphology, Ecology" by Bibikov (1985). To our knowledge, few studies on wolf morphometry, including craniometry, have been published over the past two decades.

Wolf craniometric variability in the Russian Caucasus (Republics of Kabardino-Balkaria, North Ossetia, Dagestan, and Adygea) and Transcaucasia (Azerbaijan and Georgia) was analyzed with 67 skulls (Tembotova and Kononenko, 2007a,b). The authors performed a comparative study of the sexual and geographic variation. In all regions of the study area, they found a high sexual dimorphism in size. The largest wolf skulls were found in Azerbaijan. Wolves from Russian Caucasus had intermediate skull sizes, while the smallest skulls were found in Georgia.

Studies on morphometric body parameters of wolves from a huge area of Western Siberia detected a significant geographic variation of the wolf sizes (Bondarev, 2012b). However, neither Allen's (Allen, 1877) nor Bergman's (Bergman, 1847) rules were confirmed. The largest wolves of Siberia inhabit areas of the northern and middle taiga followed by wolves of tundra, while the smallest dwell in the forest-steppe zone (Bondarev, 2012b). Despite the huge dataset, the author did not find taxonomic differences in wolves of the Western Siberia.

Large geographic variation of craniometric parameters and sexual dimorphism in skull size was found at the Russian Far East and Kamchatka based on 410 skulls (Yudin, 2013). Patterns of variability showed the complex population structure and no direct i.e., clinal variation. A possible reason for the significant variation of the population craniometric measurements is the geographic isolation and direct adaptive response of the populations to the environmental conditions (Yudin, 2013).

Morphometric study of 363 skulls and 242 carcasses of polar and forest wolves from Yenisei Siberia (Krasnoyarsk Region and the Republic of Khakassia) drew the same conclusion about the wolf population structure (Suvorov, 2017a,b). There also was no clinal variability; craniometric differences between polar and forest wolves were not found. The largest Russian wolves live in the northern and temperate forests while smallest live in the forest-steppe zone. Overall, wolf body and skull dimensions are shaped by environmental conditions, which, in turn, vary significantly across the study area (Suvorov, 2017a,b).

Wolf craniometric variability was studied in details in the center of European Russia (Korablev N. P. et al., 2021). With 326 skulls collected over 65 years from Tver, Smolensk, Yaroslavl, and Vologda regions, the authors analyzed various drivers of population craniometric polymorphism. A high craniometric variability and sexual dimorphism of skull sizes has been found. Polymorphism is mostly determined by temporal and spatial trends, sex and age, in order of the effect size. For example, female skulls are 3.6% smaller due to sexual selection as well as differences in male and female diets. Temporal polymorphism i.e., a weak increase of morphological parameters with time is likely driven by increase of moose and wild boar population abundance, leading to prevalence of both species in wolves' diet. Stochastic drivers are also at play e.g., high total mortality and disruption of the population social structure as a result of hunting pressure.

POPULATION GENETICS

The rapid development of molecular genetic techniques gave rise to population genetic studies of wolves in Europe (Randi, 2011; De Groot et al., 2016; Hindrikson et al., 2017). However, in Russia, this area of species biology is still poorly understood. So far, there are only a few publications on the wolf population genetics in Russia, most of them with Siberian wolves.

Based on the study of 97 individual wolves with 6 microsatellite markers, the taxonomic status of the forest-steppe and mountain-taiga wolves of Altai was clarified: the populations inhabiting various biotopes belong to the same subspecies *C. lupus altaicus* (Vorobyevskaya and Baldina, 2011).

High genetic diversity was found among 163 individuals from Siberian regions including Altai Krai, Altay Republic, Tyva Republic, Republic Buryatia, Republic Khakassia, Krasnoyarsk Krai, and Zabaykalsky Krai (Bondarev et al., 2013). Expected heterozygosity He was 0.72–0.82 and a mean number of alleles Na was 9.83–12.67 with an average He and Na of 0.65 and 7.67, respectively. The mountain-taiga populations of Altai and Sayan mountains had the highest genetic diversity, as did steppe wolves at south-west of Altai Krai, perhaps due to prey abundance in these areas. Plain-taiga populations of Krasnoyarsk Krai, Evenkia and Salairskiy Kryazh in Altay Krai had the smallest genetic diversity. In general, described genetic structure coincided with landscape zones.

Talala et al. (2020) broadened a geographical span of 2 above-described papers (Vorobyevskaya and Baldina, 2011; Bondarev et al., 2013) with samples from Yakutia Republic thus analyzing 270 individuals and 7 microsatellite loci. Relatively high genetic diversity of Siberian wolves was confirmed: He 0.60–0.71 and Na 4.50–5.83 with an average He and Na of 0.68 and 5.18, respectively. Siberian wolf populations are connected by the active gene flow. However, geographical distribution of previously described subspecies (*Canis l. sibiricus, C. l. altaicus, C. l. turuchanensis, Canis l. var. orientalis*) was confirmed by the genetic data.

A detailed genetic study of wolves in European Russia genotyped 101 wolves and 32 dogs at 11 microsatellite loci from Tver and Pskov regions (Korablev M. P. et al., 2021). The study's goal was assessment of the spatial and temporal dynamics of wolf population structure and genetic diversity over 30 years during population number increase, and assessment of wolf-dog hybridization rate. The authors found that the studied area is inhabited by a single wolf population confirming previously reported data (Pilot et al., 2006; Sastre et al., 2011). This population has high genetic diversity (He = 0.79 and Na = 10.00) which is more than most of European populations have (Korablev M. P. et al., 2021). The studied wolves represent a highly polymorphic part of the continuous *Canis lupus lupus* population with a relatively low rate of hybridization (around 3%) and, hence, can be viewed as a natural reservoir of the subspecies' gene pool.

WOLF HELMINTHOLOGY

Wolf helminths have been studied in several Russian regions. Two methods are mainly used: (1) a complete helminthological examination of wolf carcasses with the Scriabin method (Skryabin, 1928) and (2) the identification of eggs and cysts with microscopes (Esaulova et al., 2015). Eighty seven species of wolf helminths found in the Holarctic: 29 species of cestodes 4, 37 nematodes, and 17 trematodes. Out of 87, 68 were found in Russia (Konyaev and Bondarev, 2011). Overall, helminthological studies highlight importance wolves as a reservoir for helminths and potential source of infection for domestic and synanthropic animals.

Several papers cover wolf helminths in Russian regions. For example, 15 species of wolf helminth was found in Volgograd region: 7 nematodes, 6 cestodes, and 2 trematodes. Toxascaris leoninae (64.7%), Dirofilaria immitis (47%) and Toxacara canis (35.2%) are the most common nematodes. Taenia pisiformis (41.1%) and Echinococcus granulosus (23.5%) are the most common cestodes (Shinkarenko and Kolesnikov, 2011).

In Dagestan, 18 species of wolf helminths were found including trematodes, cestodes, and nematodes. Notably, helminth species composition differed between mountain, foothill and lowland Dagestan wolves. Single-host helminths (nematodes) and two-host (cestodes) were the most common (Bittirov et al., 2010).

In the North-West Caucasus 17 species of wolf helminths were identified (Itin and Kravchenko, 2016). In Kabardino-Balkaria Republic, also part of the North Caucasus, 12 species of wolf cestodes and nematodes were found (Kabardiev and Bittirov, 2020) including, as well as in Dagestan (Bittirov et al., 2010), dangerous to humans *Echinococcus granulosus* and *Dipylidium caninum* with prevalence of 80.0 and 40.0%, respectively.

Only 6 species of wolf helminth species were found in Kaluzhskiye Zaseki Nature Reserve, and 3 species—in Kalmykia (Esaulova et al., 2018), perhaps because the search for helminths was done with wolf feces rather than with carcass surveys.

In Kirov region, 19 species of helminths were identified including 1 trematode, 7 cestodes, and 11 nematodes. These were helminths such as *Alaria alata*, *Dipylidium caninum*, *Taenia hydatigena*, *Taenia krabbei*, *Taenia pisiformis*, *Tetratirotaenia polyacantha*, *Echinococcus granulosus*, *Echinococcus multilocularis*, *Crenosoma vulpis*, *Thominx aerophilus*, *Capillaria plica*, *Capillaria putoria*, *Trichinella nativa*, *Uncinaria stenocephala*, *Toxascaris leonina*, *Toxocara canis*, *Toxocara canis*, *Ancylostoma caninum*, *Strongiloides vulpis*, *Molineus patens*. The most common species was the trematode *Alaria alata* (73%), the cestodes *Taenia hydatigena* and *Echinococcus granulosus*, and the nematodes *Uncinaria stenocephala* and *Trichinella native* (Maslennikova, 2012).

In Ivanovo region, wolves were infested with 12 species of helminths (Andreyanov et al., 2009; Kryuchkova et al., 2011; Abalikhin et al., 2013). One species of trematodes, *Alaria alata*, was found in the intestines of animals, with prevalence of 93.8% of infected animals and infection intensity (number of helminths in each infected individual) of 8–1,056 specimens.

There are several papers where researchers focused on one or more species of the same genus, as a rule, especially dangerous helminth diseases. For example, Andreyanov (2020) described reservoirs of alveococcus infection in game carnivore species at hunting grounds of Vladimir, Nizhny Novgorod, Moscow, Tver, Oryol, and Bryansk regions of Central Russia as well as the Karelia Republic in 2007–2018. These regions have high human population density as well as high number of hunters and pet owners. A complete or partial helminthological autopsy was conducted with Scriabin method (Skryabin, 1928) for 262 animals, including 193 common red foxes, 28 feral dogs, 16 raccoon dogs, 16 feral cats, 6 wolves, 2 brown bears, and 1 lynx. Cestodes of *Echinococcus multilocularis* was found in 46 foxes (23.8%), 3 raccoon dogs (18.7%), 3 wolves (50%), and 1 feral dog (3.6%). The peak tapeworm prevalence in carnivores was noted for foxes and raccoon dogs.

