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Author
Shawler, Avery Lin

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Ecological and social dimensions of wolf-livestock conflict in the Greater Yellowstone Ecosystem

By

Avery Lin Shawler

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Committee in charge:

Professor Arthur D. Middleton, Chair
Professor Justin S. Brashares
Professor Nathan F. Sayre

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Abstract

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The recovery of large carnivores beyond protected areas presents significant conservation and management challenges as both wildlife and humans adapt to shared landscapes. This issue is particularly acute in working landscapes where carnivores, such as wolves, frequently prey on livestock, causing hardship for rural ranching communities and potentially hindering carnivore recovery efforts. Thus, research investigating the factors driving and mitigating carnivore depredation on livestock is needed to better inform conflict reduction management practices. This study takes place in a working lands frontier east of Yellowstone National Park in northwest Wyoming, near the towns of Cody and Meeteetse, where ranchers and wildlife managers have contended with wolf-livestock conflict for over two decades. Given that conflict dynamics are influenced by both wildlife behavior and management decisions, this research employs both quantitative and qualitative methods to investigate ecological and social dimensions of conflict. The first two chapters focus on predator-prey dynamics between wolves and migratory elk, as prey availability and distribution are believed to impact wolf-livestock conflict patterns. In Chapter 1, I use elk and wolf GPS collar data to investigate how wolves respond to seasonal elk migrations and describe conditions conducive to migratory coupling and decoupling. In Chapter 2, I collected wolf predation data from kill sites in winter and summer to characterize wolf seasonal predation patterns. In Chapter 3, I delve into the human dimensions of conflict mitigation using data from in-depth interviews with ranchers and wildlife managers, relationships developed during the course of the ecological research. I investigated the socioeconomic challenges of mitigating conflict by identifying factors that influence the adoption of conflict reduction practices and examining the roots of social conflict and intolerance towards wolves. Highlighting social constraints to conflict mitigation offers valuable lessons for communities facing similar challenges with recovering wolf populations. These findings can guide wildlife managers, wolf conservationists, and researchers in developing effective conflict mitigation strategies that balance the needs of both wolves and people, as wolves, already the most widespread large carnivore in the Northern Hemisphere, continue to expand their range.

DEDICATION

To everyone who supported me throughout this PhD journey

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INTRODUCTION

Background

Protected areas have increased in number and area worldwide over the last century; however, most remain isolated within human-dominated landscapes (Scott et al. 2001; Watson et al. 2014). Many of these adjacent areas consist of working lands, which provide economic resources and ecosystem services while also facilitating connectivity and buffering against more intensive land uses (Kremen & Merenlender 2018; Hilty et al. 2019). They are often characterized by high levels of human-wildlife conflict due to wildlife moving beyond adjacent protected areas (Gittleman et al. 2001). Reducing these conflicts is a central issue in conservation science and policy and will likely require adaptations from both humans and wildlife (Woodroffe et al. 2005; Chapron et al. 2014; Carter & Linnell 2016).

Large mammalian carnivores pose particularly difficult challenges for conservation in working landscapes and recent estimates found that 82% of carnivore range falls outside protected areas (Braczkowski et al. 2023). After a century of widespread declines (Ripple et al. 2014), large carnivore populations are recovering in some areas, including recolonization of some fragmented, human-dominated landscapes (Chapron et al. 2014; Ingeman et al. 2022). The recovery process is often hampered by large carnivores' ability reduce the availability of wild ungulates for human hunters (Hobbs et al. 2012; Jonzén et al. 2013), harm livestock (Baker et al. 2008), and, in some cases, kill and injure humans (Dhanwatey et al. 2013). The resulting conflict can lead to high levels of human-caused mortality making the success of these recovery efforts uncertain (Noss et al. 1996; Woodroffe & Ginsberg 1998). Large carnivore conservation hinges on progress in mitigating such conflicts (Carter & Linnell 2016; Ingeman et al. 2022).

Predation on domestic livestock is the most common source of conflict between humans and large carnivores (van Eeden et al. 2018). Livestock depredation can cause financial losses and other hardships for livestock producers (Woodroffe et al. 2005; Wang & MacDonald 2006; Lindsey et al. 2013). The most common management response is lethal control of predators, via population culls or targeted killing of 'problem individuals' (Creel & Rotella 2010). However, the effectiveness of lethal control varies widely by carnivore species, region, method of implementation, and number of individuals removed from a social group or population (Bradley et al. 2015; Lennox et al. 2018). Common limitations on the effectiveness of lethal control are the labor and expense involved, the difficulty of identifying problem individuals, and the potential for rapid recolonization of vacant habitat (Conover 2001, Mitchell et al. 2004; Bradley et al. 2015). Even when lethal control is effective, it can lead to undesirable ecological outcomes or political conflicts (McManus et al. 2015). These various critiques have fueled growing interest in nonlethal alternatives, such as preventive livestock husbandry (e.g., fencing, increased human presence, and guard dogs), deterrents (e.g., audio/visual devices or shock collars), and predator translocation – as well as changes in land and wildlife management (e.g., altered grazing strategies or native prey availability) (Shivik 2006; Linnell et al. 2012). However, the effectiveness of many non-lethal interventions is also unclear (Miller et al. 2016; Eklund et al. 2017; van Eeden et al. 2018).

The gray wolf (*Canis lupus*) is one of the most widespread large carnivores in the world, and is known to kill livestock in many areas of its range (Mech 1995; Bangs et al. 2005). Though the wolf was extirpated from many landscapes during the 20th Century, the species has recently recovered into human-dominated and working landscapes of Europe and North America (Young & Goldman 1944; Chapron et al. 2014; Gompper et al. 2015). In the western United States, the wolf has recolonized some areas through natural dispersal, and others – namely Yellowstone National Park, central Idaho, and most recently, Colorado – through active reintroduction (Ream et al. 1991; Bangs & Fritts 1996; Ditmer et al. 2022). In the northern Rocky Mountains, the species was federally protected until 2011 in Idaho and Montana, and 2017 in Wyoming, resulting in transfer of wolf management to the states (Windh et al. 2019). Wolf depredation on livestock is a significant management challenge in these states and is generally managed through lethal control and regulated recreational hunting (Bradley et al. 2015). Depredation can be locally chronic (Niemeyer et al. 1994; Collinge 2008), and its costs exacerbate intolerance for wolves and even for wildlife conservation more generally (Naughton-Treves et al. 2003). These challenges have more recently followed the wolf to Washington, Oregon, California, and Colorado where wildlife managers and livestock producers are also working to understand and mitigate livestock depredation by wolves.

Study System

This research takes place in the eastern region of the Greater Yellowstone Ecosystem (GYE) near the towns of Cody and Meeteetse in northwest Wyoming. The GYE is a temperate ecosystem covering up to 10.8 million ha around the Yellowstone plateau and encompassing several surrounding mountain ranges in the states of Wyoming, Montana, and Idaho (Noss et al. 2002). The high-elevation habitats are dominated by alpine meadows, subalpine forests, and rocky slopes; middle elevations are dominated by coniferous and deciduous forests; and the low elevations by shrub-steppe, grasslands, and agricultural fields (Rickbeil et al. 2019). The climate is continental and characterized by warm summers and cold winters. The GYE is characterized by a complex mosaic of public and private lands. Federal lands include Yellowstone and Grand Teton National Parks, 1.6 million ha of national forests, and extensive lands Bureau of Land Management (BLM), US Fish and Wildlife Service (USFWS), and the state lands (Noss et al. 2002). Approximately 36% of the GYE is private land, which is comprised of multiple uses including oil and gas development, ranching, amenity properties, and residential developments (Wright et al. 2003; Sawyer et al. 2017). This research is situated within the Shoshone and Greybull River valleys of the eastern GYE, where elk, wolves and cattle overlap and conflicts occur on private and public land. Cattle are the primary livestock and number around 8,000.

Dissertation Structure

In my research, I address key knowledge gaps in our understanding of wolf-elk interactions and the social challenges of wolf-livestock conflict mitigation. This research takes place where recolonizing wolves, their native ungulate prey, and range cattle have commingled for over 20 years, leading to chronic cycles of wolf-livestock conflict and lethal control in some areas. In my first two chapters, I investigated whether and how a key ecological dynamic in the GYE, the migratory behavior of elk – wolves' primary prey – influences these cycles of conflict. I approached this question in two steps, represented in the first two chapters of my dissertation. First, Chapter 1 evaluates wolf movement patterns in response to migratory elk. In Chapter 2, I investigated how wolves then cope with the departure of migratory elk in spring and early summer, focusing on wolf packs that hunt elk in the Cody herd – the elk population with perhaps the largest number of long-distance migrants in the GYE. Understanding this ecological dynamic can shed light on how native prey distribution influences patterns of wolf depredation on livestock. However, managing wolf-livestock conflict is influenced by more than ecological drivers and through the course of my ecological investigations it grew very clear that many people I met harbored deep experience with these issues. Thus, in Chapter 3, I interviewed livestock producers and wildlife managers to understand their perceptions of a range of conflict mitigation approaches and the challenges they have faced addressing conflict with wolves. By tapping into these groups' decades of experience dealing with these issues, I provide insight into the challenges of wildlife conflict mitigation not only for the GYE, but also the growing number of communities in working lands globally learning to share the landscape with recovering large carnivores.

CHAPTER 1. WOLVES EMPLOY DIVERSE MIGRATORY COUPLING STRATEGIES TO TRACK A PARTIALLY MIGRATORY ELK HERD

Abstract

Understanding the predator-prey behavioral response race and its downstream effects on ecosystems is an essential part of community ecology. One of the least-understood interactions within this response race occurs between predators and migratory prey. Although migration is hypothesized to be beneficial to prey by maximizing resource exploitation while minimizing spatial overlap with predators, there are many examples of predators of various taxa and ecosystems exploiting migratory prey. Many studies focus on the spatiotemporal movement patterns of migrant prey, yet relatively little research investigates behavioral responses from the predator perspective. Predators can respond to migrant prey along a continuum of movement strategies, from remaining resident to making large-scale movements beyond their home ranges (i.e., migratory coupling). These behavioral responses are further complicated where predators and prey exhibit considerable individual variation and behavioral plasticity, such as systems with partially migratory ungulate prey and cognitively sophisticated large carnivores. This study examined the space use of gray wolves (*Canis lupus*) in response to the seasonal movement of a large partially migratory elk (*Cervus canadensis*) herd on the eastern frontier of the Greater Yellowstone Ecosystem (GYE). Using GPS data from 99 elk and 19 wolves from 2019 and 2021, we first categorized elk migration strategies into long-distance migrants, short-distance migrants, and residents. We then quantified wolf movement strategy based on overlaps between wolf packs' winter and summer range and between wolf summer range and elk summer ranges. We found evidence of wolves exhibiting a range of movement responses including migrating, commuting, and remaining resident. Importantly, we show the same wolf pack can adopt multiple migratory coupling strategies. In addition, packs with pups shifted from their den sites on elk winter ranges to multiple rendezvous sites along elk spring migration routes and into long-distance migratory elk summer range – challenging the long-accepted notion that pups act as spatial anchors. These new insights into the considerable plasticity of wolf behavior in response to seasonal changes in prey availability will prove particularly salient in the coming years as elk and other ungulate prey continue to change the timing, distance, and prevalence of their migrations in response to climate and land use change. This work contributes new information to the growing body of research on the conditions conducive to migratory coupling or decoupling, which lacks examples of terrestrial predators and prey.

Introduction

Understanding predator-prey interactions is essential to community ecology not only because of their effects on predator and prey fitness and population dynamics, but also their wide-ranging effects on ecosystem function (Schmitz 2010). How predators and prey interact is often characterized as a behavioral response race or "space race" where prey attempt to minimize and predators try to maximize spatial overlap (Sih 1984; Mitchell & Lima 2002). Hence, escaping predation is one of the key benefits of migration. Moving beyond the range of predators and only seasonally being available decreases predators' ability to numerically respond and is thought to decouple migratory prey from predators (Fryxell et al. 1988). For example, some of the most spectacular migrations of ungulates moving across the Serengeti, coincide with when predators, such as lions, are limited by immobile young (Holdo et al. 2011). However, migratory prey may not always successfully escape predators as some predators can respond to prey migration by adopting large-scale movement strategies to track prey, a phenomenon known as migratory coupling (Furey et al. 2018).

Occurring in multiple taxa and at a range of scales, various predators have adopted diverse strategies to exploit migrant prey (Furey et al. 2018). Some predators adjust their migratory routes to exploit migrant prey. Red knots (*Calidris canutus rufa*) take detours of up to 1,000 km during their 10,000km+ migration between the Canadian Arctic and Tierra del Fuego to feed on the eggs of spawning horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay (Buehler & Piersma 2008). Other species intercept prey on their migrations. Pacific salmon (*Oncorhynchus* spp.) migrations attract predators such as brown bears (*Ursus arctos*), bald eagles (*Haliaeetus leucocephalus*), and salmon sharks (*Lamna ditropis*) that travel tens to thousands of miles to reach spawning salmon (Glenn & Miller 1980; Weng et al. 2008; Wheat et al. 2017). Some predators even track migrant prey on their migration, which has been observed in the few examples involving large carnivores and migratory ungulates. In the Canadian Arctic tundra, wolves (*Canis lupus*) follow barren-ground caribou (*Rangifer tarandus groenlandicus*) for up to 1350km on their migrations, representing not only the longest migratory coupling but also the longest terrestrial migration (Walton et al. 2001; Musiani et al. 2007; Joly et al. 2019).

A unique challenge to understanding predator response to migratory ungulate prey is that many ungulates exhibit considerable variation in migration tactics within and between populations. In fact, most migratory ungulate populations are partially migratory, where some individuals in a population migrate and some remain resident (Dingle & Drake 2007; Chapman et al. 2011). Many studies have suggested that the diverse migratory portfolios of ungulates might be best understood as continuum between resident and migratory behavior (Cagnacci et al. 2011; Sawyer et al. 2016; Lowrey et al. 2020; Kauffman et al. 2021; Xu et al. 2021). However, little is known about how predators respond when migratory prey are capable of varying migratory strategies.

The Greater Yellowstone Ecosystem (GYE) provides a prime opportunity to better understand predator response to variability in migratory prey behavior. GYE is home to some of the highest concentrations of migratory ungulates in North America such as elk, a species that exemplifies diverse migratory tactics and exhibits a range of migration propensity, routes, timing, and distance (Eggeman et al. 2016; Rickbeil et al. 2019; Morrison et al. 2021; Martin et al. 2022, Zuckerman et al. 2023). Within the GYE there are 26 elk herds that share summer range in and around Yellowstone National Park, including 18 partially migratory herds (Gigliotti et al. 2022; Zuckerman et al. 2023). Furthermore, recent studies have shown that individuals within partially migratory herds are capable of switching between different migratory tactics in response to changing environmental conditions (Rickbeil et al. 2019; Zuckerman et al. 2023). Wolves, the primary predator of elk, have established their territories and den sites on the low-elevation winter range of these elk herds beyond the boundaries of Yellowstone (Middleton et al. 2013; Cole et al. 2015). Because the pup-rearing period coincides with elk migration from winter ranges outside of Yellowstone into summer ranges within the park, most wolves outside of Yellowstone are traditionally assumed to be decoupled from migratory elk in the summer (Garrott et al. 2005). Yet research conducted by Nelson et al. (2012) in the northeastern region of the GYE challenged this assumption by showing that migrating and resident elk within the same herd can elicit different wolf responses as wolves may also adapt to spatiotemporal changes in elk prey density and distribution. However, Nelson et al. (2012) classified elk into binary categories of resident or migratory. Development of tracking technology has provided new opportunities to incorporate a gradient of migratory tactics to better understand individual variation within partially migratory populations. This detailed knowledge could provide valuable insight into how predators might respond to the range of ungulate migratory strategies.

In this study, we investigated how wolves respond to the seasonal movements of a large partially migratory herd with a broad diversity of individual behaviors, including long-distance migration. First, we identified distinct subpopulations within the Cody elk herd based on shared migratory strategies. Then we evaluated evidence for different types of migratory coupling behaviors based on seasonal wolf distributions and the degree of overlap between wolf pack and elk subpopulation summer ranges. Previous studies have provided evidence that wolves can adopt at least three responses to their migratory prey leading to varying levels of migratory coupling: remaining resident (no coupling), commuting (some coupling), and tracking, or migrating (full coupling) (Frame et al. 2004; Musiani et al. 2007; Nelson et al. 2012). Hence, we hypothesized wolf packs would exhibit one of three different behavioral responses to elk migration: residency, commuting, and migrating (i.e., range shift) – with the latter two indicating migratory coupling. We predicted that resident wolves would exhibit high overlap between their winter and summer ranges and have the most overlap with resident and/or short-distance migrant elk subpopulations. We predicted that commuting wolves would have larger summer ranges than winter ranges, exhibit partial overlap between winter and summer ranges, and overlap with a range of elk subpopulations. Lastly, we predicted that migrating wolves would exhibit little to no overlap between winter and summer ranges and overlap the most with long-distance migrant elk subpopulations. Additionally, to evaluate the degree to which wolf pups act as a spatial constraint decoupling wolf packs from migratory elk, we looked at changes in homesite location and range size for packs with pups. We identified den and rendezvous sites (collectively referred to as homesites) and predicted that resident and commuting packs would either not shift or have short shifts from den to rendezvous site(s), but that migratory packs would shift rendezvous sites towards long-distance elk subpopulation summer range. We also predicted that the presence of pups would impact seasonal range sizes depending on the pack's response to elk departing for their summer ranges. Research questions and predictions are summarized in Figure 1. We tested our predictions using GPS collar locations from sympatric wolves and elk recorded over three years in the eastern GYE.

