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Wildlife ecology in a human-dominated world: Insights from migratory animals, large carnivores, and ungulate prey

By

Kristin Jennifer Barker

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Arthur D. Middleton, Chair

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## Abstract

Wildlife ecology in a human-dominated world: Insights from migratory animals, large carnivores, and ungulate prey

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Kristin Jennifer Barker

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Arthur D. Middleton, Chair

The ecological consequences of animal behaviors range from the fitness of individuals to the functioning of ecosystems. As historic patterns of animal behaviors change in response to changes in climate, land use, and human presence, there is a growing need to better understand the mechanisms by which wildlife perceive and respond to anthropogenic and environmental influences. Understanding how and why animals alter their behavior in anthropogenic spaces requires moving beyond general descriptions of behavioral patterns to investigate the biological mechanisms underpinning these behavioral responses. Such investigations would fill gaps in current theories of animal cognition and behavioral ecology while improving effectiveness of management and conservation efforts. In this dissertation, I aim to help fill these knowledge gaps by investigating the behavioral ecology of large carnivores, their ungulate prey, and migratory wildlife moving through areas where people live, work, and play. In chapter 1, I provide a brief introduction to key themes of wildlife behavioral ecology in the context of anthropogenic influence. In chapter 2, I work with collaborators to synthesize key insights from migration restoration efforts spanning diverse taxa and ecosystems. We use lessons learned to draw broad inference about the conditions under which lost migratory behaviors can be restored. In chapter 3, I use new data collected from wolf kill sites to investigate how humans change natural patterns of predation on native ungulates. Building on this work, chapter 4 investigates how ungulates perceive and respond to these human-influenced patterns of wolf predation risk. I conclude by discussing the considerable opportunities that exist to restore and facilitate the wildlife behaviors on which ecosystems are built. I urge ecologists, natural resource professionals, and policymakers to expand their concept of conservation beyond physical landscapes and species to include the behavior of wild animals moving through an increasingly human-dominated world.

## **DEDICATION**

*For Anna  
who taught me the meaning of life*

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# Chapter 1. Introduction

## BACKGROUND

From transcontinental seasonal migrations to daily species interactions, the behavior of animals affects the structure and function of the ecosystems through which they move (Westneat and Fox 2010). For example, predatory behavior of large carnivores can alter the habitat use of their migratory ungulate prey (Messier 1991, Creel et al. 2005), whose antipredator and foraging behavior can alter the structure and function of vegetative communities across their seasonal ranges (McNaughton 1984, Holdo et al. 2007). Vegetation, in turn, provides food and cover for species across trophic levels while influencing hydrological processes, nutrient cycling, and soil retention (Wedin and Tilman 1990, Tabacchi et al. 2000). The ecological consequences of animal behaviors range from the fitness of individuals to the functioning of ecosystems, but historic patterns of animal behaviors are changing in response to changes in climate, land use, and human influences.

The effect of humans on the behavior of wildlife plays a critical yet underappreciated role in ecosystem functioning across the globe (Wilson et al. 2020). A large body of research reveals that, more often than not, wild animals change their behavior when they encounter humans or anthropogenic environments. The prevailing view holds that wild animals generally avoid humans, for example by altering their use of space, timing of activity, or extent of movement (Frid and Dill 2002, Gaynor et al. 2018, Tucker et al. 2018). However, studies also reveal instances in which animals preferentially use rather than avoid human-dominated areas. Evidence ranges from the global scale (e.g., higher animal density worldwide in suburban and agricultural areas vs. wilderness areas, Tucker et al. 2021) to the local scale (e.g., ungulate selection for areas closer to roads and trails, Berger 2007, Rogala et al. 2011), but the conditions under which humans serve as a benefit rather than a detriment to wild animals are not well understood.

When anthropogenic or environmental changes exceed the historic range of conditions experienced by a species, some types of behavior may be altered to the point of complete loss. For instance, a growing body of work reveals that seasonal migratory behaviors have been lost across diverse taxa including birds (Baskin 1993), fish (Reid et al. 2020), herpetofauna (Pearson et al. 2003), and mammals (Harris et al. 2009). The well-known importance of animal migration to both ecological and human systems (Lundberg and Moberg 2003, Dobson et al. 2010) has recently prompted major science, policy, and management initiatives to protect extant migratory behaviors (e.g., International Convention on Migratory Species, Harris et al. 2009; Global Initiative for Ungulate Migration, Kauffman et al. 2021; United States Department of the Interior Secretarial Order 3362, Middleton et al. 2020; Wyoming Migration Corridor Executive Order 2020-1, Gordon 2020). Alongside this important work to conserve remaining migrations, relatively little attention has been given to restoring the migratory behaviors we know have already been lost. Unbeknownst to many researchers and conservationists, lost migrations have successfully been restored in all major vertebrate taxa and across diverse ecosystems including grasslands (Bartlam-Brooks et al. 2011), deserts (Burnside et al. 2020), forests (Jesmer et al. 2018), wetlands (Sun et al. 2015), ponds (Ward et al. 2016), and rivers (Quinn et al. 2017). Because most restoration efforts by necessity focus on single species at local scales, siloed management and taxa-specific dialogue to date have precluded broad inference about the key shared factors underpinning the success of varied restoration efforts. As animal behaviors

continue to change – and in some cases disappear – across the world, elucidating common drivers of differing behaviors will provide key insights for both ecological understanding and applied work across spatial and temporal scales.

Common drivers of wildlife behavior are difficult to discern because animals decide how to move through the world based on how they perceive their surroundings, but it is impossible to directly measure an animal's perception of what is beneficial or costly. Unfortunately, this incomplete understanding of animal perception can stymie the effectiveness of efforts to restore or conserve the wildlife behaviors upon which ecosystems are built. For instance, despite the well-known effects of top predators on the functioning of ecosystems (Estes et al. 2011), reintroducing top predators does not always result in the expected restoration of ecosystem functions (Alston et al. 2019). One particularly well-studied but still hotly contested example is the reintroduction of the gray wolf (*Canis lupus*) into the western United States in the mid-1990s with the explicit goal of restoring the ecological role large carnivores historically played in regulating ungulate populations (Hayward and Somers 2009)

Many studies took advantage of the natural experiment afforded by wolf reintroduction to investigate whether and how the predatory behavior of wolves changed population sizes, distributions, and behaviors of their ungulate prey and associated ecosystem processes (e.g., Laundre et al. 2001, Fortin et al. 2005, Mao et al. 2005, Gude et al. 2006, Creel et al. 2008, White et al. 2011, Ripple and Beschta 2012, Woodruff et al. 2018). Still, after decades of concerted investigations into behavioral interactions between wolves and ungulates, researchers still “know almost nothing” about how these prey perceive and respond to predation risk measured empirically in natural landscapes (Creel et al. 2019). The reason for this lack of knowledge is at least three-fold. First, measuring predation risk requires considerable effort and resource expenditure (Moll et al. 2017). Second, predation risk varies markedly across space and time (Gaynor et al. 2019, Wirsing et al. 2021, Palmer et al. 2022), making it extremely difficult to tease apart the specific aspects of predation risk to which prey respond. Third, most studies of predator-prey interactions have occurred in protected landscapes under limited human influence despite the strong effects that humans can have on animal behavior (Dellinger et al. 2018). As carnivore populations continue to expand across North America (Gompper et al. 2015) while ungulate populations increasingly use human-dominated areas (Thompson and Henderson 1998), improved understanding of predator-prey interactions will be particularly important to anticipate and manage the effects of large carnivores on both ecosystems and human societies.

Determining how and why animals alter their behavior in response to anthropogenic and environmental change requires moving beyond general descriptions of behavioral patterns to investigate the biological mechanisms underpinning these behavioral responses. Such investigations would fill gaps in current theories of animal cognition and behavioral ecology while improving effectiveness of management and conservation efforts. My dissertation research aims to help fill these knowledge gaps by investigating the behavioral ecology of large carnivores, their ungulate prey, and migratory wildlife as they move through an increasingly human-dominated landscape.

## **STUDY SYSTEM**

All new data included in this dissertation were collected in the southeastern portion of the Greater Yellowstone Ecosystem (GYE) during winters 2018/2019, 2019/2020, and 2020/2021. Often touted as one of the largest intact ecosystems in the world, the GYE covers more than 20 million acres in the United States' intermountain West (Middleton and Allison 2016). The area is

generally characterized by grassland and shrub-steppe ecosystems at low- and mid-elevations giving way to subalpine spruce-fir forests and high-elevation alpine mountain ranges. Yellowstone and Grand Teton National Parks comprise the central pieces of this landscape, which also includes 5 National Forests and 3 National Wildlife Refuges as well as land owned by the Bureau of Land Management, native tribes, 3 state governments, and countless private landowners. Land uses across the GYE range from vast expanses of undeveloped natural areas to densely populated towns surrounded by subdivisions, exurban developments, and ranchlands. Similarly, human influences range from heavily restricted activities in protected Parks and wilderness areas to largely unregulated activities on private lands.

This complex mosaic of land supports the highest concentration of mammals in the continental United States, including eight species of ungulates and seven large carnivores (bison [*Bison bison*], pronghorn antelope [*Antilocapra americana*], Rocky Mountain bighorn sheep [*Ovis canadensis*], Rocky Mountain goats [*Oreamnos americanus*], moose [*Alces alces*], elk, white-tailed deer [*Odocoileus virginianus*], mule deer [*O. hemionus*], black bears [*Ursus americanus*], grizzly bears [*U. arctos horribilus*], pumas [*Puma concolor*], lynx [*Lynx rufus*], wolverines [*Gulo gulo*], coyotes [*Canis latrans*], and gray wolves). Since their reintroduction into Yellowstone National Park in 1995, wolves have expanded far beyond protected recovery areas and are increasingly coming into contact with a rapidly growing human population.

Perhaps more than any other region in the GYE, Jackson Hole valley in western Wyoming provides a microcosm of every type of human influence that may alter carnivore and ungulate behavior and interactions. Jackson Hole is well-known for its bustling outdoor recreation and tourism industry as well as its century-old supplemental elk feeding programs subsidizing the large Jackson Elk Herd (~11,000 individuals), which serves as wolves' primary prey. Jackson Hole is well-poised for fine-scale mechanistic studies of human influences on predator-prey dynamics, and the broader ecosystem in which it is embedded provides further opportunity to investigate broad patterns of animal space use across diverse landscapes. Research in the area therefore holds great power to inform science and wildlife management regionally, nationally, and even globally.

## **STRUCTURE OF THE DISSERTATION**

My dissertation begins at the global scale, with Chapter 2 presenting a new framework for understanding whether, how, and where lost wildlife migrations can be restored. This work is the first to examine the restoration potential for lost terrestrial and freshwater vertebrate migrations worldwide. My coauthors and I bring together case studies of restoration efforts across diverse taxa and combine the resulting insights with those gleaned from behavioral research and ecological theory. We first introduce how recent advances in migration ecology can inform restoration research and management efforts. Then, we review empirical studies and reports to identify common themes of restoration success across four major vertebrate groups, highlighting strategies and outcomes of key case studies. Next, we advance a conceptual framework that distinguishes seven effective means of restoring lost migrations, and we explore the biological mechanisms that underpin the potential of each for success. Finally, we discuss how the work of researchers, conservation practitioners, and policymakers can directly influence restoration efforts to regain important migratory behaviors we have lost.

Chapter 3 moves from a global to a regional scale to focus on a mechanistic understanding of how humans change the behavior of a species that may have a disproportionately strong effect on ecosystem functioning. The field data I gathered with considerable help from field technicians

and local wildlife managers informs my investigation into how wolf perception of humans drives changes in predatory behavior. Results help resolve complexity around wolf response to human influences, shed new light on the drivers of large carnivore behavior in anthropogenic areas, and improve understanding of predator-prey dynamics in and around the wildland-urban interface.

Next, Chapter 4 builds on the findings from Chapter 3 to evaluate how prey perceive and respond to these human-influenced patterns of predation risk. To investigate the effects of wolf predation on ungulate behavior, we quantified associations between behaviors of elk and different proxies of wolf predation risk to which elk may respond - including environmental drivers of vulnerability, proximity to wolves, and temporal variation in individual risk exposure. To our knowledge, this is the first study that uses empirically derived estimates of both spatial and temporal predation risk (based on wolf kill site field investigations and concurrent elk-wolf GPS collar locations, respectively) to evaluate how elk perceive and respond to different indicators of human-influenced predation risk.

Lastly, in Chapter 5 I combine lessons from the global to the local scale to consider how animal behaviors are changing, key drivers of adaptability, and opportunities to influence the behavior of wildlife to benefit both ecological and human systems. I explore insights from each chapter within the context of behavioral ecology, conservation, and anthropogenic influence writ large. I also identify remaining knowledge gaps and offer suggestions for future research. Because this work represents a collaborative effort that would have been impossible alone, and because dissertation chapters were written for publication in scientific journals, I use the collective “we” through the remainder of the dissertation.

## Chapter 2. Toward a new framework for restoring lost animal migrations

This chapter has been previously published and is included here with permission from co-authors.

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### ABSTRACT

Global declines in wildlife migrations have prompted new initiatives to conserve remaining migratory behaviors. However, many migrations have already been lost. Important attempts have been made to recover extirpated migrations, and our understanding of restoration remains narrowly confined to these particular species and landscapes. Here, we examine diverse restoration efforts through the unifying lens of behavioral ecology to draw broader inferences regarding the feasibility and effectiveness of restoring lost migrations. First, we synthesize recent research advances that illuminate key roles of exploration, learning, and adaptation in migratory behavior. Then, we review case studies to identify common themes of restoration success across four major vertebrate groups: fish, birds, mammals, and herpetofauna. We describe three broad strategies to effectively restore lost migrations: reestablishing migratory populations, recovering migratory habitats, and reviving migratory behavior itself. To guide conservation and research efforts, we link these strategies with specific management techniques, and we explore the biological mechanisms underpinning the success of each. Our work reveals a previously underappreciated potential for restoring lost migrations in terrestrial and freshwater vertebrates, and it provides guidance on whether and how conservation practitioners, researchers, and policymakers can work to restore the valuable migrations we have lost.

### INTRODUCTION

Migration is a widespread behavioral adaptation that has evolved in every major vertebrate group and affects ecosystems and societies across the world (Bauer and Hoye 2014). Migratory wildlife provide seasonal influxes of food that support species in higher trophic levels, from Pacific salmon (*Oncorhynchus* spp.) sustaining populations of grizzly bears (*Ursus arctos horribilus*) in North America (Hilderbrand et al. 1999) to dusky rats (*Rattus colletti*) driving seasonal abundance of water pythons (*Liasis fuscus*) in Australia (Madsen and Shine 1996). Meanwhile, nitrogen deposited by dead and defecating migrants fuels plant growth and nutrient cycling in systems ranging from the Mara River of the Serengeti (via wildebeest [*Connochaetes taurinus*], Subalusky et al. 2017) to the salt marshes of eastern Canada (via lesser snow geese [*Anser caerulescens*], Cargill and Jefferies 1984). In addition to contributing to ecosystem function, migrants also contribute economic inputs (Gislason et al. 2017) and cultural services (López-Hoffman et al. 2017) to human societies.

In recent decades, changes in climate, vegetation, biotic communities, and human influences have altered some migrations to the point of complete loss (Harris et al. 2009). Migrations may be lost due to population extirpation, as when the introduction of a predatory

non-native trout caused the local extinction of migratory long-toed salamanders (*Ambystoma macrodactylum*, Pearson et al. 2003). In other cases, a migration remains intact, but the migratory population is so depleted that it no longer supports related ecosystem functions – for example, when overhunting and habitat loss reduced migratory whooping cranes (*Grus americana*) to fewer than 15 individuals (Glenn et al. 1999). Alternatively, migration can be lost when a previously-migratory population becomes nonmigratory, like the anadromous alewives (*Alosa pseudoharengus*) that evolved resident freshwater traits after dams blocked passage to estuarine habitat for hundreds of years (Reid et al. 2020). Such losses have recently prompted efforts to conserve migration at the international, national, and local levels (e.g., International Convention on Migratory Species, (Harris et al. 2009); Global Initiative for Ungulate Migration, (Kauffman et al. 2021); United States Department of the Interior Secretarial Order 3362, (Middleton et al. 2020); Wyoming Migration Corridor Executive Order 2020-1, (Gordon 2020)).

With attention focused on conserving existing migratory behaviors, a critical question has been mostly overlooked: Once a migration has been lost, how can it be restored? Some research casts strong doubt on the potential for restoration, highlighting migrants' reliance on particular environmental or social conditions (Jesmer et al. 2018, Brooks et al. 2019). Other research, however, suggests more restoration potential by highlighting plasticity in some migratory species (Xu et al. 2021).

Efforts to restore lost migrations have been reported in all major vertebrate taxa (e.g., Fig. 1), but the success of existing attempts remains highly idiosyncratic. Species in unrelated taxonomic groups can display remarkably similar responses to restoration, while animals of the same species do not. For example, removing barriers to movement allowed both bull trout (*Salvelinus confluentus*) and zebras (*Equus burchelli antiquorum*) to swiftly restore lost migrations on their own (Bartlam-Brooks et al. 2011, Quinn et al. 2017). Yet the construction of passage structures around dams did not restore fish migrations in South America as it had in North America (Oldani et al. 2007). Likewise, elk (*Cervus canadensis*) transplanted into the American Midwest did not migrate seasonally like their montane counterparts (Wichrowski et al. 2005). These inconsistencies suggest a need to synthesize lessons learned across varied case studies to elicit more general insights.

Here, we assess the prospects for restoring lost vertebrate migrations worldwide, defining migration broadly as synchronized movement between seasonal ranges (Dingle and Drake 2007). First, we introduce key recent advances in the study of wildlife migrations that reveal opportunities for restoration. Next, we bring together case studies of restoration attempts across four major taxonomic groups (fish, birds, mammals, and herpetofauna) to synthesize common themes influencing restoration success among terrestrial and freshwater vertebrates. From this evaluation, we develop a conceptual framework to help inform restoration efforts across taxa. Our review reveals three broad strategies comprising seven specific techniques capable of effectively restoring lost migrations, and we explore the biological mechanisms that underpin their potential for success. Finally, we discuss how the work of researchers, conservation practitioners, and policymakers can directly influence restoration efforts.

## RECENT DEVELOPMENTS IN MIGRATION ECOLOGY

Innovations in animal tracking equipment, remote sensing technology, and computing approaches now allow us to link animals' behavioral choices and fates more effectively to

environmental attributes. The resulting advances in our understanding of migratory behavior now inform prospects for restoring migrations by revealing migrants' capacities for learning, exploring, and adapting to changing environments. These advancements include increasing recognition of 1) variation among individual-level behaviors, 2) variation among population-level behaviors, 3) the role of cultural knowledge in perpetuating behaviors, and 4) the scale and predictability of relevant environmental variations.