Trichinosis is another wolf's helminthosis dangerous for humans. Across Russia, trichinosis prevalence is 18.5% (Tulov et al., 2013), for example 20% in Altay Krai and Altay Republic (Malkina and Konyaev, 2013). In all cases, wolves had *T. nativa*.

RABIES

In spite of rare occurrence of rabies in wolves as compared to red fox, wolves still carry this disease. For example, in 2013, 19 cases of rabies were registered in wolves in Russia (Novikova and Petrova, 2015). In Central Russia, in Lipetsk, Moscow, Tver' and Yaroslavl' regions, there was 5 cases of rabies in wolves, or 0.5% of all cases (N = 1,089 animals). In Tver' region, the most often rabies hosts are raccoon dogs (39%), and perhaps wolves contract rabies while preying on raccoon dogs (Nesterchuk et al., 2019).

In Yakutia, rabies also has been reported in wolves, although polar foxes are the main rabies reservoir there (Zakharova, 2019).

Recently, rabies rates have increased in many regions of Russia. The most cases are observed in the south of Western Siberia and the central and southern parts of European Russia (Poleshchuk et al., 2012, 2019). Number of rabies cases have increased in Transbaikalia, Buryatia, and Krasnoyarsk Regions (Sidorova et al., 2007; Botvinkin et al., 2019). Meltsov et al. (2020) provide a detailed analysis of the rabies situation in Irkutsk region, the only Russian region free from rabies, including prevalence of rabies in red foxes and wolves. Rabies transmission can be curbed with peroral regular vaccination. Meltsov et al. (2020) identified the areas of the most likely rabies penetration into Irkutsk region, and initiated peroral vaccination of foxes and wolves in these areas up to 50 km depth from a point of possible penetration. This strategy has been highly efficient. However, Meltsov et al. (2020) warn about the risk of rabies transmission through pets.

In adjacent to Irkutsk region Buryatia Republic, two outbreaks of rabies have been reported in wild animals in 2011–2013 and 2017–2019. The most affected species was red fox. Only few cases of rabies have been reported among wolves. Both outbreaks of rabies in Buryatia took place during the years of red fox peak numbers and low numbers of wolves (Shchepin et al., 2019). Rabies was also registered in Transbaikalia (Botvinkin et al., 2019).

In summary, the rabies situation in Russia is becoming challenging. Recently, there has been a shift from natural (autochthonous) foci and carriers of the disease to synanthropic ones, with feral dogs and cats as a main source of infection. Large-scale vaccination of wild, feral and domestic animals is needed as an effective measure to curb rabies (Novikova and Petrova, 2015; Meltsov et al., 2020).

WOLF PALEONTOLOGY

Paleontological studies is a special section of our review. There are few of them but usually it is high-quality research published in high-ranked journals. Usually, these studies are co-authored by big international teams including Russian specialists who found some paleontological remains on Russian territory. For example, Lee et al. (2015) analyzed mDNA of 14 canid remains aged 17,000–360,000 years before present. One of these samples was identified as a separate species named Canis cf. variabilis. All the samples had affinity with pre-domesticated as well as modern dogs leading Lee et al. (2015) to question an opinion about European origin of domestic dogs.

Ní Leathlobhair et al. (2018) analyzed ancient wolves to look into the origin of American dog. American dogs arrived from Siberia through Beringia about 9 thousand years ago. Genetic analysis reveals that American dogs are closer to Siberian wolves than to American ones. Sinding et al. (2020) came to similar conclusions regarding sled dogs. Present-day sled dogs are closely related to Siberian 9,500-year-old dogs and 33,000-year-old Pleistocene Siberian wolves, but not modern American wolves. The importance of the Beringia wolf expansion during the last glacial maximum is demonstrated by Loog et al. (2019): "Our results suggest that contemporary wolf populations trace their ancestry to an expansion from Beringia at the end of the Last Glacial Maximum and that this process was most likely driven by Late Pleistocene ecological fluctuations that occurred across the Northern Hemisphere. This study provides direct ancient genetic evidence that long-range migration has played an important role in the population history of a large carnivore, and provides insight into how wolves survived the wave of megafaunal extinctions at the end of the last glaciation. Moreover, because Late Pleistocene gray wolves were the likely source from which all modern dogs trace their origins, the demographic history described in this study has fundamental implications for understanding the geographical origin of the dog."

Canid remains from the Yana paleolithic site (Republic of Yakutia) shed light on the early wolf domestication (Nikolskiy et al., 2018). Most remains belongs to "intermediate" between wolves and dogs canids with worn, partially missing teeth and various bone pathologies, often small in body size. As modern experiments show, such pathologies accompany tolerance to people. Perhaps, those canids used human settlements as a food source in spite of human-wildlife conflict risk due to their tolerance to humans, at the cost of accumulating various anomalies. Also, some evidence of wolf totemic cult was found at the Yana site. Thus, self-domestication of Yana wolves could be considered one of the first steps of wolf domestication (Nikolskiy et al., 2018).

Various wolves from Siberia aged 14–50 thousand years reveal two lines of wolves: Pleistocene wolves morphologically close to modern Siberian wolves, and shorter-faced "Paleolithic dogs" morphologically intermediate between wolves and dogs (Ramos-Madrigal et al., 2021). Both lineages do not form a monophyletic group. Pleistocene wolves are represented by several extinct lines that could be ancestral forms of Arctic and some Asian dog breeds (Ramos-Madrigal et al., 2021). Remains of Pleistocene wolves aged 40,000–50,000 years were found in 2 caves of Altay mountains, Razboynichya and Fanatikov. A new wolf species was identified based on its gracile skull shape and smaller brain size and named *Canis subtilis* (Ovodov and Martynovich, 2011).

TABLE 1 | Distribution of publications by significance level in databases.

	Web of Science Q1	Web of Science Q2	Web of Science Q4	Scopus	Other journals	Monographs	Compilation (Collection)	Ph.D. thesis
Introduction			2			10	1	
Distribution, number, density					2	3	6	1
Management					7	4	2	
Wolf-ungulates					3	1	1	
Diet, prey					2	1	1	
Space use			1	3	2		2	
Behavior			4			2	1	
Morphology				2	3	2	2	
Genetics		2	1		2			
Helminthology				1	9		5	
Rabies			2		7			
Paleontology	4	2			3			
Total	4	4	10	6	40	23	20	1

CONCLUSION

Papers on Russian wolves have been published in sources of varying accessibility and varying scientific significance. A brief analysis of the sources we listed shows an extremely uneven distribution of works depending on a study subject. **Table 1** shows the distribution of works depending on the subject (corresponding to our review) by journals, monographs and compilation. We divided publications into journals indexed in Web of Science by quartiles, Scopus (if the journal is not cited in Web of Science but is cited in Scopus), other journals, Monographs or chapters in monographs, compilation combining thematic publications and Ph.D. dissertations thesis (**Table 1**). The distribution of works showed a sharp skew in the direction of hard-to-reach and low ranked sources. Only 24 studies (22%) are published in the international Web of Science or Scopus databases, while the remaining 85 studies (78%) are difficult to access for international scientific community preventing the integration of Russian wolf specialists to the world scientific community. Only paleontological research stand out being published in high-ranked journals, primarily due to large highly professional scientific teams in which Russian specialists take an active part. Such research areas as regional distribution, abundance, population density, relationship with ungulates, trophic ecology and management generally do not reach international scientific databases making results unavailable for the international scientific community.

Among all the countries overlapping with wolf, the Russian part of the wolf range is the largest one. Russian wolves live almost everywhere, with minor exceptions such as large cities and some Arctic and Pacific islands. Wolves occupy various habitats and geographical zones. Our knowledge about wolves has many gaps to fill; the lack of deep understanding is the main obstacle to the comprehensive assessment of wolf impacts on diverse ecosystems.

AUTHOR CONTRIBUTIONS

AP, MK, and JH-B collected literature and wrote the text (partially). EB carried out the general revision of the work. All authors contributed to the article and approved the submitted version.

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Spatial Determinants of Livestock Depredation and Human Attitude Toward Wolves in Kailadevi Wildlife Sanctuary, Rajasthan, India

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Gray wolves are capable of adapting to human-dominated landscapes by utilizing domestic prey as a source of food. Livestock depredation by wolves incurs a heavy economic loss to the villagers, resulting in negative attitudes toward the species and leading to increased conservation conflict. We used multi-state occupancy modeling on the interview data to assess the ecological factors governing livestock depredation by wolves. We also assessed the socio-demographic factors that may govern the attitude of villagers toward the wolf using ordinal regression. Over the past year, 64% of respondents reported a loss of livestock, in which goats (63%) comprised the major share, followed by sheep (22%) and cattle calves (15%). Wolves tend to hunt medium-sized domestic prey (sheep and goats) that commonly graze in open agricultural areas. The estimated livestock depredation probability of wolves was 0.84 (*SD* = ± 0.23). Depredation probability was influenced by habitat use by wolves, the extent of agricultural areas, scrubland area, and settlement size. Respondents with prior experience of livestock loss held more negative attitudes. Shepherds held more negative attitudes than other occupations. Increases in the respondent's age and education level reflected a positive shift in attitudes toward the wolf. High economic loss caused by livestock depredation by wolves can lead to retaliatory persecution of wolves. Adequate compensation for livestock loss, along with better education and awareness can help lead to coexistence between wolves and humans in multi-use landscape of Kailadevi Wildlife Sanctuary, Rajasthan, India.