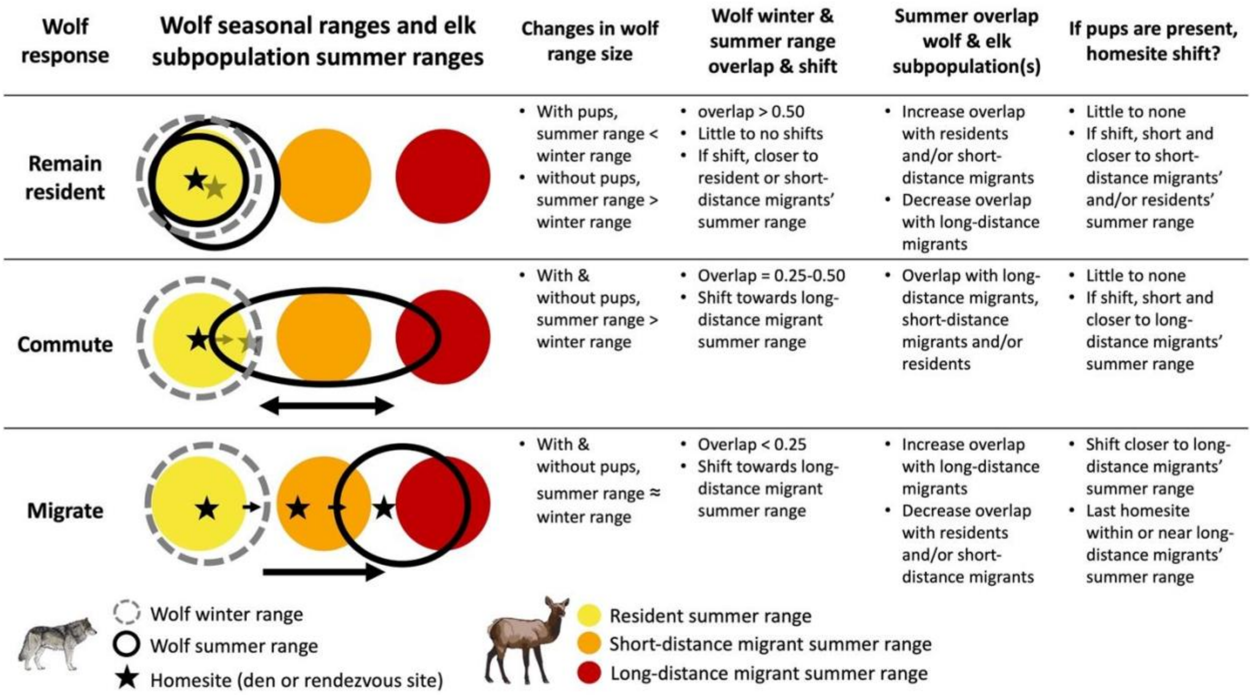


Figure 1. *Predictions regarding wolf response to the departure of long-distance migrants from their winter range to their summer range*

Methods

Study area

This study was conducted in northwest Wyoming east of Yellowstone National Park in the Absaroka Mountains. The elevation of the study area ranges from 1700m to 3400m, with high-elevation habitats dominated by alpine meadows, subalpine forests, and talus slopes; mid-elevation habitats dominated by Douglas fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*) and lodgepole pine (*Pinus contorta*) in coniferous forests and aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and shrubs in deciduous forests; and low-elevation areas dominated by sagebrush (*Artemesia* spp.) steppe, grasslands and agricultural fields. A mix of U.S. Forest Service (USFS), Bureau of Land Manager (BLM), Wyoming state land, and private land were included in this study.

Study species

We focused on the wolves that predate on the Cody elk herd, whose winter ranges are along drainages near the towns of Cody and Meeteetse. The Cody elk herd is one of the largest in the GYE with approximately 6,000-7,000 predominantly migratory individuals that winter on private, state, and BLM and USFS land – often on or near working ranches and public grazing allotments. The elk that migrate cover a range of distances, some as long as 117 miles, into their summer ranges in the southeast corner of Yellowstone National Park and surrounding National Forests (Rickbeil et al. 2019; Kauffman et al. 2020). Other subpopulations of elk complete short-distance migrations, often to the stopover sites of the long-distance migrants in the Shoshone National Forest. The wolf packs we studied occupied different areas of the Cody elk herd's winter range and varied in their overlap with human-dominated areas, with the Western and Central packs occupying more remote areas than the Eastern packs. While the Western and Central packs have remained relatively stable and have occupied their territories for over a decade, the packs that occupy the eastern region (during our study, Eastern packs, A, B & C) tend to experience high rates of turnover due to conflicts with livestock. During our study, the Western and Central pack maintained mostly the same individuals while the Eastern packs did not.

Capture and GPS collar deployment on elk and wolves

In January and February 2019 and 2020, we worked with Wyoming Game and Fish (WGFD) and Native Range Capture Services to deploy GPS collars on 99 individual cow elk (70 in 2019 and 29 in 2020) that were fitted with Lotek GPS Litetrack Iridium-420 collars (Newmarket, Ontario, Canada) in 2019 and Vectronic Vertex Plus GPS Iridium collars (Berlin, Germany) in 2020. We collared 19 wolves (9 in 2019, 4 in 2020, and 6 in 2021) and fitted them with Lotek GPS LiteTrack Iridium-420 collars in 2019 and Telonics Gen4 GPS-Iridium collars (Model TGW-4577-4, Telonics, Mesa, Arizona, USA) in 2020 and 2021. Wildlife captures and handling were approved by University of California Berkeley's Institutional Animal Care and Use Committee AUP-2018-07-11261. Elk GPS collar recorded locations every two hours, while wolf GPS collar recorded locations every two hours during the winter and every 20 minutes to 1 hour in the summer. Elk GPS collars were deployed across the winter range of the Cody herd. We deployed GPS collars in seven wolf packs that occurred within the range of the Cody elk herd. Due to GPS collar malfunctions, human-caused wolf mortalities (e.g., harvest, poaching, lethal control), and dispersals out of the study area, five of the seven packs with GPS collared wolves were analyzed in this study. Pack names and number of collars in each pack each year are as follows: Western pack (1 in 2019, 2 in 2020, 1 in 2021), Central pack (2 in 2019, 2 in 2020, 3 in 2021), Eastern A pack (2 in 2019, 2 in 2020), Eastern B pack (2 in 2021), and Eastern C pack (2 in 2021). Only one individual wolf had continuous GPS data throughout our study.

Classifying Cody elk herd subpopulations and their seasonal range dates

To capture the diversity of migratory tactics within the Cody herd, we split it into five distinct subpopulations based on migratory strategy and geographic region. We determined migratory strategy by plotting distance and elevation net-squared displacement (NSD) curves with an interactive map (Zuckerman et al. 2023) that used the `nsd()` function in the `amt` package (Bunnefeld et al. 2011). Once elk were split into migrant and resident categories, we further split the migratory elk based on migration distance (long and short) and summer range location (northern and southern), which resulted in five subpopulations: 1) long-distance southern, 2) long-distance northern, 3) short-distance southern, 4) short-distance northern, and 5) resident. In our study, some elk embarked on short elevational migrations, but because they remained accessible to resident wolves we classified them as resident. To further evaluate distinctiveness of elk subpopulations and how each subpopulation shifted their distributions from winter to summer, we measured overlap of elk subpopulations in winter and summer (Supplementary Materials Table 1)

We calculated the average start and end dates of the spring and fall migration of the long-distance migrants (both northern and southern populations) between 2019 and 2021. We used the dates of the long-distance migrants because they comprise the majority of the Cody elk herd, and their migration represents a major seasonal shift in the distribution of prey availability for wolves. We used two methods to determine start and end dates for each individual long-distance migrant. First, we used the NSD curves we plotted using the interactive interface of Zuckerman et al. (2023). Then following the method used by Aikens et al. (2017) and Rickbeil et al. (2019), we visually inspected the individual NSD profiles and locations on the accompanying map to determine start and end dates for spring and fall migrations. Secondly, we used a function called `segclus2d`, which performs segmentation of bivariate time-series data into homogeneous segments using Lavielle's method – typically used to identify home range shifts (`segclus2d`, Patin 2021). Segmenting elk GPS data using `segclus2d()` allowed us to identify distinct seasonal ranges. However, there were some instances where the segments representing seasonal ranges included parts of migratory routes. Therefore, using a combination of the two methods allowed us to cross-check start and end dates. Once migration dates were determined, we identified the mean ordinal dates of the spring and fall migration start and end dates for each year of the study (similar to Anton et al. 2020). Using the mean migration start and end dates, we set dates for four different seasons: 1) spring migration, 2) summer range, 3) fall migration, and 4) winter range for each year (Supplementary Materials Table 2). Years were kept separate because of large differences between migration start and end dates across the three years.

Calculating overlap and changes in size of wolf winter and summer ranges

To quantify the extent to which wolves shift their space use after the spring migration of elk, we calculated changes in size, location, and overlap of wolf winter and summer ranges. Using the season dates from long-distance migratory elk, we calculated winter and summer ranges of each wolf pack using 95% autocorrelated kernel density estimation (AKDE) from the `ctmm` package (Fleming & Calabrese 2022; Fleming et al. 2015). This method allows the estimation of range distribution with accurate confidence intervals from autocorrelated data sets without the need to coarsen the sampling rate or stratify across individuals as it also accounts for irregular sampling in time (Silva et al. 2022). We then calculated the area of each AKDE (km2).

Next, we used 'overlap' in the *ctmm* package to measure overlap between each wolf pack's' winter and summer ranges. This measure of similarity, the Bhattacharyya coefficient, can accurately estimate overlap even between individuals with different movement strategies (Winner et al. 2018). We used 95% contours to minimize the influence of extraterritorial movements and outliers (White and Garrot 1990, Getz et al. 2007) However, because the season dates of long-distance migratory elk used to determine winter and summer range did not align with when wolves were on their winter and summer ranges, we recalculated the size and overlap of wolf winter and summer range using only one month of winter (Feb 15th - Mar 15) and summer (Aug 1 - Sep 1) - when elk and wolves were on their winter and summer ranges.

Calculating overlap of wolves and elk subpopulations winter and summer ranges

We calculated winter and summer range overlap of wolf packs and elk subpopulations using the winter and summer range dates calculated using long-distance migratory elk migration dates to evaluate whether wolf packs shifted seasonal ranges after long-distance migrants departed. We calculated individual elk AKDEs for winter and summer range and then calculated population range estimates for each of the five subpopulations. We used the `pkde()` (population kernel density estimation (PKDE)) function from the `ctmm` package. This is a hierarchical kernel density estimation function with bias correction, which places kernels of density on every sampled time, with a bandwidth optimized for population-range estimation, while also accounting for autocorrelation and irregular sampling (Fleming et al. 2022). Once each of the elk subpopulation PKDEs were calculated, the `overlap()` function was used to calculate overlap of every wolf pack AKDE with every elk subpopulation PKDE for every winter and summer range between 2019 and 2021. We also noted if the shifts were closer to any elk subpopulation summer ranges. Overlaps of each elk subpopulation were also calculated during summer and winter to further analyze distinctness and fidelity of each subpopulation (Supplementary Materials 1a).

Calculating homesite shifts and distances to summer range

To investigate how packs with pups responded to the departure of migratory elk, we identified if any shifts occurred between wolf homesites (i.e., den and rendezvous sites). Shifts were easily identified with wolf GPS collar data as the den or rendezvous site acted as a central “basecamp” that collared wolves returned to frequently and were easily distinguishable from other GPS clusters. On a net-squared displacement curve, den and rendezvous sites were represented by a line of points at the same distance/elevation (Supplementary Materials Fig. 1). Additionally, ground-truthing by Wyoming Game and Fish Department wolf monitoring efforts and by our team during the field season further confirmed rendezvous sites. We then extracted the distance and direction of the shifts and whether the shift was towards a specific elk subpopulation summer range.

Wolf behavioral responses and metrics for migratory coupling

We evaluated evidence for residency, commuting, and migration based on 1) changes in wolf range size from winter to summer, 2) relative degrees of wolf winter and summer range overlap, 3) overlap with which elk subpopulations’ summer range, and 4) presence or lack of homesite shifts (if pups present). We consider increases in wolf range size from winter to summer to indicate commuting or residency without pups, while decreases in wolf range size from winter to summer to indicate residency with pups. While little to no changes in wolf range size indicates migratory behavior. We considered seasonal overlaps of at least 0.5 to indicate residency, 0.25-0.5 to indicate commuting, and 0-0.25 to indicate migration. We considered most overlap with long-distance migratory elk to indicate migration, most overlap with resident/short-distance migratory elk to indicate residency and overlap with both long-distance migratory and resident/short-distance migratory elk to indicate commuting. If wolves had pups, we considered little to no shifts in homesite to indicate residency or commuting, while multiple shifts to multiple homesites towards long-distance migratory elk to indicate migration. We consider both commuting and migration to be migratory coupling and residency to be migratory decoupling.

Results

Elk subpopulation seasonal range dates

Each elk subpopulation displayed a distinct temporal pattern of migration, and these patterns differed among years (Fig. 2; Supplementary Materials 1b). For example, the short-distance southern subpopulation tends to have later spring migration start dates and hence, shorter duration on summer ranges than other subpopulations. Figure 2 also highlights differences among the years of the study (e.g., the 2019 fall migration start and end dates were earlier than in 2020 and 2021).

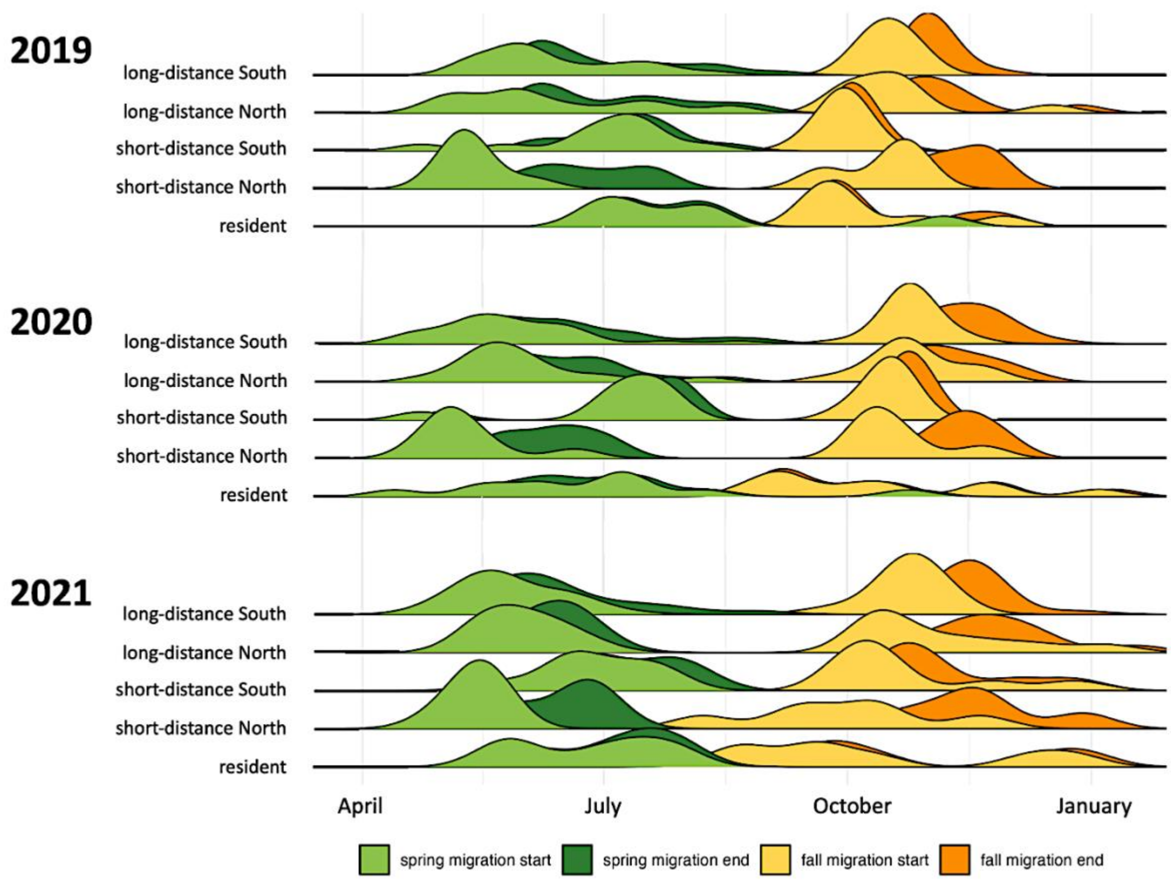


Figure 2. *Distribution of spring and fall migration start and end dates of each elk subpopulation for each year of the study.*

Changes in range distribution and size of wolf winter and summer ranges

Overlap of one month of wolf winter range (Feb 15 - Mar 15) and one month of summer range (Aug 1 - Sep 1) shows the degree to which wolves shift their range distribution from winter to summer (Fig. 3; Supplementary Materials Table 3). The percent overlap of winter and summer ranges for the Western and Central packs were all under 0.29, while overlap of the resident Eastern packs remained above 0.67. However, while the Central pack had 0.27 overlap in 2019, in 2020 and 2021 there was 0.0 overlap of winter and summer ranges. The Western pack had varying levels of overlap percentages of winter and summer ranges (0.4 in 2019, 0.06 in 2020, 0.29 in 2021). Due to GPS collar malfunctions and lethal control actions, only a few Eastern packs had GPS collar data past August 1st (Eastern A in 2020 and Eastern B in 2021), so winter and summer overlap could not be calculated. For the Eastern packs that did maintain GPS collars past August 1st, overlap percentages were over 0.5 (Eastern A 2019 = 0.67, Eastern C 2020 = 0.75). The Eastern C pack had the highest winter and summer range overlap of any pack. After calculating these overlaps, we realized that only looking at winter and summer overlap alone did not show us how the changes in wolf distribution throughout the year. Thus, we conducted a more nuanced post hoc analysis evaluating the overlap between the winter range and each monthly range from March to December. This analysis revealed a clear seasonal pattern of decreasing overlap when wolves were commuting and migrating (Fig. 3) and gave us a more complete picture of how wolf pack distribution shifts (if any) throughout the year.