### **Migratory behavior varies among individuals**

The ability to radio track more animals over longer time spans and at finer temporal resolutions has uncovered far more variation in individual behavior than previously recognized. Whereas early research posited that characteristics of individual movements remained fixed (Farner 1950), contemporary studies find that many animals alter the timing, direction, and duration of yearly migrations in response to environmental fluctuations. Such flexibility occurs across diverse vertebrates including fish (Meager et al. 2018), birds (Fraser et al. 2019), mammals (Xu et al. 2021), and herpetofauna (Jourdan-Pineau et al. 2012). Perhaps more surprisingly, all taxonomic groups include some individuals that go so far as to alternate between migratory and nonmigratory behavior (e.g., striped bass [*Morone saxatilis*], (Secor et al. 2020); wood storks [*Mycteria americana*], (Picardi et al. 2020); spotted salamanders [*Abystoma talpoideum*], (Kinkead and Otis 2007); and elk, (Eggeman et al. 2016).

Such behavioral flexibility reveals considerable potential for individuals to naturally restore lost migrations under appropriate conditions. In species that alternate behaviors between years, for instance, individuals not currently migrating but retaining relevant knowledge or genetics can resume the behavior in future years if conditions prove beneficial and the cues of movement remain intact. Yellow-bellied toads (*Bombina variegata*), for example, can forego yearly migrations but resume them if rainfall again becomes sufficient to support breeding (Cayuela et al. 2014). Additionally, species that alter aspects of migratory behavior in response to environmental fluctuations can naturally restore migrations under suitable external conditions. For instance, eight waterfowl species rerouted migrations to recolonize historic seasonal habitats after environmental conditions improved (Fang et al. 2006), thereby restoring migrations that had been functionally lost from the area.

### **Migratory behavior varies among populations**

Partial migration - in which only part of a population migrates - has long been acknowledged, but more nuanced studies now reveal that partial migration does not manifest as a simple dichotomy of migration vs. residency. Rather, migration is best conceived as a continuum that also includes intermediate movement tactics (e.g., making multiple trips; moving for abbreviated times or distances; (Boel et al. 2014). This population-level variation in behavior has proven far more diverse than previously recognized, and populations even within the same species and geographic area can exhibit markedly different variations (Weimerskirch et al. 2017, Barker et al. 2019).

Populations with a higher diversity of individual behaviors often prove more resilient to variable environmental conditions, because different individuals can prosper under different conditions (i.e., the portfolio effect, (Schindler et al. 2010). Therefore, diversity in population-level behavior suggests considerable potential for restoring migrations amid changing environments. Indeed, translocating behaviorally diverse source populations of fish was more effective at long-term restoration of migration than translocating less-diverse populations

(Waldman et al. 2016). Furthermore, diverse extant populations may naturally re-establish extirpated local migrations, as when individuals from a genetically diverse population of Canada geese colonized a new seasonal breeding range in Greenland (Scribner et al. 2003). Of course, environmental fluctuations beyond the scope of variations historically experienced by a population may still result in permanent migration loss if the range of behavioral diversity does not allow adaptation to the new conditions.

### **Cultural knowledge perpetuates migratory strategies**

Recent work highlights the role of cultural knowledge transmission in maintaining migration across taxa including mammals (Festa-Bianchet 2018), birds (Mueller et al. 2013), and fish (Brown and Laland 2003). Translocated moose and bighorn sheep, for instance, adopted the migratory behavior of their new population rather than retaining that of their natal population, revealing that social learning had a stronger influence than genetic encoding in driving migratory behavior in these species (Jesmer et al. 2018).

Social migratory animals with knowledge of past behaviors may naturally restore lost migrations if conditions again become beneficial, whereas loss of cultural knowledge can impede or eliminate the possibility of re-establishing migrations (Jesmer et al. 2018). Alternatively, if knowledge of migration has been lost from a population or species but retained by humans, it may be possible to re-teach animals to migrate, as demonstrated by pioneering work in which researchers led Canada geese (*Branta canadensis*) along historic migration routes with ultralight aircraft (Lishman et al. 1997). Although research on social learning has historically focused on birds and mammals, reptiles and fish also demonstrate proclivities for communication and learned behaviors (Brown and Laland 2003). Bearded dragons (*Pogona vitticeps*), for example, can learn to open trap doors by mimicking conspecifics (Kis et al. 2015), and archer fish (*Toxotes jaculatrix*) learn to hunt simply by observing others (Schuster et al. 2006). If the learning of behavior extends to space use and seasonal movement, species in these taxa may be capable of learning migration from conspecifics as well.

### **Migration relies on predictable resource variation at appropriate spatiotemporal scales**

Whether individuals move based on social cues, past experience, or fixed internal mechanisms, recent studies reveal that migration typically occurs where variable resource patches are aggregated at broad spatial scales and where resources vary predictably each year (Bastille-Rousseau et al. 2017, Barker et al. 2019). Predictability is important not only for animals that track resources in near real-time but also for those that migrate in anticipation of future resources. For example, barnacle geese (*Branta leucopsis*) are more likely to arrive at stopover sites during peak forage conditions if climatic conditions vary more predictably (Kölzsch et al. 2015). Relatedly, reticulated flatwoods salamanders (*Ambystoma bishop*) can fail to reproduce when high environmental stochasticity disrupts the relative timing of male and female arrival on seasonal breeding grounds (Brooks et al. 2019).

Restoring a lost migration is therefore most likely where resources vary predictably enough that migrants can effectively track, and benefit from, seasonal changes. Evaluating the variability and distribution of resource patches across biologically relevant spatial scales may help inform feasibility of restoration. For example, facilitating movement across broad spatial scales was more effective than local habitat restoration in maintaining resilience of migratory fish species in Australia (Marshall et al. 2016). Temporal scales of variation also influence the



feasibility of re-establishment. For instance, if the cues triggering migration no longer align temporally with seasonal resource benefits, long-term restoration of migration is unlikely. Such phenological mismatches have already reduced population sizes of migratory birds unable to adjust the timing of seasonal movements to match climate-driven changes to seasonal breeding or brood-rearing habitats (Saino et al. 2011). Ongoing climate change will likely exacerbate mismatches for such species and may contribute to further declines of extant migrations.

## **EFFECTIVE MEANS OF RESTORING LOST MIGRATIONS**

Given the recent advances in our understanding of migration ecology, it is timely to explore whether, when, and how lost migrations can be restored. To provide a foundational understanding of the prospects for restoring lost migrations worldwide, we review and synthesize insights from case studies of restoration across four major vertebrate groups – fish, birds, mammals, and herpetofauna (e.g., Fig. 1). We focus on terrestrial and freshwater vertebrates due to a relative dearth of research on restored migrations in marine species, which are likely limited by technical and logistical constraints. Because the field of migration restoration lacks consistent terminology that would allow for a systematic search of the literature, and because many restoration efforts are described in technical reports rather than peer-reviewed scientific journals (e.g., (Soorae 2016, Brink et al. 2018), our review was more opportunistic than exhaustive. We located key examples of both successful and unsuccessful restoration attempts by (a) searching peer-reviewed literature in Google Scholar and Web of Science for relevant taxa, species, and all forms of the keywords “migration,” “restoration,” “recovery,” “re-establishment,” and “recolonization,” and (b) following threads of citations through relevant publications.

From our review, we identify three non-mutually exclusive strategies encompassing seven specific techniques capable of effectively restoring lost animal migrations (Fig. 2). First, lost migratory populations can be re-established (via techniques of either translocating wild animals or releasing captive-bred animals). Second, lost habitats can be recovered (by techniques aimed at restoring seasonal ranges, re-establishing habitat connectivity, or restoring stopover sites). Third, lost behavioral patterns can be revived (using techniques involving teaching animals or facilitating social learning). We discuss each strategy below, combining lessons learned from case studies with those gleaned from behavioral and ecological theory to illuminate the biological mechanisms underlying the success of each.

### **Re-establishing migratory populations**

Several case studies demonstrate that when migration is lost due to extirpation of a migratory population, releasing either wild or captive-bred individuals into a previously occupied seasonal range can result in restored migratory behavior (Fig. 2, techniques 1 & 2, respectively). Successful examples exist in all major vertebrate groups and include wild alewives translocated into historic spawning lakes (Reid et al. 2020), captive-bred loggerhead shrikes (*Lanius ludovicianus migrans*) released into areas where wild populations had become endangered (Imlay et al. 2010), and wild-born but captive-reared agile frogs (*Rana dalmatina*) released into historic breeding ponds (Fig. 1; Ward et al. 2016). In addition to underlying biological considerations, this strategy should be considered along with relevant aspects of the habitat restoration strategy to ensure adequate habitat exists to support a restored population.

Biologically, the success of population re-establishment in a target area hinges primarily on mechanisms of movement that are often genetically controlled. For example, some species

will readily migrate to and from a release site (e.g., Asian houbara bustard [*Chlamydotis macqueenii*], Burnside et al. 2020), whereas others appear genetically predisposed to return to their birth site or other non-target area (e.g., cuckoos [*Cuculus canorus*], Thorup et al. 2020). Genetics may also determine whether an individual will migrate at all, though the immediate trigger of movement typically consists of complex interactions between internal and external mechanisms (Kendall et al. 2015), and some genotypes considered migratory or nonmigratory may in fact display the opposite behavior (Kelson et al. 2019). Understanding the genetic basis of migration is important for understanding where and whether translocated animals will migrate, as well as for deciding whether wild or captive-bred individuals will be the most effective source population for restoration.

In addition to genetic traits of individuals, population-level genetic diversity also influences effectiveness of efforts to re-establish migratory populations. Low genetic diversity caused unsuccessful restoration of Atlantic salmon migrations (*Salmo salar*, Fraser et al. 2007), whereas retention of diverse native genetic traits allowed successful restoration of migratory rainbow trout (*O. mykiss aquilarum*, Carmona-Catot et al. 2012). Even where temporary local-scale restoration remains feasible, lack of genetic diversity can limit the ability to restore a sustainable metapopulation. For instance, efforts to re-establish Atlantic salmon migration in Canada were thwarted when immigration from nearby populations could not compensate for lack of genetic diversity in the released population (Fraser et al. 2007). Potential hybridization between released and extant individuals constitutes another important genetic consideration. Limited existing work suggests hybrids sometimes prove less adept at migrating (e.g., Reid et al. 2020), though results may be specific to species or areas. Opportunities to restore migratory populations may be limited where genetic diversity has already been lost, for instance if changing anthropogenic influences or environmental conditions have selected against the more migratory genotypes.

Characteristics of the area into which animals are released can also influence the success of re-establishment. Because animals often migrate to access temporally variable resources, re-establishing populations in resource-limited habitats is most likely to result in migration because such areas become seasonally less hospitable. For example, trumpeter swans reintroduced into their migratory summer range naturally restored migrations out of necessity when ponds froze during winter (Baskin 1993), and European bison (*Bison bonasus*) reintroduced into forested areas migrated to open grassland to take advantage of the higher forage availability during the growing season (Kowalczyk et al. 2013). Moreover, the habitat into which animals are released must provide adequate resources for continued seasonal use. For instance, American shad (*Alosa sapidissima*) introduced into high-quality breeding grounds above dams consistently returned to their release sites each year (Fig. 1; Brown and Pierre 2001), whereas giant kokopu (*Galaxias argenteus*) released into a stream with suboptimal water flow moved to other drainages rather than re-establishing historic migrations in the release area (Soorae 2016).

### **Recovering migratory habitats**

Habitat loss and barriers to movement rank among the most common causes of migration loss (Wilcove and Wikelski 2008). Provided the fitness benefits of migration remain intact, simply removing physical barriers between seasonal habitats or otherwise re-establishing habitat connectivity (Fig. 2, technique 4) can allow species across taxa to naturally restore migration (e.g., dam removal for bull trout, (Quinn et al. 2017); fence removal for zebras, Bartlam-Brooks et al. 2011; highway crossing structures for salamanders, (Pagnucco 2010); Fig. 1). In addition,

recovery efforts can improve fitness benefits provided by seasonal habitats or along migration routes (Fig. 2, techniques 3 and 5, respectively). However, some recovery efforts prove insufficient to restore behaviors, as when alewives landlocked for centuries evolved freshwater-specific traits rendering them unable to restore historic seaward migrations (Reid et al. 2020). Effectiveness of habitat recovery therefore depends not only on the quantity and quality of the restored habitat but also on the ability of animals to discover and use restored areas.

The scale of required habitat recovery can vary widely, from spanning multiple continents to discrete localized areas, depending on the distance across which the species ranges, the portion of the historic range across which restoration is desired, and the nature of threatening habitat characteristics. Habitat recovery areas are best identified based on their ability to provide the fitness benefits afforded by the original migratory habitat. In addition to determining which habitat type across the potential migratory range has limited behavior (i.e., seasonal ranges vs. migration paths vs. stopover sites), habitat recovery efforts must identify and ameliorate the specific habitat characteristic(s) threatening migration. Considerations should extend beyond physical aspects of the habitat (e.g., connectivity; invasive species; (Randall et al. 2016) to include ecological processes on which migrants also rely (e.g., river runoff regimes, Travnichek et al. 1995). Where limiting aspects are uncertain or complex, adaptive management strategies can help discern whether recovery efforts are effectively addressing the initial cause of migration loss.

The primary biological mechanism underpinning the success of habitat recovery efforts is the capacity of animals to perceive and respond to changing external conditions rather than relying on memory of past experiences. Examples of species rapidly colonizing new habitats occur in all major vertebrate groups, revealing considerable promise for naturally restoring migrations. Great crested newts (*Triturus cristatus*) took less than three years to discover and use seasonal ponds constructed to mitigate construction impacts (Jarvis et al. 2019); Atlantic salmon and alewives recolonized upstream areas within two years of dam removal (Hogg et al. 2015); and reed warblers (*Acrocephalus scirpaceus*) established a sustainable breeding population in a new habitat within two years of its restoration (Sætre et al. 2017).

A particular benefit of habitat recovery is the potential to restore multiple migrations simultaneously without directly manipulating wild populations. For example, habitat restoration projects in the central Yangtze River allowed at least eight waterfowl species to re-establish use of historic wintering grounds (Fig. 1; Fang et al. 2006), and enhancing a flow regime doubled the diversity of fish species downstream of the Thurlow Dam in Alabama (Travnichek et al. 1995). Thus, identifying shared species requirements on which to base habitat recovery goals can provide a relatively high return on project investment. Additionally, knowledge of species' responses to degraded environmental conditions can help determine the most effective habitat recovery technique. For instance, songbirds successfully migrating through corridors where recent hurricanes had significantly depleted food and shelter (Lain et al. 2017) suggest that habitat recovery efforts for such species may be more effective if focused on seasonal breeding grounds rather than stopover sites along migration corridors.

### **Reviving migratory behavior**

In some cases, existing habitat can support migration, and migratory species remain present, but animals no longer move seasonally. For species in which migration is learned rather than strictly inherited, case studies reveal that lost behaviors can be restored by either facilitating learning among conspecifics or teaching behavior to remaining individuals (Fig. 2, techniques 7 and 6,

respectively). In perhaps the most well-known example of a restored behavior, researchers taught Canada geese to migrate between Ontario and Florida (Lishman et al. 1997), a story adapted into the major motion picture *Fly Away Home*. The most successful examples of revived behavior across taxa capitalize on cognitive capacities of the target species by focusing on when, what, and from whom animals most readily learn to migrate. Underlying cognition of migratory behavior is therefore the primary biological mechanism influencing success of this restoration technique.

Though most migrants accumulate experiential and cultural knowledge as they age, they typically learn the basics of migration during early life stages. One restoration effort learned this lesson the hard way, when the majority of translocated adult elk returned to the areas from which they were captured. The subsequent translocation of yearlings proved far more successful as the younger animals more readily learned to migrate in novel environments (Allred 1950). Similarly, lesser spotted eagles (*Clanga pomarina*) that learned as juveniles from experienced conspecifics were more likely to migrate along the correct flyway than translocated juveniles that did not learn appropriate behavior during their first migration (Meyburg et al. 2017). Though migration-focused studies of social learning in fish remain rare, existing evidence similarly points to a heightened propensity for learning in juveniles relative to adults (Brown and Laland 2003).

In addition to learning migration during the most beneficial life stage, individuals must also learn the most beneficial type of migratory behavior. Successful restorations typically entail animals learning not to migrate along a fixed path at a predetermined time, but rather to actively perceive and respond to their environment. Translocated bighorn sheep and moose, for example, tracked seasonal changes in forage more optimally the longer they lived in novel areas, and extant native populations tracked forage most optimally (Fig. 1; Jesmer et al. 2018), suggesting that accumulated knowledge of flexible behavior improves fitness of migrants and contributes to sustainable restoration. Similarly, young whooping cranes migrated more efficiently and effectively when they learned flexible behaviors from more experienced conspecifics (Mueller et al. 2013).

Successful restoration efforts also incorporate information about from whom animals learn. Some migrants primarily learn from one closely-related individual (e.g., white-tailed deer [*Odocoileus virginianus*], Nelson 1995), whereas others learn from multiple unrelated conspecifics (e.g., short-toed snake eagles [*Circaetus gallicus*], Agostini et al. 2016; and sockeye salmon [*O. nerka*], Berdahl et al. 2017). Appropriate teachers can further vary among individuals within populations; for example, great bustards (*Otis tarda*) learn migration only from members of the same sex (Palacín et al. 2011). In many social species, a small number of individuals disproportionately influence population behavior by acting as group leaders (e.g., European bison, Ramos et al. 2015). The importance of individual leadership is increasingly recognized in behavioral ecology (Couzin et al. 2005) and holds particular promise for informing efforts to revive lost migrations. Because leaders tend to be older and more experienced, efforts to retain such individuals in restored populations may help build self-sustaining migrations with minimal management intervention.

## **KEY CONSIDERATIONS IN RESTORATION DECISIONS**

Our work reveals promising avenues for restoring lost migrations, as well as instances in which restoration may not be feasible or desirable. In addition to evaluating which aspect(s) of migration require restoration, decisions related to restoration efforts should consider whether, where, and how migration can effectively be restored (Table 1). Clearly identifying conservation

goals associated with restoration initiatives, the threats that originally caused migration loss, and the spatiotemporal scale of required initiatives can help improve the success of restoration efforts.

Importantly, migration is not always vital – or even desirable – for populations in which the behavior has been lost. Individuals may achieve higher fitness by not migrating, as in the blackbirds (*Turdus merula*) whose nonmigratory populations exhibited higher population growth than their migratory counterparts (Møller et al. 2014). Furthermore, migratory animals can transmit diseases across species and habitats, with potentially detrimental effects on the health of both ecosystems and humans (Altizer et al. 2011). Environmental alterations driven by climate change may intensify these and other issues if migrants establish new seasonal ranges and pathways that alter expected ecosystem interactions. Alternatively, a migration that is suboptimal for migratory individuals may still merit restoration to benefit other species or ecosystem functioning – for instance if migrants provide an important food source for predators (Hilderbrand et al. 1999), contribute to nutrient cycling (Subalusky et al. 2017), or shape vegetative communities in seasonal ranges (Cargill and Jefferies 1984).