Keywords: coexistence, human-wolf interactions, Indian grey wolf, interview surveys, multi-state occupancy modeling, spatial predation risk

INTRODUCTION

Wildlife conservation and management in India is mostly limited to protected areas (Ghosal et al., 2013). Large carnivores due to their large home ranges are more likely to come in contact with humans, with most of the human-wildlife interactions occurring at the edge of the protected areas where carnivores, people, and livestock overlap (Nyhus and Tilson, 2004; Woodroffe et al., 2005). Therefore, large carnivores residing outside the protected areas in highly human-dominated landscapes require effective management for their conservation (Linnell et al., 2001). For instance, snow leopards (*Panthera uncia*) in the Himalayan region and leopards (*Panthera pardus*) in India and Pakistan tend to kill more livestock near the human habitation where the livestock is high in number and easily accessible (Dar et al., 2009; Aryal et al., 2014; Miller et al., 2015), whereas tigers (*Panthera tigris*) generally depredate livestock inside the forest, away from villages and human habitation (Wang and Macdonald, 2006; Miller et al., 2015). However, due to the degraded status of their habitats, wolves (*Canis lupus pallipes*) in India generally reside outside the protected areas where most of the interactions between wolves and humans occur (Mahajan and Khandal, 2021). Conservation of carnivores in shared landscapes is the major challenge for the persistence of large carnivores (Chapron et al., 2014; Majgaonkar et al., 2019), therefore achieving harmonious coexistence of humans with carnivores is the ultimate goal for the survival of the carnivores in these shared landscapes (Linnell et al., 2001; Carter and Linnell, 2016).

The social drivers of human–wildlife interactions also play an important role in achieving coexistence (Dickman, 2010). Considering the importance of livestock to the local economy, understanding people's attitudes toward carnivores is also important for effective conservation planning (Bagchi and Mishra, 2006). It is thus crucial to identify and address both the ecological and social factors to understand the complex interactions between humans and wildlife (Gálvez et al., 2018; Lischka et al., 2018). People's perceptions and attitudes toward a species are based on personal experiences, social and cultural norms, knowledge of their surroundings, and beliefs associated with the species (Dickman, 2010), which affect the level of tolerance toward a particular species. Therefore, to ensure long-term persistence of a carnivore in a human-dominated landscape, it is pertinent to assess the relative roles of potential ecological and social drivers of human-carnivore interactions to better understand the social carrying capacity of a carnivore in a landscape.

Livestock depredation by carnivores is a complex phenomenon governed by multiple factors (Inskip and Zimmermann, 2009). Areas predisposed to livestock depredation are influenced by ecological factors like the availability of wild prey (Gurung et al., 2008; Kaartinen et al., 2009; Sharma et al., 2015), density of livestock (Mech et al., 2000; Wang and Macdonald, 2006; Aryal et al., 2014; Carvalho, Zarco-Gonzalez et al., 2015; Suryawanshi et al., 2017), habitat characteristics (Treves et al., 2004; Kaartinen et al., 2009; Suryawanshi et al., 2013; Davie et al., 2014), and livestock husbandry management (Kolowski and Holekamp, 2006; Wang and Macdonald, 2006; Abade et al., 2014). Apart from these, social factors like gender (Ogra, 2009: Koziarski et al., 2016), education level (Mkonyi et al., 2017; Behmanesh et al., 2018), religion (Dickman et al., 2014; Arbieu et al., 2019), and economic importance of livestock to a community, shape the attitudes, perceptions, and belief systems of people toward a carnivore (Dickman, 2010) and govern the type and severity of human response toward them. Identifying relevant ecological and socio-economic factors associated with livestock depredation is crucial to understanding complex human-carnivore interactions and accordingly prioritizing conservation activities.

Wolves, due to their large home ranges and dietary requirements, are difficult to conserve in small protected areas of India, where the average size is 240 km^2 (UNEP-WCMC, 2021). Moreover, most of these protected areas are surrounded by high densities of human settlements, and wolves in such human-dominated landscapes can utilize domestic prey as a source of food. Wolf predation on livestock severely affects the economy of the pastoral communities that barely manage to eke out a living from the highly overgrazed and degraded landscapes of semi-arid India (Mahajan and Khandal, 2019). This often brings them into conflict with wolves (Kumar and Rahmani, 2000; Krithivasan et al., 2009; Palei et al., 2013; Behmanesh et al., 2018), sometimes leading to retaliatory persecution of wolves by indirect means such as smoking out dens to kill pups (Shahi, 1982; Kumar and Rahmani, 2000; Singh and Kumara, 2006) and by using poison (Jhala, 2003; Mahajan and Khandal, 2019). For the small-scale households living near the protected areas, the loss arising due to livestock depredation poses a challenge to rural development and biodiversity conservation (Treves and Karanth, 2003; Khorozyan et al., 2015). This is particularly important for the conservation of wolves in India due to their persistence in human-dominated landscapes. Unlike tigers and leopards which commonly reside within the dedicated protected areas, wolf habitats do not come under the protected area network, and most human-wolf interactions occur due to the Wolf's dietary dependence on livestock and lack of wild prey (Mahajan et al., 2021).

In present study, we used a socio-ecological framework for examining human-wolf interactions in the human-dominated landscape of Kailadevi Wildlife Sanctuary. The covariates used to model the attack on livestock by wolves were selected based on earlier studies conducted on human-wolf interactions (Agarwala and Kumar, 2009; Krithivasan et al., 2009; Majgaonkar et al., 2019; Srivathsa et al., 2019; Rehman et al., 2021). We hypothesized that attacks on livestock will be more frequent in areas or habitats that are used by wolves (Majgaonkar et al., 2019; Srivathsa et al., 2019). Earlier studies have shown that wolves use habitats where livestock is easily accessible (Agarwala and Kumar, 2009; Mahajan et al., 2021). Presence of water and scrubland are defined as important limiting factors for wolves (Jhala, 2003; Singh and Kumara, 2006), therefore, we predicted that these areas will have a positive influence on the probability of attack on livestock. High forest cover areas are generally avoided by wolves (Mahajan et al., 2021), therefore, we predicated those areas with high forest cover will have negative influence on the probability of livestock attack. Moreover, predation on livestock by wolves has also been linked to low densities of wild prey in Southern Europe (Meriggi and Lovari, 1996) and North America (Mech et al., 2000; but see Treves et al., 2004). In a few protected areas in India, where native ungulate wild prey species such as blackbuck (*Antilope cervipera*) and chinkara *(Gazella bennettii)* are readily available, wolves prefer wild prey over livestock (Kumar and Rahmani, 1997; Jhala, 2003). However, due to low availability of wild prey in the study area (Mahajan and Khandal, 2021), we hypothesized that wolf will switch to alternative prey i.e., livestock, which is easily available and assessable. We therefore, predicted that availability of wild prey will have the negative influence while domestic prey availability will have the positive influence on the probability of livestock attack. Moreover, we hypothesized that anthropogenic factors like large human settlements will have a negative influence on the probability of livestock attack, since more disturbance can deter the presence of wolves (Srivathsa et al., 2019). However, open agricultural areas are generally grazing grounds for medium sized livestock and thus provide an opportunity to wolves to hunt livestock in those areas (Majgaonkar et al., 2019; Mahajan et al., 2021), we therefore speculated that agricultural areas would aid wolves to attack livestock.

Certain socio-demographic factors were also selected to model the attitude of people toward wolves. Caste of the respondents, for example can negatively or positively influence perceptions toward animals based on cultural values associated among different caste systems (Dickman, 2010; Arbieu et al., 2019). Age is another important factor which influences the behavior of respondents toward wolf. Based on previous studies on wolves we hypothesized that older people would hold more negative attitudes than younger people (Kellert, 1985; Kaltenborn et al., 1999; Røskaft et al., 2007; Majić and Bath, 2010). Similarly, we predicted that people with more formal education would be more likely to respond positively toward wolf (Kellert, 1985; Majić and Bath, 2010; Mkonyi et al., 2017). Different types of occupation can also positively or negatively impact the attitude of people toward wolf conservation (Kellert, 1985; Kaltenborn et al., 1999; Williams et al., 2002; Carlson et al., 2020). We hypothesized that shepherds would hold more negative attitude than other occupations as they encounter wolves more frequently. Moreover, people with prior experience of livestock loss to wolves would hold a more negative attitude than respondents who have not suffered any livestock loss (Williams et al., 2002; Røskaft et al., 2007).

We combined both ecological and social aspects of human-carnivore interactions in a single coherent framework using the approach developed by Gálvez et al. (2018). We used interview surveys with local people which provide both cost-effective and reliable information for the conservation of species at large spatial scales (Zeller et al., 2011; Rich et al., 2013). We first collected ecological data on habitat use by wolves (Mahajan et al., 2021), and on the same spatial scale, we conducted socio-ecological interviews to determine the drivers of livestock depredation by wolves. We further used the interviews to assess the socio-demographic factors shaping the perceptions of the respondents toward human-wolf interactions. We used occupancy models to determine the suite of ecological and social factors that govern livestock depredation by wolves. Occupancy models are based on the detection and non-detection of species over multiple surveys to reduce the chances of "false negative" which helps in accounting for the detection probability (MacKenzie and Royle, 2005). Using occupancy models with interview data has been applied across multiple studies to understand human-wildlife interactions (Goswami et al., 2015; Srivathsa et al., 2019; Puri et al., 2020; Bista et al., 2021). Based on the results of our study we provided recommendations for conserving the highly neglected species of semi-arid landscapes of India that can aid the overall coexistence of carnivores and humans in shared landscapes.

MATERIALS AND METHODS

Study Area

Kailadevi Wildlife Sanctuary (KWLS) forms the northern boundary of Ranthambhore Tiger Reserve (RTR) (26°13′40.05″N–26°15′17.42″N, 76°35′52.68″E–77°13′52.45″E). It is located in the Karauli district of the western Indian state of Rajasthan (**Figure 1**). The sanctuary covers an area of 673 Km^2 and for its effective management the sanctuary is further divided into four administrative ranges (**Figure 1**) namely Kailadevi, Karanpur, Mandrail, and Nainyaki. The KWLS falls within the semi-arid climatic zone. It experiences three distinct seasons, monsoon, winter, and summer. More than 90% of the annual precipitation occurs during monsoon (July–September) with an average of 750–800 mm of rainfall. October is a transition period between monsoon and winter. The two major rivers Chambal and Banas form the southern and western boundaries of the sanctuary, respectively. The parallel running ridges forming deep gorges are an important geographical feature of the sanctuary and are locally known as "Khoh."