Changes in wolf pack range sizes from winter to summer did not appear to show any patterns. However, packs with pups had smaller range sizes than packs without pups. For example, when the Central pack did not have pups in 2019, they had bigger summer range sizes compared to 2020 and 2021 when they had pups. The Eastern packs generally had larger seasonal ranges than the Western or Central packs throughout most of the year. However, the Eastern C pack had pups and had much smaller monthly seasonal ranges than any of the other Eastern packs.

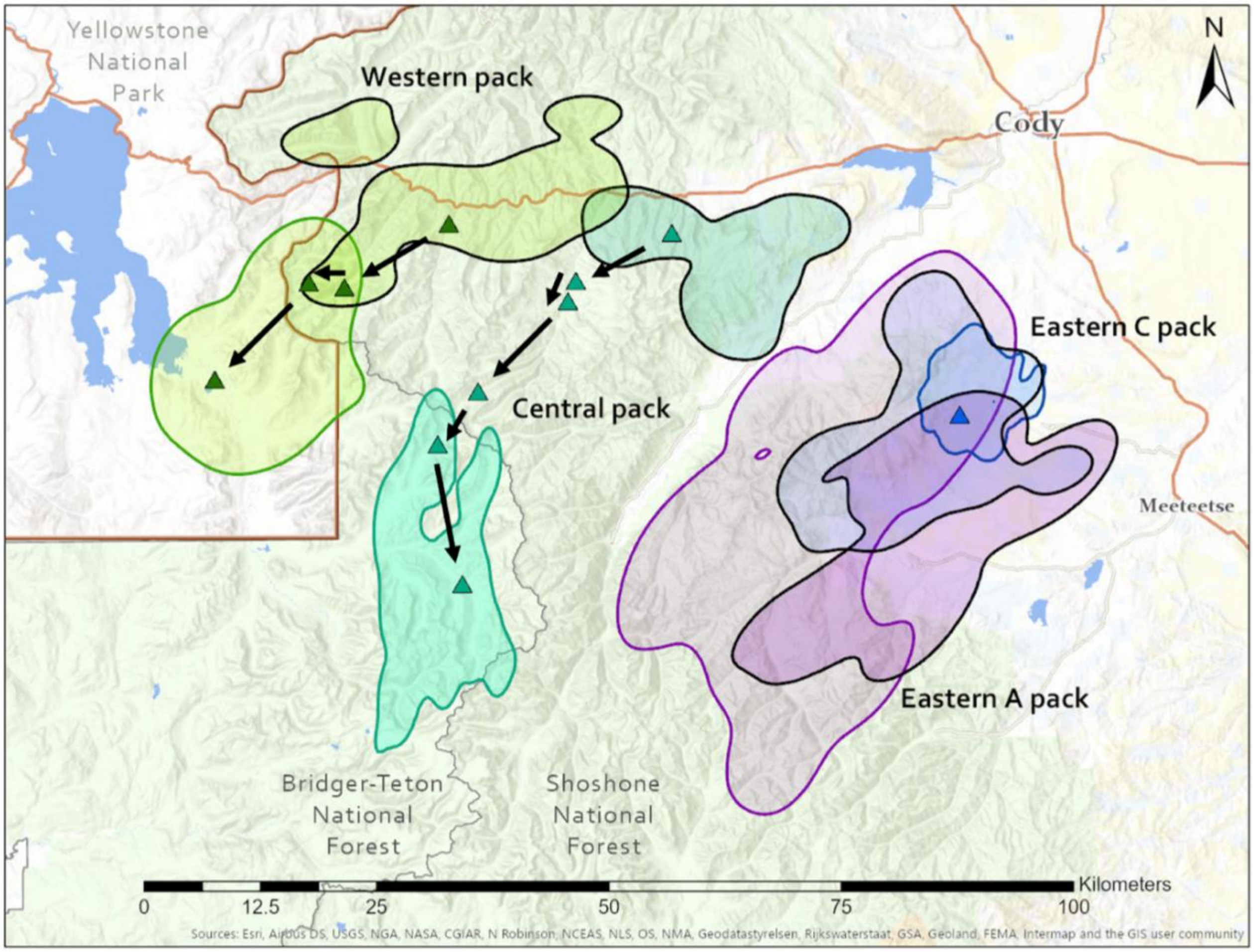


Figure 3. *Overlap of wolf winter AKDE (Feb 15th - March 15th; black outline) and summer AKDE (Aug 1st - Sept 1st; color outline) for each pack. The Western, Central, and Eastern C pack AKDEs are from 2021, while the Eastern A pack AKDEs are from 2019. Triangles represent homesites (den and rendezvous sites) and arrows note the direction of the shift. Eastern A pack did not have pups and so no homesites were marked. The Central pack had no overlap between their winter and summer range - showing a complete seasonal range shift. The Western pack has little overlap between their winter and summer range. Both Eastern pack A (in purple) and Eastern pack C (in blue) have more overlap than the other packs. However, the Eastern A pack has a larger summer range than winter range, while the Eastern C pack has a smaller summer range than winter range. The Eastern C pack also did not shift homesites and pups remained at or close to the den site until late summer.*

Wolf pack and elk subpopulation overlaps

Different wolf packs had varying levels of overlap with the elk subpopulations in winter and summer (Fig. 4). The Western pack mostly overlapped with the long-distance northern elk subpopulation and had moderate overlap with long-distance southern elk subpopulations. The Central pack mainly overlapped with the long-distance southern elk subpopulation with a little bit of overlap with resident, short-distance southern, and long-distance northern elk subpopulations. The Eastern packs mostly overlapped with short-distance southern and resident elk subpopulations.

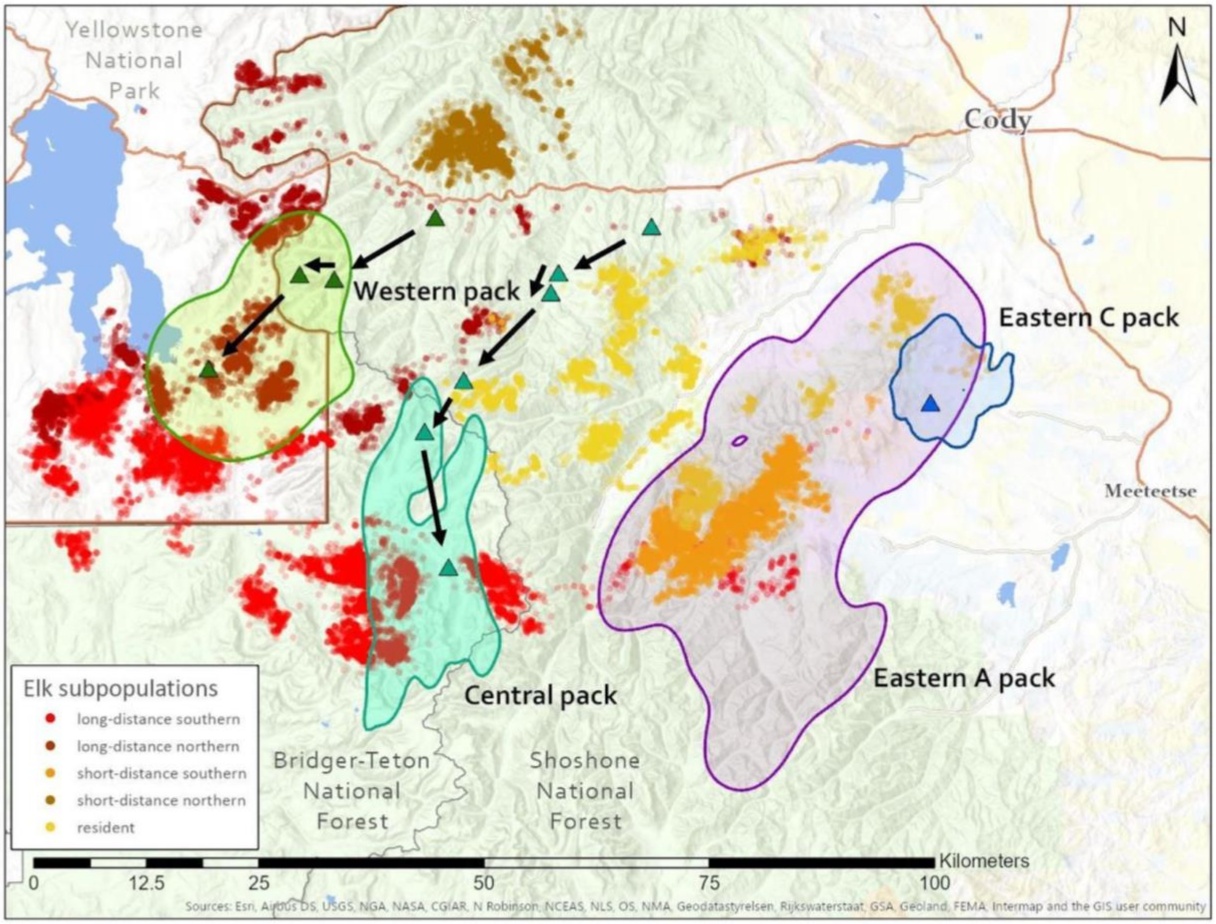


***Figure 4**. Summer range of wolf packs in 2021 (Western, Central and Eastern C) and 2019 (Eastern A) overlapped with elk subpopulation GPS points during the summer from 2019 to 2021. Elk subpopulations are represented by different colors in the legend. Summer range dates are August 1st to September 1st. Triangles represent wolf homesites (den and rendezvous sites) of wolf packs with pups and arrows show the direction of shifts. The Western pack had the most overlap with the long-distance northern elk subpopulation. The Central pack had the most overlap with the long-distance southern elk subpopulation. The Eastern A pack had the most overlap with the short-distance southern, resident, and long-distance southern elk subpopulations. The Eastern C pack had the most overlap with the short-distance southern and resident elk subpopulations.*

Wolf homesite shifts towards long-distance migratory elk summer range

Wolf packs in the study area did not consistently have pups during the study period except for the Western pack, which had pups in all three years of the study and shifts from the den site to multiple rendezvous sites were observed in all years. The Western pack's den site and first rendezvous site (R1) are 13.2km apart (Euclidean distance) and have been historically used by this pack. The Western pack's final rendezvous sites for 2020 and 2021 were within the long-distance northern migrants' summer range (due to collar failure in 2019, the final rendezvous site was unknown). The Central pack had pups in 2020 and 2021 and shifted from the den site to multiple rendezvous sites (two in 2020; five in 2021). The longest shift was from their den site to R1 in 2020, which was 23.92km. All the Central pack's shifts were movements closer to long-distance southern migrants' summer range. Of the three packs that occupied the eastern region during the study, only one had pups (Eastern C). They had two rendezvous sites very close to the den site (R1 = 2.74km; R2 = 0.69km), which they used in August along with the den site. They never made complete shifts like the Western and Central packs, often returning to the den site with the pups. The den site, R1 and R2 were within resident elk summer range and near short-distance southern migrants' summer range. Figures 5 and 6 show Western, Central and Eastern C packs‘ homesites on a map (homesite shift distances and dates can be found in Supplementary Materials Table 4).

Discussion

The goal of this study was to evaluate how wolves changed their space use in response to seasonal changes in elk availability where they had access to a large herd that exhibited a wide range of migratory tactics. Wolves in our study area employed a variety of behavioral responses to a partially migratory elk herd, from remaining resident to engaging in two migratory coupling behaviors – commuting and migrating. However, contrary to our prediction that each wolf pack would employ a singular behavioral strategy, we found packs that exhibited migratory coupling behaviors did so through a combination of commuting and fully migrating. Our findings also challenged the assumption that wolves are decoupled from migratory elk because the packs are spatially anchored to immobile young (Garrott et al. 2005), allowing elk to spatially separate from wolves in the spring and early summer. Instead, we found that migratory packs shifted homesites and young pups along elk migration routes toward long-distance migratory elk summer range.

Our results provide evidence of migratory coupling between migratory elk and gray wolves. Wolves that exhibited migratory coupling moved between discrete winter and summer ranges by tracking elk along their migration routes (Fig.3). Our post hoc analysis that calculated wolf monthly overlap with winter range found a clear pattern of decreasing overlap that began in late spring and early summer when wolves embarked on commutes before fully migrating later in the summer. This provided a more complete picture of seasonal movements of wolves than our initial winter and summer range overlap analysis. Therefore, we believe that commuting is a crucial behavior enabling full migratory movements by acting as scouting forays for wolves to gather information to track migratory elk (and potentially other wolf packs) more effectively before and during their migrations. Since elk in the study area are known to demonstrate plasticity in migratory strategy, timing, and distance (Rickbeil et al. 2019; Zuckerman et al. 2023), these costly forays may be important for ensuring that the timing of long-distance shifts to migratory elk summer range aligns with prey availability and accessibility. Wolves could also be using commutes to scout elk environmental cues (e.g., greenwave or snowmelt), which may prove to be more predictable than elk themselves – despite changes in greenwave timing (Rickbeil et al. 2019). Thus, while the increasing unpredictability of migratory behavior may threaten to decouple predators and migratory prey, our results show that wolves may have adopted a strategy to cope with this unpredictability. Nelson et al. (2012) also observed wolves engaging in commutes or extraterritorial forays, suggesting that this behavior may be common in wolves that track partially migratory elk. Studies of spotted hyenas in the Serengeti have found that hyenas will make long commutes of up to 140km to access migratory herbivores when resident prey abundance is low, and that despite the increasing unpredictability of environmental cues, hyenas can effectively locate and track migratory herbivores using past experience and possibly visual cues (Gicquel et al. 2022). Other large carnivores with similar cognitive abilities may use similar strategies to predict and track migratory behavior of prey and related environmental cues.

Our findings challenge the long-held assumption that elk can effectively minimize predation risk by migrating to high elevation areas, spatially separating from wolves that are anchored to den and rendezvous sites because of the need to feed immobile pups throughout the the pup-rearing period between May and August (Bergerud et al. 1984; Garrott et al. 2005; Mao et al. 2005). On the contrary, we found instances of packs with pups tracking elk on long-distance migrations and packs without pups remaining resident. Instances of wolves with pups tracking migratory prey have been observed in the arctic and subarctic regions of North America in late summer when pups are old enough to travel with adults (Ballard et al. 1997; Walton et al. 2001; Michelot et al. 2023). But to our knowledge, this study is the first to show adults and young pups shifting rendezvous sites closer to migratory prey in spring and early summer (Fig. 5 & Fig. 6). While wolves have been observed shifting rendezvous sites 1-8km, this usually occurs later in the summer when pups are larger (Mech & Boitani 2003). Nelson et al. (2016) observed a pack make a 5.5km rendezvous site shift in late July. The pack that consistently moved one-month-old pups more than 13km to the same rendezvous site in mid-May every year of our study have been observed to do so for many years prior. Many of these homesites were used for multiple years of the study and for several years prior (personal communication with P. Quick at Wyoming Game and Fish Department). Using the same homesites year after year may make long-distance homesite shifts less risky and worth the benefit of being closer to migratory elk on their summer ranges.