Foundational to any successful restoration project is eliminating or reducing the original cause of loss. Acute, easily-manipulatable threats allow for relatively straightforward restoration approaches, whereas chronic or more complex threats prove more challenging to alleviate. Not only the original cause of loss but also potential future threats can affect the feasibility of migration restoration, most notably unpredictable environmental fluctuations and extreme weather events associated with climate change. Considering and integrating elements of adaptability – with respect to both management approaches and animal behavior – can bolster the likelihood of success amid uncertain future conditions.

Successful restoration culminates in the re-establishment of a self-sustaining migratory population. However, many key examples of ostensibly successful restorations rely on continual management intervention to bolster populations or behaviors (Fig. 1). Whooping cranes, for example, require artificial insemination to effectively reproduce (Brown et al. 2019); American shad require human-operated lifts to migrate past dams (Pierre 2003); and northern leopard frogs (*Lithobates pipiens*) require continual re-introductions to reinforce migratory populations (Randall et al. 2016). Thus, restoration projects should be initiated with consideration not only of immediate but also of long-term resource needs to ensure continued viability of migratory populations. Efforts can run the gamut from continually facilitated (e.g., yearly translocations; ongoing habitat treatments) to temporarily facilitated (e.g., population reintroductions across a discrete number of years or areas) to largely unfacilitated (e.g., waiting for animals to naturally restore behaviors after a single habitat restoration). Capitalizing on animals' inherent flexibility may provide the most cost-effective means of restoring migrations with minimal ongoing interventions.

### **Future directions in migration policy and management**

Despite the promising research and applied work we review here, environmental policies and management strategies generally do not include migration restoration as an explicit goal, particularly for terrestrial taxa. Instead, they tend to focus on conservation to prevent further loss of migrations, and on the physical environment rather than species ecology and behavior (e.g., (Gordon 2020, Middleton et al. 2020, Kauffman et al. 2021). The omission of migration restoration as a policy and management goal likely stems in part from a lack of knowledge about, or confidence in, the ability to restore such behavioral phenomena. Our work suggests an important need for governmental and non-governmental organizations to incorporate restoration

of lost wildlife migrations more clearly into policy goals and conservation strategies (Table 1).

Efforts ranging from top-down policy regulations to bottom-up community-led efforts can drive successful restoration initiatives. Policies can promote restoration across broad spatiotemporal scales by ensuring long-term protection for recovering populations, regulating threats to migratory behavior, and addressing issues of environmental justice. Practical examples include strengthening requirements for developers to include migration recovery in mitigation planning; increasing protections for migratory species across historic ranges; requiring infrastructure such as fences and dams to maintain wildlife permeability; recognizing and elevating indigenous rights to wildlife stewardship; and shifting population objectives from being primarily numerical to being more flexible and behaviorally or diversity based (e.g., target percentage of the population migrating seasonally; objective ranges of population-level genetic diversity).

Working in support of or independently from policy requirements, management strategies can effectively restore migrations by directly manipulating wild populations and habitats, building local support for conservation projects, and maintaining flexibility in restoration efforts. Land management agencies, conservation organizations, grassroots groups, tribes, and private landowners can implement habitat improvement projects, remove barriers to animal movement, and establish conservation easements with explicit migration-related objectives (Middleton et al. 2020). Wildlife management agencies, zoos, and museums can use captive breeding programs and research into animal husbandry to provide source animals capable of restoring lost behaviors (Soorae 2016). Effective management goals incorporate relevant logistical as well as biological considerations (Table 1).

## **CONCLUSION**

Preventing migration loss is likely a simpler and cheaper alternative to restoring lost migrations, yet failing to recognize the potential for restoration needlessly constrains future conservation efforts. Our synthesis of the literature reveals that migrations can be restored across vertebrate taxa and ecosystems, highlighting both opportunities and challenges in recovering lost migratory behaviors and related ecological processes. Popular attention typically focuses on the immediate aftermath of dramatic reintroductions or the human-wildlife relationships on display in the retraining of charismatic megafauna, but we show that restoring migratory behaviors more often requires long-term and painstaking efforts, significant investments, and a wide range of techniques to manage populations, habitats, and behaviors.









Countless opportunities exist to restore lost migrations worldwide. Although no single management technique can reliably restore migrations under all circumstances, explicitly considering each possibility and its potential for success can help guide restoration efforts and direct limited resources. The most successful restoration efforts will likely be those that recognize and facilitate migrants' adaptability, particularly in light of likely ongoing environmental changes. To date, the field of migration conservation has focused primarily on recovering damaged habitats and retaining extant migrations. We now invite conservationists to expand their thinking beyond environmental resources and population sizes to include restoration of large-scale behavioral phenomena.

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**FIGURE 1.** Key examples of efforts to restore lost migrations across four major vertebrate groups

	Species & Location		Pre-restoration status	Restoration technique*	Post-restoration status**
Fish	American shad ( <i>Alosa sapidissima</i> ), Susquehanna River, New England, USA		Effective loss of population by 1928 due to construction of multiple hydroelectric dams	2, 3, 4	<i>Partially restored:</i> Human-operated lifts at dams provide fish passage; pollution reduced; hatcheries still supplement juvenile population [1, 2]
	Bull trout ( <i>Salvelinus confluentus</i> ), Elwha River, Washington, USA		Complete loss of migration to estuary due to blockage by dam	4	<i>Fully restored:</i> Dam removal resulted in re-establishment of migratory life history strategy [3, 4]
Bird	Whooping crane ( <i>Grus americana</i> ), North America		Fewer than 15 wild adults by 1938 due to hunting and habitat loss	1, 2, 3, 4, 5, 6, 7	<i>Partially restored:</i> More than 600 individuals; individuals can migrate on their own but require human assistance with reproduction [5, 6]
	Siberian crane ( <i>Grus leucogeranus</i> ) and other species, Poyang Lake Ecosystem, Jiangxi, China		Drastic decrease of bird species diversity and population sizes due to conversion of overwintering habitat	3	<i>Partially restored:</i> Increased number of species and population sizes recorded anecdotally after wetland size recovered (lack of explicit pre-treatment counts) [7, 8]
Mammal	Bighorn sheep ( <i>Ovis canadensis</i> ), western United States		Some populations extirpated due to disease and overhunting; others reduced to point of high risk of migration loss	1, 7	<i>Partially restored:</i> Some, but not all, translocated individuals migrated. In successful cases, individuals learned from historic migrating populations how to track environmental cues [9]
	Zebra ( <i>Equus burchelli antiquorum</i> ), Botswana		Historic migration fully lost due to construction of veterinary fence	4	<i>Fully restored:</i> Historical migration that had not occurred from 1968-2004 was completely restored four years after fence removal [10]
Herpetofauna	Agile frog ( <i>Rana dalmatina</i> ), Channel Island of Jersey, United Kingdom		Critically Endangered; population limited to a single 10-ha area by 1988	2, 3	<i>Partially restored:</i> Two new migratory sites established; evidence of wild breeding in new areas; principal breeding sites protected [11]
	Long-toed salamander ( <i>Ambystoma macrodactylum</i> ), Waterton Lakes National Park, Alberta, Canada		Strong decline in migratory population; 10% mortality of migrants yearly due to road crossings	4	<i>Partially restored:</i> Installation of roadside fences and underpass tunnels reduced migrant mortality during road crossings to fewer than 2% [12]

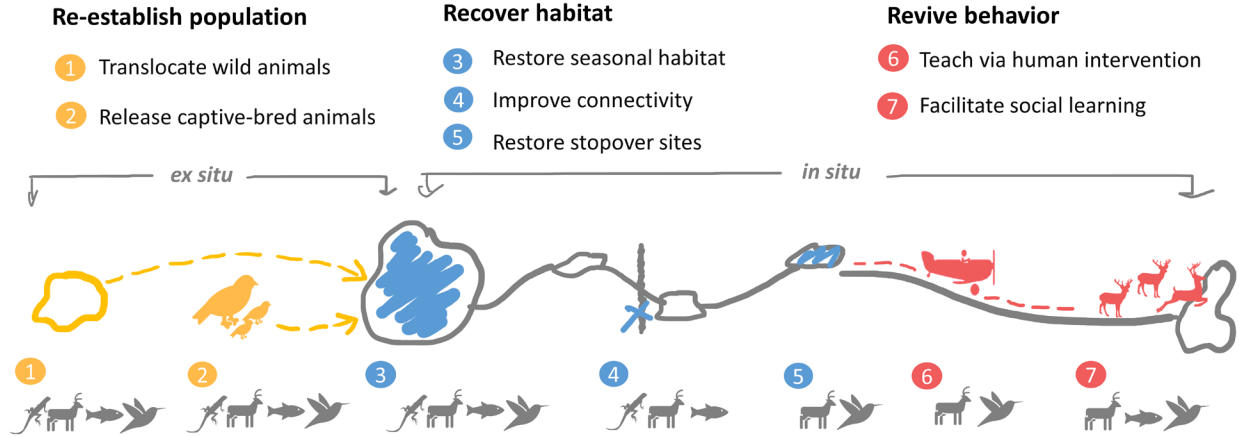
\* 1) Translocate wild animals, 2) Release captive-bred animals, 3) Restore seasonal habitat, 4) Improve connectivity, 5) Restore stopover sites, 6) Teach via human intervention, 7) Facilitate social learning (as in Fig. 2)

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**FIGURE 2.** Lost migrations can be restored ex situ or in situ using three broad strategies: re-establishing populations (yellow), recovering habitats (blue), and reviving behaviors (red). Each strategy encompasses multiple techniques (numbers 1 – 7) that have proven effective for terrestrial and freshwater vertebrates. Animal icons represent taxa in which the restoration technique has been successfully applied (herpetofauna, mammals, fish, and birds).



**TABLE 1.** Decisions regarding whether, there, and how to restore lost aspects of vertebrate migrations can be guided by careful consideration of management goals, species biology and ecology, and logistical constraints.

<b>Decision point</b>	<b>Management considerations</b>	<b>Biological influences</b>	<b>Logistical factors</b>
<b>Why restore migration?</b>	Benefit migratory species	Threat types and characteristics	Socioeconomic impacts of migration and of the restoration effort
	Improve ecosystem function	Effect of migration on target populations, other species, and ecosystem processes	Current and future manipulability of threats
<b>How can you conduct restoration efforts?</b>	Ongoing initiatives	Species behavioral plasticity and propensity for learning	Amount and timespan of funding
	Multiple efforts over limited time	Demographic and fitness requirements for a self-sustaining population	Available staff and resources
	One intervention		Quality of sociopolitical support
<b>Where can you restore?</b>	Historic habitat	Species flexibility and response to new environments	Availability of adequate locations
	New area(s)	Quality and manipulability of habitat in target area	Likelihood of ongoing suitability for migration
<b>Which aspect(s) of migration have been lost?</b>	Population	Relevant genetics and/or memory of migration	Source population availability
		Ontogeny: How genes and experience interact to influence migratory behavior	Moving animals across jurisdictions
	Habitat	Relative importance of seasonal ranges, movement paths, and stopover sites	Adequate habitat across yearly range
		Selective advantage: How target areas support fitness	Likely future changes to climate and land use practices
Behavior	Relevant aspects of social learning and knowledge transmission	Feasibility of removing barriers to movement	
	Control: Trigger of a migratory event	Regulations allowing manipulation of wild populations	
			Human knowledge of past migration

## Chapter 3. Large carnivores avoid humans while prioritizing prey acquisition in anthropogenic areas

*This chapter has been previously published and is included here with permission from co-authors.*

Barker, K. J., Cole, E., Courtemanch, A., Dewey, S., Gustine, D., Mills, K., Stephenson, J., Wise, B., & Middleton, A. D. (2023). Large carnivores avoid humans while prioritizing prey acquisition in anthropogenic areas. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.13900>

### ABSTRACT

1. Large carnivores are recovering in many landscapes where the human footprint is simultaneously growing. When carnivores encounter humans, the way they behave often changes, which may subsequently influence how they affect their prey. However, little research investigates the behavioral mechanisms underpinning carnivore response to humans. As a result, it is not clear how predator-prey interactions and their associated ecosystem processes will play out in the human-dominated areas into which carnivore populations are increasingly expanding.
2. We hypothesized that humans would reduce predation risk for prey by disturbing carnivores or threatening their survival. Alternatively, or additionally, we hypothesized that humans would increase predation risk by providing forage resources that congregate herbivorous prey in predictable places and times.
3. Using gray wolves (*Canis lupus*) in Jackson Hole, Wyoming, USA as a study species, we investigated 170 kill sites across a spectrum of human influences ranging from heavily restricted human activities on protected federal lands to largely unregulated activities on private lands. Then, we used conditional logistic regression to quantify how the probability of predation changed across varied types and amounts of human influences, while controlling for environmental characteristics and prey availability.
4. Wolves primarily made kills in environmental terrain traps and where prey availability was high, but predation risk was significantly better explained with the inclusion of human influences than by environmental characteristics alone. Different human influences had different, and even converse, effects on the risk of wolf predation. For example, where prey were readily available, wolves preferentially killed animals far from motorized roads but close to unpaved trails. However, wolves responded less strongly to humans, if at all, where prey were scarce, suggesting they prioritized acquiring prey over avoiding human interactions.
5. Overall, our work reveals that the effects of large carnivores on prey populations can vary considerably among different types of human influences, yet carnivores may not appreciably alter predatory behavior in response to humans if prey are difficult to obtain. These results shed new light on the drivers of large carnivore behavior in anthropogenic areas while improving understanding of predator-prey dynamics in and around the wildland-urban interface.

## INTRODUCTION

Large carnivores can influence trophic dynamics and ecosystem productivity by regulating the abundance and distribution of their herbivorous prey (Estes et al. 2011). After being extirpated from large portions of their historic ranges by the early 20<sup>th</sup> century (Ceballos and Ehrlich 2002, Mattson and Merrill 2002, Oakleaf et al. 2006), large carnivores across the globe are now recovering and expanding into rapidly growing human-dominated areas (Chapron et al. 2014, Gompper et al. 2015). Carnivores frequently alter their behavior in response to human influences, yet relatively little research explicitly integrates humans into studies of trophic interactions (Haswell et al. 2017). As a result, it is not clear how human-driven changes in predator behavior may affect prey populations, and related ecosystem functions, in the anthropogenic areas with which large carnivores are increasingly coming into contact.

Conventional wisdom holds that large carnivores avoid humans in shared landscapes, for instance by avoiding roads and structures (Wilmers et al. 2013, Carricondo-Sanchez et al. 2020), acting more nocturnally (Wang et al. 2017, Frey et al. 2020), using habitat types with better concealment (Ordiz et al. 2011), or moving more quickly through anthropogenic areas (Valeix et al. 2012). Large carnivore avoidance of humans has most commonly been interpreted as a fear response (Oriol-Cotterill et al. 2015, Smith et al. 2017, Suraci et al. 2019). However, it is plausible that human influences which directly threaten carnivore survival elicit a fear response, whereas carnivores perceive other human influences not as a direct threat but merely as a disturbance or nuisance (Frid and Dill 2002). This distinction between fear and disturbance is important because an animal that perceives danger typically behaves differently from one that merely feels disturbed (e.g., Stankowich 2008, Paton et al. 2017, Visscher et al. 2017). If carnivores perceive humans as a risk rather than a disturbance, patterns of predation by carnivores on their prey should differ between areas where humans do and do not directly threaten carnivore survival.

Explicitly investigating whether and how different types of human influences effect different changes in the predatory behavior of carnivores would help elucidate the relative efficacy of different management techniques aimed at manipulating populations of predators or their prey. For instance, such investigation could reveal whether carnivore behavior would be similarly affected by changing carnivore hunting regulations as by revising general recreation guidelines. Further, investigating the behavioral mechanisms underlying carnivore response to humans would help refine ecological theories of predator-prey dynamics in anthropogenic areas.

Despite their characteristic avoidance of humans, carnivores sometimes capitalize on benefits associated with anthropogenic areas, thereby increasing the risk of predation for their prey. For instance, predators preferentially travel along anthropogenic linear features such as roads, seismic lines, pipelines, railways, and transmission lines that increase hunting efficiency or access to prey (DeMars and Boutin 2018, Dickie et al. 2020). Furthermore, even where carnivores actively avoid human influences, behavioral alterations such as decreased feeding time can result in equivalent or even higher kill rates to fulfill energetic needs in anthropogenic areas (Smith et al. 2015). Evaluating how the risk of predation changes across a range of human influences would reveal whether and how different human influences differentially affect carnivore behavior to a degree that may alter prey distribution or demography (Elbroch et al. 2018b, Suraci et al. 2022).

To improve understanding of predator-prey interactions in anthropogenic areas, we tested three alternative hypotheses posited to explain how and why different human influences may alter the risk of predation for the prey of large carnivores (Table 1). We hypothesized that

humans would reduce predation risk either by disturbing carnivores via general activity (i.e., disturbance avoidance hypothesis) or being perceived as a direct threat to carnivores' survival (i.e., fear response hypothesis). Alternatively, or additionally, we hypothesized that humans would increase predation risk by providing forage for ungulates that congregates prey in predictable places and times (i.e., resource subsidy hypothesis). Our null hypothesis was that human influences would not affect the risk of predation (i.e., environmental hypothesis).

In support of the disturbance avoidance hypothesis, we predicted wolf kills would be less likely to occur close to human activity (near roads and trails), particularly when the risk of encountering humans was higher (during daytime and in high-visibility areas). In support of the fear response hypothesis, we predicted wolves that had been exposed to hunting by humans would exhibit a particularly strong avoidance of humans and would therefore be less likely than nonhunted wolves to make kills close to human activity or when the risk of encountering humans was higher. In support of the resource subsidy hypothesis, we predicted that wolf kills would be more likely to occur near areas where ungulate prey had access to human-provided forage. We recognize that carnivores may exhibit differing simultaneous responses to differing human influences (i.e., kills could be less likely to occur near disturbing or frightening human influences while also being more likely to occur near human-provided ungulate forage), so we explore this possibility by combining predictions from multiple hypotheses (Appendix A). Alternatively, if carnivores did not respond to humans, we predicted that predation risk would primarily be associated with environmental characteristics known to influence predation success such as snow, vegetation structure, topography, and prey availability.

To test these hypotheses, we studied the predation patterns of gray wolves (*Canis lupus*) in Jackson Hole, Wyoming, USA along a wide spectrum of human influences ranging from highly restricted human presence to unrestricted activity. First, we quantified associations between wolf kill site selection and aspects of the environment. Then, we tested whether inclusion of varied human influences better explained observed patterns of kill site selection than environmental characteristics alone. The study area was ideal for our purpose because land uses in Jackson Hole range from a densely developed town surrounded by suburban and exurban developments to broad swaths of undeveloped public land. Two different linear features facilitated human travel through the study area: paved plowed roads which received vehicle traffic day and night, and unpaved oversnow travel routes (i.e., trails) used by snowmobilers or nonmotorized recreationists primarily during the day. Wolf hunting was prohibited in some portions of the study area and allowed in others, providing an opportunity to evaluate the influences of both mortality risk and disturbance effects from humans on predation risk. Furthermore, supplemental feeding of ungulates during winter allowed us to explicitly account for the effects of human-provided forage on predation risk.