The forests of the KWLS are mainly composed of Northern Tropical Dry Deciduous forests, Zizyphus scrub, dry deciduous scrub, and dry Grass lands (Champion and Seth, 1968). Dhonk (*Anogeissus pendula*) is the dominant tree species in the sanctuary constituting nearly 80% of the vegetation cover. The KWLS supports a rich diversity of mammalian species such as the Tiger, Leopard, Indian Gray Wolf, Golden Jackal (*Canis aureus*), Sloth Bear (*Melursus ursinus*), Indian Striped Hyena (*Hyaena Hyaena*), Indian Fox (*Vulpes bengalensis*), Indian crested Porcupine (*Hystrix indica*), Wild-pig (*Sus scrofa*), Honey badger (*Mellivora capensis*), Jungle cat (*Felis chaus*), Caracal (*Caracal caracal*), Rusty Spotted Cat (*Prionailurus rubiginosus*), Common Civet (*Paradoxurus hermaphroditus*), Small Indian civet (*Viverricula indica*), Sambar (*Rusa unicolor*), Cheetal (*Axis axis*), Bluebull (*Boselaphus tragocamelus*), and Chinkara (*Gazella bennettii*).

KWLS is a human-dominated landscape and is home to several agro-pastoralist communities that are substantially dependent on its resources for their livelihood. Currently, there are 60 villages inside the KWLS with a total of 4,773 households and 18,344 people (Mahajan and Khandal, 2019). Most of the villages have a multi-caste composition among which *Meenas* and the *Gurjars* are the most predominant communities. Villages inside the forest and in its peripheries exert immense pressure on the forest for resources like timber, fodder, etc.

Field Surveys

To record the presence of livestock depredation by wolves, we conducted semi-structured questionnaire surveys from October 2018 to December 2018 in grids of 14.4 km^2 each, across the KWLS for the events pertaining to the previous year. We collected both presences of indirect signs of the wolf (Mahajan et al., 2021)

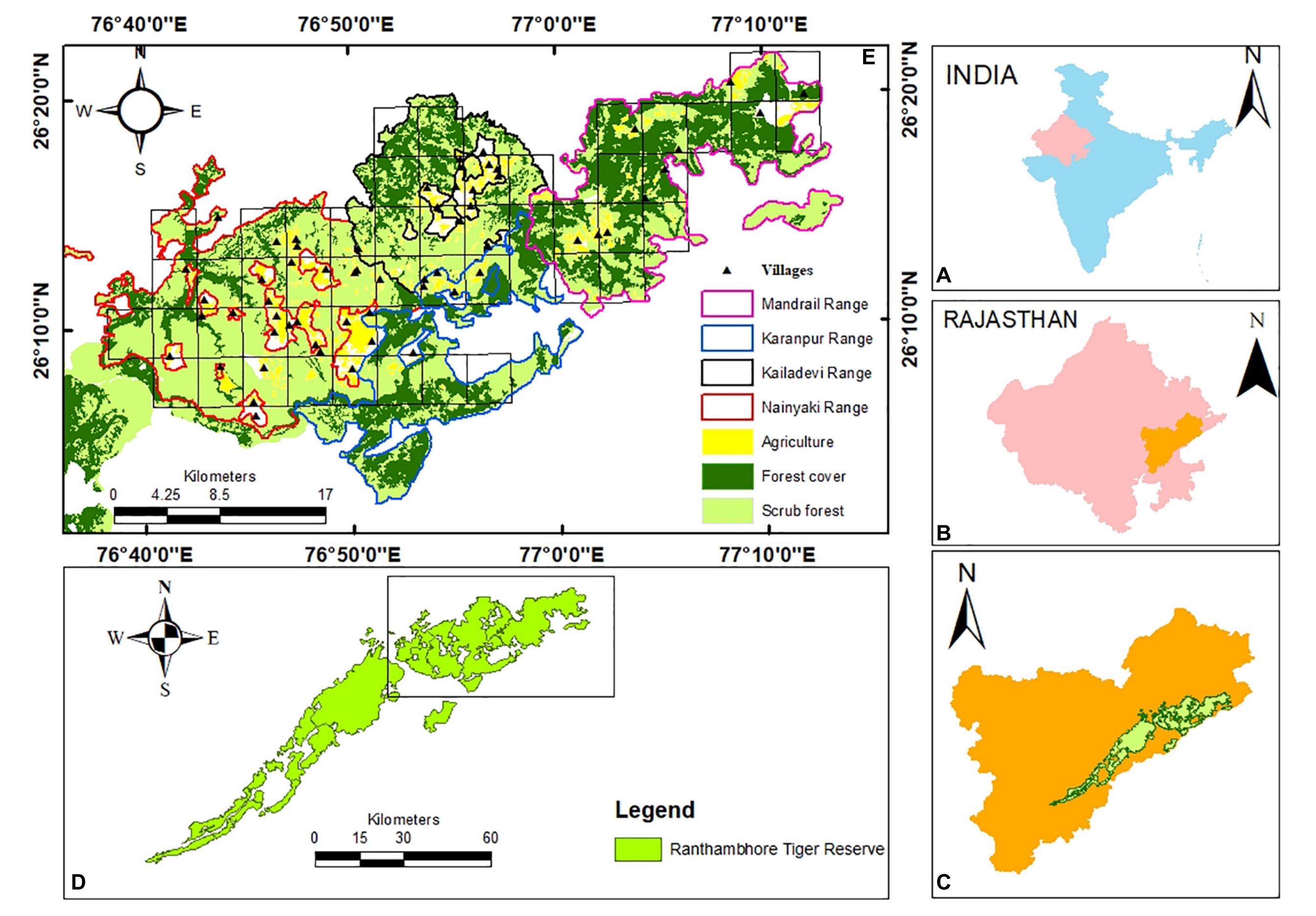

FIGURE 1 | Study area showing the grids with villages inside the Kailadevi Wildlife Sanctuary, Rajasthan, India. **(A)** The state of Rajasthan, India. **(B)** District in Rajasthan where the study area is located. **(C)** Location of study area within the district. **(D)** Ranthambhore Tiger Reserve, where the marked block represents the KWLS. **(E)** Kailadevi Wildlife Sanctuary, Rajasthan, India.

and the presence of any depredation event at the same spatial scale (Zeller et al., 2011; Gálvez et al., 2018; Srivathsa et al., 2019). The presence of indirect signs was observed in each grid by searching for indirect signs near roads and trails. Each kilometer walked inside a grid was considered as a single spatial replicate. The presence/absence data thus generated was used to estimate the habitat-use of wolves with the suite of ecological and anthropological covariates using a single-season correlated detection occupancy modeling approach (Mahajan et al., 2021). Using the same grids as our sampling units, we conducted socio-ecological interview surveys to know the presence of livestock attack by wolves in KWLS. Out of 48 grids, villages were present in 29 grids and we, therefore, conducted interviews in those grids only. We selected local residents of the KWLS to conduct questionnaire interviews. Prior to the survey, all these volunteers were trained on how to conduct interviews and to avoid any ambiguity generated through the respondent's answers. These volunteers held more than 10 years of experience in conducting ecological surveys (Mahajan and Khandal, 2019). To avoid any false positives, respondents were shown pictures of different species found in the study area and were asked to identify wolves. Upon correct identification, the respondents were asked if they have encountered or seen the wolves in and around their village and their responses were validated through the presence of indirect signs if the encounter was recent (not more than 5 days). They were also asked about incidents of livestock depredation by wolves for the last 12 months (Puri et al., 2020). Respondents that were unable to correctly identify wolves from photographs were discarded and were considered as "missing observations" for the occupancy analysis. We further collected information on the respondent's family demographics which included the number of males and females in the family, age of different family members, education level, caste, and occupation of the respondent. Other information like number of different livestock holdings, various measures to mitigate livestock depredation, and compensation claimed for the loss of livestock by wolves was also collected. To understand the attitude and perceptions of respondents toward livestock depredation by we asked specific questions like their opinion on what should be done regarding the loss of livestock caused by wolves and what they believe regarding wolf conservation in KWLS. We conducted a total of 442 interviews across the KWLS