Figure 5. *Western pack breeding female carrying pup from den site to rendezvous site in June 2020 (WGFD camera trap)*

***Figure 6**. Central pack female (not breeding) leading pups from one homesite to another in Aug 2020 (WGFD camera trap)*

While pups do act as a spatial anchor to some degree during the denning season, wolves have found ways to cope by making long-distance movements to situate themselves near the routes and summer ranges of migratory prey. In our study, although packs with pups had smaller summer range sizes than packs without pups (Supplementary Materials Fig. 2), shifting rendezvous sites closer to migratory elk summer range as elk embark on their spring migration allows wolves to concentrate movements in a smaller area and lessens the need to travel long distances to search for prey. However, Michelot et al. (2023) found that some wolves in Northern Quebec make long-distance movements *before* caribou start their spring migration and establish dens within the vicinity of caribou migration routes and summer ranges so they can intercept caribou on their migration while being spatially constrained by young pups. Because high fidelity to calving grounds, high temporal consistency for calving, and a relatively brief calving pulse are defining features of arctic caribou herds (Joly et al. 2021), we hypothesize the predictability of movement and parturition patterns of ungulate prey may determine whether wolves make large-scale shifts before or after pups are born. Wolves in our study area may wait to shift homesites until after pups are born because migratory elk timing are highly variable from year-to-year with a calving period that spans almost two months and individual calving locations spread across winter range, migratory routes, and summer range (Rickbeil et al. 2019; unpublished VIT data). Evaluating how both prey and predators adjust to changing resources is an aspect of migratory coupling that will prove increasingly important in the face of ongoing environmental changes.

Although two wolf packs engaged in migratory coupling, three wolf packs in our study area remained resident during the same period. The packs that did engage in migratory coupling were relatively large and had been on the landscape for more than a decade, whereas the resident packs experienced high rates of turnover due to human-caused mortality (e.g., hunting, lethal control), and were likely less familiar with the landscape and elk movement behaviors. We therefore hypothesize pack stability and longevity play a key role in determining whether wolves engage in migratory coupling. Gathering information on nearby wolf packs could be another reason why wolves make commutes prior to fully migrating. We did observe resident packs in our study making a few commutes into migratory elk summer range, but not the full migration into the areas already occupied by the migratory packs. The high density of wolves in adjacent Yellowstone National Park may have a considerable effect on the seasonal movements of wolves in our study area. While the Western pack had separate seasonal ranges, they were not spatially distinct because they consistently used a small portion of their territory that borders Yellowstone National Park year-round. This area includes their long-time first rendezvous site and is situated along the migration route of the long-distance northern elk subpopulation, allowing access to both their winter and summer ranges (Fig. 3). The need to defend this core part of their territory from nearby Yellowstone packs may explain why this pack does not make a complete shift between winter and summer ranges. Wolves in Yellowstone occur at very high densities which require them to maintain and defend consistent annual territories against neighboring packs (Trapp 2008; Smith et al. 2015; Metz. et al. 2020) and therefore do not engage in migratory coupling. Future studies, especially those in places where large carnivore densities are higher within protected areas than adjacent areas, can examine the role of population density and familiarity with the landscape in determining a predator's propensity for engaging in migratory coupling.

Another reason resident wolves may not follow migratory prey could be the availability of alternate prey - either elk that don't embark on long-distance migrations or other prey species (i.e., prey switching; Kjellander & Nordström 2003). In our study area, resident wolves had the greatest overlap with resident and short-distance migrant elk subpopulations, suggesting resident wolves were spatially tracking resident elk. Results from our related wolf predation and diet study (Chapter 2) found a greater percent biomass of alternate ungulate prey (non-elk ungulate prey such as deer, pronghorn, and moose) and cattle for resident wolves compared to migratory wolves.

Management Implications

Migratory coupling has wide-ranging conservation and management implications. For many decades ecologists have cited seasonal escape from predators as a key benefit of ungulate migration (Fryxell & Sinclair 1988). However, our findings challenge this idea. Despite elk in the GYE exhibiting resilience to environmental and anthropogenic change through plasticity in migratory timing and switching between migratory tactics (Rickbeil et al. 2019; Zuckerman et al. 2023), some migratory subpopulations are declining due to reduced recruitment and survival (Middleton et al. 2013; Cole et al. 2015). Yet, the extent to which environmental or anthropogenic changes in driving these declines remains uncertain. If predation is a primary driver, migratory coupling may accelerate population shifts if wolves outside of Yellowstone can track and exploit migratory elk, emphasizing that the benefits of migration may be smaller than widely believed. Other ungulate migrations across the globe are declining, despite demonstrating high levels of behavioral plasticity, while large carnivores are recovering in many regions (Kauffman et al. 2021; Xu et al. 2021; Candino et al. 2022; Ingeman et al. 2022; Laforge et al. 2023). Additionally, migratory coupling, or decoupling, could alter carnivore behavior and distribution, creating new or exacerbating existing human-wildlife conflicts. Exploring predator-prey interactions where declining migratory ungulates and recovering carnivores overlap may illuminate the effects of migratory coupling on species dynamics, necessitating novel approaches to conservation and management for both carnivore and ungulates. Currently, few studies have explored the factors enabling or hindering carnivores' ability to track migratory prey. Understanding migratory coupling dynamics requires evaluating changes not only in migratory prey, but also in the predators that follow them.

Supplementary Materials

Supplementary Materials Table 1. Percent overlaps of winter and summer ranges for each elk subpopulation

Winter overlap of elk subpopulations

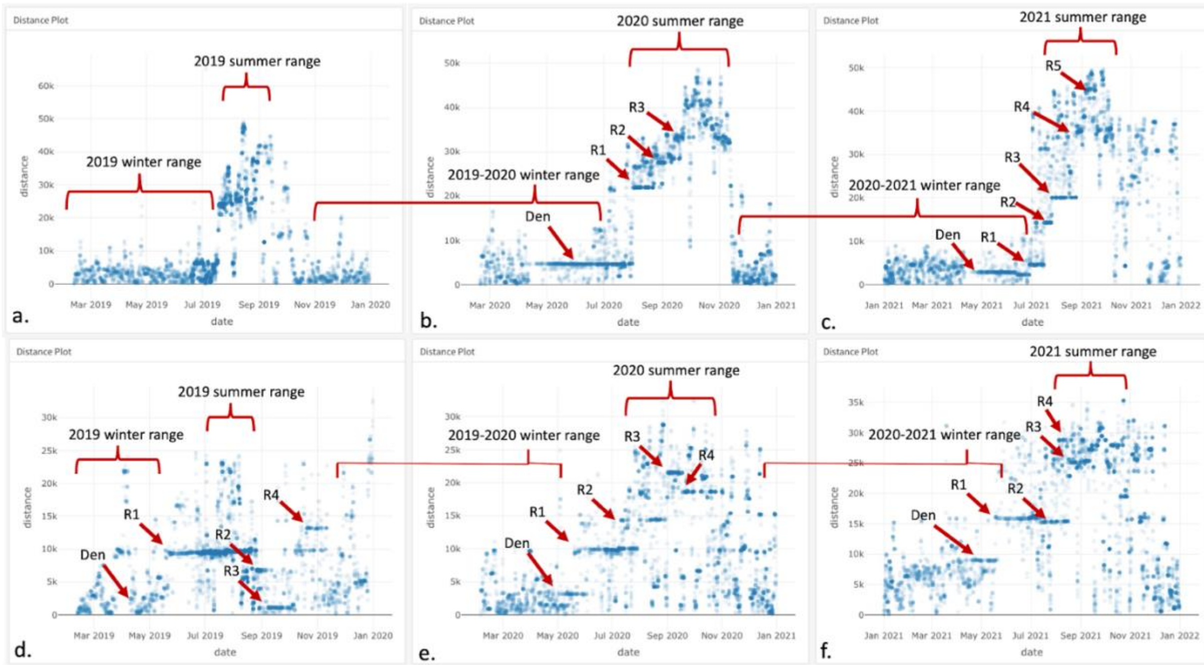
	long-distance northern	long-distance southern	short-distance northern	short-distance southern	resident
long-distance northern	1	0.75	0.75	0.21	0.77
long-distance southern	0.75	1	0.67	0.89	0.79
short-distance northern	0.75	0.67	1	0.01	0.31
short-distance southern	0.21	0.89	0.01	1	0.16
resident	0.77	0.79	0.31	0.16	1

Summer overlap of elk subpopulations

	long-distance northern	long-distance southern	short-distance northern	short-distance southern	resident
long-distance northern	1	0.60	0.17	0.10	0.11
long-distance southern	0.60	1	0.03	0.19	0.14
short-distance northern	0.17	0.03	1	0.31	0.09
short-distance southern	0.10	0.19	0.31	1	0.77
resident	0.11	0.14	0.09	0.77	1

Supplementary Materials 1a. Elk subpopulation overlaps on winter & summer range results

In winter there was a high percentage of overlap between both long-distance migrant groups (75%) and between long-distance migrants and short-distance within the same geographic area - 75% (northern subpopulations) and 89% (southern subpopulations). The least amount of overlap occurred between the two short-distance migrant groups (1%). Also in the winter, there was more overlap between long-distance migrant winter range and resident winter range (77% for northern, 79% for southern), than short-distance migrant winter range and resident winter range (31% for northern, 16% for southern). This is likely because long-distance migrants had larger winter ranges than short-distance migrants, and therefore overlapped with residents more. There were more stark differences in percentage overlaps in summer elk subpopulation overlaps. The only groups that had meaningful overlaps in the summer, were the two long-distance subpopulations (60%), as well as residents and the short-distance southern migrants (77.4%). But even on the summer range, each subpopulation seemed to maintain distinct core areas with only edges overlapping- the northern long-distance migrants tended to use the northern part of the summer range and the southern long-distance migrants tended to use the southern part of the summer range. While there was more overlap in the winter than summer, the subpopulations still maintained distinct winter range areas. Except for the long-distance and short-distance southern groups, which overlapped spatially during the winter, but appeared to use areas at different times because of differences in their migratory timing. Comparing migratory strategies of collared elk with multiple years of data showed that most of the collared elk remained within their subpopulation during the study period. A handful of individuals shortened (n=4) or lengthened (n =3) their migrations but remained within the geographic areas. Only two individuals moved to different elk herds (Jackson herd, and Gooseberry herd), with one of those individuals returning to the Cody herd from the Jackson herd. Notably no collared individuals moved between the northern and southern populations between 2019 and 2021.



Supplementary Materials Figure 1. Net-square displacement plots of the Central (top) and Western (bottom) pack with winter and summer ranges as well as den and rendezvous sites identified. Commutes can be seen as points between summer range and winter range (i.e., points closer to the 0 on the y-axis). The Central pack in 2020 (1b) and 2021 (1c) had very few commutes back to winter range compared to the Western pack in 2019 (1d), 2020 (1e), and 2021 (1f).

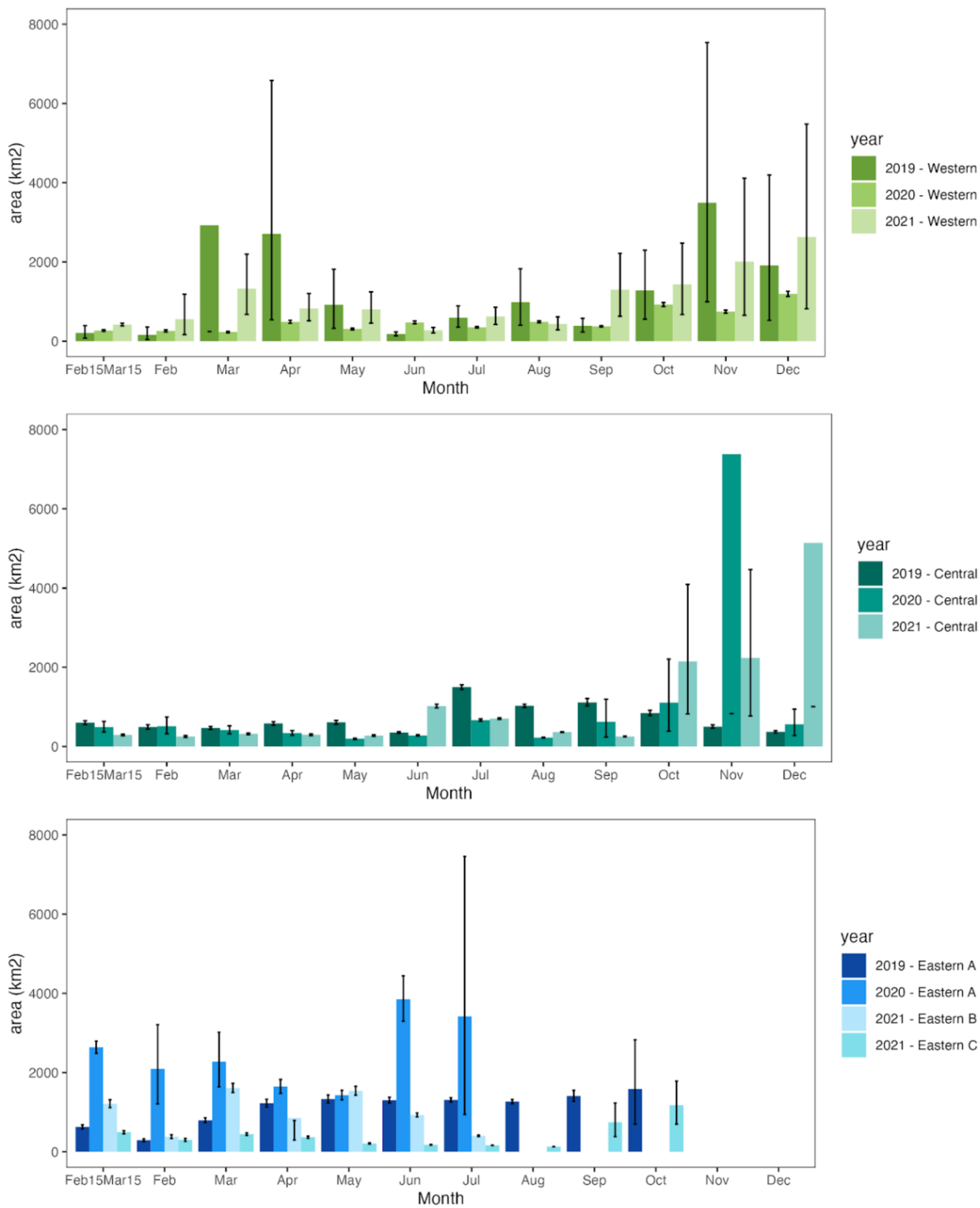
Supplementary Materials Table 2: The seasonal dates for each year of the study calculated using `nsd()` and `segclus2d()`: winter range, spring migration, summer range, and fall migration.

Seasonal range and migration start/end dates	2019 (n=26)	2020 (n=42)	2021(n=31)
Winter range	Capture dates in Jan/Feb 2019 to June 9th	Nov 1st 2019 or capture date (Jan/Feb 2020) to May 29th	Nov 10th 2020 to May 29th 2021
Spring migration	June 10th - 26th	May 30th to June 15th	May 30th to June 12th
Summer range	June 27th – Oct 15th	June 16th – Oct 25th	June 13th to Oct 23rd
Fall migration	Oct 19th-Oct 30th	Oct 25th to Nov 9th	Oct 24th to Nov 13th

Supplementary Materials Table 3. Wolf winter (Feb 15th - Mar 15th) and summer range (Aug 1st – Sept 1st) overlap percentages

pack	year	lower CI	overlap percent	upper CI
Western	2019	0.07	0.40	0.92
Central	2019	0.25	0.27	0.30
Eastern A	2019	0.66	0.67	0.68
Western	2020	0.06	0.06	0.07
Central	2020	0.00	0.00	0.00
Eastern A*	2020	NA	NA	NA
Western	2021	0.14	0.29	0.53
Central	2021	0.00	0.00	0.00
Eastern B*	2021	NA	NA	NA
Eastern C	2021	0.74	0.75	0.76

*packs were removed before August and therefore did not have summer AKDEs to calculate overlap



Supplementary Materials Figure 2. Monthly range sizes of wolf packs in the study area from 2019 to 2021 with y-axis maximum limit set to 8000km2.