## **MATERIALS AND METHODS**

### **Study area**

Jackson Hole, Wyoming is a high-altitude (1,900–3,500 m) intermountain basin spanning about 2,000 km<sup>2</sup> in the southeastern Greater Yellowstone Area, USA (Fig. 1). Winters are generally cold and snowy, with yearly average total snowfall exceeding 5 m and average temperatures varying from -2°C to 5°C. Sagebrush-steppe dominates low elevations; quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*) dominate intermediate elevations; and subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea*

*engelmannii*) dominate high elevations.

Approximately 94% of the study area was federally owned, either by the US Forest Service (Bridger-Teton National Forest), the US Fish and Wildlife Service (National Elk Refuge), or the National Park Service (Grand Teton National Park). The remainder of land was either privately-owned (5%) or administered by state or local governments (1%). Winter recreation on federal land was strictly regulated, with large areas closed to public use or restricted to trail-only travel. Trails (i.e., unpaved oversnow travel routes) are primarily used during the day for snowmobiling by local residents and commercial tour groups, with the exception of trails in Grand Teton National Park which are restricted to non-motorized uses such as snowshoeing, cross-country skiing, and skate skiing. In contrast, plowed roads typically allow travel only by motorized vehicles (i.e., cars, trucks), with the exception of approximately 4km of the National Elk Refuge Road immediately adjacent to town which is commonly used by local residents for nonmotorized recreation including biking, hiking, and dog walking.

Wolves recolonized Jackson Hole in the late 1990s shortly after being reintroduced to nearby Yellowstone National Park. Between 2019-2021, the area supported 4-6 established packs consisting of 2-17 individual wolves; pack numbers, sizes, and territory boundaries changed yearly and seasonally due to inter-pack territory disputes, hunting by humans, and control removals. Wolf hunting occurred on the National Forest yearly on a quota system from September 1 – December 31; we began field seasons in early January just after the close of hunting seasons. At least two of the wolf packs we studied each winter had not been exposed to hunting, whereas at least two had been hunted in the season preceding fieldwork. We only considered wolf experience with hunting, not with control removals, in our evaluation of a potential fear response because (a) hunting occurred during winter immediately prior to our study, whereas control removals occurred during the summer, and (b) control removals may occur from the air or the ground, whereas hunting is always ground-based and occurs across broad swaths of the study area rather than only on specific parcels of private property.

The Jackson Elk Herd constitutes local wolves' primary prey (Woodruff and Jimenez 2019) and is provided forage via supplemental winter feeding programs in three areas that vary in their degrees and types of human influence: the National Elk Refuge bordering the busy town of Jackson, which is largely closed to public recreation (Cotterill et al. 2018), the Patrol Cabin Feedground immediately adjacent to a popular snowmobile trail and an inhabited home (Woodruff et al. 2018), and the Fish Creek Feedground that receives intermittent and inconsistent human influence from elk feeders and recreationists (Woodruff et al. 2018). During the time of our study, between 6,000 - 8,000 of the 11,000 individuals in the Jackson Elk Herd typically overwintered in large groups on the National Elk Refuge; about 1,000 - 2,000 individuals congregated on and around the other two feedgrounds; and the remainder lived in smaller groups on native winter range. Sympatric winter ungulates include bighorn sheep (*Ovis canadensis*), American bison (*Bison bison*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and a small number of white-tailed deer (*Odocoileus virginianus*). Cougars (*Puma concolor*) and sometimes coyotes (*Canis latrans*) also predate on ungulates in Jackson, as do black (*Ursus americanus*) and grizzly bears (*Ursus arctos*) which were largely denning through the duration of the study.

### **Animal capture and field investigations**

Wolves were captured by helicopter net gunning and darting (Native Range Capture Services,

Ventura, CA, USA and Leading Edge Aviation, Clarkston, WA, USA) and immobilized with tiletamine hydrochloride and zolazepam hydrochloride during winters 2018-2021. Wolves were outfitted with GPS collars (Telonics, Mesa Arizona, USA) programmed to record one location every two hours. Animal capture and handling was conducted in accordance with guidelines established by the American Society of Mammalogists (Sikes and Mammalogists 2016) and protocols approved by the National Park Service Institutional Animal Care and Use Committee (permits WY\_GRTE\_Stephenson\_Wolf\_2020.A3 and IMR\_GRTE\_Gustine\_Wolves\_2017.A3).

We conducted our study in winter, when adult ungulates are most vulnerable to wolf predation (Brodie et al. 2013) and are congregated at lower elevations closer to areas typically used by humans (Skovlin et al. 1989, Haggerty et al. 2018). To find kill sites, we investigated clusters of wolf locations (i.e.,  $\geq 2$  GPS collar locations recorded within 100 m in a 4-day period, Webb et al. 2008), indicating areas where wolves may have spent time killing and feeding on prey. We randomly prioritized cluster sites to visit by pack to ensure random sampling and even coverage of the study area. We accessed clusters via skis, snowmobiles, snowshoes, and hiking, and we waited to visit clusters until at least 2 days after wolves had left the area to avoid influencing movements and feeding. We classified carcasses as kills based on presence of hemorrhaging in areas typical of wolf kills or if tracks or other sign showed clear evidence of a chase and kill (Acorn and Dorrance 1990). We recorded kill sites as the locations of wolf-killed carcasses unless they had been dragged or otherwise moved, in which case we recorded the location of the hair mat and rumen as the kill site.

## **Environmental covariates**

We used remotely sensed data to determine the aspect, terrain position, canopy cover, and snow depth at each kill site or non-kill site. We calculated aspect and terrain position index (relative position of a pixel relative to neighboring pixels, e.g., ridgetops vs. drainages) from USGS's 1/3 arc-second digital elevation model using the raster package (Hijmans 2022). We converted aspect to northness (i.e.,  $\cos(\text{aspect})$ ) to represent ecological differences between north- and south-facing slopes. For canopy cover we used the National Landcover Database percent canopy cover at a 30 m<sup>2</sup> scale. We estimated snow depth as the depth recorded on that date at the SNOTEL or National Weather Service station within our study area that was closest in elevation. Though not specific to exact sites, we consider this estimation to represent a relative index of snow depth based on a significant positive linear relationship between these snow data and snow measurements taken at a subsample of our field sites ( $p = 0.0003$ ).

We estimated an index of relative prey availability using data from aerial and ground counts of elk recorded by WGFD and USFWS biologists every winter. Surveys occur during February, the month considered most representative of core winter distribution for native ungulates. Counts are conducted visually from a helicopter across all elk winter ranges in the study area and from the ground via horse-drawn sleigh or mechanized feeding equipment on feedgrounds. For each of the 3 winters (2019-2021), we used these spatially explicit elk count data to generate a number of points per count location equal to the number of elk observed at that location. We then used the kernel density estimator in the `adehabitatHR` package (Calenge 2006) to generate a utilization distribution from those points using a grid cell size of 1 km<sup>2</sup>. We used the volume of the utilization distribution in each pixel as a proxy for relative prey availability. We normalized the index by removing values  $>99$  and then taking the natural log of 100 minus each value (Kertson and Marzluff 2011).

## Human influence covariates

Candidate human influence covariates were daytime; wolf exposure to hunting by humans; and distances to paved roads, unpaved over-snow travel routes that were mostly used by snowmobiles during daytime hours (hereafter, trails), and elk supplemental feeding areas. We defined daytime as a binary yes/no representing whether humans could see without the use of artificial light (i.e., when humans were most likely to be active outdoors) using daily timing of civil twilight from the `suncalc` package (Thieurmel and Elmarhraoui 2019). We defined wolf exposure to hunting as a binary yes/no representing whether the individual was in a pack that had been hunted based on annual harvest and poaching data (WGFD et al. 2020, 2021, 2022).

Distances to all human influences were measured in 30 m increments to correspond to the spatial scale of environmental covariates. We digitized paved roads and unpaved winter trails using a combination of US Forest Service open roads and trails shapefiles (USFS 2019), roads and easements shapefiles (Teton County 2019, Sublette County 2019, WYDOT 2019), study area-specific recreation keyhole markup language (kml) files from the Jackson Ranger District (J. Wilmot, unpublished data), and personal experience of road closures observed during fieldwork. We hand-digitized feedground locations to most accurately represent the spatial extent of feeding areas that were actively used during the period of the study.

## Predation risk models

We used a multi-stage approach to evaluate whether and how humans altered the risk of wolf predation for ungulate prey (Fig. 2). Briefly, we first developed a well-supported model of the environmental characteristics that best explained kill site selection by wolves. Then, we used Akaike's information criteria corrected for small sample size (AICc; (Burnham and Anderson 2004) to compare support for this environmental model with that for other models that also included combinations of human influences designed to test predictions supporting each of our hypotheses (Table 1). Analyses were conducted in Program R version 4.0.5 (R Core Team 2021) and modeled using the `survival` package (Therneau 2022) unless otherwise noted. All covariates were centered, scaled, and had Pearson's correlation coefficients  $< 0.5$ .

We used matched case-control logistic regression models (Boyce et al. 2003) to quantify associations between the probability of a wolf kill occurring in a given area and the environmental and human-related characteristics of that area. For each used location (i.e., wolf-killed carcass) we randomly selected five matched locations (Cooper and Millsbaugh 1999) from a circular area with a 10 km radius (the maximum distance we observed a wolf traveling in 2 hours) centered at the collar location immediately preceding the kill. This method allowed us to compare characteristics of a used location with those of alternative locations in which a wolf could feasibly have killed an animal, given that wolves frequently shifted territory boundaries during the study.

First, we determined which combination of environmental characteristics most strongly influenced selection of kill sites by wolves using the seven-step process for covariate selection (Hosmer et al. 2013). Broadly, this approach involves identifying potentially informative covariates using univariate models, evaluating influences of statistically informative covariates all together in a multivariate model, iteratively removing statistically uninformative covariates, and evaluating interactions between covariates to arrive at a multivariate model containing the



combination of covariates that are most strongly associated with the response variable (Hosmer et al. 2013). Covariates considered for the environmental model were snow depth, terrain position index, prey availability, aspect, and canopy cover, all of which serve as key drivers of wolf habitat selection and predation patterns in similar areas (Oakleaf et al. 2006, Lesmerises et al. 2012, Woodruff et al. 2018), along with biologically relevant interactions and quadratic terms.

Next, for each of our three human-related hypotheses (Table 1), we evaluated support among a small suite of candidate models representing hypothesis predictions. We compared support among each of the individual hypotheses to draw inference regarding the relative strength of each explanation independently. We then used covariates included in any of the best-supported models for each individual hypothesis to develop additional models that encompassed multiple hypotheses by considering additions and interactions among supported covariates (e.g., adding effects of feedgrounds to fear response models). Finally, we compared support among these multiple-hypothesis models, the best-supported models representing each individual hypothesis, and the top environmental model. We evaluated model fit of supported models using 100 repetitions of 10-folds cross validation for conditional logistic regression models (Fortin et al. 2009). We also tested whether the inclusion of individual wolf or pack-year as random effects improved explanatory power of models to a degree that merited their increased complexity based on a  $\Delta\text{AICc}$  value of 2.0. We defined these models using `glmmTMB` to allow for the additional random effects (Brooks et al. 2017).

## RESULTS

### Kill site investigations

During 72 days of field investigations conducted January-March 2019-2021, we visited 1038 cluster sites from 24 individual collared wolves in 8 packs. Of these clusters, we identified 170 (16%) as probable or likely wolf kills, 657 (63%) as beds, 47 (5%) as scavenges, 13 (1%) as revisits to previous clusters, and 151 (15%) as other or unknown. Elk comprised the vast majority of kills (87%), followed by moose (7%) and other ungulates (6%). Eleven of the 170 kill sites had two carcasses; none had more than two.

### Predation risk models

Wolves primarily selected kill sites in areas of high prey availability and spatial vulnerability based on environmental characteristics, but we found more statistical support for models that included human influences than for those that included environmental characteristics alone (Table 2; Appendix A; environmental-only model  $\Delta\text{AICc} = 11.05$ ). The environmental covariates for which we found support were linear effects of relative prey availability, terrain position index, snow depth, and canopy cover, as well as an interaction between prey availability and canopy cover. We found support for six models ( $\Delta\text{AICc} \leq 2.0$ ), and we report results from the two best-supported models. The other four supported models (models 3-6) did not include additional covariates with effects distinguishable from zero; therefore the top two models capture the most substantive effects on predation risk (Table 2). Additionally, each of the top two models each have approximately double the  $\text{AICc}$  weight of models 3-6 (Table 2). Model validation indicated high predictive accuracy for both models with mean observed Spearman rank correlation  $0.83 \pm 0.14$  sd and  $0.84 \pm 0.11$  sd, whereas the model of environmental influences

alone had lower predictive accuracy with mean observed Spearman rank correlation  $0.73 \pm 0.18$  sd.

The two best-supported models generally agreed on the relative strength and effects of shared covariates (Fig. 3) and indicated that wolves were most likely to make kills in areas of relatively high prey availability, especially in more heavily forested areas, as well as in drainages and valley bottoms (i.e., low terrain positions) and shallow snow. Both models also indicated that kills were more likely to occur close to trails and feedgrounds but not paved roads. Neither model included an influence of wolf exposure to hunting. The key difference between the two supported models was that model 1 indicated that wolves preferentially killed prey closer to trails during the night, whereas model 2 indicated that selection for or against trails and roads depended on the relative availability of prey. This second model indicated that where prey availability was high, wolves were more likely to kill close to trails but far from paved roads, whereas where prey availability was low, wolves responded less strongly to anthropogenic linear features (Fig. 4). Neither the addition of wolf nor pack random effects improved model explanatory power to a degree that merited the increased complexity ( $\Delta AICc = 2.04$  with  $\log(L)$  essentially equivalent to that of the fixed effect-only model for both models). Further, parameter estimates and associated standard errors in these models were statistically equivalent to those in models that did not include the additional random effects.

## DISCUSSION

Wolves prioritized acquiring prey over avoiding humans, yet failing to account for human influences considerably reduced our ability to explain observed patterns of predation risk for ungulate prey. Of the hypotheses we tested (Table 1), we found the strongest support for the disturbance avoidance and resource subsidy hypotheses. We did not find support for either the fear response hypothesis or the null hypothesis that human influences would not affect patterns of wolf predation. Our results reveal that multiple human influences alter the predatory behavior of wolves, and that wolf avoidance of humans may stem more strongly from a disturbance avoidance than a fear response.

Despite the opposing nature of the predictions associated with the disturbance avoidance and resource subsidy hypotheses, both were supported within the same models of kill site selection, revealing that wolves did not unequivocally perceive humans as either disturbing, threatening, or rewarding. Rather, they actively distinguished between relative costs and benefits of different human influences. For example, wolves avoided killing prey near trails during the day when humans were most active, but they were more likely to kill prey near human-run elk feedgrounds during both day and night regardless of human activity, suggesting the considerable food benefit on feedgrounds outweighed any perceived costs of human interactions. Indeed, the effect of prey availability on the risk of predation far exceeded that of any human influence, and in areas of particularly low prey availability wolves responded less strongly – if at all – to humans.

To date, the effects of anthropogenic linear features like roads and trails on predation risk for ungulates have appeared highly idiosyncratic. Wolves select for linear features in some areas (DeMars and Boutin 2018, Dickie et al. 2020) and against them in others (Rogala et al. 2011), and linear features can increase (Leblond et al. 2013), decrease (DeCesare et al. 2012, McKay et al. 2021), or have no effect on (Hebblewhite et al. 2005) predation risk for ungulate prey. Our

work indicates that these incongruous results may stem from differences in how predictably or intensely humans are using linear features, not physical aspects of the linear features themselves. For example, during the night, wolves killed prey closer to trails but did not alter behavior in response to roads. In our study area during winter, humans predictably use trails almost exclusively during the day, whereas use of roads continues sporadically and unpredictably throughout the night. Therefore, the differing response of wolves to roads and trails during the night may indicate wolves most consistently avoid areas where human activity occurs most predictably, regardless of the relative frequency of encounter. Similarly, pumas (*Felis concolor*) in North America and Eurasian lynx (*Lynx lynx*) in Norway more strongly avoided using habitat or killing prey in areas of more predictable human activity (Bunnefeld et al. 2006, Wilmers et al. 2013). We would further expect wolf responses to linear features to differ based on the detectability and availability of prey, based on our finding that wolves prioritize acquiring prey over avoiding humans.

Wolves are typically classified as coursing predators due to their propensity for chasing down prey in flat, open areas (Kauffman et al. 2007, McPhee et al. 2012, Torretta et al. 2017), but our work corroborates that of other studies in North America, Europe, and Asia showing that wolves can also kill effectively in the environmentally complex habitats traditionally associated with ambush predation. As in our study area, wolf predation risk in parts of Canada (Hebblewhite et al. 2005, DeCesare et al. 2012) and Mongolia (Caroline et al. 2009) was highest in forested areas, while wolves elsewhere were more likely to kill prey in ravines than on flat terrain (U.S.: Kunkel and Pletscher 2001; and Poland: Gula 2004). Such flexibility in wolf hunting strategies may stem from differences in detectability or catchability of primary prey in different areas. For example, wolves in Scandinavia preferentially made kills in opposite types of landscapes (e.g., open vs. forested areas) depending on whether they were preying on moose or roe deer (Gervasi et al. 2013). Supporting this idea, wolves in our study tended to kill key secondary prey (moose and bison, 11% of kills) in more thickly vegetated areas than elk (median canopy cover 31% vs. 11%). Our work additionally suggests that not only differing prey species but also differing human influences or amounts of prey availability may interact with environmental characteristics to drive predation strategies of wolves.

Human-altered patterns of predation risk, when they occur, could influence population dynamics of ungulate herds if they disproportionately affect particular sexes or cohorts (i.e., demographic classes) of prey relative to others. For example, different demographic classes of elk are associated with different group sizes – larger groups typically consist of fecund adult females and their recent offspring, whereas males and senescing females live in smaller groups (McCorquodale 2001, Hebblewhite et al. 2005, Woodruff et al. 2018). A key benefit of the small group strategy is that the relatively high individual mortality risk should be offset by a low probability of encountering a predator (Hebblewhite and Pletscher 2002). However, other studies have documented increased encounter rates and predation risk for ungulates near linear features (Whittington et al. 2011, Mumma et al. 2017). Our finding of heightened predation risk near trails regardless of prey availability suggests that wolf use of trails could increase encounter rates for prey living in smaller groups, thereby reducing survival rates of males and old females relative to those of the fecund females that contribute to increasing population sizes.