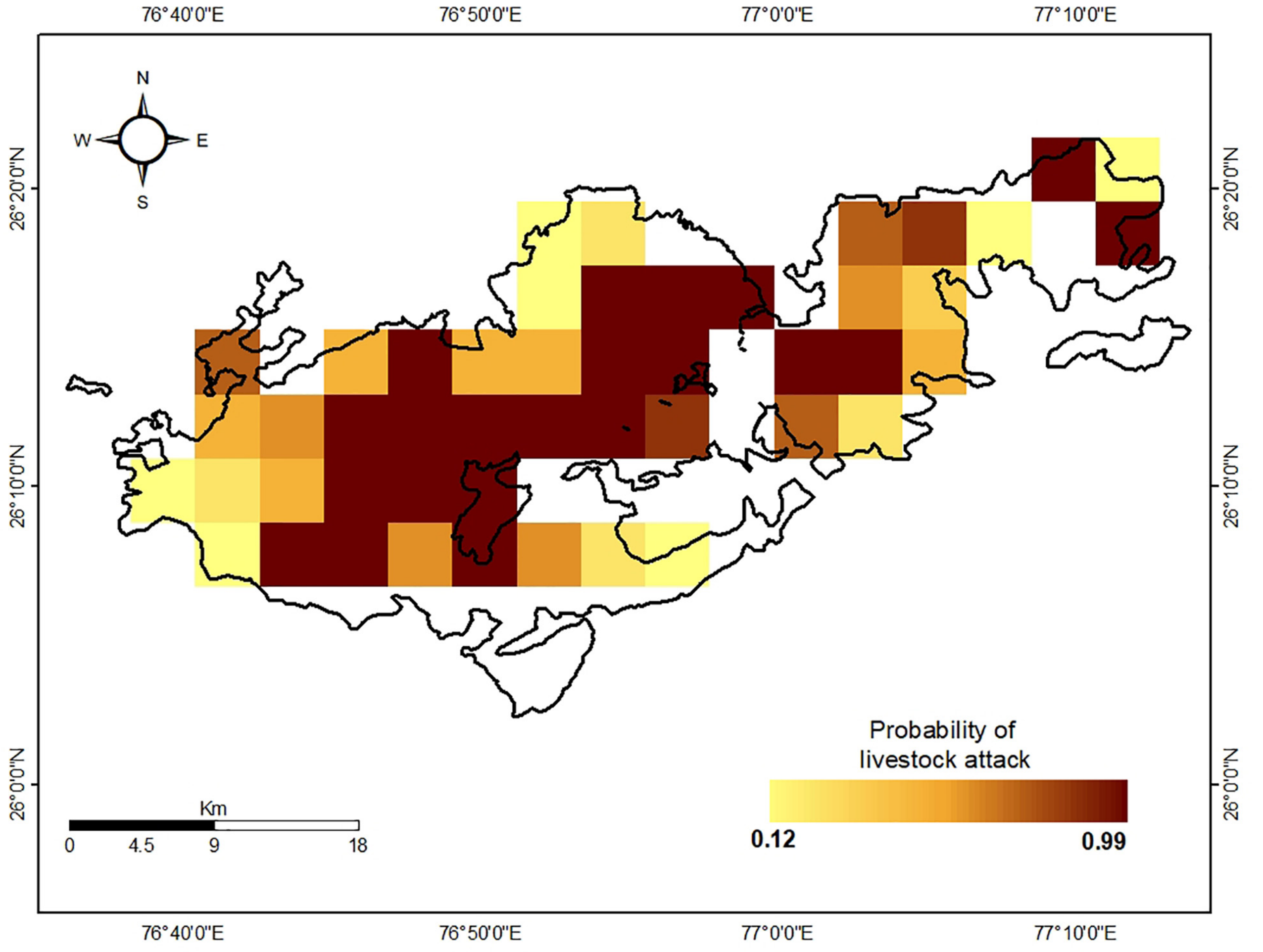

FIGURE 2 | Map showing estimated probability of livestock attack by wolves based on interview surveys across the Kailadevi Wildlife Sanctuary, Rajasthan, India.

to assess the effect of socio-demographic factors on people's attitudes toward the wolves. Out of multiple respondents in grids, each respondent was considered a survey-specific replicate that allows estimation of detection probability (MacKenzie et al., 2006). Out of 442 we only considered 271 (maximum of 10 replicates in each grid) interviews to avoid correlations among multiple replicates within a grid. Also, we assumed that due to high detection probability of livestock depredation by wolves, fewer replicates would be enough to model detection probability (MacKenzie and Royle, 2005).

Model Covariates for Livestock Depredation and Human Attitudes Toward Wolf

Values of wolf habitat use, availability of water, scrubland, forest cover, wild prey availability, domestic prey availability, anthropogenic disturbance, and presence of agricultural land in the grids were taken from another study on habitat-use by wolves (for information on how these values for each grid were generated; see Mahajan et al., 2021). The area of human settlements in each grid was calculated by digitizing human settlements using Google Earth imagery (2017–2018). Boundaries of settlements were hand drawn to form polygons and the area of human settlements in each grid was computed in QGIS (Version 2.18.25- Pisa, QGIS Development Team, 2018). All covariates were standardized by calculating z-scores $(y-\bar{y})/SD_y$. Prior to developing any model, Pearson's correlation values were calculated to minimize the effect of correlations among covariates and only one variable among the highly correlated pairs ($r > 0.7$) was retained (Dormann et al., 2013).

For modeling the attitudes, socio demographic factors were selected from the interview data. The predictor variables were age, caste, education, occupation and previous attack on livestock. Age was the only continuous variable while other factors were categorical. Caste was categorized into 3 groups where "1," "2," and "3" represents *Gurjar*, *Meena*, and others, respectively. Similarly, level of education was also categorized into 3 groups where "1" represents respondents whose education level was up to 5th standard or below, "2" represents respondents whose education level was from 6th to 10th standard and "3" represents respondents who were educated above 10th standard.

TABLE 1 | Demographic characteristics of surveyed villages and livestock holdings across the ranges of Kailadevi Wildlife Sanctuary, Rajasthan, India.

Ranges	No. of villages surveyed	Total no. of respondents	Caste			Total livestock holding					Mean no. of livestock per respondent (SD) per range	
			Gurjar	Meena	Others	Cow	Buffalo	Goat	Sheep	Others	Goat	Sheep
Nainyaki	25	189	140	13	36	260	673	5,928	869	43	31.36 (21.06)	4.6 (19.72)
Kailadevi	14	115	64	45	6	298	624	2,985	644	60	25.96 (24.76)	5.6 (15.74)
Karanpur	11	66	36	22	8	241	46	2,471	420	0	37.44 (24.5)	6.36 (16.57)
Mandrayal	8	72	38	6	28	44	342	960	20	0	13.91 (23.79)	0.29 (2.39)
Total	**58**	**442**	**278**	**86**	**78**	**843**	**1,685**	**12,344**	**1,953**	**103**	**28.12 (24.11)**	**4.45 (16.68)**

The occupation was categorized into four groups in which "1" represents laborer, "2" represents farmer, "3" represents shepherd and "4" represents respondents belonging to other occupations. Respondents who had experienced wolf attack on livestock were labeled as "1" while those who did not experience any attack by wolves were labeled as "0."

Estimating Determinants of Livestock Depredation

We used a multi-state occupancy model to assess the pattern of livestock depredation by wolves (MacKenzie et al., 2009). The data generated from the interview surveys were classified as "0," "1," and "2" in the design matrix, where "0" represents the absence of wolf in a grid, "1" represents the presence of wolves in a grid but without depredation, and "2" represents depredation by wolves in a grid. The following parameters were estimated: Ψ_p—probability of wolf presence in a grid (without depredation); Ψ_d—probability of depredation by wolves in a grid; p_{pp}—probability of detecting wolf presence in a grid; p_{dd}—probability of detecting depredation in a grid; p_{pd} —probability of detecting only presence although there may be depredation in the grid. The probability of depredation in a site was modeled as a function of covariates using the multinomial-logit link function (MacKenzie et al., 2009). To estimate detection probability we used the number of interviews in a grid (i.e., survey effort) as a covariate (Srivathsa et al., 2019; Puri et al., 2020). Since our parameter of interest was the probability of depredation (Ψ_d), the probability of wolf presence (Ψ_p) was retained as intercept-only to avoid issues of overfitting and to maintain parsimony. We ran a set of 10 plausible models with different covariates for modeling the probability of depredation (**Supplementary Table 1**). We also ran a null model without covariates. We used Akaike's Information Criterion (AIC) to rank and select the best models. Akaike weights (w) were also computed for the models in the candidate set to compare the weight of evidence (Burnham and Anderson, 2002). Since no model stood out as the best based on AIC values, averaging of models with values $\Delta AIC < 2$ was used to derive estimates of depredation probability at the site level (Burnham and Anderson, 2002). We selected the five best models out of 10 using AIC with the lowest AIC value and Akaike weights (cumulative wi of 0.99, $\Delta AIC < 2$). β-coefficients and associated Standard Errors (SE) of selected models were assessed to know the effect of the covariates on the probability of depredation. Analyses were performed using the single-season multi-state model in program PRESENCE (Version 2.12.22, Hines, 2006). A spatially explicit map depicting the grids with high and low model-average probabilities of depredation by wolves across the different sites was generated using QGIS (**Figure 2**).

Patterns of Livestock Depredation and Socio-Demographic Determinants Associated With Attitudes of Respondents Toward the Wolf

We used descriptive statistics to characterize patterns of livestock depredation by wolves. The Chi-square goodness of fit test was used to examine (i) the association between the range

TABLE 2 | Frequency of livestock depredation by wolves across the ranges of Kailadevi Wildlife Sanctuary, Rajasthan, India.

Ranges	Cattle calf	Buffalo calf	Goat	Sheep	Mean livestock depredation (*SD*) per range per category
Nainyaki	36	4	170	40	62.5 (53.5)
Kailadevi	48	10	193	62	78.25 (70)
Karanpur	41	0	178	29	62 (51.75)
Mandrayal	5	1	52	74	33 (31.75)
Total	**130**	**15**	**593**	**205**	**235.75 (207)**

TABLE 3 | Model comparisons for probability of presence-only without depredation (ψ_p), probability of depredation (ψ_d), and associated detection probabilities (p_{pp}, p_{dd}, p_{pd}) in the Kailadevi Wildlife Sanctuary, Rajasthan, India, 2018.

Model	AIC	Δ AIC	AIC weight	Model likelihood	Parameters
ψ_p (.), ψ_d (occp), p_{pp} (ints), p_{dd} (ints), p_{pd} (.)	470.78	0.00	0.26	1	8
ψ_p (.), ψ_d (agri), p_{dd} (ints), p_{dd} (ints), p_{pd} (.)	471.08	0.30	0.23	0.86	8
ψ_p (.), ψ_d (sett+occp), p_{dd} (ints), p_{dd} (ints), p_{pd} (.)	471.09	0.61	0.19	0.74	9
ψ_p (.), ψ_d (occp+scrb), p_{pp} (ints), p_{dd} (ints), p_{pd} (.)	471.62	0.84	0.17	0.66	9
ψ_p (.), ψ_d (agri+sett), p_{pp} (ints), p_{dd} (ints), p_{pd} (.)	472.07	1.29	0.14	0.52	9

The top five models (based on AIC ranks) are presented. scrb, scrubland cover; sett, area of human settlements; agri, area of agriculture land; occp, occupancy probability of wolf; ints, number of interviews per site; models do not include combinations of highly correlated covariates ($r > |0.7|$).

TABLE 4 | β-coefficients (± *SE*) from most-supported models used to assess the effect of variables on Ψ_d (Depredation probability) of wolves in Kailadevi Wildlife Sanctuary, Rajasthan, India.