Supplementary Materials 1b. Distinct migratory tactics and timing and intra-herd switching of Cody elk herd's subpopulations

The Cody elk herd has at least five subpopulations exhibiting a range of migratory tactics with distinct spatial and temporal patterns (Supplementary Materials Table 2). Despite spatial separation in winter range, both long-distance subpopulations had similar average migratory dates for spring and fall migrations for all three years of the study. This is likely because individuals are experiencing the same environmental cues such as vegetation green-up and snow conditions, which has been shown to be a major driver of migration timing for elk herds across the entire GYE (Rickbeil et al. 2019). While these results are expected, we observed differences in migration timing between the northern and southern short-distance and long-distance subpopulations. The starkest migratory timing difference was observed with the long-distance southern and short-distance southern subpopulations. Despite spatiotemporal overlap for much of their winter range, the short-distance southern individuals average spring migration start dates were consistently about a month later than the long-distance southern individuals in all three years of the study. The delayed timing of the short-distance migrants may be due to other mechanisms that have stronger influence than environmental cues. This finding highlights that asynchrony in migration timing can occur even within the same herd and not just among different herds (Rickbeil et al. 2019).

During the three years of the study, none of the GPS collared elk switched between northern and southern elk subpopulations, despite overlap of long-distance migrants in their summer range. Historically, the Cody elk herd was managed as two separate herds, which occupy the same regions as the northern and southern subpopulations we identified. In the 1980s and 1990s, researchers found that 80% of the North Fork Shoshone herd and more than 90% of the Carter Mountain herd were migratory (long-distance migrants) while also finding an interchange of more than 10% of these herds in their summer range leading to both herds being managed as one – the Cody herd. (Rudd 1982; Hurley 1996). In our study we found that about 52.4% of the Cody elk herd are long-distance migrants, while 25.2% are short-distance and 18% are resident or elevational migrants. While our GPS collar data did not detect switching between the northern and southern subpopulations, we did observe switching between long-distance and short-distance subpopulations in the same region, with two individuals switching from short to long and three individuals switching from long to short. We also had on collared elk spend one winter on the Jackson elk herd winter range before returning to the Cody area the following winter. Future research and monitoring of the Cody elk herd should keep track of these switches to better understand how individuals are changing migratory tactics. Being able to parse out the different subpopulations and their unique movements will better inform future studies looking into the drivers of the decline of long-distance migratory behavior.

Supplementary Materials Table 4. Den and rendezvous site (Rx) shifts observed from the Western and Central packs during the study period with dates and Euclidean distances noted.

	Western pack			Central pack	
year	**2019**	**2020**	**2021**	**2020**	**2021**
Den start date	Apr-10	Apr-11	Apr-18	Apr-13	Apr-9
Den to R1 shift date	May-16	May-19	May-20	Jul-31	Jun-12
Den to R1 shift distance	**13.2** km	**13.2** km	**13.2** km	**23.92** km	**11.53** km
R1 to R2 shift date	Aug-20	Jul-29	Jul-9	Aug-23	Jun-28
R1 to R2 shift distance	**20.4** km	**12.67** km	**2.4** km	**7.14** km	**2.36** km
R2 to R3 shift date	Sep-11	Aug-29	Aug-16	Sep-14	Jul-15
R2 to R3 shift distance	**6.29** km	**7.77** km	**14.56** km	-	**13.7** km
R3 to R4 shift date	Oct-16	Sep-17	Aug-18	-	Jul-25
R3 to R4 shift distance	-	-	-	-	**7.19** km
R4 to R5 shift date	-	-	-	-	Aug-25
R4 to R5 shift distance	-	-	-	-	**15.22** km
R5 departure date	-	-	-	-	Sep-25

CHAPTER 2. UNGULATE MIGRATION ALTERS SEASONAL DIET COMPOSITION OF WOLVES ALONG A WORKING LANDS FRONTIER

Abstract

The recovery of wolves into human-dominated regions has led to conflicts stemming from their impacts on native wild prey populations and depredation on livestock. Understanding wolf predation and diet ecology across various habitats is crucial for addressing these conflicts and ensuring the long-term success of wolf recovery efforts. This study evaluated the seasonal predation patterns of wolves tracking an elk herd with diverse migration strategies across a wilderness to working lands gradient in the eastern Greater Yellowstone Ecosystem (GYE). Most of what is known about seasonal wolf diets in the GYE comes from Yellowstone National Park, where elk are present during all seasons and are the primary prey of wolves year-round (Metz et al. 2012). We tested the alternative prey hypothesis, positing that wolves living outside Yellowstone National Park decrease predation on elk and increase predation on alternate prey (wild prey and/or livestock) from winter to summer as most elk in the Cody elk herd migrate into Yellowstone. However, despite these shifts, we predicted that wolves that track migratory elk would maintain elk as their primary prey, while resident wolves would not. From 2019 to 2021, we conducted cluster searches to investigate wolf-killed prey, and scat analysis to determine wolf dietary patterns, across winter and summer seasons. We found wolves that follow long-distance migratory elk not only maintained elk as primary prey, but actually increased the proportion of elk in their diet, marking the first recorded instance of migratory wolves increasing predation on their primary prey during the summer pup-rearing period. Meanwhile, the short-distance migratory pack maintained elk as their primary prey in one year but switched to cattle in the next. Both resident wolf packs decreased proportion of elk kills and increased proportion of alternate prey kills from winter to summer, supporting the alternative prey hypothesis. However, the resident pack that switched to mainly killing alternate wild prey such as deer and pronghorn maintained elk as their primary prey when measuring percent biomass. Whereas despite mainly killing elk during summer, the other resident pack did not maintain elk as their primary prey when measuring percent biomass and instead switched to primarily consuming livestock. Uncovering differences in predation patterns of wolves across a wilderness to working lands gradient underscores the importance of monitoring wolf predation and diet ecology to understand wolf impacts on ungulate populations and livestock depredations in landscapes beyond protected areas.

Introduction

Despite being extirpated from much of their historical range by the early 20th century, gray wolves (*Canis lupus*) are now the most widespread large carnivore in the Northern Hemisphere, where they exist across a gradient of wilderness to working landscapes (Mech 1995). However, their ability to survive in human-dominated areas has led to increased conflicts with humans, which threaten wolf recovery and conservation efforts (Graham et al. 2005). Conflict with wolves often arises from their dietary habits - from their widely debated impacts on harvested ungulate populations to predation on economically valuable livestock (Fritts et al. 2003; Muhly & Musiani 2009). Understanding wolf diet ecology is critical for the effective conservation and management of both wolves and their ungulate prey.

Wolves in multi-prey systems often show a clear preference for a primary wild ungulate species (Jędrzejewski et al. 2000; Mech & Peterson 2003; Metz et al. 2012). However, wolves are also flexible and can exhibit dietary plasticity (Newsome et al. 2016; Gable et al. 2018). When primary prey density declines, wolves may increase consumption of alternate prey - supporting the *alternative prey hypothesis* (Angelstam et al. 1984; Metz et al. 2012; Nelson et al. 2016; Tallian et al. 2017; Shave et al. 2020; Prokopenko 2022). In the context of wildlife management, when the alternative prey are livestock, the alternative prey hypothesis is more specifically known as the *prey scarcity hypothesis* (Nelson et al. 2016), which has received support from site-specific studies and global syntheses that have found that wolves kill more livestock where wild ungulates are rare, but prefer wild prey when it is abundant (Gula 2008; Meriggi et al. 2011; Imbert et al. 2016; Newsome et al. 2016; Janeiro-Otero et al. 2020). The prey scarcity hypothesis further posits that the number of livestock killed is determined by alternate wild prey availability– with the absence of alternate prey potentially exacerbating livestock depredations (Newsome et al. 2016) and the availability of alternate prey, such as other wild ungulates, potentially mediating depredations (Chavez & Gese 2005; Nelson et al. 2016). Thus, maintaining a high density and diversity of wild prey populations is consistently recommended as a strategy to mitigate livestock conflict (Meriggi et al. 2011; Newsome et al. 2016; Janeiro-Otero et al. 2020). Multi-prey systems where wolves' primary prey availability fluctuates – such as places where wolves' primary prey is migratory - offer the opportunity to evaluate how wolves respond to seasonal changes in primary prey availability and the extent to which they increase use of alternate prey.

The Greater Yellowstone Ecosystem (GYE) harbors a wide assemblage of large carnivores and migratory ungulate species, including wolves and their primary prey, elk (*Cervus canadensis*). Potential alternate prey species for wolves include wild ungulates such as deer (*Odocoileus sp.*), bison (*Bison bison*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*) (Stahler et al. 2006). While some wolves in the GYE outside of the Park have also been found to prey on livestock such as cattle (*Bos taurus*) (Nelson et al. 2016; Atkinson 2023). Most knowledge about seasonal wolf predation patterns in the GYE comes from Yellowstone National Park's northern range, where wolves maintain elk as their primary prey year-round (Metz et al. 2012; Tallian et al. 2017; Metz et al. 2020). However, most wolves in the GYE live outside of the Park on elk winter ranges and little is known about how their seasonal diet changes.

It has been assumed that wolves outside of the Park are decoupled from elk when migratory elk herds move into the Park in the summer (Garrott et al. 2005). While some wolves can make large-scale movements (i.e., long-distance migratory wolves, Table 1) to follow migratory elk to their high elevation summer ranges, a phenomenon termed migratory coupling (Nelson et al. 2012; Furey et al. 2018; Chapter 1), it is unknown whether this strategy allows them to maintain elk as their primary prey given that spatial overlap is a poor proxy for predation (Suraci et al.

2022). Indeed, wolves engaged in migratory coupling have been found to decrease predation on their primary prey during the summer pup-rearing period (Bonin et al. 2023; Michelot et al. 2023). Additionally, most wolves outside of the Park do not track long-distance migratory elk (Chapter 1). Rather, they may track elk that embark on shorter migrations (i.e., short-distance migratory wolves, Table 1) or remain on elk winter ranges (i.e., resident wolves, Table 1). Little is known about how these wolves cope with the departure of a large portion of their primary prey.

Our study evaluated how wolf predation and diet patterns changed in association with seasonal changes in primary prey availability in areas with varying degrees of overlap with cattle. Specifically, we tested the alternative prey hypothesis by examining how seasonal wolf prey composition shifts among elk (their primary wild prey) and alternate prey (wild ungulate prey or cattle). We also tested the prey scarcity hypothesis by evaluating the degree to which wolves increase predation on wild ungulate prey versus cattle when elk migrate away from wolves' winter territories. We used wolf kill site investigations and wolf scat analyses to examine whether predation patterns and diet composition vary before and after elk migrate from winter to summer range.

According to the alternative prey hypothesis, we expect all wolf packs to decrease predation on elk and increase predation on alternate prey, including wild ungulate prey or cattle. However, we predict these changes in prey composition will occur to different degrees depending on wolf movement strategy (Table 1). We expect changes in prey composition to be least pronounced in long-distance migratory wolves, with only slight decreases in elk and increases in alternate prey. We expect to see the greatest change in prey composition for resident wolves because they lose access to the majority of elk when migratory subpopulations leave their range. We predict wolves that track migratory elk (long-distance and short-distance) will maintain elk as their primary prey (>50% prey composition), but resident wolves will not. Additionally, we expect alternate prey for short-distance migratory wolves and resident wolves to include both wild ungulate prey and cattle as they overlap with cattle summer pastures - providing support for the prey scarcity hypothesis. Our research aims to uncover seasonal predation patterns to better understand how wolves adapt to living in human-dominated landscapes beyond protected areas and how changing use of their primary prey may impact wild ungulate populations and livestock depredations.

Table 1. Predictions on proportion of prey composition from winter to summer and across wolves with different seasonal movement strategies. Arrow size indicates the degree of proportion change expected with long-distance migratory wolves exhibiting the least amount of change in prey composition and resident wolves exhibiting the greatest amount of change.

Change in proportion of prey composition from winter to summer

	Elk predation	Maintain elk as primary prey?	Alternate prey (wild prey & cattle) predation
long-distance migratory wolves			
short-distance migratory wolves			
resident wolves			

Methods

Study area and species

The study area is a part of the eastern GYE, located in northwestern Wyoming east of Yellowstone National Park in the Absaroka Mountains (Fig. 1). The elevation of the study area ranges from 1700m to 3400m, with high-elevation habitats dominated by alpine meadows, subalpine forests, and talus slopes; mid-elevation habitats dominated by Douglas fir (*Pseudotsuga menziesii)*, limber pine *(Pinus flexilis*) and lodgepole pine (*Pinus contorta*) in coniferous forests and aspen (*Populus tremuloides*), cottonwood (*Populus spp.)*, and shrubs in deciduous forests; and low-elevation areas dominated by sagebrush (*Artemisia spp.*) steppe, grasslands and agricultural fields. The study area is home to a diverse assemblage of carnivores including grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), lynx (*Lynx canadensis*), and wolverines (*Gulo gulo*), as well as ungulates such as mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*). A mix of U.S. Forest Service (USFS), Bureau of Land Management (BLM), Wyoming state land, and private land were included in this study.

We focused on wolves that predate on the Cody elk herd, whose winter ranges are along drainages near the towns of Cody and Meeteetse. The Cody elk herd is one of the largest in the GYE with approximately 6,000-7,000 predominantly migratory individuals that winter on private, state, and BLM and USFS land often on or near working ranches and public grazing allotments (Rickbeil et al. 2019; Gigliotti et al. 2022). The density of wintering elk differs across the study area with the eastern region of the study area hosting the larger aggregations throughout the winter and summer. The Cody herd has at least five distinct elk subpopulations - two long-distance migratory, two short-distance migratory, and a resident subpopulation – and different wolf packs track different subpopulations (Chapter 1).

The wolf packs we studied occupied different areas of the Cody elk herd's winter range and varied in their overlap with human-dominated areas and migratory strategy. The Elk Fork and Pahaska packs (Long A & B packs) follow long-distance migratory elk in the summer occupying more remote areas than the short-distance migratory and resident packs. The Greybull pack (Short A pack) track short-distance migratory elk. The Big Chief Butte and Heart Lake packs (Resident A & B packs) track resident elk.

Capture and GPS collar deployment on wolves

In January and February 2019 and 2020, we worked with Wyoming Game and Fish (WGFD) and Native Range Capture Services to deploy GPS collars on 19 wolves (9 in 2019, 4 in 2020, and 6 in 2021) in seven packs and fitted them with Lotek GPS LiteTrack Iridium-420 collars in 2019 and Telonics Gen4 GPS-Iridium collars (Model TGW-4577-4, Telonics, Mesa, Arizona, USA) in 2020 and 2021. Wildlife captures and handling were approved by University of California Berkeley's Institutional Animal Care and Use Committee AUP-2018-07-11261. Wolf GPS collars recorded locations every two hours during the winter and every 20 minutes to 1 hour in the summer. Due to GPS collar malfunctions, human-caused wolf mortalities (e.g., harvest, poaching, lethal control), and dispersals out of the study area, five of the seven packs with GPS collared wolves were analyzed in this study: Long A pack (2 in 2019, 2 in 2020, 3 in 2021), Long B pack (1 in 2019, 2 in 2020, 1 in 2021), Short A pack (2 in 2019, 2 in 2020), Resident A pack (2 in 2021), and Resident B pack (2 in 2021). Only one individual wolf had continuous GPS data throughout our study (Long A pack).