We found activity disturbance by humans decreased predation risk irrespective of direct threats to carnivore survival (i.e., exposure to hunting by humans), yet a fear response could conceivably underlie the disturbance responses we observed. Importantly, data limitations may have precluded our ability to detect a fear response due to hunting by humans. Wolves that are

hunted may alter their behavior only when being actively hunted, whereas we evaluated kill site selection after hunting seasons ended. Additionally, wolves in packs that had been hunted may not have individually experienced the risk associated with hunters, and wolves in packs that were not hunted but had experienced control removals may still perceive humans as risky. Experimental (e.g., Smith et al. 2017, Suraci et al. 2019) or observational studies that contrast carnivore behavior during and outside hunting seasons would provide stronger support for or against the hypothesis that direct human-caused mortality elicits a fear response in large carnivores.

Large carnivores are often killed or relocated when they come into close contact with humans due to issues of livestock depredation, potential risks to humans, competition with human hunters for ungulate prey, and cultural pushback against perceived government overreach in supporting or facilitating predator recovery (Behdarvand et al. 2014, Bradley et al. 2015, Lute et al. 2018, Linnell et al. 2021). As carnivore populations continue to recover and expand following their deliberate extirpation from much of their historic range worldwide by the mid-20th century, they are increasingly pushed into areas of not only increased human activity (Linnell et al. 2001, Chapron et al. 2014) but also reduced prey availability (Basille et al. 2009). We anticipate heightened human conflict and concomitant carnivore mortality in such situations if large carnivores, like wolves in our study area, forego avoiding humans to increase opportunities for prey acquisition in areas of relative scarcity. Conservation and coexistence efforts often aim to identify likely areas of human-carnivore conflict in which to focus mitigation work (Miller 2015, Minin et al. 2016). We note that native prey availability in and around human-dominated areas may represent a particularly strong determinant of conflict likelihood (e.g., Khorozyan et al. 2015).

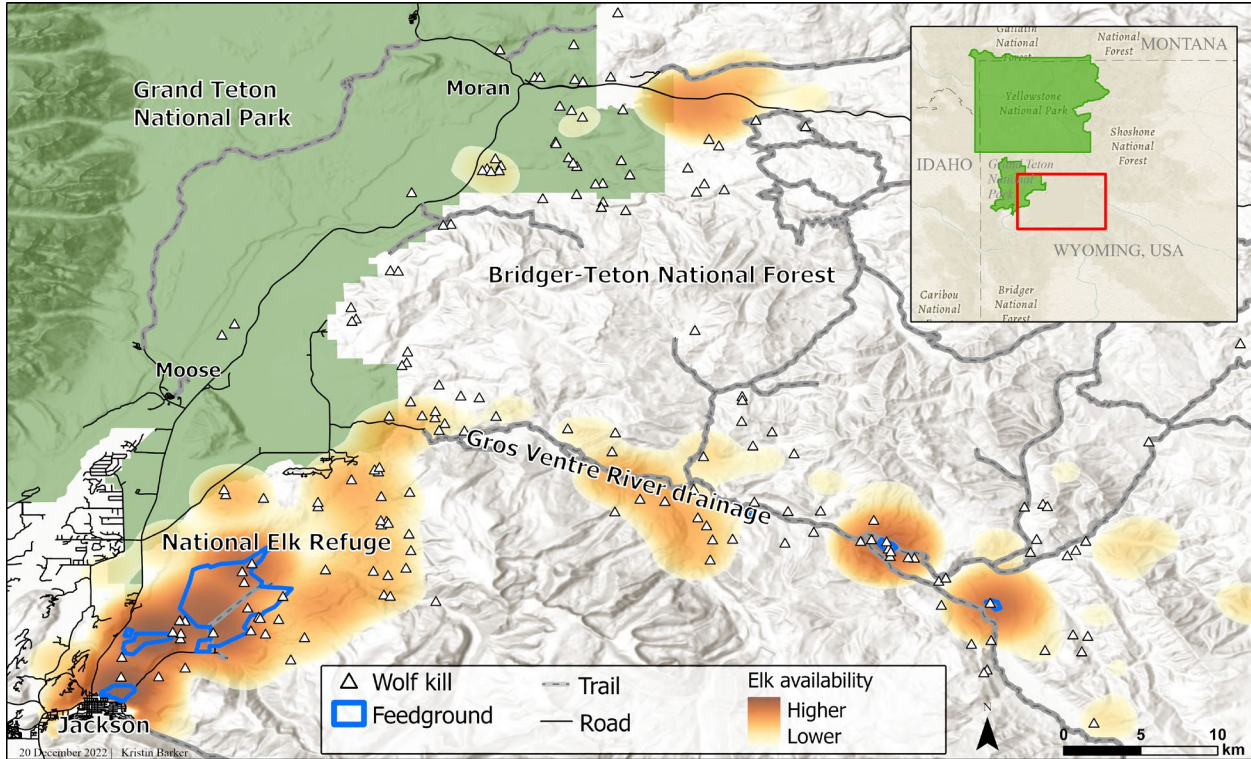
As large carnivore populations continue to spread across the globe, understanding how their distributions and behaviors will take shape in the human areas with which they inevitably come into contact will prove increasingly important to wildlife practitioners, policymakers, communities, and local stakeholders. We found that both environmental and human influences can affect the risk of wolf predation, suggesting that strong shifts in biotic or abiotic conditions such as snowpack or vegetation could alter predation risk as strongly as either intentional or unintentional human influences. Anticipating and managing predator-prey interactions in anthropogenic landscapes will rely on a strong understanding of the conditions under which the effects of humans in conjunction with environmental effects may alter predator behavior to a degree that could result in biological consequences for prey populations and potentially cascading effects on associated ecosystem processes.

## **ACKNOWLEDGEMENTS**

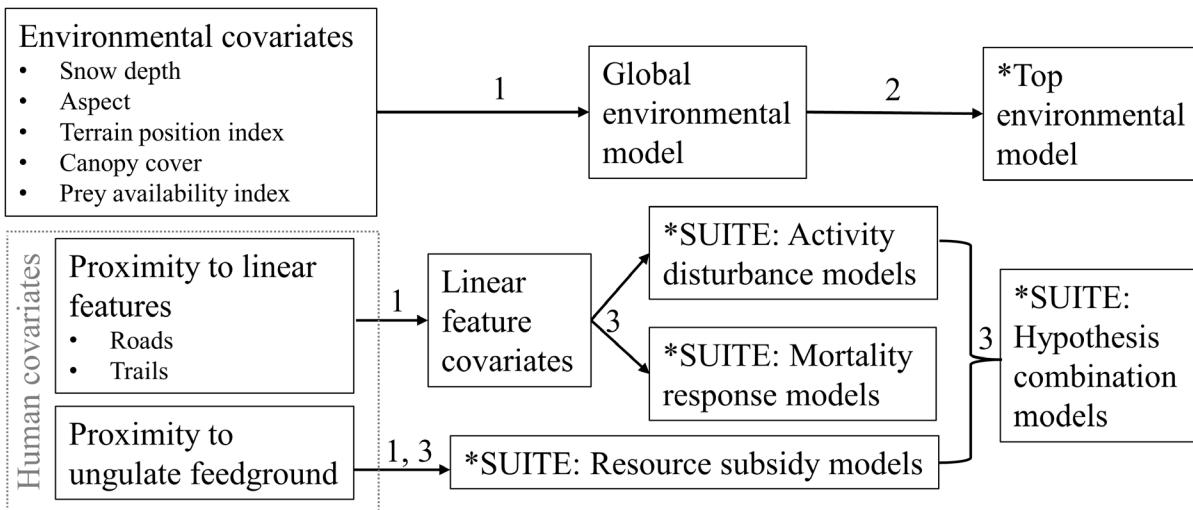
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considerably improved by helpful feedback on previous versions from Wenjing Xu, Laura Gigliotti, and Avery Shawler.

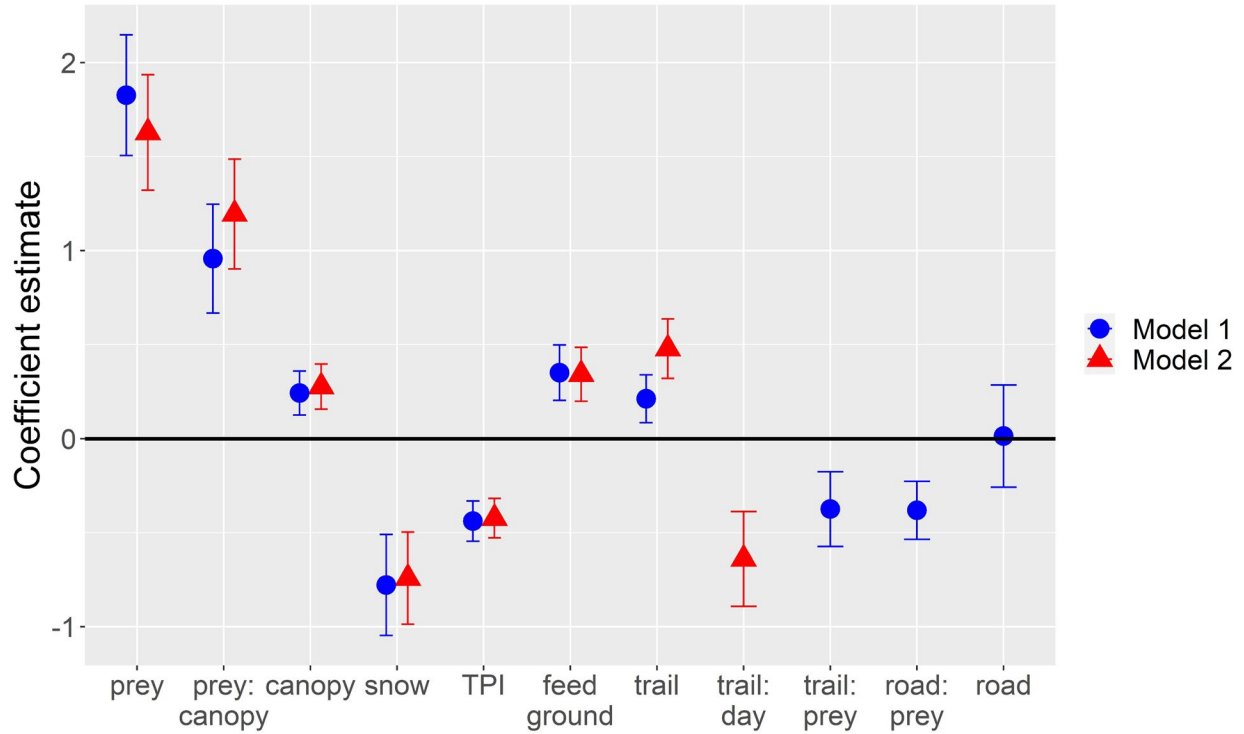
**FIGURE 1.** Locations of wolf kill sites, linear features, elk feedgrounds, and average relative prey availability across Jackson Hole, Wyoming, USA, winters 2019-2021. In addition to the orange shaded areas depicting relatively higher prey availability based on winter aerial and ground surveys, prey occur in low densities across the majority of the study area.



**FIGURE 2.** Diagram of methods used to develop and evaluate support for models that quantified how the spatial risk of wolf predation changed in association with environmental and human influences. Steps included: (1) Identify supported forms of individual covariates by evaluating covariate significance in univariate models that included linear or quadratic forms of each candidate covariate, (2) Determine best-supported combination of environmental covariates using the seven-step process of covariate selection (Hosmer et al. 2013), and (3) Develop a priori set of models based on predictions of hypotheses and supported forms of candidate covariates. \*Indicates models competed using Akaike’s information criterion corrected for small sample size (AICc, Burnham and Anderson 2004). Models in suites included combinations of environmental and human influence covariates.

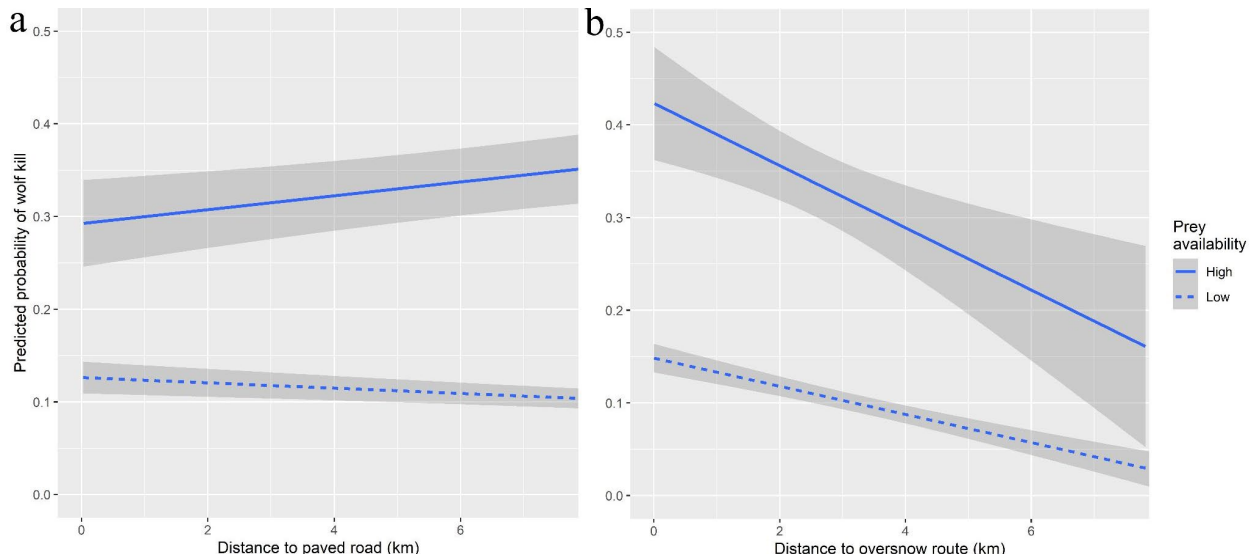


**FIGURE 3.** Estimated effects of environmental and human influences on wolf kill site selection across Jackson Hole, Wyoming, USA, winters 2019-2021. Points and lines indicate beta estimates and standard errors, respectively, from two supported models (distinguished by color and shape). Covariates are standardized and represent relative prey availability (prey), percent canopy cover (canopy), snow depth (snow), terrain position index (TPI), and proximities to paved roads (road), unpaved over-snow travel routes (trail), and elk feeding areas (feedground).





**FIGURE 4.** Predicted effects of anthropogenic linear features on the kill site selection of wolves across Jackson Hole, Wyoming, USA, winters 2019-2021. Where prey were readily available (i.e., relative prey availability index above average; solid lines) wolves responded differently to these two linear features, being more likely to make kills farther from paved roads (panel a) but closer to unpaved over-snow travel routes (i.e., trails; panel b). Conversely, wolves exhibited weaker response to trails and no distinguishable response to roads when prey availability was low (i.e., within 25% quartile; dashed lines). Shaded areas represent 95% confidence intervals. The figure represents results from the model referred to as Model 2 in the main text and Table 2.



**TABLE 1.** Hypotheses and predictions posited to explain whether and how humans influence natural patterns of wolf predation on ungulates.

<b>Hypothesis</b>	<b>Biological explanation</b>	<b>Predicted probability of wolf kill</b>
Disturbance avoidance	Avoiding human activity reduces carnivores' propensity to kill prey	Lower near roads and trails, especially during the day or in visible open-canopy areas
Fear response	Fear of mortality by humans reduces carnivores' propensity to kill prey	Lower near roads, trails, or in open-canopy areas for wolves that are hunted relative to wolves that are not hunted
Resource subsidy	Anthropogenic forage that predictably congregates prey increases carnivores' propensity to kill prey	Higher near ungulate feedgrounds
Environment (null)	Wolves do not alter predatory behavior in response to humans	Uncorrelated with human influences (environmental influences only)

**TABLE 2.** Best-supported models testing predictions regarding the influence of humans on kill site selection of wolves in Jackson Hole, Wyoming, USA. Italics indicate uninformative covariates (i.e., 95% confidence interval of beta estimate overlaps 0). All models also include the covariates from the null environment-only model reported in the last row. Covariates are: road - distance to nearest paved road; trail - distance to nearest unpaved oversnow travel route, prey - relative prey availability index; feed - distance to nearest ungulate feeding area; tpi - terrain position index; snow - snow depth (cm); can - canopy cover (%). K indicates the number of model parameters,  $\omega_i$  indicates model AICc weight, and LL refers to log-likelihood.

Model	K	$\Delta$ AICc	$\omega_i$	LL	Covariates
<b>1</b>	10	0.00	0.18	-234.30	<i>road</i> + trail + feed + prey:road + prey:trail
<b>2</b>	8	0.14	0.17	-236.41	trail + feed + trail:day
<b>3</b>	11	1.34	0.09	-233.95	<i>road</i> + <i>trail</i> + feed + prey:road + prey:trail + <i>feed:day</i>
<b>4</b>	11	1.44	0.09	-233.99	<i>road</i> + trail + feed + prey:road + prey:trail + <i>feed:can</i>
<b>5</b>	9	1.50	0.09	-236.07	trail + feed + trail:day + <i>feed:day</i>
<b>6</b>	9	1.72	0.08	-236.18	trail + feed + trail:day + <i>feed:can</i>
<b>38</b>	5	11.05	0.00	-244.90	tpi + prey + snow + can + prey*can

## APPENDIX A

Results of AICc model selection among a suite of models testing predictions regarding the influence of humans on the kill site selection of wolves in Jackson Hole, Wyoming, USA, winters 2019-2021.

Hypoth. refers to the hypothesis or combination of hypotheses the model was intended to test: disturbance avoidance (dist), fear response (fear), resource subsidy (rsc), and environment (envt). All models also include the covariates from the environment model.

Covariates are: road - distance to nearest paved road; trail - distance to nearest unpaved oversnow travel route, prey - relative prey availability index; feed - distance to nearest ungulate feeding area; tpi - terrain position index; snow - snow depth (cm); can - canopy cover (%); hunt - whether the wolf was exposed to hunting by humans. K indicates the number of model parameters,  $\omega_i$  indicates model AICc weight, and LL refers to log-likelihood.