Model	$\widehat{\beta}_{occp}$ (*SE*)	$\widehat{\beta}_{agri}$ (*SE*)	$\widehat{\beta}_{sett}$ (*SE*)	$\widehat{\beta}_{scrub}$ (*SE*)
ψ_p (.), ψ_d (occp), p_{pp} (ints), p_{dd} (ints), p_{pd} (.)	2.98 (1.77)	-	-	-
ψ_p (.), ψ_d (agri), p_{dd} (ints), p_{dd} (ints), p_{pd} (.)	-	6.94 (5.65)	-	-
ψ_p (.), ψ_d (sett+occp), p_{dd} (ints), p_{dd} (ints), p_{pd} (.)	2.85 (1.28)	-	602.04 (3.47)	-
ψ_p (.), ψ_d (occp+scrb), p_{pp} (ints), p_{dd} (ints), p_{pd} (.)	2.21 (1.75)	-	-	0.98 (1.01)
ψ_p (.), ψ_d (agri+sett), p_{pp} (ints), p_{dd} (ints), p_{pd} (.)	-	5.12 (2.15)	417.84 (2.24)	-

Scrb, scrubland cover; sett, area of human settlements; agri, area of agriculture land; occp, occupancy probability of wolf; ints number of interviews per site.

of KWLS and the frequencies of livestock killed by wolves and (ii) the difference in the frequencies of different livestock killed. Ordinal logistic regression was used to determine the effects of socio-demographic factors on people's attitudes toward the wolves. Ordinal attitudinal scores were entered in the model as response variables, and socio-demographic factors including age, caste, education level, occupation, and previous attack on livestock were considered as predictor variables. AICc scores were used to rank and select the models that accounted for a small sample size. Prior to the analysis, we performed a Spearman's Rank correlation matrix to confirm that none of the variables were inter-correlated using Spearman's rho (r_s) > 0.7 as a criterion for exclusion. The probability graphs of respondent attitudes toward wolves with the effect of different socio-demographic variables as predicted by the ordinal logistic regression were produced to know the importance of the variables. The importance of response variables ranges from 0 to 1, with importance values of 1 indicating that the variable made a strong contribution to the model. We examined the relationship of each predictor variable to predict the probability of respondent attitude. All the statistical analyses were carried out using R (v.3.5.0, R Development Core Team, 2021).

RESULTS

We conducted questionnaire interviews across 58 villages inside the KWLS (**Table 1**). We surveyed 15% of the total households present in each village. Respondents were primarily men (99%), of which 6% were educated till the 8th grade. The remaining respondents (94%) had no formal education or had dropped out of formal education before the 8th grade. The majority of the respondents were from the *Gurjar* community (63%), which are either pastoralists or agriculturists. The majority of the households (92%) were engaged in livestock rearing, of which goat (73%) formed the major livestock, followed by cattle (15%), sheep (11.5%), and donkey (0.5%).

Momentary Loss and Patterns of Livestock Depredation by Wolves

In the last 1 year, 283 (64%) respondents reported livestock losses due to wolf attacks. Respondents reported a total loss of 943 livestock due to wolf depredation (**Table 2**). Depredation of goats (63%) by wolves was significantly higher than sheep (22%), cow calves (14%) and buffalo calves (1%) (χ^2 = 799.52, d.f. = 3, $p < 0.01$). Frequency of livestock depredation was reported significantly more from villagers in the Nainyaki

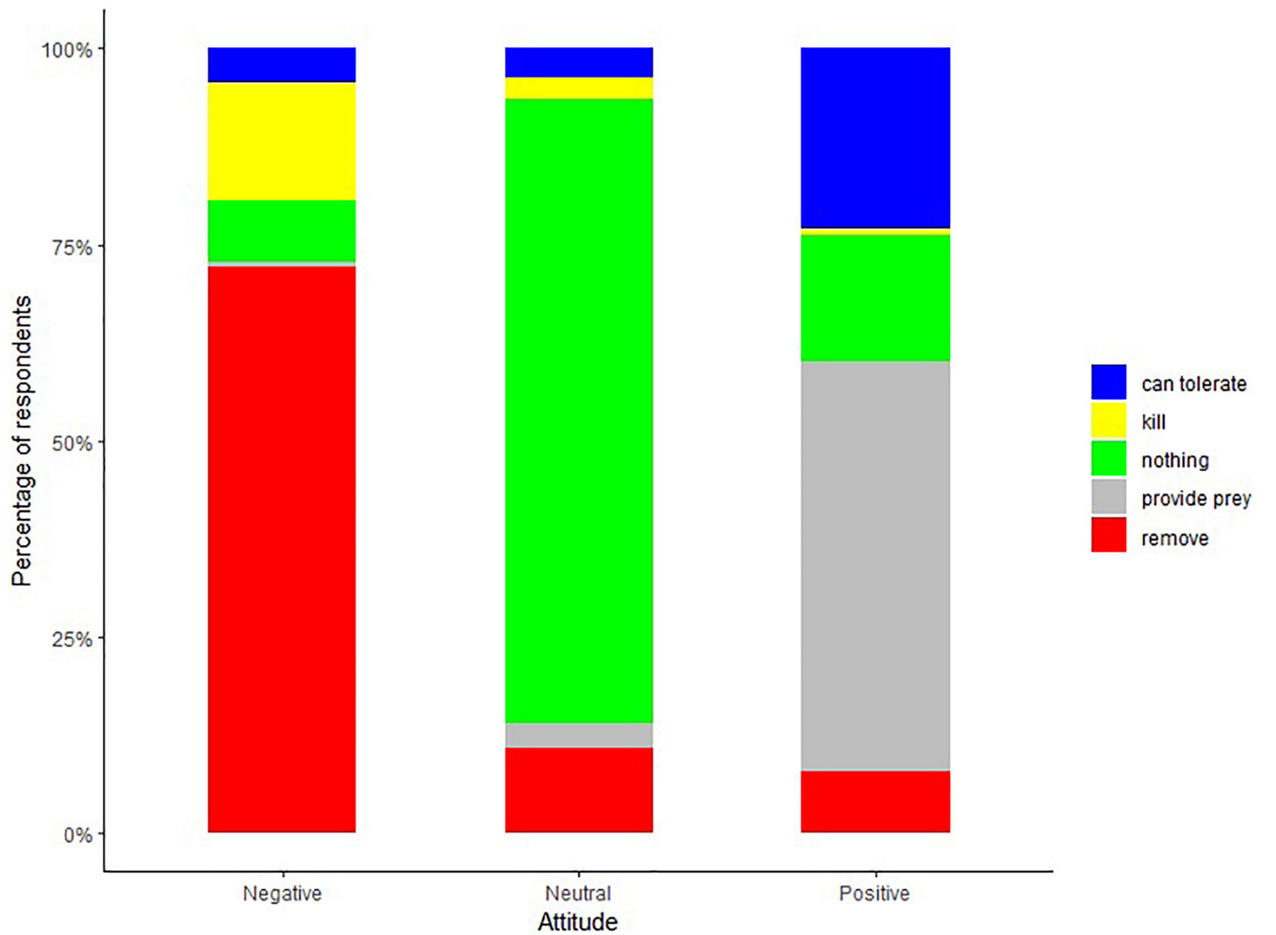

FIGURE 3 | Comparison of attitudes of respondents toward the wolves, for the question "what should be done to reduce the loss caused by wolves".

TABLE 5 | Model comparison for socio-demographic factors (Occupation, Attack, Age, Caste, Education) affecting attitudes of respondents toward the wolf in Kailadevi Wildlife Sanctuary, Rajasthan, India.

Model structure	K	AICc	Δ AICc	ModelLik	AICcWt	LL	Cum.Wt
Occupation	3	962.87	0.00	1.00	0.98	−478.42	0.98
Attack	3	971.09	8.23	0.02	0.02	−482.54	0.99
Age	3	975.30	12.44	0.01	0.01	−484.64	0.99
Caste	3	975.84	12.97	0.00	0.00	−484.91	0.99
Education	3	976.02	13.15	0.00	0.00	−485.00	1

range (44%), followed by Kailadevi (31%), Karanpur (17%), and Mandrail (8%) ranges ($\chi^2 = 81.72$, d.f. = 3, $p < 0.01$). The majority of the attacks occurred during the day time (96%) while the shepherds were herding their livestock and few instances of livestock depredation occurred during the nighttime (4%).

Out of 283 reported cases of livestock depredation, 265 (94%) reportedly did not file for compensation, while 18 (6%) respondents filed claims for the year 2017–1018. Out of the 18 who filed for compensation, 15 individuals received compensation, while 3 individuals did not receive any compensation. The majority of the respondents who didn't file for compensation stated that they were unaware of any compensation scheme for livestock loss caused by wolves (93%), while the remaining respondents stated other reasons, such as the non-receipt of compensation in a previous case, a greater investment of resources in the application than the compensation amount, and unavailability of the forest department officers when applying for compensation. Livestock depredation in terms of monetary loss was estimated using average local prices of livestock in 2017–2018. The value of each livestock type was calculated according to the species and age. The average amount of annual loss for households that reported livestock loss ($n = 283$) by wolves was valued to be around 230 USD. The total