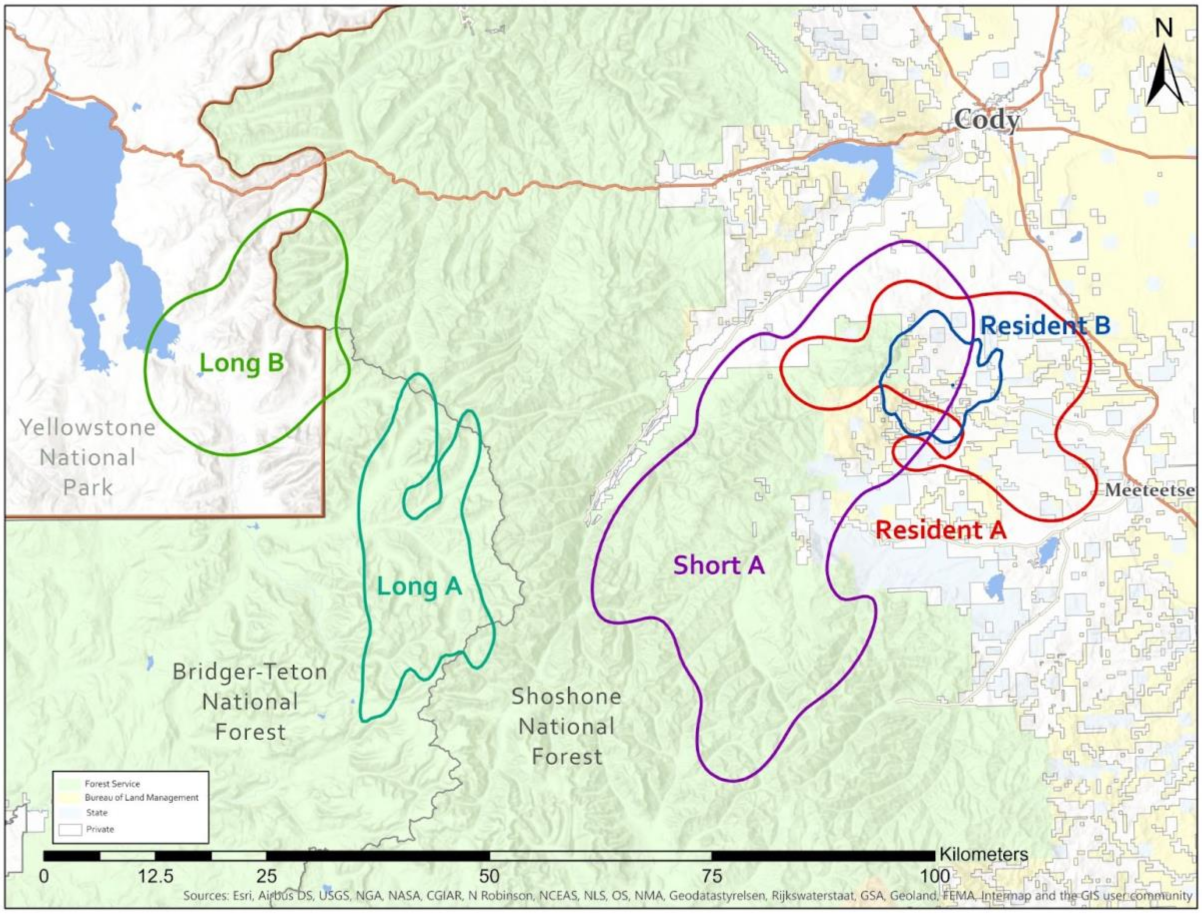


***Figure 1**. Map of study area with wolf summer ranges*

Data Collection

We assessed seasonal wolf predation and diet patterns by analyzing prey composition of wolf kills, scats, and scavenges detected during late winter (late January to late March) and summer (late June to late August) field seasons from 2019 to 2021. Kills and scavenges were located via cluster searching, while wolf scats were collected at clusters and wolf homesites (i.e., denning areas or rendezvous locations). Cluster searching alone can underestimate the presence of smaller prey, whereas scat collection alone can overestimate the presence of small species consumed. Combining these methods offers a less biased and more accurate approximation of wolf diet prey composition overall (Marucco et al. 2008; Tambling et al. 2012;).

Cluster searching

We used the cluster searching method (Sand et al. 2005) to locate and conduct necropsies on carcasses to evaluate whether they represented a predation or scavenging event. Field crews of two or more people searched clusters using similar methods to those described in Metz et al. (2012) and Nelson et al. (2016) (Supplementary Materials A). When dead livestock were found at clusters, we immediately notified Wyoming Game and Fish (WGFD) large carnivore biologists, who conducted their own necropsy as part of a collaborative agreement with WGFD and several ranches from a simultaneous study (Atkinson 2023). Per the agreement, WGFD delayed notifying producers of confirmed depredations until the end of the field season to ensure compensation without impacting wolf lethal control actions, thereby preserving the integrity of our study. All wolf-killed cattle carcasses we found were also found by producers and thus all lethal control actions that occurred during the study were from producer-detected depredations.

Scat collection, preparation, and prey item identification

We collected scats at clusters in all years. In 2020 and 2021, we added summer monthly scat collections at den and rendezvous sites (henceforth, homesites) for packs with pups. At clusters, only scats greater than 25mm in diameter were collected and were assumed to be from adult wolves. At homesites, adult and pup scats (<25mm diameter) were collected. If multiple scats were collected at a cluster, we pooled those scats into a single sample unit and estimated percent volume for each species represented in the cluster collection to avoid over-representation of prey items from multiple scats (Marucco et al. 2008; Tambling et al. 2012, Lodberg-Holm et al. 2021). For example, if we collected two scats in a cluster and one was 1.0 elk and one was 1.0 deer, we would combine those scats into a single sample with 0.5 elk and 0.5 deer. Each scat was analyzed together by the same two people to reduce potential observer bias. Scats were collected, stored, prepared, and analyzed through established methods using percent volume estimates (see Supplementary Materials A for detailed scat protocols).

Prey composition statistical analyses

We conducted Fisher's exact tests using R statistical software (Version 2022.12.0+353; R Core Team, 2023) to compare prey composition of collection methods (cluster-searched kills vs scats) to test for significant differences in prey composition (elk vs alternate prey) and prey size (large vs small) between kills and scats. Statistical significance was determined using a significance level of $\alpha = 0.05$. We defined prey size as small prey below 96kg of edible biomass (elk neonates, all deer, moose neonates, all pronghorn, all bighorn, small mammals) and large prey above 96kg (all elk except neonate, adult moose, all cows) (Morehouse & Boyce 2011; Metz et al. 2012). We used Fisher's exact tests to test for significant differences in winter vs summer kill prey composition for each pack for each year. We defined prey composition by classifying prey species into two prey types 1) elk, 2) alternate prey (wild prey & cattle). Additionally, for scat we calculated monthly prey composition values and then averaged across the seasons to reduce sampling bias because scat sample sizes varied across months (Gable et al. 2017).

We calculated two prey composition metrics: 1) percent frequency occurrence, which is the proportion of kills and shows how often a prey species is eaten, and 2) percent biomass, which is the proportion of prey acquired and shows the importance of the prey in the predator's diet. Since Fisher's exact tests require positive integers as inputs, we calculated adjusted biomass values by multiplying percent biomass by the total frequency of each pack/season/year (rather than multiplying by 100, so the numbers reflected the actual sample size of our data). We conducted Fisher's exact tests comparing winter and summer elk vs alternate prey (wild prey & cattle) prey composition using the adjusted biomass values for each pack across each year.

Percent frequency and percent biomass calculations

Percent frequency of kills was determined by dividing the frequency of prey detections by the total number of prey for each pack/season/year. For scats, we counted the number of scat samples that contained that prey species, then divided it by the total number of scat samples collected for each pack/season/year (Ciucci et al. 1996). Percent biomass of each species is expressed as a percentage of total estimated biomass consumed based on all prey species found for each pack/season/year and uses estimates of average live mass of individual prey derived from wolf predation and scat studies conducted in the GYE (Metz et al. 2012; Lodberg-Holm et al. 2021). Ungulates were divided by adult and juvenile body masses, and for elk and deer, the most common prey, we used data derived from growth curves (Murphy et al. 1998; Metz et al. 2012) to estimate live mass of elk and deer of different age classes and sex for each season (Supplementary Materials B).

Biomass of kills and scavenges were calculated using frequency occurrence of prey detections, live body mass of prey, and edible biomass percentages based on body size - 68% for large-bodied prey (≥97kg) and 79% for small-bodied prey (<96kg) (Metz et al. 2012; Morehouse & Boyce 2011). We did not include scavenges in the official analysis because of uncertainty surrounding how much of the scavenged carcass was consumed; however, we compared predation (kills) to prey consumption (kills + scavenge carcasses) as a descriptive analysis.

To calculate percent biomass for scats we used Weaver's (1993) regression equation, which converts percent volume to percent biomass for mammalian prey and is used for mammals to correct bias of smaller prey having a larger proportion of indigestible material in scats than larger prey (Gable et al. 2017; Lodberg-Holm et al. 2021). The equation is: $\hat{Y} = 0.439 + 0.008X$, where X is the average live mass (kg) of a prey species and $\hat{Y}$ is the estimated prey mass (kg) per scat. Percent biomass is calculated by multiplying the $\hat{Y}$ by the percent volume. Prey biomass associated with each scat ($\hat{Y}$) was multiplied by the number of scats containing that particular prey for each season/pack/year to estimate the total amount of biomass consumed for each prey. We only calculated biomass of mammalian prey and did not include prey items in our "other small prey" category such as fish, insects, birds, plants, and trash. We conducted Fisher's exact test of adult and pup scat prey frequency occurrence and percent biomass to see if adult and pup scats could be pooled for our analyses.

Results

a. Collection summary – kills, scavenges, scats

We investigated 1265 clusters (534 winter, 733 summer) and found 172 kills and 56 scavenged carcasses. Of those kills, we used 157 from five packs (3 resident, 2 migratory) in our analyses. We did not include long-distance migratory wolf pack data (Long A & B packs) for 2019 because of low sample sizes of clusters and kills. We investigated a higher percentage of short-distance migratory and resident wolf clusters (n = 898, 71%) than long-distance migratory wolf clusters (n = 359, 29%), and thus, found more overall and summer kills from short-distance migratory and resident wolf packs (winter = 37, summer = 63), compared to long-distance migratory packs (winter = 44, summer = 13).

We collected 740 wolf scats in winter and summer between 2019 and 2021. We removed 44 scats due to insufficient prey remains, and during scat analysis we removed 63 scats because we were unable to identify the prey. Of the 632 scats remaining, we pooled scats that were collected from the same cluster, leaving 489 individual scat samples that we used for the scat prey composition analysis. For the packs where we collected adult and pup scats (Resident B, Long A, Long B), we did not find significant differences between adult and pup scat prey composition, therefore in our analyses we pooled adult and pup scats together (Supplementary Materials C Table 1). Summary of kills, scavenges, and scats for each season for resident and migratory wolves can be found in Supplementary Materials C Table 2 and Figure 1.

b. Winter vs summer prey composition: Kills

Long-distance migratory wolf packs (Long A & Long B)

Long-distance migratory packs increased the proportions of elk in their diet during summer in 2020 (Long A, 38% to 75% frequency, 65% to 92% biomass; Long B, 63% to 100% frequency, 78% to 100% biomass) and 2021 (Long A, 36% to 50% frequency, 70% to 98% biomass) - maintaining elk as their primary prey year-round when measuring percent biomass (Fig. 2a; Supplementary Materials C Fig. 1 & Table 3). Meanwhile, they consumed decreased proportions of alternate wild prey such as deer, moose, and bighorn sheep in 2020 (Long A, 63% to 25% frequency, 35% to 8% biomass; Long B, 38% to 0% frequency, 22% to 0% biomass). However, the differences in prey composition between seasons were not statistically significant, likely due to low sample sizes (all $p > 0.05$, Supplementary Materials C Table 4). We did not have sufficient sample sizes for the Long A or Long B packs in 2019, or the Long B pack in 2021, to conduct analyses. No cows were killed by long-distance migratory packs.

Short-distance migratory wolf pack (Short A)

We found contrasting results between Short A's seasonal prey composition shifts in 2019 and 2020 (Fig. 2b; Supplementary Materials C Fig. 1 & Table 3). In 2019, Short A maintained the same proportions of elk when using percent frequency (78% to 78% frequency) and slightly increased the proportions of elk when using percent biomass (63% to 70% biomass) maintaining elk as their primary prey from winter to summer - although the seasonal differences were not significant ($p > 0.05$). In 2020, Short A significantly decreased the proportion of elk killed in summer (92% to 17% frequency, 97% to 10% biomass) and did not maintain elk as their primary prey (Supplementary Materials C Table 4). Rather, they increased the proportion of alternate prey killed (8% to 83% frequency; $p = 0.003$) - mostly cattle. The changes in percent biomass of elk versus alternate prey further highlighted these differences (3% to 89% biomass; $p = 0.0005$).

Resident wolf packs (Resident A & B)

All resident packs decreased proportions of elk and increased proportions of alternate prey, with one pack increasing predation on alternate wild prey and the other pack on cattle (Fig. 2c; Supplementary Materials C Fig. 1 & Table 3). Resident A and Resident B packs both decreased elk proportions from winter to summer. Resident A significantly decreased elk biomass proportions (100% to 40% biomass; $p = 0.013$). Meanwhile, Resident B pack significantly decreased elk kill proportions (100% to 25% frequency, $p = 0.0001$) with significant differences in biomass proportions as well (100% to 58% biomass, $p = 0.03$; Supplementary Materials C Table 4). Resident A pack (64%) maintained elk as primary prey when using percent frequency as a prey composition metric, but not Resident B pack (25%). However, when using percent biomass as a prey composition metric, Resident B pack (58%) maintained elk as primary prey and Resident A pack (40%) did not (Fig. 3).

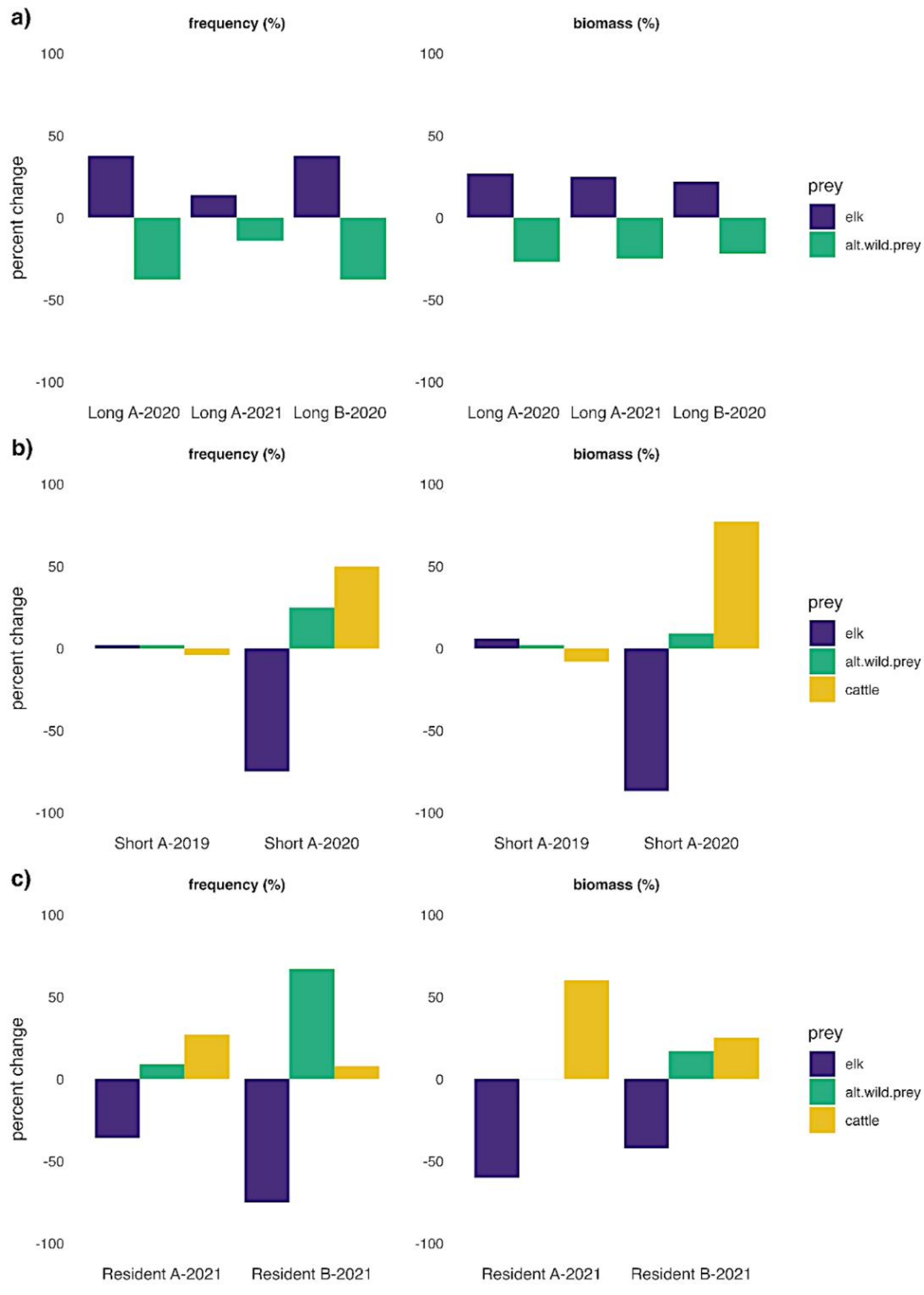


Figure 2. *Percent change of prey composition of kills (percent frequency and percent biomass) from winter to summer of a) long-distance migratory packs, b) short-distance migratory packs, and c) resident packs.*