<b>K</b>	<b><math>\Delta</math>AICc</b>	<b><math>\omega_i</math></b>	<b>LL</b>	<b>Covariates</b>	<b>Hypoth.</b>
10	0.00	0.18	-234.30	road + trail + feed + prey:trail + prey:road	dist + rsc
8	0.14	0.17	-236.41	trail + feed + trail:day	dist + rsc
11	1.34	0.09	-233.95	road + trail + feed + prey:trail + prey:road + feed:day	dist + rsc
11	1.44	0.09	-233.99	road + trail + feed + prey:trail + prey:road + can:feed	dist + rsc
9	1.50	0.09	-236.07	trail + feed + trail:day + day:feed	dist + rsc
9	1.72	0.08	-236.18	trail + feed + trail:day + can:feed	dist + rsc
9	2.18	0.06	-236.41	road + trail + feed + trail:day	dist + rsc
10	3.53	0.03	-236.06	road + trail + feed + trail:day + day:feed	dist + rsc
9	3.75	0.03	-237.19	road + trail + prey:trail + prey:road	dist
10	3.76	0.03	-236.18	road + trail + feed + trail:day + can:feed	dist + rsc
7	3.88	0.03	-239.29	trail + trail:day	dist
8	4.05	0.02	-238.36	trail + feed + can:hunt	fear + rsc
7	4.55	0.02	-239.63	trail + feed	dist + rsc
8	5.58	0.01	-239.13	road + trail + trail:day	dist
9	5.95	0.01	-238.29	road + trail + trail:day + road:day	dist
9	5.99	0.01	-238.31	trail + feed + can:hunt + hunt:feed	fear + rsc
9	6.08	0.01	-238.36	road + trail + feed + can:hunt	fear + rsc
8	6.10	0.01	-239.38	road + trail + prey:road	dist
8	6.58	0.01	-239.62	trail + feed + feed:hunt	fear + rsc
6	7.05	0.01	-241.89	feed	rsc
10	8.03	0.00	-238.31	road + trail + feed + can:hunt + hunt:feed	fear + rsc
7	8.07	0.00	-241.39	trail + can:hunt	fear
7	8.30	0.00	-241.50	trail + can:trail	dist
6	8.85	0.00	-242.79	trail	dist
7	8.86	0.00	-241.78	feed + I(feed^2)	rsc
7	8.87	0.00	-241.79	feed + can:feed	rsc
7	9.06	0.00	-241.88	feed + snow:feed	rsc

7	9.27	0.00	-241.99	trail + prey:trail	dist
8	9.74	0.00	-241.21	road + trail + can:hunt	fear
8	10.21	0.00	-241.44	road + trail + can:trail	dist
7	10.48	0.00	-242.59	trail + trail:hunt	fear
7	10.51	0.00	-242.61	road + trail	dist
9	10.52	0.00	-240.58	road + trail + can:trail + can:road	dist
8	10.79	0.00	-241.73	road + trail + can:road	dist
7	10.81	0.00	-242.76	trail + can:day	dist
8	10.88	0.00	-241.78	feed + snow:feed + can:feed	rsc
8	10.92	0.00	-241.80	road + trail + prey:trail	dist
5	11.05	0.00	-244.90	tpi + prey + snow + can	envt
8	11.68	0.00	-242.18	road + trail + road:day	dist
8	12.17	0.00	-242.42	road + trail + trail:hunt	fear
8	12.42	0.00	-242.54	road + trail + road:hunt	fear
8	12.46	0.00	-242.56	road + trail + can:day	dist
9	13.95	0.00	-242.29	road + trail + trail:hunt + road:hunt	fear

## **Chapter 4. Individual experience with risk affects antipredator behavior of elk**

### **ABSTRACT**

Indirect effects of predators on their prey can have important ecological consequences but are challenging to measure empirically. Prey may alter their behavior in risky places, at risky times, or both, and the amount of time that prey allocate to antipredator behavior may further vary based on the degree and duration of risk experienced by an individual. Here, we leverage a novel dataset integrating field-based wolf kill site investigations with concurrent GPS collar locations of elk and wolves to test predictions of the risky places, risky times, and risk allocation hypotheses. After inferring elk behavior states from movement patterns using hidden Markov models, we used mixed effects multinomial regression to estimate the relative probability that an elk would be resting, foraging, or traveling based on (a) the immediate spatial or temporal risk of predation (i.e., whether the elk was located in an area characteristic of those where wolves readily kill prey or was within 1km of a collared wolf), and (b) the risk generally experienced by the individual (i.e., how much of its time it spent in these immediately risk conditions). We found no consistent behavioral response of elk to the immediate presence of a wolf, regardless of the underlying spatial risk in which the encounter occurred. Rather, elk response to predation risk varied primarily as a function of environmental characteristics and individual experience with predation risk. Elk that often experienced immediate predation risk were much more likely than their counterparts to forage or rest in spatially risky places where wolves could readily kill prey. Conversely, elk that had little experience with immediate predation risk allocated their behaviors differently in spatially risky places, sacrificing foraging for traveling. These results support predictions of the risk allocation hypothesis and reveal that the risk generally experienced by an individual can affect how it navigates the risk landscape. Our work suggests that the considerable variation in antipredator behavior reported within and among elk populations to date may stem from differences in individual elk experiences with predation risk, in addition to frequently considered factors such as differences in study sites or methodologies. As populations of wolves and other predators continue to expand across the northern hemisphere, our results suggest antipredator behavior of ungulates may weaken as their accumulated experiences with risk increase.

### **INTRODUCTION**

Predators affect ecosystem functioning by directly reducing prey population sizes and by indirectly changing prey behaviors (Estes et al. 2011). In some cases, the biological and ecological consequences of predators' indirect effects on the behavior of their prey exceed those of their direct consumptive effects (Preisser et al. 2005, Matassa and Trussell 2011). For example, prey that shift to using safer habitats may subsist on suboptimal forage (Muhly et al. 2010, Barnier et al. 2014) that does not adequately support reproductive needs (Bourbeau-Lemieux et al. 2011). Concurrently, changes in prey distribution can alter mortality risk for sympatric species (Holt 1977, Matassa and Trussell 2011), and changes in foraging behavior of herbivorous prey can alter vegetation structure and function (McNaughton 1984, Kuijper et al. 2013). Even animals that do not alter their space use can suffer energetic costs from escaping immediate encounters with predators that reduce their body condition (Martin and Lopez 1999)

and render them more susceptible to future threats. Increasing recognition of the important indirect influences of predators on their prey has spurred a new emphasis on determining how prey alter their behavior to reduce the risk of predation.

Understanding how prey respond to predation risk requires first identifying which aspects of risk prey perceive as most consequential (Ford and Goheen 2015), but prey perception of predation risk is notoriously difficult to quantify. Even in the extremely well studied wolf-elk systems of North America (Say-Sallaz et al. 2019), researchers still “know almost nothing” about how ungulate prey perceive and respond to predation risk measured empirically in natural landscapes (Creel et al. 2019). Some studies suggest elk (*Cervus canadensis*) respond so strongly to the risk of predation by gray wolves (*Canis lupus*) that the effects of their altered behavior cascade throughout the ecosystem (Ripple and Beschta 2012), whereas other work finds little evidence that wolves generate meaningful changes to elk behavior or related ecosystem processes (Creel and Christianson 2009, Winnie 2012, Middleton et al. 2013b, Cusack et al. 2020). Given the widespread distribution and continued growth of wolf (Gompper et al. 2015) and ungulate (Thompson and Henderson 1998) populations across the northern hemisphere, resolving this ambiguity is important to advance both ecological theory and the effectiveness of management and conservation efforts.

One key challenge in linking prey behavior to predation risk stems from the considerable variation in risk across the landscape in both space and time (Gaynor et al. 2019, Wirsing et al. 2021, Palmer et al. 2022). Three complementary hypotheses have been posited to explain how prey navigate this complex risk landscape. First, animals can proactively mitigate risk by selecting against or moving more quickly through areas where they are particularly vulnerable to predation (i.e., the risky places hypothesis). Second, animals can reactively mitigate risk by altering their behavior to avoid detection or attack specifically when a predator is nearby (i.e., the risky times hypothesis). Third, animals can exhibit a targeted mitigation approach in which they alter their behavior during risky times if those times occur in risky places (i.e., the ‘risky places at risky times hypothesis,’ Dröge et al. 2017).

Alongside the differing behavioral responses to landscape-scale variation in risk, a growing body of evidence suggests that prey response to predation risk is mediated by temporal variation in the background risk to which an individual has been exposed (i.e., the risk allocation hypothesis, (Lima and Dill 1990, Ferrari et al. 2009). In other words, the way an animal responds to the immediate risk of predation depends on the context in which that animal has generally experienced risk overall. The risk allocation hypothesis suggests that individuals that spend more time in dangerous situations should respond less strongly to the risk of predation because frequent or constant antipredator responses would have severe energetic costs or drastically limit food acquisition or other essential behaviors (Verdolin 2006). By this logic, individual prey animals that rarely experience risk should respond more strongly, because an animal that can safely allocate sufficient time to foraging can afford to exhibit a strong behavioral response during the limited times in which it experiences predation risk. This hypothesis is particularly salient in large ungulate systems where individual behaviors can vary considerably within and among populations (Lowrey et al. 2020, Xu et al. 2023).

In addition to the difficulty of finding commonalities among the highly variable individual responses to predation risk, studies of predator-prey interactions in large carnivore-ungulate systems suffer from practical limitations. Most notably, measuring predation risk requires considerable effort and resource expenditure (Moll et al. 2017). Kill site selection models, which quantify the probability of a kill occurring in a given place and time based on

characteristics of kill sites and non-kill sites (Anderson and Lindzey 2003, Merrill et al. 2010), are one of the best-known representations of spatial predation risk (Prugh et al. 2019). However, these models rely heavily on field data (Elbroch et al. 2018a) that are particularly resource-intensive and often infeasible to collect (Webb et al. 2008). Therefore, much research relies out of necessity on proxies for predation risk such as vegetation characteristics (Ripple and Beschta 2003), predator space use (Latombe et al. 2014, Flagel et al. 2016), or olfactory cues (van Ginkel et al. 2019, Calkoen et al. 2021, Palmer et al. 2021). Though often the best data available, these proxies do not always accurately represent the risk of predation experienced by individuals (Suraci et al. 2022).

To help resolve divergent findings about the effects of large carnivores on ungulate behavior, we used a novel empirical dataset to disentangle the effects of spatial predation risk, temporal predation risk, and individual risk experience on the behavioral responses of elk to the risk of wolf predation. Specifically, we evaluated how the relative probability of an elk either foraging, resting, or traveling varied in association with: (a) spatial predation risk (i.e., ‘risky places’), based on an empirically derived spatial model of wolf kill site selection, (b) wolf encounters (i.e., ‘risky times’), based on documented proximity of wolves and elk using GPS collar locations, and (c) individual prey experience with risk (i.e., ‘risk allocation’), based on the proportion of time each elk spent in the particularly-risky upper quartile of spatial predation risk and on the proportion of encounters it experienced in these particularly-risky places relative to safer places where wolves were less likely to make kills.

Under the risky places, risky times, or ‘risky places at risky times’ hypotheses, we expected elk would be more likely to travel than to forage or rest in places where wolves were most likely to kill ungulates, during times when wolves were nearby, or under both conditions, respectively. Under the risk allocation hypothesis, we further predicted elk that had more experience with risk would be less likely to alter their behavior in response to risky places or times than elk that rarely experienced risk (i.e., there would be an interaction between individual risk experience and immediate spatial or temporal risk). We tested these predictions using data collected in the southeastern Greater Yellowstone Ecosystem (GYE) during winter, the season in which adult elk experience both the highest degree of food stress and the highest risk of predation. By illuminating the importance of individual experience with predation risk, our work provides new insight into how similar interactions between predators and prey can yield different outcomes in different places and times.

## **METHODS**

### **Study area**

The study took place across Jackson Hole, Wyoming, USA, a high-elevation (1,900-3,500 m) intermountain basin spanning approximately 2,000 km<sup>2</sup> in the southeastern GYE. The area is characterized by cold, snowy winters and warm, shorter summers (yearly average snowfall >5 m, average temperatures -8 - 5 °C in winter and 13 - 17 °C in summer). Sagebrush flats and grasslands dominate the lower elevations. Deciduous trees and shrubs primarily occur along riparian corridors, with quaking aspen (*Populus tremuloides*) stands intermittently scattered outside of riparian zones at intermediate elevations. Higher elevations are characterized by spruce-fir forests and bare windswept ridges.



Most land in the area (94%) is federally owned by either the US Forest Service (Bridger-Teton National Forest), US Fish and Wildlife Service (National Elk Refuge), or National Park Service (Grand Teton National Park), or administered by local governments (1%). Private land makes up the remaining 5%, consisting of residential and exurban developments in and around the town of Jackson. Public land is used primarily for recreation by locals and tourists; activities consist primarily of snowmobiling in the Gros Ventre area, snowshoeing and cross-country skiing in Grand Teton National Park, and roadside wildlife viewing and walking along the small portion of road on the National Elk Refuge open to the public. The majority of the Elk Refuge is closed to the public, and recreation on much of the designated ungulate winter range is limited to existing roads and trails.

The large Jackson Elk Herd (~11,000 individuals) is provided supplemental food during the winter by the US Fish and Wildlife Service on the National Elk Refuge and by the Wyoming Game and Fish Department on feedgrounds in the Gros Ventre River drainage. The majority of the Jackson Elk Herd overwinters on the National Elk Refuge (6,000 – 8,000 animals during 2018-2021), where feeding dates are primarily determined based on the pounds per acre of natural forage available across the native grassland. On the Elk Refuge, elk are fed pressed alfalfa pellets distributed by large machinery typically before 0900h. The remainder of the herd generally overwinters across the Bridger-Teton National Forest, with about 1,000 – 2,000 animals using the state-run feedgrounds in this area. In these feedgrounds, elk are fed alfalfa hay from horse-drawn sleigh; food is typically distributed in the morning before 1000h. Jackson Hole provides strong habitat connectivity that allows elk to move between the Elk Refuge and the National Forest throughout the season, and space use by individuals is often in flux.

The number, size, and location of wolf packs fluctuated considerably within and among years due to interpack conflict, harvest, and control removals. During our study, the area supported between 4 - 6 packs each year with pack sizes ranging from 2 – 17 individuals. Other large carnivores in the area include black bears (*Ursus americanus*) and grizzly bears (*U. arctos horribilis*), both of which were generally hibernating during the study, and mountain lions (*Puma concolor*), which represent relatively little predation risk for adult elk compared to wolves, particularly during winter (Evans et al. 2006, Elbroch et al. 2015), due to their low population size and role as subordinate predators in this system (Kortello et al. 2007, Elbroch et al. 2018b). In addition to the elk that serve as the wolves' primary prey, sympatric ungulates during winter are moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), and a small number of white-tailed deer (*O. virginianus*).

## **Animal locations**

We used GPS collar locations from elk and wolves collected by the Wyoming Game and Fish Department, National Park Service, and US Fish and Wildlife Service during winter (December – March) 2018/2019, 2019/2020, and 2020/2021. Elk were captured via dart-delivered chemical immobilization from over-snow vehicles on selected National Elk Refuge feedgrounds, from helicopter net-gunning in the Gros Ventre River drainage area, and in corral elk traps operated by WGFD on feedgrounds in the Gros Ventre and Elk Refuge. All elk capture and handling was conducted in compliance with WGFD Chapter 33 Permit numbers 394 and 1201. Elk collars used for this study were programmed to collect a location every 1, 1.5, or 2 hours.

At least 1 wolf was collared in each pack that inhabited the study area each year. Wolves were captured via helicopter net-gunning; capture and handling was conducted in accordance

with guidelines established by the American Society of Mammalogists (Sikes and Mammalogists 2016) (Sikes et al., 2016) and using protocols approved by the National Park Service Institutional Animal Care and Use Committee (permits WY\_GRTE\_Stephenson\_Wolf\_2020.A3 and IMR\_GRTE\_Gustine\_Wolves\_2017.A3). Wolf collars were programmed to collect a location every 2 hours (Telonics, Mesa, Arizona, USA). We used program R version 4.2.2 (R Core Team 2021) to process animal locations and perform all subsequent analyses.

## **Environmental effects**

We identified three environmental influences that had a particularly strong effect on the resting, foraging, and traveling behaviors of elk based on data summaries, ecological knowledge, and research precedent. First, because elk periodically move between feeding and resting areas throughout the day, we included a cyclical effect of the time of day calculated as two covariates,  $\sin(2\pi \cdot \text{hour}/24)$  and  $\cosine(2\pi \cdot \text{hour}/24)$ . Second, because deep snow can impede both mobility and access to forage (Parker et al. 1984), we included a linear effect of snow depth. We estimated snow depth in centimeters across the study area at a 30 m x 30 m spatial resolution using SnowModel (Liston and Elder 2006, Liston et al. 2020). We assimilated snow water equivalent observations from local Natural Resources Conservation Service (NRCS) Snow Telemetry (Snotel) and NRCS snow course sites into the model, and we ground-truthed resulting model estimates by comparing them to measurements we gathered from snow pits and line transects across the study area. This effort represented an interdisciplinary approach to merge snow and wildlife expertise to produce more wildlife-relevant, spatially distributed snow information (Reinking et al. 2022).

Third, because elk typically feed in open areas and rest in forested areas, we calculated the distance to forest edge using National Landcover Database percent canopy cover data. We defined forest as an area with >20% canopy cover based on visual comparisons between canopy cover values and aerial imagery of the study area; this classification aligned well with USGS Primary Landcover classifications but was slightly more accurate at a fine scale. We multiplied distances within the forest by -1 so that large negative numbers represented areas deep in the forest, large positive numbers represented open areas far from forest cover, and numbers close to 0 represented the transition between open and closed canopy areas. We note that although many studies use open areas as a proxy for high predation risk from coursing predators, wolves in our study area also use forested areas where thick vegetation and complex terrain facilitate trapping and killing prey (Barker et al. 2023).

The high-quality winter forage supplied on elk feedgrounds provided a strong feeding incentive and also supported relatively large groups of elk (Barker et al. 2023). To account for the potential resultant effects on elk behavior, we included a binary variable indicating whether each elk location was recorded on a feedground (within 5m). Unless otherwise noted, we used the raster package (Hijmans 2022) in program R to extract these and other spatial covariates at each elk location.

## **Predation risk effects**

We calculated two metrics representing the spatial and temporal risk experienced by each elk at each recorded location: spatial predation risk (i.e., risky places) and wolf encounter (i.e., risky

times). We estimated the relative spatial predation risk associated with each elk location using an empirically derived kill site selection model. Detailed methods of kill site investigations and risk modeling are reported in Barker et al. (2023). In short, we used cluster searching methods to investigate a representative sample of wolf kill sites across the study area each winter, then used matched case-control logistic regression to model the probability of a wolf kill occurring in a given area as a function of environmental and human influences. For this study, we used the coefficient estimates from the kill site selection model to predict spatial predation risk across the study area at a 30m scale. We used the same model to predict risk separately for each of the 3 winter seasons to account for differences in prey availability and snow among years. To identify encounters between collared wolves and elk, we used ‘conProcess’ in the *wildlifeDI* package (Long et al. 2021). We defined encounters as locations of GPS collared wolves and elk  $\leq 1$ km apart (Middleton et al. 2013b, Cusack et al. 2020) within a 2hr timespan aligning with the fix rate of the wolf collars. We recorded the number, distance, and duration of encounters at each elk location.