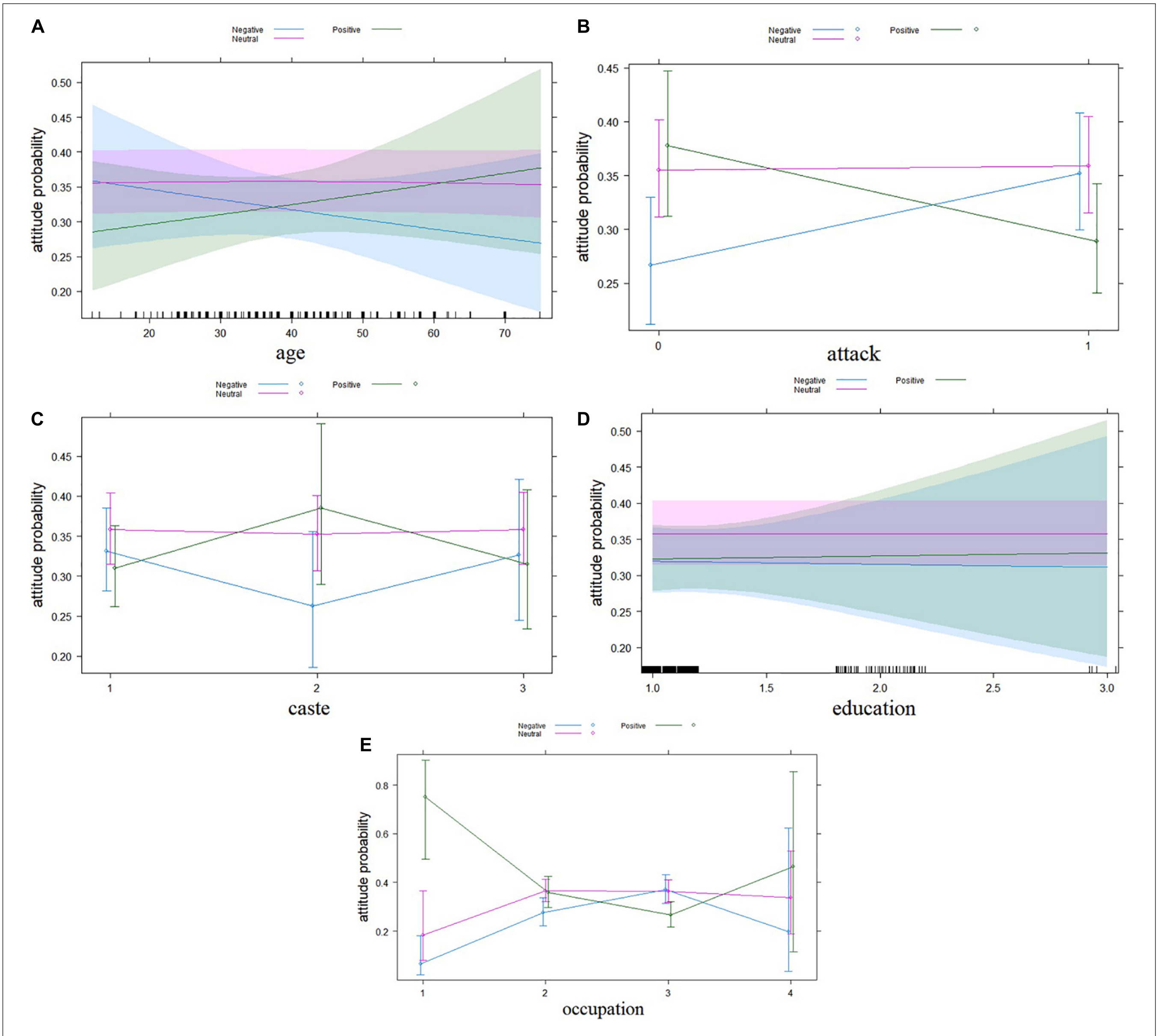

FIGURE 4 | Probability of attitude responses in ordinal models for predicting attitudes toward wolves. **(A)** Effect of Age. **(B)** Effect of livestock attacked by wolves (0 = No attack, 1 = attack). **(C)** Effect of caste (1 = Gurjar, 2 = Meena, 3 = Others). **(D)** Effect of Education (1 = 5th and below, 2 = 6th-10th standard, 3 = 10th and above. **(E)** Effect of Occupation (1 = Laborer, 2 = Farmer, 3 = Shepherd, 4 = Others).

amount of compensation received by the 15 people who had filed for compensation was 761 USD for a total of 60 livestock heads comprising 40 goats, 8 sheep, 11 cow calves, and 1 buffalo calf. Based on the total number of livestock holdings of the respondents (**Table 1**), the percentage of goat and sheep loss over a year due to wolves was 5 and 1%, respectively.

Based on interview surveys, we established that livestock in the Kailadevi Wildlife Sanctuary is pastured from early morning (approximately 2–3 h after sunrise) to 1.5–2 h before sunset (Mahajan and Khandal, 2019). Respondents revealed that cattle were usually unguarded, but for goats and sheep at least one person remained on guard while the animals were grazing. The majority (67%) of the respondents stated that they stayed with their livestock and made loud noises during herding in order to protect their livestock from wolves, while other 18% of the respondents stated that they did nothing to protect their herd against the wolves. Only 7% of the respondents stated that they keep their livestock in a fenced enclosure during the night time, while 8% stated that they used vigilance both during the day and night time to prevent livestock from wolf attack and used fencing in the night time to guard their livestock. The mesh pens used to guard the livestock are not very well constructed and cannot keep the wolves away from attacking livestock (Krithivasan et al., 2009). Most of the livestock guarding techniques used by shepherds in KWLS is not very effective to prevent livestock depredation.

Determinants of Livestock Depredation and Attitudes of Respondents Toward Wolves

The probability of depredation across the sites in KWLS was modeled using the data from 271 interviews conducted with the villagers. The naïve probability (proportion of grids in which livestock depredation was reported without taking detection probability into account) of livestock depredation was 0.58 in KWLS during the survey. There was a high correlation between the availability of agricultural land and the habitat use of wolves (r = 0.73) and also between the domestic prey and availability of agricultural land (r = 0.77). Therefore, these two pairs were not included together while building the models. The estimated depredation probability by wolves after model averaging was estimated at 0.84 ($SD = \pm 0.23$). Based on the ΔAIC and Akaike weight, the habitats frequently used by wolves, the presence of agricultural areas, the presence of scrubland, and the area of settlements were the most reliable in explaining the probability of livestock depredation at a site (**Table 3**). β-coefficient values indicated that the depredation probability at a site was positively influenced by the habitat-use probability by wolves, extent of agricultural area, scrubland, and settlement size depending on the model (**Table 4**). The direction of slopes for all covariates except the settlement size were consistent with our a *priori* predictions. Therefore, the areas which had a high intensity of usage by wolves, the presence of agriculture, scrubland, and human settlements had a higher probability of livestock attack by wolves

When asked if wolves should be conserved or not, 66% of the respondents said that they had no opinion (Neutral) about conserving wolves, 18% responded positively toward wolf conservation, while the remaining 16% (Negative) believed that wolves should not be conserved and should be either removed or exterminated from the area near their villages. In response to the question "what should be done to reduce losses due to wolves?," a majority of 54% of respondents believed that nothing could be done as wolves are wild animals who need food for survival and thus, will continue to kill their livestock, whereas 29% of the respondents believed that wolves should be entirely removed from the area with another 7% of the opinion that wolves should be killed to reduce livestock losses. Conversely, 10% of the surveyed people were tolerant of the losses caused by wolves (**Figure 3**). The majority of respondents (94%) either had no formal education or had dropped out before the 8th grade, out of which 63% held neutral attitudes toward wolves while 17 and 14% held positive and negative attitudes, respectively. Most of the respondents held neutral attitudes toward wolves irrespective of whether they had suffered from livestock losses or not.

Using ΔAIC and Akaike weight (wi of 0.98, $\Delta\text{AIC} < 2$) the ordinal regression revealed that the occupation of respondents had the greatest influence on the attitude toward wolf (**Table 5**). Shepherds held more negative views toward the wolf than farmers and other occupations. Also, with an increase in a respondent's age, the attitude shifted more toward positive, although respondents with prior experience of livestock loss held more negative attitudes. Moreover, shepherds with previous experience of livestock loss were more likely to hold negative attitudes than shepherds who didn't have any experience of livestock loss. Education did not have a significant effect on the attitude of respondents toward the wolf.

DISCUSSION

Patterns and Determinants of Livestock Depredation by Wolves

Our study examined the relevant social and anthropogenic factors that govern the attack on livestock by wolves. The attack on livestock in a site was majorly influenced by four factors which included, the probability of habitat used by the wolf in a site, the extent of agricultural area, settlement size, and availability of scrubland. As predicted, the probability of an attack on livestock was higher in those sites which are used more by wolves and have higher availability of scrubland and agricultural area. However, contrary to our prediction the size of settlements positively influenced the attack on livestock. Our results show that goats and sheep were the major livestock depredated by wolves. Previous studies have also shown that goats and sheep form the major prey of wolves outside the protected areas (Kumar and Rahmani, 2000; Behmanesh et al., 2018; Srivathsa et al., 2019; Khan et al., 2020; Rehman et al., 2021). Depredation of sheeps and goats may be related to higher vulnerability associated with their easy handling due to medium body size and absence of anti-predator behavior. Moreover, in our study area due to the low availability of wild prey (Jhala et al., 2020; Mahajan and Khandal, 2021), wolves might be dependent upon livestock. Livestock depredation by carnivores is also related to high carnivore density in an area (Kolowski and Holekamp, 2006). Our results reveal that the frequency of depredation was greater in the Nainyaki range than in other ranges, which might be attributed to the high density of wolves in the Nainyaki range (Mahajan and Khandal, 2021) and also due to greater availability of sheep and goats which might attract the wolves toward them due to large livestock holdings (Mech et al., 2000; Palei et al., 2013; Srivathsa et al., 2019). In our study, most of the livestock depredation by wolves occurred during the day, which was consistent with the other studies (Kumar and Rahmani, 2000; Palei et al., 2013) and might be due to an overlap of wolf activity pattern with peak livestock grazing activity away from the human settlements during the day. However, Krithivasan et al. (2009) recorded that among the nomadic shepherds, most of the attacks on the livestock occurred during the night.

The predictions of our factors were in accordance with the other studies conducted on human–wolf interactions. For instance, in Mongolia, Davie et al. (2014), also found that the risk of livestock depredation reflects the patterns of space use by wolves. Mahajan et al. (2021) and Majgaonkar et al. (2019) in Rajasthan and Maharashtra, respectively, found that harvested agricultural plots attract wolves since these areas are grazed by livestock after crops are harvested, providing an opportunity for the wolves to hunt sheeps and goats. Past and existing destruction of wolf habitats can cause wolves a future ecological loss known as extinction debt (Tilman et al., 1994). As a strategy to escape the extinction debt, wolves have adapted to living in agricultural lands through their dependence on livestock (Agarwala and Kumar, 2009). Moreover, in a study in Western Iran, Behdarvand et al. (2014) found that areas away from human settlements and a higher proportion of dry farms increased the probability of livestock depredation by wolves. However, where wolves depend on wild prey, the presence of wolves in agricultural lands is mostly due to the use of agricultural lands by wild prey (Chavez and Gese, 2006). In contrast to other studies (Behdarvand et al., 2014; Majgaonkar et al., 2019; Srivathsa et al., 2019), we found that the size of the human settlements was positively related to the livestock depredation by wolves in a site. This may be due to the fact that larger settlements have larger livestock holdings, and thus attracting wolves. However, it is important to demarcate the threshold at which the probability will be positively influenced by livestock holdings, beyond which it would either become stable or would exert a negative influence (Sharma et al., 2015). Our results do not reflect the presence of wild prey on the probability of livestock depredation, which may be an artifact of low wild prey density in the study area (Mahajan and Khandal, 2021).