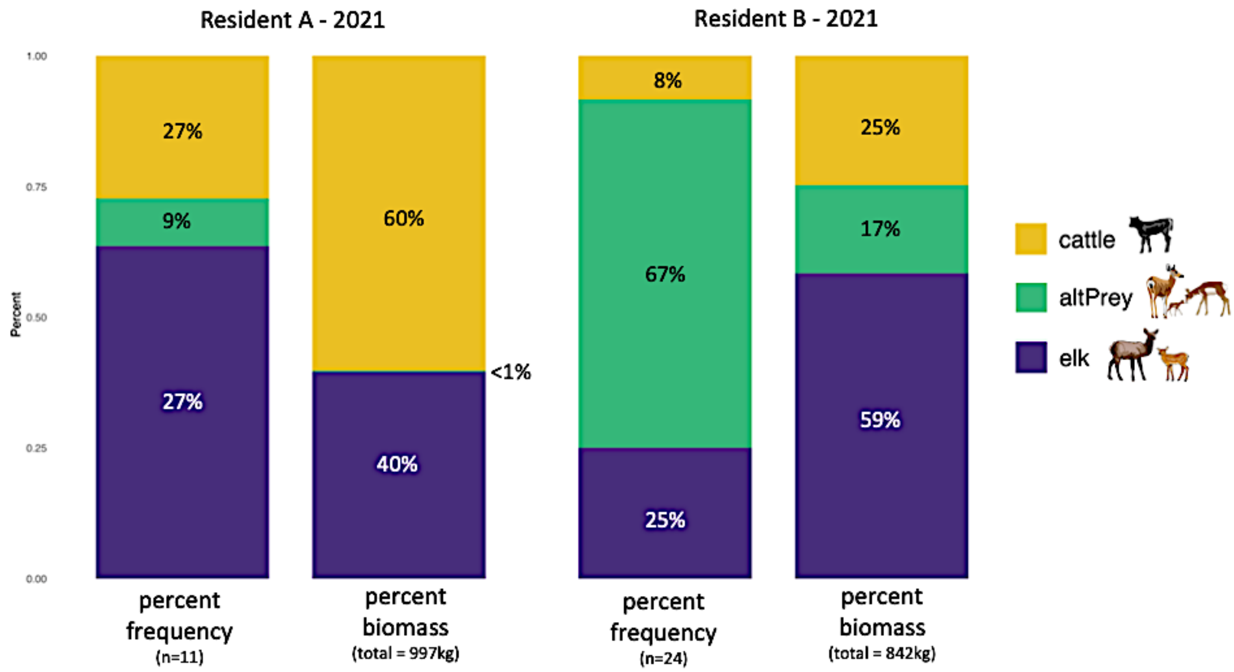


Figure 3. *Comparing percent frequency and percent biomass of Resident A & B packs' summer kills prey composition. Based on percent frequency (i.e., proportion of animals killed), elk would be considered the primary prey for Resident A pack, and alternate native ungulate prey (pronghorn and deer) would be considered the primary prey for Resident B pack. Conversely, percent biomass (i.e., proportion of prey biomass consumed) indicates cattle are the primary prey for Resident A pack, and elk are Resident B pack's primary prey.*

c. Winter vs summer prey composition: Scats

We did not detect significant differences between kills and scats prey composition for any packs (Fig. 4; Supplementary Materials C Table 5), nor we did not detect any significant differences in the proportion of large vs small prey between kills and scats (Supplementary Materials C Table 6).

Long-distance migratory wolf packs (Long A & B)
The scat data for long-distance migratory wolves largely reflected the pattern observed in kills, with increased proportions of elk in 2020 (Long A, 33% to 75% frequency, 28% to 96% biomass; Long B, 44% to 68% frequency, 66% to 92% biomass) and 2021 (Long A, 76% to 83% frequency, 93% to 97% biomass) in summer and elk maintained as primary prey (Fig. 3a & 3b; Supplementary Materials C Table 7). Both the Long A (p = 0.00009) and Long B (p = 0.047) packs in 2020 had significantly higher percent biomass of elk in summer - which differed from the kill data that did not find the differences to be significant (likely due to small sample sizes)

Short-distance migratory wolf pack (Short A)

Short A pack scat data mostly reflected the same patterns as the kill data (Supplementary Materials C Table 7). In 2019, Short A pack maintained elk as their primary prey, which was significantly higher than winter when measuring percent biomass, but not percent frequency (55% to 93% biomass, $p = 0.04$; 41% to 74% frequency, $p = 0.07$), which differs from the kill data that found differences were not significant. In 2020, Short A pack had significantly lower proportions of elk biomass (44% to 1% biomass, $p = 0.04$), which aligned with the kill data findings.

Resident wolf packs (Resident A & B)

Resident B pack scat data reflected the same patterns as the kill data (Supplementary Materials C Table 7). They maintained elk as their main prey for percent biomass (69%). They decreased percent frequency and biomass of elk; however the differences were not significant (93% to 69% biomass, $p = 0.18$; 71% to 63% frequency, $p = 1$) (Fig. 4e & 4f). We did not collect scats for the Resident A pack in summer.

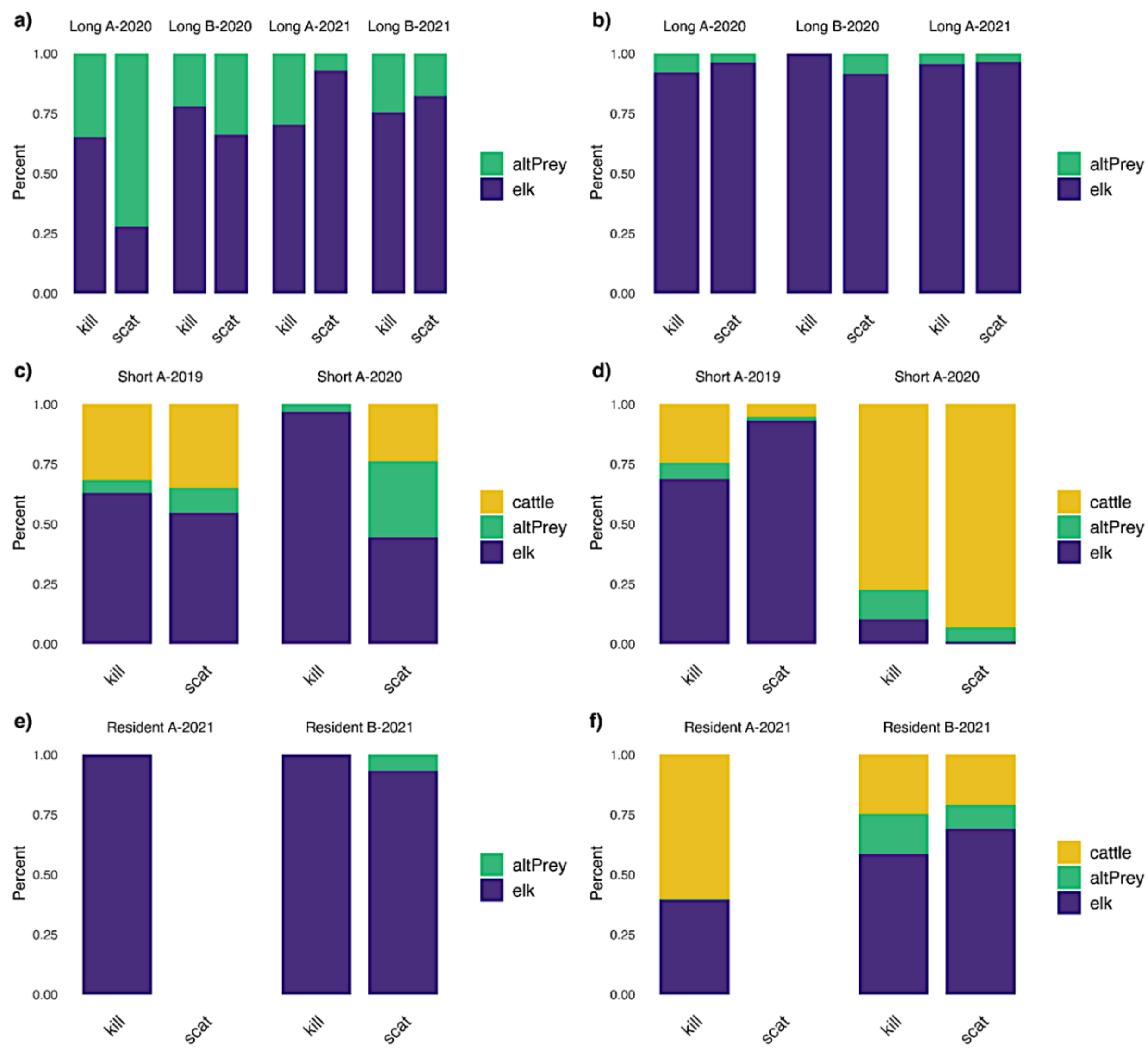


Figure 4. *Percent biomass of prey composition of kills versus scats in winter (left) and summer (right) for long-distance migratory packs (top), short-distance migratory packs (middle), and resident packs (bottom) - a) long-distance migratory winter, b) long-distance migratory summer, c) short-distance migratory winter, d) short-distance migratory summer, e) resident winter, f) resident summer.*

Discussion

Our study revealed a variety of ways that wolves can shift prey composition seasonally in response to the migration their prey. We found mixed support for our hypothesis that wolves would increase predation on cattle or alternative native ungulates after elk migrated away from their shared winter ranges. Aligning with predictions of the alternative prey hypothesis, we found short-distance migratory and resident wolf packs largely decreased their use of elk and increased their use of deer, pronghorn, and/or cattle during summer. Conversely, migratory wolves *increased* their use of elk during summer, directly contradicting the alternative prey hypothesis. Overall, despite shifting seasonal prey composition, we found that most packs maintained elk as their primary prey from winter to summer. All short-distance migratory and resident packs overlapped with cattle and engaged in depredations during the summer, providing support for the prey scarcity hypothesis. However, while the resident pack that increased predation on alternate wild prey maintained elk as their primary prey, the two packs that increased predation on livestock did not maintain elk as their primary source of prey biomass. Our findings suggest that migratory strategy and primary prey availability are not the only drivers of seasonal prey composition for wolves that predate on partially migratory ungulates.

Our study is the first to record wolves engaged in migratory coupling increasing the proportion of primary prey in their diet in the summer, challenging the commonly held notion that wolves on elk winter range outside of Yellowstone are decoupled from migratory elk in the summer (Garrott et al. 2005). These findings differ both from other packs in the study area and from neighboring wolves in northern Yellowstone, where predation on elk decreased and predation on deer increased from winter to summer (Metz et al. 2012). The only other documented example of wolves engaging in migratory coupling occurs in the Canadian Arctic where wolves decreased consumption of their primary prey, barren-ground caribou (*Rangifer tarandus groenlandicus*), and increased consumption of alternate species during the summer months (Ballard et al. 1997; Bonin et al. 2023; Michelot et al. 2023). Our research shows that for long-distance migratory packs, migratory coupling is an effective strategy to maintain predation on primary prey during the summer pup-rearing period.

The differences in seasonal diet across wolf packs show potential tradeoffs of different migratory strategies. While long-distance migratory wolves kill a smaller proportion of elk in winter due to the lower densities of elk on their winter range, they are better positioned to track and prey on migratory elk in the spring and summer because of their proximity to migration routes. Conversely, resident wolves establish territories on elk winter ranges with higher densities of elk, which may counteract the disadvantages of losing access to migratory elk in late summer. While short-distance migratory wolves can maintain access to large aggregations of wintering and summering elk year-round, that access comes at the cost of having to defend a larger home range.

Despite maintaining the same summer range and overlap with elk, the short-distance migratory pack maintained elk as their primary prey in one year but not the next, revealing that movement strategy alone does not determine seasonal prey composition. We hypothesize that differences in ability to maintain elk as primary prey may be impacted by pack size, specifically the number of adults capable of hunting, which may determine wolves' ability to acquire biomass from adult elk in the summer. While Yellowstone wolves prey mainly on elk neonates in summer, most biomass comes from adult elk, which comprise 34% of wolf-killed elk (Metz et al. 2012; Metz 2021; Lodberg-Holm et al. 2021). The only two packs in our study area that overlapped with cattle and still maintained elk as their primary prey biomass in the summer were relatively large (Short A-2019, Resident B), whereas the smaller two packs killed much smaller proportions of adult elk (Short A-2020, Resident A) (Fig. 3 & 4; (Supplementary Materials C Table 8). Short A pack's decrease in size from 4-5 adult wolves in 2019 to 2-3 adult wolves in 2020 may explain why they killed fewer adult elk. In Yellowstone, packs with at least four wolves are more successful at hunting elk than packs with fewer wolves (MacNulty et al. 2020). Prey vulnerability is an important aspect of summer prey availability for wolves, and small pack sizes may render larger prey less vulnerable, especially in the summer when adult elk are in peak nutritional condition and more difficult and dangerous to hunt (MacNulty et al. 2012; Metz et al. 2012). Killing insufficient numbers of adult elk may limit small packs' ability to meet their nutritional requirements during summer, the season in which they acquire the least biomass, and may increase their likelihood of killing cattle (Metz et al. 2012). While larger packs are associated with higher depredation levels in the study area (Atkinson 2023), our findings suggest there may also be a minimum pack size threshold above which conflict likelihood increases.

Alternative ungulate prey availability in resident wolf summer range may also influence the likelihood of livestock depredation**.** For example, the Resident B pack denned on a ranch with high densities of cattle and elk, but instead of primarily depredating cattle they preyed on migratory elk that remained on their winter ranges through July and then increased predation on alternative native ungulate prey as elk became scarcer in August. When most migratory elk vacated the area in August, the biomass this pack acquired from alternate prey (mostly pronghorn) increased more than five-fold, from 8% to 47% of their diet (Supplementary Materials C Table 9). This pack capitalized primarily on the seasonal resource pulse of a large pronghorn herd that migrated near their den site (Sawyer & Telander 2022). Smaller prey like pronghorn, despite their lower biomass, may help wolves compensate for the reduced availability of primary prey and may be particularly crucial for packs constrained to pups at dens (Borg et al. 2002; Brown 2002; Sand et al. 2008; Latham et al. 2013). Although they killed one cow in August, the availability of pronghorn and deer may have allowed the Resident B pack to meet their remaining energy needs, reducing their propensity to prey on additional cattle. If a predator is satiated, high encounter rates do not necessarily increase predation risk (Suraci et al. 2022). Our findings align with Nelson et al. (2016), who found that wolves increased predation on deer when migratory elk departed, potentially mediating conflict.

Grizzly bears, which occur in high densities throughout the study area, may also influence prey composition by limiting wolf biomass acquisition through interference competition. In Yellowstone, grizzlies shorten wolf handling time of large carcasses, possibly because larger carcasses attract more bears, prompting wolves to abandon their kills sooner (Tallian et al. 2022). Thus, grizzlies may reduce the benefits of killing adult elk in the summer, particularly for smaller wolf packs that take longer to consume large carcasses and thus have more to lose. Grizzlies may also hinder wolves' scavenging opportunities. Most dead cattle we found were scavenged, suggesting scavenged cattle could be a significant biomass source. Yet there were no significant differences in biomass percentages of cattle between kills and scats, indicating limited consumption from scavenged carcasses. Scavenging bison is a major biomass source for Yellowstone wolves in winter - a time when grizzlies are less active (Metz et al. 2020). We also found evidence of at least two kleptoparasitism events, where grizzlies stole wolf-killed cattle, which resulted in wolves killing another cow nearby, suggesting grizzlies may exacerbate conflicts.

We found that most cattle kills were spatiotemporally aligned with elk presence and elk kill locations (Supplementary Materials D), suggesting that these depredations were likely incidental as wolves tracked elk (Nelson et al. 2016; Atkinson 2023). Short-distance migratory wolves killed cattle in or near migratory elk locations throughout the summer. Meanwhile, all but one of the resident wolf depredations occurred on migratory elk winter range earlier in the summer before most elk had migrated. However, our summer field season spanned a time period when many migratory elk were still present on their winter ranges assume collared elk did not migrate until August. Because we investigated clusters only through August and depredations often continue through September, our findings could be biased towards depredations associated with migratory elk presence. Atkinson (2023) observed most wolf depredations in the study area from 2012-2020 occurred on private land rather than public grazing allotments, meaning most conflict occurred on elk winter range. This suggests that historically resident wolves have engaged in more conflict than short-distance migratory wolves. Future research could analyze depredation data across the summer into early fall and compare it with corresponding GPS collar data from the Cody elk herd to determine whether most depredations were linked to the presence or absence of migratory elk. Across the GYE, average summer migration start times have become increasingly later (Rickbeil et al. 2019). Thus, if depredations are closely associated with elk availability, future research could investigate whether depredation timing has also followed this trend.

Management Implications

Wolf recovery reignites old disputes and sparks new conservation and management challenges. Because wolf conflict stems from predation on both wild and domestic prey, investigating wolf diet ecology is crucial for understanding wolf ecological impacts and mitigating conflict with livestock producers. Ecologically, wolf predation may have important impacts on the population dynamics of migratory subpopulations of elk, which are largely in decline across the Northern Rocky Mountains. In addition to climate and land use change making migration more difficult, recovering wolf and grizzly populations in protected areas have increased predation risk for some migratory elk, reducing survival and recruitment (Hebblewhite & Merrill 2007; Barber-Meyer et al. 2008; Middleton et al. 2013; Berg 2023). Meanwhile, in more human-dominated landscapes, hunting and conflict management have reduced carnivore densities, while year-round agricultural subsidies contribute to higher densities of resident elk (Hebblewhite et al. 2006; Middleton et al. 2013; Barker et al. 2019). In Canada's Banff National Park, the altered predation risk gradient in the last two decades has shifted the elk population from mostly migrant to mostly resident (Williams et al. 2024). A similar trend may occur in the GYE if wolves outside of Yellowstone can track and exploit migratory elk, potentially further accelerating their decline. Additionally, wolves that don't track long-distance migratory elk may impact other ungulate populations when they seasonally increase predation on alternate wild prey such as deer and pronghorn. Monitoring changes in density and movement of elk and other ungulates can help reveal long-term impacts of wolves on migratory populations, as well as wolf-livestock conflict dynamics.