We calculated two additional metrics representing exposure to predation risk for each individual in order to test the risk allocation hypothesis (Lima and Dill 1990). First, we calculated the proportion of time spent in high-risk areas ( $p$ ) based on how many of the individual’s total locations occurred in the upper quartile (75%) of spatial predation risk; we considered these areas particularly risky because 65% of recorded encounters occurred in this upper quartile. Second, we calculated the comparative risk each individual experienced in high-risk vs. low-risk situations (encounter ratio) to test the prediction of the risk allocation hypothesis that antipredator behavior is further mediated by how dangerous the high-risk situations are relative to the low-risk situations. Specifically, if risky situations are much more dangerous than less risky situations, then antipredator behavior should be stronger in high-risk situations. We calculated the encounter ratio by dividing the number of encounters the individual experienced per unit time in high-risk situations by the number of encounters per unit time experienced in low-risk situations. We added 0.01 to zeros to avoid non-numeric ratios.

## **Elk behavior models**

We took a two-stage approach to evaluate associations between elk behaviors and the risk of wolf predation, explained in detail below. We originally intended to use a hidden Markov model (HMM; (Franke et al. 2004) with all the explanatory variables of interest as predictors of the probability of an elk transitioning between behavior states. However, the common approach of accommodating individual heterogeneity using discrete random effects was not sufficient for the variation in our data set; a large number of random effects mixtures were supported but computationally infeasible, and using a small number of groups would likely have biased our estimates (McClintock 2021). Therefore, we fit one HMM per individual to infer the behavior state underlying each elk location. Then, we fit a population-level multinomial logistic regression to evaluate how the probability of an elk being in a particular behavior state varied in association with the explanatory variables of interest.

In the first stage, we fit an HMM with three behavior states to each elk, omitting covariates so they could be independently investigated in the next stage. We then identified which behavioral state corresponded to: (1) sedentary behavior, characterized by very low speeds and a wide range of turning angles, (2) meandering behavior, characterized by intermediate speeds and tortuous turning angles, and (3) relocating behavior, characterized as relatively high-

speed, directed movement. We refer to these movement types as “resting,” “foraging” and “traveling,” respectively, through the remainder of the paper (Franke et al. 2004, Chimienti et al. 2021). The three behavior states were inferred based on step lengths (via gamma distribution) and turning angles (via Von mises distribution) between consecutive elk locations, which we calculated using ‘prepData’ from the *momentuHMM* package (McClintock and Michélot 2018). This method allowed us to impute missing locations along a movement trajectory, but if a gap in locations exceeded 6 hours, we created a separate trajectory rather than imputing a large number of contiguous timesteps. We followed guidance in McClintock and Langrock (McClintock et al. 2020) to select starting values, and we accounted for zero-inflated step lengths by including a zero-mass parameter.

In the second stage, we fit a multinomial logistic regression model to evaluate how the probability of an elk being in one behavior state as opposed to another varied as a function of environmental and predation-related influences. To extract independent samples from the autocorrelated behavioral states, we randomly selected up to three locations per individual per day that were recorded at least six hours apart: one each during the daytime, nighttime, and crepuscular time periods. To propagate uncertainty, we used 35 imputations of behavioral states from the individual HMMs using ‘MifitHMM’ from *momentuHMM*. Each imputation uses different parameters from the distribution of parameter uncertainty and also different draws of behavioral states from the conditional state distribution calculated from the Viterbi algorithm. We repeated the multinomial logistic regression for each imputation, and we report pooled parameter estimates and confidence intervals calculated using ‘MIcombine’ from the *mitools* package (Lumley 2019). This population-level model included all covariates of interest, and statistical significance was determined by whether 95% confidence intervals excluded zero.

Environmental covariates included in the multinomial model were time of day, distance to forest edge and its square, snow depth, and whether the location was recorded on a feedground. Individual risk experience covariates were encounter ratio and proportion of time spent in high-risk areas. To evaluate whether cumulative individual risk experience influenced behavioral response to immediate risk, we included interaction terms between each of these individual risk covariates and each of our two immediate risk experience covariates: spatial predation risk and wolf encounter risk. To determine the measure of encounter risk to which elk responded most strongly, we used a  $\Delta$ AIC cutoff value of 2 to evaluate relative support among models in which the encounter risk covariate was either: a) a binary indicator of whether an encounter had occurred at the previous timestep, b) a categorical indicator of encounter risk based on distance (<50m, 200m, 500m, 1000m), c) a binary indicator of whether the encounter was the first encounter (i.e., the start of an encounter that spanned multiple elk locations or a singular encounter), or d) encounter duration. We also included an interaction between wolf encounter and feedground to evaluate the effect of forage availability on risk response, as well as an interaction between wolf encounter and snow depth as we expected elk may respond differently to predators in shallow vs. deep snow. All covariates were centered, scaled, and had Pearson’s correlation coefficients < 0.60. We included random effects of individual and fix rate to account for heterogeneity in behavior.

## RESULTS

We recorded 246,071 GPS collar locations from 199 individual elk-years (127 elk over 3 winters), resulting in 241 elk-year trajectories for which we separately inferred latent behavior states. Step length and turning angle parameters were largely consistent across individuals and

aligned well with our biological expectations of behavior patterns (Fig. 1). The number of locations recorded per elk trajectory ranged from 111 – 2903 (mean 1113, median 1191, Q1 719, Q3 1569). We recorded 36,852 GPS collar locations from 48 wolf-years, comprising 30 wolves in 11 packs.

We detected encounters between elk and wolves at 6,548 recorded elk locations (~2.7%). Approximately 6% of individuals ( $n = 12$  of 199) did not encounter a wolf during the time of the study. The closest recorded encounter occurred at a distance of 14 m; median encounter distance was 656 m. Encounters were most likely to occur during the night and least likely to occur during the day ( $p < 0.001$  in all time period comparisons). The vast majority (75%) of encounters lasted for 5 hours or less; the longest recorded wolf encounter lasted 28 hours.

Nearly all elk spent at least some time in the high-risk areas (92%,  $n = 184$ ) where wolves were particularly likely to make kills. On average, elk that did use high-risk areas spent a little over half of their time there ( $54\% \pm 27\%$  SD). A moderate majority of the 187 elk that encountered wolves did so most frequently in these high-risk areas (62%,  $n = 124$ ). Encounter ratios, which represented the number of encounters per unit time (hour) an individual experienced in high-risk areas relative to low-risk areas, were strongly right-skewed, with median of 5.5 and maximum 46 ( $Q1 = 2$ ,  $Q3 = 16$ ). The median encounter rate regardless of underlying spatial risk was approximately 1 encounter every 9.4 days (maximum average rate of 1.6 encounters/day).

We found evidence that the type of behavior exhibited by elk varied with respect to both environmental and risk-related influences (Fig. 2). We found the best support for the model that used the binary indicator of whether a wolf encounter had occurred at the previous location ( $\Delta AIC > 2$  in all cases, Supplementary Table 1), so we report results from that model and note that we were unable to detect an effect of wolf encounter risk regardless of the covariate we used to represent it. Overall, elk were least likely to be traveling and most likely to be foraging (foraging vs. traveling intercept estimate  $0.82 \pm 0.77$ ,  $p < 0.001$ ), especially if they were on a feedground. However, elk were more likely to travel than to either forage or rest in open areas far from forest cover. The only situation in which elk were most likely to be resting was in deep snow.

Elk that spent more time in high-risk areas generally allocated more of their time to traveling and less of their time to resting than their peers (resting vs. traveling  $\text{riskExp} = -0.18 \pm 0.08$ ,  $p = 0.03$ ). However, these elk were less likely to travel, and more likely to forage or rest, in riskier places compared to safer places. In contrast, elk that spent less time in high-risk areas were more likely to travel and less likely to forage or rest in riskier places relative to safer places ( $\text{spatRisk} * \text{riskExp} = 0.19 \pm 0.03$  and  $0.18 \pm 0.03$  for foraging and resting vs. traveling, respectively;  $p < 0.001$  in both cases). We did not find an effect of risky times ( $\text{encPrev} = -0.14 \pm 0.16$  and  $-0.14 \pm 0.18$  for foraging and resting vs. traveling, respectively;  $p$ -values for this covariate and all related interactions  $> 0.35$ ). Common behavioral responses of elk to wolf predation risk were evident only among individuals that shared similar experiences with risk; we did not detect common behavioral responses across all individuals in the population (Fig. 3).

## DISCUSSION

The physical presence of a wolf did not have a consistent effect on the behavior of elk, regardless of how close the wolf was, how long it remained nearby, or whether it was encountered in an area where wolves were particularly likely to make kills. Rather than unequivocally altering their

behavior in response to nearby wolves, some elk in our study area took a more proactive approach to risk management by altering their behavior in risky places regardless of whether wolves were immediately nearby. Consistent with predictions of the risk allocation hypothesis, individuals responded differently to risky places based on their personal experience with risk. We only observed the proactive approach to risk reduction in elk that experienced relatively little risk overall – although these individuals generally traveled less than their peers, they were increasingly likely to travel through increasingly riskier places. Elk that spent higher proportions of time in risky places were more likely to forage or rest in riskier places than in safer places. However, the patterns of behavior driven by individual risk experience were obscured at the population level (Fig. 3).

Our finding that individual risk experience affects antipredator behavior may help explain why studies of the same predator-prey interactions in different places and times have yielded such different results. Much of the debate around the degree to which wolves affect elk behavior comes from comparison between studies from Yellowstone National Park in the earlier days of wolf introduction and studies that occurred after the wolf population was more strongly established. Because we found elk that experience more spatial predation risk behave differently than elk that rarely experience risk, it is possible that the behaviors of elk in the same or similar areas have changed over time as individuals gain experience with wolves. Temporal changes in antipredator behavior of elk have previously been reported in the GYE; vigilance levels of elk populations increased initially as wolves moved into their areas but then stabilized within two to three years (Laundre et al. 2001).

The differences we observed in how individuals with different risk experiences allocated their behaviors were not limited strictly to risky times. Despite their reduced propensity for travel in risky places, elk that experienced more risk overall generally traveled more than their peers. In a post hoc investigation of these different behavioral baselines, we found elk that experienced a high degree of risk (i.e., spent at least 70% of their time in risky areas) were also more likely to spend time on feedgrounds than elk that spent less than half of their time in risky areas (chi-squared  $p$ -value  $< 0.001$ ,  $df = 1$ ). Additionally, we noted a particularly high propensity for movement in these high-risk elk during the morning spanning the typical timing of forage distribution on feedgrounds (Fig. 4). We speculate that the higher propensity for travel in elk that experience more risk may be more strongly related to their foraging than their antipredator behavior. If in fact this increased movement is due to moving on and off the feedgrounds, it is not likely to indicate an energetic expenditure with negative fitness consequences.

Alongside common experience-based behaviors, we also found common behavioral responses to environmental influences across all elk irrespective of individual risk experiences. Unsurprisingly, foraging was the most common behavioral state, especially on feedgrounds. Elk were most likely to be resting in deep snow and traveling through open areas far from forest cover. However, contrary to our prediction, elk response to wolf encounters did not differ on and off of feedgrounds. We speculate this lack of response may reveal the effects of nutritional constraints, elk group size, or both. One possible explanation is that the nutritional limitation elk experience in the winter requires them to prioritize acquiring food over avoiding predators (i.e., the starvation-predation hypothesis), as has been found with moose elsewhere in the GYE (Oates et al. 2019) and bison in Alaska (Simon et al. 2019). Alternatively, or additionally, the lack of response to wolves on feedgrounds could be a consequence of the larger group sizes that these areas typically support. Anecdotally, elk in the Jackson herd tend to gather in groups that are orders of magnitude higher than those of elk foraging on native winter range. Because larger

groups allow each individual more foraging time as they share the duties of vigilance (Hunter and Skinner 1998, Hebblewhite and Pletscher 2002), elk on feedgrounds may not need to change their behavior as strongly in these areas. Additional work with carefully designed GPS collar distributions could add valuable insight into the role of elk group size in conjunction with individual experience in driving antipredator behaviors.

Both Middleton et al. (2013) and Cusack et al. (2018) noted extreme variation in individual experiences with predation risk (20-fold and 12-fold variation in the rates of wolf encounters among individual elk, respectively). We also found considerable variation among individual elk experience with risk, and this varied risk experience drove varied behavioral responses of elk to spatial predation risk. However, despite allocating their behaviors differently in risky places, elk allocated about half of their time overall to foraging regardless of their individual risk experience. This suggests a possible mechanism by which elk attain similar fitness despite individual differences in risk response (Middleton et al. 2013b) – reduced allocation of behavior to foraging in one area is compensated by increased foraging in other areas.

After 15 years of concerted studies on predator-prey interactions, the story emerging from the GYE is that elk alter their behavior in response to the risk of predation by wolves (Fortin et al. 2005, Gude et al. 2006, Creel et al. 2008, Gower et al. 2008, Proffitt et al. 2009), but antipredator behaviors may stabilize or even decrease over time as elk experience with predation risk increases (Laundre et al. 2001, this study). Behavioral changes alone do not appear to meaningfully alter the fitness (White et al. 2011, Middleton et al. 2013b) or distributions (Mao et al. 2005, Cusack et al. 2020) of elk, possibly because elk allocate their behaviors differently in different areas to balance the costs of antipredator behavior with the benefits of nutritional intake and rest. We note, however, that this understanding stems primarily from studies conducted during the winter. Further study during the growing season would provide a particularly valuable contribution to this story, because nutritional intake during summer and fall affects ungulate survival and reproduction much more than foraging during the winter (Cook et al. 2013, Middleton et al. 2013a, Monteith et al. 2014).

Our results align well with Verdolin's (2006) meta-analysis that found antipredator behavior of prey was more consistently linked with habitat structure than with actual presence of predators. The temporal scale of our work may explain why we differed from other studies that documented elk behavioral responses to wolf presence (e.g., Creel et al. 2008, Middleton et al. 2013b). First, examining elk behaviors at 1- to 2-hour time intervals precluded our ability to capture immediate yet temporary responses to predator presence such as swift displacement to avoid detection by an approaching wolf. Our estimates of elk response to predation risk may therefore be biased low; consequently, the differences in antipredator behavior of elk with different experiences may be more pronounced than we were able to detect. Second, it is important to note that our classification of behavior states could not distinguish vigilance from resting or foraging, and some behaviors classified as resting could potentially include foraging. To account for these limitations, we primarily focused our predictions and inference on traveling behavior. Because ungulates can chew and ruminate while scanning for predators (Fortin et al. 2004), neither vigilance nor differences between foraging and resting behavior are likely to substantially affect nutritional intake (Gower et al. 2008).

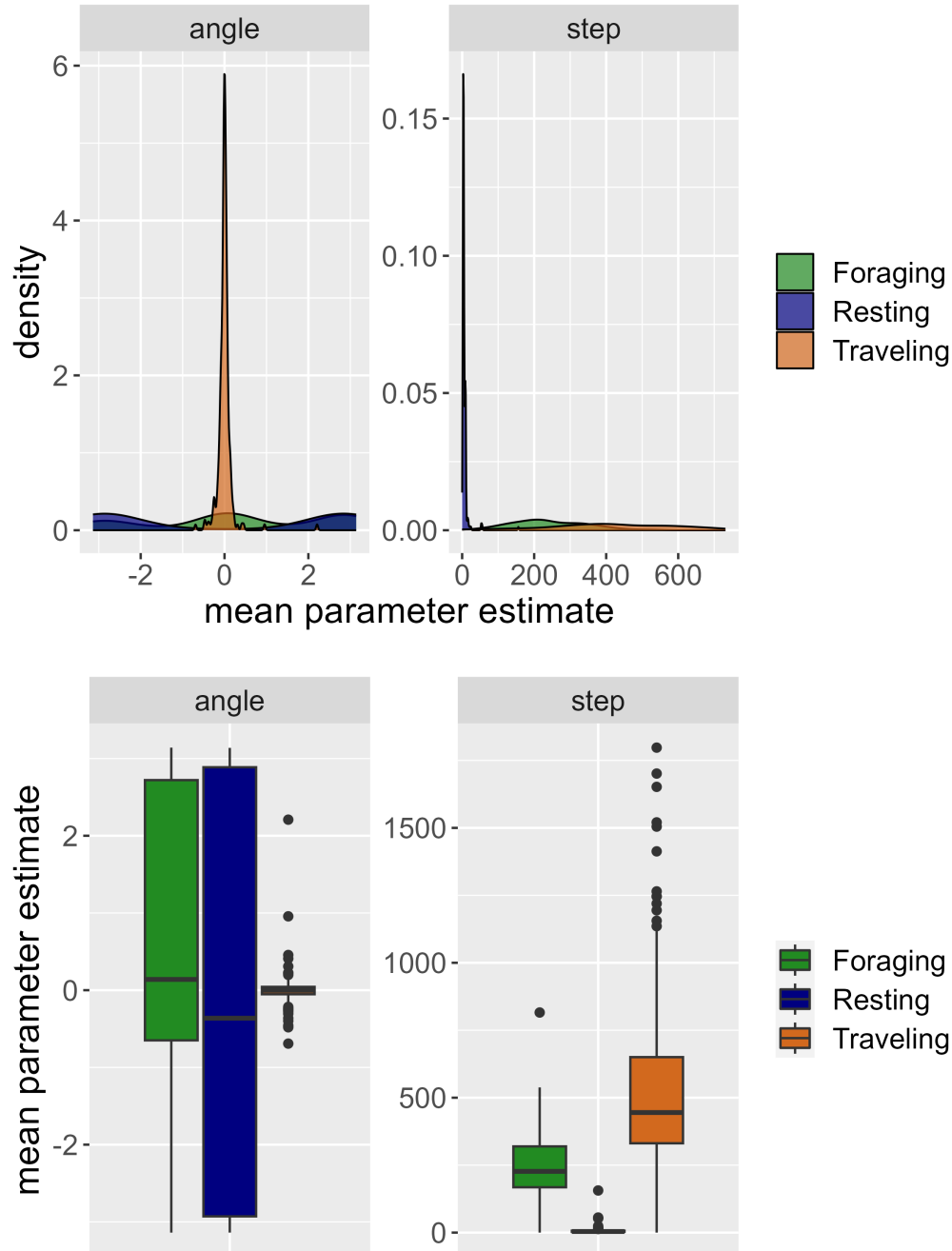
Our methods were designed to test the prediction of the risk allocation hypothesis that differing individual experiences with risk cause differing degrees of antipredator behavior. Conversely, however, our results could indicate that it is differing risk tolerance or boldness that

causes differing individual experiences with risk – i.e., rather than reducing their antipredator behavior because they have experienced chronic risk, elk may experience chronic risk because they are more tolerant of it. Regardless of the direction of causation, our key inference still holds that individuals with similar experiences of risk exhibit similar allocations of antipredator behavior, and that broad variation in individual risk experience can obscure common antipredator behaviors when viewed at the population level.