Socio-Demographic Factors Govern the Attitude Toward the Wolf

The perception of a conflict can be quite different from the actual scale of a problem (Suryawanshi et al., 2013). The attitude toward a species can therefore misrepresent the scale of conflict causing people to take retributive action. Even though wolves in KWLS cause substantially high economic loss, the villagers are quite tolerant of the species. People were generally accepting of wolves in their surroundings but did not want them to depredate their livestock as they are heavily dependent upon their livestock, and having more livestock is a symbol of wealth. Therefore, if no immediate mitigation actions are taken to resolve livestock depredation by wolves, the attitudes of people can shift negatively, which can be detrimental to the conservation of wolves in KWLS.

The direction of the slope of people's attitude was consistent with our prior hypothesis for most of our selected socio-demographic factors (**Figure 4**). Many studies on carnivores have found that older people hold more negative attitudes than the younger population (Røskaft et al., 2007; Majić and Bath, 2010; Liu et al., 2011). Deep rooted cultural beliefs and traditions mostly shape the attitude of older people toward wolves. In contrast, older people's positive attitudes may result from personal experiences related to their prolonged residency and exposure to wolves (Mkonyi et al., 2017). Our results similarly suggest that older people in KWLS hold less negative attitude, although the results were not significant. On the contrary, younger people had more negative attitudes toward wolves, which may be attributed to their occupation. Most of the younger population in KWLS comprises shepherds, an occupation that entails greater encounters with wolves, and livestock depredation (Mahajan and Khandal, 2021). Such negative experiences, sometimes very frequent, often manifest as negative attitudes in the younger generation especially among shepherds who hold more negative attitudes than those in other occupations. Our results were consistent with other studies that have also found people with large livestock holdings or occupations related to the rearing of livestock, hold more negative attitudes than any other occupations (Kaltenborn et al., 1999; Williams et al., 2002; Liu et al., 2011; Carlson et al., 2020). Our results suggest that prior experience of losing livestock to a carnivore can also generate negative attitudes among villagers. Shepherds having prior experience of livestock loss hold more negative attitudes than people who did not experience any loss. In China, Liu et al. (2011) observed that individuals who did not suffer damage due to the Asiatic black bear (*Ursus thibetanus*) held 4.8 times more positive attitudes than the people who have experienced loss to bears. Dickman et al. (2014), in Tanzania's Ruaha Landscape, also reported that people hold more negative attitudes if they have prior experience of livestock depredation.

Our models suggest that among all the socio-demographic factors, education has the least effect on attitudes of people toward wolves, although education has often been suggested as the preferred management tool for reducing conflict (Johansson et al., 2016). Previous studies have shown that the role of education is the most important factor that influences the perception about carnivores (Mkonyi et al., 2017; Behmanesh et al., 2018; Arbieu et al., 2019). Moreover, only 5% of the respondents were educated up to 10th grade or above, therefore there was not much variation in the data to generate the differences in the attitude of the respondents. Education when combined with other interventions like the use of a compensation scheme and involvement of local people in management as a means of developing trust, can be helpful in reducing negative attitudes toward carnivores (Johansson et al., 2016). Therefore, further studies should focus on the assessment of attitudes post successful implementation of educational programs to better address human–wolf interactions (Baruch-Mordo et al., 2011).

The data collected on livestock depredation through interviews with the locals might have several limitations. Overestimation of loss by livestock owners is a common source of error in interview-based studies (Amit et al., 2013; Boast et al., 2016). Our estimates, therefore, represent a probable upper limit for our reported figures. Nonetheless, these interviews serve as an important source of information to understand the determinants of livestock depredation and the attitudes of villagers, which is crucial for the management of conservation conflict (Redpath et al., 2015).

Compensation Scheme as a Tool for Co-existence

In our study, we found that wolves caused a relatively high annual economic loss (180 USD) per household as compared to other studies where wolves depredated sheep and goats. For instance, in Maharashtra, the economic loss caused by wolves per person annually by depredating on sheep and goats was 60 USD (Agarwala et al., 2010), and in eastern India annual livestock (sheep and goats) loss per household was 125 USD (Palei et al., 2013). In Pakistan, at two different sites, the livestock (sheep and goats) loss per household annually was 95 USD (Ali et al., 2016) and 78 USD (Khan et al., 2020), respectively. In areas such as Wisconsin where wolves depredate on larger livestock such as cattle calf, the annual loss reached high as 602 USD per person (Agarwala et al., 2010).

Many studies in India have recommended adequate compensation schemes to ensure wolf conservation (Kumar and Rahmani, 2000; Jhala, 2003). Currently, in India, compensation schemes are variable across states and are usually prioritized for more charismatic mega fauna, including the tiger, leopard, lion, elephant, and sloth bear (Madhusudhan, 2003; Johnson et al., 2018). The State of Maharashtra has a good compensation policy scheme for ensuring wolf conservation (Agarwala et al., 2010). In the KWLS, the forest department of Rajasthan also started providing compensation for the loss of livestock due to wolves. However, only a few people are aware of the program, as they believe that the compensation scheme is primarily applicable for livestock loss by tigers and leopards. Even though wolves cause high economic loss in the KWLS, in our survey we found that only 6% of the victims filed for compensation against livestock depredation by wolves. To claim compensation, it is necessary to produce photographic documentation of the kill. Since it is difficult to locate the kill made by the wolf, claiming compensation is rather difficult (Behdarvand et al., 2014). Also, the process of receiving compensation is often delayed due to bureaucratic issues (Barua et al., 2013) which usually involve a veterinarian's report, and cost, time, and effort of the applicant. As a result, the value of the compensation received is often considerably less than the market value of the animal killed (Krithivasan et al., 2009). Such a discrepancy in losses vs. compensation likely instills greater negative attitudes among people of KWLS. Therefore, greater awareness among the people of the KWLS is required through education and outreach about the compensation program for livestock depredation by wolves. There should be an effective and efficient compensation scheme to reduce negative perceptions among villagers. Moreover, the procedure for applying the compensations should be easy to follow with minimal requirement of documentation. In our study area, we recommend that a trained team with veterinarians and forest department personnel should be deployed in each range to report and file the compensation as soon as depredation is reported.

CONCLUSION

Our study highlights the importance of both ecological and social determinants of livestock depredation by Indian wolves in the semi-arid landscape of western India. Previous studies were mostly based on characterizing losses caused by wolves but did not highlight the factors behind the depredation. This study demonstrates that the combined use of ecological and social factors can help generate a better understanding of the complex human-wolf interactions. Our spatial risk map identifies the areas with a high probability of depredation, which can help the managers to prioritize and mitigate conflict in those areas. It is always better to prevent wolf attacks on livestock, however, given the current scenario, it seems inevitable to avoid much of the interaction between humans and wolves. We suggest that better livestock management can help minimizing the rates of depredation. During the day, shepherds should be more vigilant and graze their livestock closer to villages. We found that only a small proportion of respondents use pens to safeguard their livestock from wolves and most of these pens are poorly constructed, made of dry thorny scrub branches (**Supplementary Figure 1**) or soft metal wire mesh (**Supplementary Figure 2**) which are not strong enough to keep wolves away. More emphasis should be placed on using appropriate husbandry methods including better construction of pens, to prevent future depredation events. A compensation program, as suggested above, is the most efficient method to resolve human-wolf interactions and reduce negative attitudes among the villagers toward wolves. More awareness should be created regarding the compensation program through education and outreach. The present study can be replicated in other wolf-occupied regions of India where they cause high economic loss to the marginalized communities through livestock depredation.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are included in the article/ **Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Verbal consent was gained from all participants before the interviews, but written informed consent and ethical review and approval was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

PM and DK conceived the study. PM designed, performed the data collection, analyzed, and drafted the manuscript. RC conducted the data analysis. AK revised the manuscript. All authors reviewed and approved the final draft.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.855084/full#supplementary-material

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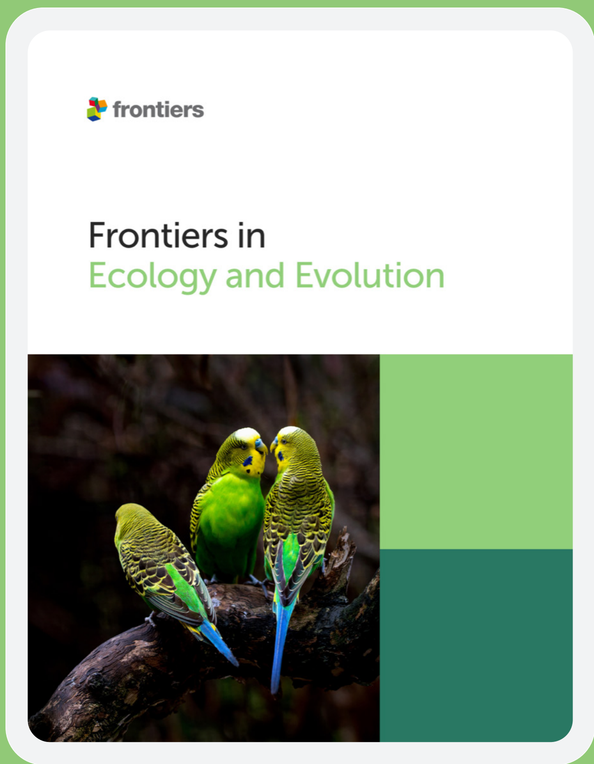

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