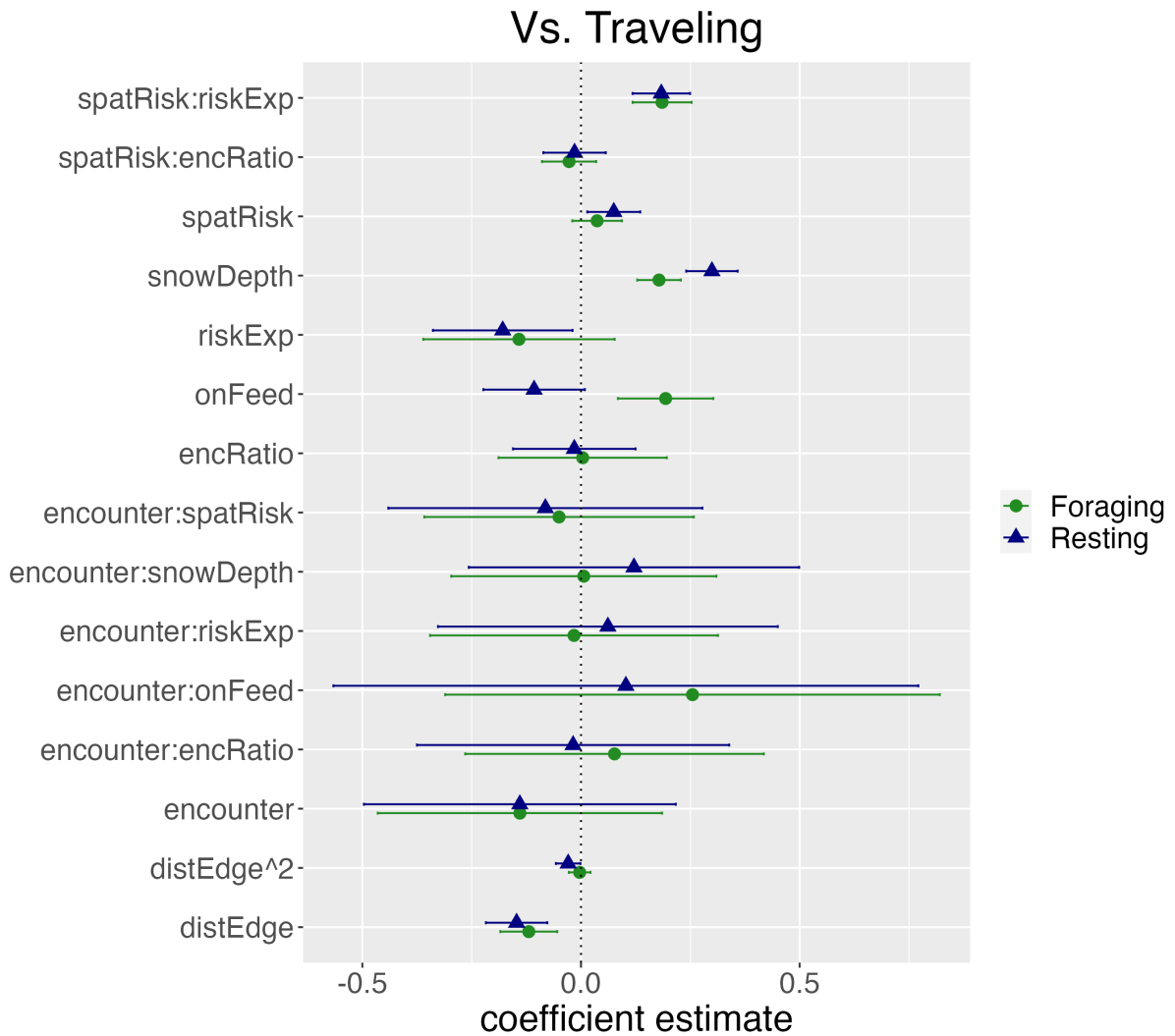
Even when prey behavior can be linked with specific aspects of predation risk as in in our study, these behavioral changes may not prove strong enough to incur fitness costs (Middleton et al. 2013b, Prugh et al. 2019), nor is it always evident whether behaviors have changed to a degree that affects other species or related ecosystem processes. As with behavioral studies, studies of the indirect consequences of predation risk on prey fitness have also yielded equivocal results in wolf-elk systems. Some studies have found associations between prey fitness and predation risk (Proffitt et al. 2014, Gehr et al. 2018) while others have found stable or even improved elk fitness with higher predation risk (White et al. 2011). With no mechanistic link between predation risk, prey behavior, and prey fitness (Lind and Cresswell 2005), it remains unclear whether the indirect behavioral effects of wolves on elk result in meaningful changes to elk survival or reproduction, much less cascading changes throughout the ecosystem. Our work reveals that identifying and accounting for commonalities among individual prey experiences with risk could help elucidate common consequences of varying ungulate behaviors in the face of fluctuating environments and risk landscapes.



**FIGURE 1.** Mean angle (radian) and step length (m) parameter estimates of three behavior states evaluated by fitting hidden Markov models to 241 elk trajectories. Behaviors with relatively long step lengths and directed movement were typically classified as “traveling,” those with very short steps and a broad range of angles as “resting,” and those with intermediate parameters as “foraging.”

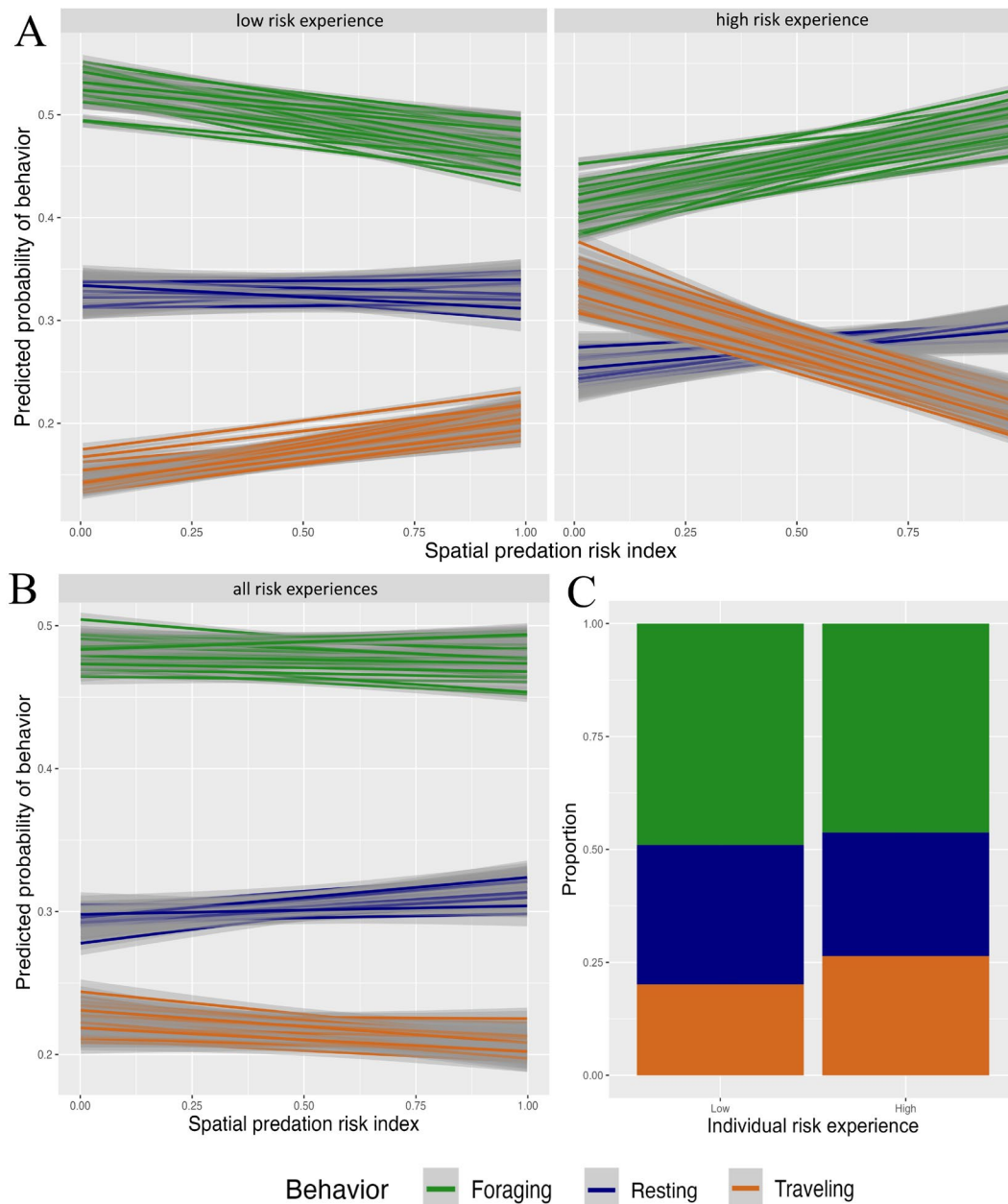


**FIGURE 2.** Pooled coefficient estimates  $\pm$  95% confidence intervals from multinomial logistic regression models evaluating the log odds of an elk exhibiting different types of behaviors as a function of environmental and risk-related covariates (foraging [green] or resting [blue], as opposed to traveling [reference category]). In addition to the covariates described below, models included a cyclical effect of day (cosine/sin of hour) and a quadratic effect of distance to forest edge. Estimates with confidence intervals that do not overlap the dashed horizontal line were considered statistically significant.

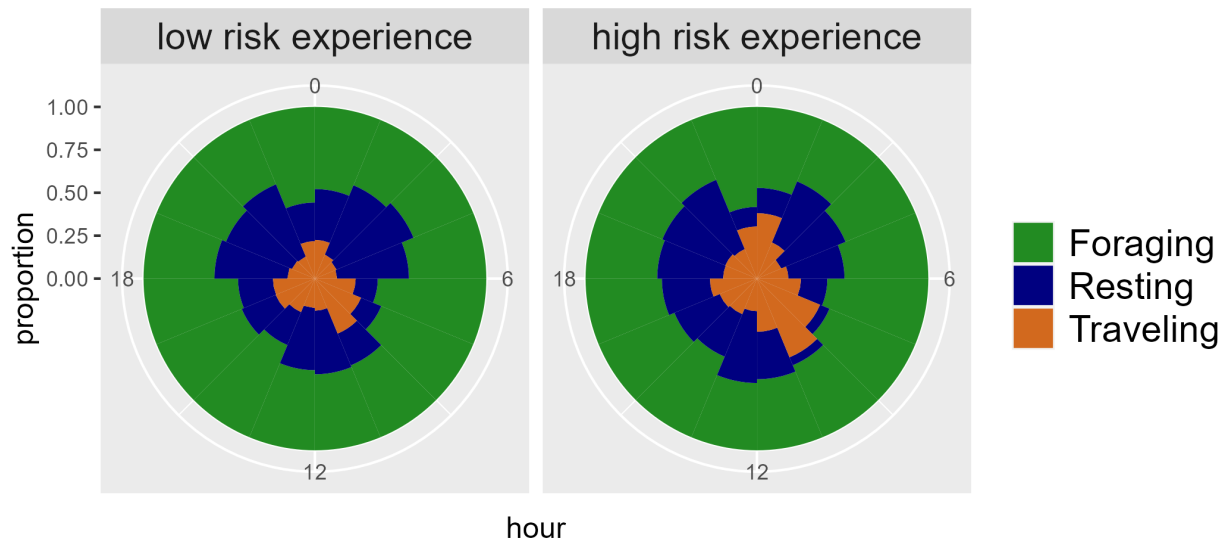


spatRisk - spatial risk index, based on wolf kill site selection model  
 riskExp - proportion of time spent in high-risk areas (i.e., individual risk experience)  
 snowDepth – depth of snow at location, estimated using SnowModel (cm)  
 onFeed - whether the location occurred on an elk feedground (Y/N)  
 encounter - whether a wolf was encountered at the immediately previous timestep (Y/N)  
 encRatio - encounter ratio; encounters per unit time in high-risk vs. low risk areas  
 distEdge – distance to nearest forest edge (m); positive values in forest, negative values outside forest

**FIGURE 3.** The predicted probability of an elk foraging (green), resting (blue), or traveling (orange) varied based on the risk the individual generally experienced (panel A). Lines represent predictions and 95% confidence intervals from each of 35 model imputations, all other variables being held at their means. Elk that spent at least 70% of their time in risky places (“high risk experience”) were most likely to forage or rest in areas where wolves were more likely to kill prey, whereas elk that spent less than half of their time in risky places (“low risk experience”) traded foraging for traveling in these areas. Behavioral responses to spatial predation risk were not detectable without explicitly considering individual experience (panel B). Elk spent about half their time foraging regardless of the risk they experienced, but elk that spent less time in risky places spent slightly less time traveling overall than their counterparts (panel C).



**Figure 4.** The proportion of time spent foraging, resting, or traveling differed throughout the day among elk that spent less than half of their time in risky places (“low risk experience”) and those that spent at least 70% of their time in risky places (“high risk experience”). High-risk elk were more likely to travel overall, particularly in the morning after sunrise (~0800-1000 hr) and to a lesser extent late at night (~2300-0100 hr).



**Supplementary Table 1.** AICc results comparing relative support for models that used different proxies for wolf encounter risk: a) a binary indicator of whether an encounter had occurred at the previous timestep, b) a binary indicator of whether the encounter was the first encounter (i.e., the start of an encounter that spanned multiple elk locations or a singular encounter), c) duration of the encounter, or d) a categorical indicator of encounter risk based on distance (<50m, 200m, 500m, 1000m). Mean and standard deviation of  $\Delta$ AIC and model weights are calculated across results of 35 model imputations. Adjusted  $\Delta$ AIC indicates the difference from the lowest average AIC value.

<b>Encounter covariate</b>	<b>adjusted <math>\Delta</math>AIC</b>	<b>mean <math>\Delta</math>AIC (std. dev.)</b>	<b>mean weight (std. dev.)</b>
Binary yes/no	0	3.58 (4.60)	0.44 (0.40)
Initial encounter	2.70	6.28 (8.50)	0.36 (0.40)
Duration	6.69	10.29 (9.11)	0.14 (0.25)
Distance classification	17.92	21.49 (9.77)	0.06 (0.23)

## Chapter 5. Concluding remarks

The work presented in this dissertation explores wildlife behavior at scales ranging from global patterns of movement to direct interactions between individuals. Through this broad lens, we bring into focus a clearer picture of the considerable flexibility and adaptability inherent in animal behavior across the globe. Alongside important environmental influences, we draw attention to key human influences driving behavioral change. We show that animals actively respond to external changes, and we illuminate some common drivers of individual movement decisions.

Although the prevailing perception of human influence on wildlife has primarily been one of exploitation and destruction, our work uncovers many examples of humans conserving and even restoring important wildlife behaviors on which ecosystems rely. In Chapter 2, “Toward a new framework for restoring lost wildlife migrations,” we find evidence of humans facilitating the restoration of lost migrations in all major vertebrate taxa across the globe. The insights gleaned from our synthesis of restoration efforts highlight the fundamental role of behavioral ecology in effective restoration strategies. From the dam removals allowing migratory fish to return to historic spawning sites to the ultralight aircraft leading whooping cranes along historic flight paths, conservation efforts have made great strides towards restoring not only wild species but also their functional roles in ecosystems.

As we dig deeper into the role humans play in restoring lost behaviors, we add nuance to our understanding of anthropogenic influence on wild animals. In Chapter 3, “Wolves avoid humans while prioritizing prey acquisition in anthropogenic areas,” we take a more mechanistic research approach to investigate not only how humans can effect behavioral change but also how animals perceive and respond to different human influences. Gray wolves served as a particularly germane study species with which to explore themes of anthropogenic influence on wildlife behavior due to their fraught relationship with humans. After being deliberately extirpated by humans across most of the United States by the early 1900s, gray wolves were deliberately reintroduced by humans in the late 1990s, and now they are deliberately hunted and trapped by humans in some areas but not others. As a result, it is not clear whether wolves perceive humans as a helpful ally, a dangerous threat, or a mere annoyance. By distinguishing between different types of anthropogenic influences in our investigation of wolf predation, we discovered wolves do not see humans in black and white. Rather, they actively distinguish between, and respond differently to, different types and amounts of human influences. Importantly, these behavioral changes do not affect only the wolves themselves. Because our analysis specifically focused on the kill site selection of wolves, we were able to show that human influences on wolves propagated through the ecosystem, affecting not only the behavior of wolves but also the spatial vulnerability of their prey.

In addition to affecting prey by directly eating them, predators sometimes have even stronger indirect effects by causing prey to alter their behavior to reduce the risk of predation. To form a more complete picture of the influence of humans in wolf-elk systems, we built on our previous work to investigate how elk changed their behavior in response to the predation risk we characterized. In Chapter 4, “Individual experience with risk affects antipredator behavior of elk,” we showed that elk change their behavior as they move through areas where wolves are most likely to make kills. Because elk behaviors are influenced by the spatial predation risk underlying the areas through which they move, and because that spatial predation risk is influenced by humans, we unveil a chain reaction in which humans drive not only behavioral

changes of one species but also interactions between two species that can have considerable implications for ecosystem function. However, we did not find that all elk responded to predation risk in the same way. A key insight from our elk behavior analysis was that an elk's individual experience with risk influences how it responds to that risk. Elk that rarely experienced risk were much more likely than their peers to exhibit antipredator behavior in risky places, revealing that the way an animal behaves may depend as much on its general experience as on the immediate situation at hand. Only by incorporating individual experiences into our analyses were we able to tease out common themes among the wide diversity of individual behaviors we observed.

This work provides new insight into wildlife adaptability, but much remains to be learned about the causes and consequences of these changing behaviors. It would be helpful to know, for instance, if human-driven changes to natural patterns of predation allow wolves to kill more elk. Similarly, although we know elk change their behavior in response to the risk of wolf predation, we do not know whether those behavioral changes are drastic enough to affect individual fitness or ecosystem functions. Identifying key patterns and processes is a foundational step towards building a more comprehensive understanding of how human influences on wildlife behavior reshape the ecosystems in which those behaviors evolved. Future work can build on this understanding by evaluating the degree to which human-driven behavioral changes affect the fitness of animals or the species with which they interact.

Altogether, our work reveals that wildlife behaviors are far more diverse and flexible than may have previously been appreciated. This behavior adaptability bodes well for the persistence of ecologically important wildlife behaviors into the future, but not without careful consideration by humans. Ecosystems are built not on static animals but on wildlife interacting with the world around them. Conservation initiatives and policies from global to local scales aim to conserve our wild lands and the animals that live on them. With very few exceptions, these initiatives do not include wildlife behavior as a key objective or target. Conserving the physical environment and meeting target numbers of animals are laudable goals, but we neglect a key component of ecology if we don't broaden our conservation and management plans to include not just physical pieces of the environment but also how those pieces move together to drive a functional ecosystem. With this dissertation, I hope to have made some small contribution towards our understanding of how wild animals perceive and respond to their habitats - and to each other - amidst ongoing environmental and anthropogenic change.

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