Shifting distributions of migratory elk between protected areas and adjacent working lands in the GYE may intensify conflict as later migration departure dates and increasing resident elk populations may result in more elk comingling with cattle throughout the summer (Middleton et al. 2013; Cole et al. 2015; Nelson et al. 2016; Rickbeil et al. 2019). Some researchers have recommended reducing overlap of wolves, cattle, and elk by decreasing resident elk populations and removing large depredating packs, or by shifting where cattle graze (Bradley & Pletscher 2005; Bradley et al. 2015; Nelson et al. 2016; Atkinson 2023). However, our study found examples of wolf packs co-occurring with high densities of elk and cattle engaging in low levels of conflict - including a pack with pups denned on a ranch. We also found smaller packs of 2-3 wolves killing more cattle than larger packs of 4+ wolves occupying similar summer ranges. This indicates that prey availability and wolf density alone do not determine depredation levels, making it difficult to identify specific management strategies that will effectively address patterns of conflict.

While our findings challenge common assumptions about conditions conducive to conflict, our study took place during a period with low occurrences of cattle depredation. Since wolves were removed from the Endangered Species list in 2017, wildlife managers in Wyoming have been able to use lethal control more decisively. Additionally, ranchers in the study area have adapted to having wolves on the landscape and have adopted practices such as increasing human presence to reduce livestock depredations (Chapter 3). The combination of lethal and nonlethal measures has reduced depredation numbers in the study area. As management actions significantly influence conflict dynamics, these lower levels of conflict may represent a new norm for conflict dynamics in the later stages of the wolf recovery process.

Supplementary Materials A – Methods

Supplementary Materials 1a. Cluster searching protocol

We defined clusters as two or more locations within 100m of each other. Wolf GPS collar data was downloaded twice a week in the winter and every other day during the summer and run through a cluster algorithm in R statistical software (Version 2022.12.0+353; R Core Team, 2023 that identified clusters (cite Kristin's cluster code?) and created a randomized list of clusters to prioritize in order to reduce bias for clusters that are easier to access. Several clusters were inaccessible due factors such as unnavigable terrain, avalanche danger, high water preventing river crossings, grizzly bear presence, or would require more than two days to get there. Although we were able to obtain permission to access most clusters on private land, there were a couple where we either could not get in contact with the landowner or were denied permission. Clusters associated with known wolf homesites weren't searched until the wolves had left the area.

Field crews of two or more people searched clusters using similar methods described in Metz et al. (2012) and Nelson et al. (2016), making sure to investigate every point within the cluster even when a carcass was located. If multiple GPS collared wolves from the same pack were present at the cluster at the same time, we counted them as one cluster and searched points of both wolves. However, if the clusters were at separate times, we treated them as separate clusters. If there was no evidence of a carcass, we searched for other wolf sign that matched the timeframe of the cluster such as tracks, scat, hair, and day beds. We collected wolf scat that matched the time frame of the cluster. Day beds were located by looking for flattened vegetation and depressions in the ground that contained wolf hair. When clusters contained no evidence of wolves, we classified them as unknown. The cluster was also assessed for signs of struggle (e.g., blood spatter, broken vegetation) as well as potential terrain traps that could have given wolves an advantage in capturing prey (e.g., dense vegetation, downed trees, water, ice, fences, etc.). For neonate ungulates detected during the summer season, we assumed wolves had killed the prey unless specific evidence suggested otherwise (e.g., when a carcass had been cached by a cougar) (following the protocol in Metz et al. 2012). We conducted necropsies of found carcasses to determine cause of death and approximate time of death to see if it matched the cluster generation date. The hide was investigated for characteristics and locations of canine teeth punctures, raking, and hemorrhaging to distinguish between different types of predator kills. We categorized each carcass as either a possible wolf kill, probable wolf kill, scavenge (and then indicated what the estimated cause of death was), or unknown cause of death. We noted prey species, age class, sex, and took samples from the carcass that could provide us more information on the demographic and condition of the prey, such as bone marrow, teeth, and hair. If the incisors of an adult ungulate were present, its age at time of death was determined by counting cementum annuli of teeth (Matson's Laboratory, Milltown, MT, USA). We obtained year-specific ages from 48 of 152 adult ungulates that we necropsied. When dead livestock were found at clusters, we immediately notified WGFD large carnivore biologists who would conduct their own necropsy to confirm the cause of death.

Supplementary Materials 1b. Scat analysis protocol

Scat collection protocol

We collected 740 wolf scats in winter and summer between 2019 and 2021. In 2019, scats were only collected at clusters, but in summer 2020 we added den and rendezvous site (henceforth, homesite) scat collections to assess monthly patterns in wolf pack diet through the summer (See scat collection protocol document). Because scats were only collected at GPS clusters and homesites, the likelihood of confusing wolf scats with sympatric canid species scats (mainly, coyotes) was small. However, at GPS clusters we only collected scats that were greater than 25mm in diameter and assumed all to be adult scats. At homesites we collected both adult and pup scats and assumed scats <25mm to be from pups and grouped them separately for analysis because pup diets may differ because some pack members (e.g., breeding individuals) bring disproportionally greater amounts of food to the pups or pups consume food that are abundant around homesites (Gable et al. 2017; Bryan et al. 2006). Separating scats by season and month is important because wolf diets can change quickly in response to the availability and abundance of prey (Van Ballenberghe et al. 1975; Gable et al. 2017) and monthly homesite scat collections can help us to better understand shifting patterns of wolf diet throughout the summer (Steenweg et al. 2015; Gable et al. 2017). In addition to grouping scats by age class (adult vs pup) time period (season and month), we also grouped scats by pack because packs experience different levels of prey availability in each territory or packs specializing on particular prey (Gable et al. 2017; Fuller & Keith 1980). During the scat preparation process, we removed 72 scats due to insufficient prey remains or very degraded old scats that seemed older than the cluster or homesite collection. We did not include 28 of the 668 scats analyzed because we were not able to identify the prey – leaving us with 640 scats for the scat prey composition analysis.

Scat Preparation

After wolf scats were collected, they were labeled and placed in a freezer at -20°F. Once scats were ready to be analyzed they were removed from the freezer and placed in nylon stockings (pantyhose or knee-high stockings) with individual embossed tape labeled with a unique scat ID (pack name abbreviation and number) that would not fade in the washer. One nylon stocking could hold multiple scats with knots tied between each sample. Then scats were placed in a washing machine (purchased a used washing machine specifically for washing scats) and soaked in water to thaw for several hours. Then we ran the scats through a wash cycle using cold water at the lowest spin cycle with a double rinse. No detergent was used and no more than 25 scats were placed in the washing machine at the same time. Once all soluble material was removed (sometimes larger scats needed to be washed twice), labels and prey remains were removed from nylon stockings and placed on paper plates and left to dry completely (at least 48 hours). After drying, prey remains were placed in labeled Ziplock bags until ready for analysis.

Scat prey species identification and percent volume estimation

Despite the systematic approach of the point-frame method that is commonly used to randomly select hairs to identify prey species in scat, it does not always capture all the prey remains in a scat. Even after identifying randomly selected hairs, the entire scat is visually inspected and percent volume is estimated if there are more than one species identified. Therefore, we did not use the point-frame method. For each dried scat, we spread out each scat sample across a sheet of white paper and divided by prey remain type (e.g., hair, bones, hooves, teeth, feathers, claws, plant material, trash, etc.). Several scat samples that had very few hairs and lacked other identifiable prey remains were removed from the analysis as hair can get temporarily stuck in the digestive tract and may not reflect the species most recently consumed (n = 72) (Ciucci et al. 1996). Next, macroscopic inspection was used to divide hairs into groups based on similar characteristics such as color, size, and texture. Then guard hairs were selected from each hair group and analyzed under a compound microscope at 40x and 100x to look at medulla and cuticular scale patterns. Scale patterns were analyzed by brushing clear fast-drying nail polish onto a microscope slide and gently pressing the hair into the nail polish. Once the nail polish dried, we carefully removed the hair using tweezers trying not to scratch the nail polish. This creates a cast, or impression of the hair, which makes the scale patterns easier to see than on the hair itself. We used hair identification guides specific to species in the region to aid in species identification, as well as reference hairs we collected from wolf kill sites in the field (Kennedy & Carbyn 1981; Moore 1974). We also compared prey remains to museum specimens, which were collected from the GYE, from the Draper Natural History Museum at the Buffalo Bill Center of the West in Cody, Wyoming. For scats collected during the summer that had ungulate hair, we noted whether it was a neonate or an adult. Neonate cervid hair is distinguishable from that of adults based on the width of hairs until juveniles are about 5 months old (Lodberg-Holm et al. 2021; Calhoun et al. 2023). Because the earliest parturition period for ungulates in the GYE starts in mid-May (elk) and the latest scats were collected in August, all scats collected during the summer field seasons were within a period when adult and juvenile ungulate hairs could be easily distinguished. When present, deciduous teeth, hooves and degree of bone ossification were also used to distinguish between adults and juveniles. Mule deer and white-tailed deer (*Odocoileus sp.*) are present in the study area and because distinguishing between the two species is very difficult, we classified them into one category as “deer”. When we were able to identify rodents to species, genus, or family, we made sure to record it. However, all rodents except marmots (*Marmota flaviventris*) were categorized into the “small rodent” category. Each scat was analyzed together by the same two people to reduce potential observer bias. Once all prey remains were identified, if there were >1 prey species identified in the scat, then percent volume of each species was estimated and recorded. Prey remains that occurred in trace amounts within a single scat (<= 5%) were not included in the analysis as remnants of previous prey can get trapped in the digestive tract of wolves (Ciucci et al. 1996).

Supplementary Materials B – Live Mass Estimates

prey species	age class	sex	season winter = March summer = July	live mass (kg)	edible biomass (%)	edible biomass (kg)	Live mass source
elk	adult	male	winter	266	0.68	180.88	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	337.2	0.68	229.296	average of all July estimated weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
		female	winter	226	0.68	153.68	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	240.56	0.68	163.5808	average of all July estimated weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
		unknown	winter	230.8	0.68	156.944	calculated using estimated weight for each season based on adult male and female weights and known proportions of adult males (9.1%) and adult females (66.2%) in the Cody elk herd from Wyoming Game & Fish winter aerial surveys (WGFD 2021).
			summer	252.2	0.68	171.496	calculated using estimated weight for each season based on adult male and female weights and known proportions of adult males (9.1%) and adult females (66.2%) in the Cody elk herd from Wyoming Game & Fish winter aerial surveys (WGFD 2021).
	yearling	male	winter	167	0.68	113.56	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	246.09	0.68	167.3412	average of all July estimated adult weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
		female	winter	162	0.68	110.16	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	215.64	0.68	146.6352	average of all July estimated adult weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
		unknown	winter	162.6	0.68	110.568	calculated using estimated weight for each season based on adult male and female weights and known proportions of adult males (9.1%) and adult females (66.2%) in the Cody elk herd from Wyoming Game & Fish winter aerial surveys (WGFD 2021).
			summer	219.32	0.68	149.1376	calculated using estimated weight for each season based on adult male and female weights and known proportions of adult males (9.1%) and adult females (66.2%) in the Cody elk herd from Wyoming Game & Fish winter aerial surveys (WGFD 2021).
	calf	male	winter	108	0.68	73.44	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	175.35	0.68	119.238	average of all July estimated calf weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
		female	winter	97	0.68	65.96	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012

			summer	151.69	0.68	103.1492	average of all July estimated calf weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
		unknown	winter	98.3	0.68	66.844	calculated using estimated weight for each season based on adult male and female weights and known proportions of adult males (9.1%) and adult females (66.2%) in the Cody elk herd from Wyoming Game & Fish winter aerial surveys (WGFD 2021).
			summer	154.6	0.68	105.128	calculated using estimated weight for each season based on adult male and female weights and known proportions of adult males (9.1%) and adult females (66.2%) in the Cody elk herd from Wyoming Game & Fish winter aerial surveys (WGFD 2021).
	neonate	unknown	summer	52.33	0.79	41.3407	average of all July estimated neonate weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
deer	adult	male	winter	83.2	0.79	65.728	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	91.54	0.79	72.3166	growth curves from Murphy et al. 1998 via Metz et al. 2012
		female	winter	50.9	0.79	40.211	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	56.19	0.79	44.3901	growth curves from Murphy et al. 1998 via Metz et al. 2012
		unknown	winter	67.05	0.79	52.9695	average of adult male and female mass
			summer	79.295	0.79	62.64305	average of adult male and female mass
	yearling	male	winter	53.9	0.79	42.581	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	62.83	0.79	49.6357	growth curves from Murphy et al. 1998 via Metz et al. 2012
		female	winter	40.4	0.79	31.916	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	51.39	0.79	40.5981	growth curves from Murphy et al. 1998 via Metz et al. 2012
		unknown	winter	47.15	0.79	37.2485	average of yearling male and female mass
			summer	54.99	0.79	43.4421	average of yearling male and female mass
	calf	male	winter	35.3	0.79	27.887	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	47.18	0.79	37.2722	growth curves from Murphy et al. 1998 via Metz et al. 2012
		female	winter	26.8	0.79	21.172	March estimated mass from growth curves from Murphy et al. 1998 via Metz et al. 2012
			summer	36.24	0.79	28.6296	growth curves from Murphy et al. 1998 via Metz et al. 2012
		unknown	winter	31.05	0.79	24.5295	average of calf male and female mass
			summer	41.71	0.79	32.9509	average of calf male and female mass
	neonate	unknown	summer	8.8	0.79	6.952	average of all July estimated neonate weights from growth curves from Murphy et al. 1998 via Metz et al. 2012
pronghorn	adult	male	summer	54	0.79	42.66	Byers 2003, in Feldhamer et al.
		female	summer	51	0.79	40.29	Byers 2003, in Feldhamer et al.

		unknown	summer	52.5	0.79	41.475	average of male and female neonate weights
	neonate	unknown	summer	3	0.79	2.37	Averaged mass from Schmidly and Bradley (2016)
moose	adult	male	winter	299	0.68	203.32	Matson 1997
			summer	446	0.68	303.28	Matson 1997
		female	winter	258	0.68	175.44	Matson 1997
			summer	385	0.68	261.8	Matson 1997
	neonate	unknown	summer	60	0.79	47.4	Averaged mass from Blood et al. (1967) and (Coady, 1973)
bighorn sheep	adult	male	winter & summer	79	0.79	62.41	Kraussman and Bowyer 2003, in Feldhamer et al.
		female	winter & summer	59	0.79	46.61	Kraussman and Bowyer 2003, in Feldhamer et al.
cow	adult	female	winter & summer	577	0.68	392.36	Average adultrange cattle weights from range cattle grazing on US Forest Service land from Uresk (2010)
	calf	unknown	summer	153	0.68	104.04	Average live calf weights from range cattle grazing on US Forest Service land from Uresk (2010)
bison	adult	male	winter	784	0.68	533.12	Matson 1997
horse	adult	unknown	winter	316	0.68	214.88	Metz et al. 2012

Supplementary Materials C – Results

Supplementary Materials C Table 1. Summary of Fisher's exact tests' p-values comparing adult wolf scats vs juvenile wolf scats prey composition (frequency occurrence and percent biomass) for resident and migratory wolf packs in summer. No p-values were < 0.05.

year	metric	pack	elk vs altPrey/cows
2020	frequency	Long A	0.73
	biomass	Long A	1
	frequency	Long B	0.48
	biomass	Long B	0.6
2021	frequency	Long A	0.4
	biomass	Long A	1
	frequency	Resident B	1
	biomass	Resident B	0.63

Supplementary Materials C Table 2. Summary of all kills, scavenges, and scats analyzed divided by season and resident and migratory packs.

prey composition frequency occurrence		resident packs						short-distance migratory packs						long-distance migratory packs					
		winter			summer			winter			summer			winter			summer		
prey class	prey species	kills	scavenges	scats	kills	scavenges	scats	kills	scavenges	scat	kills	scavenges	scats	kills	scavenges	scats	kills	scavenges	scats
elk	adult elk	9	-	10	2	1	41	12	3	17	4	2	19	15	5	68	4	-	83
	yearling elk	3	-	-	1	-	-	1	-	-	1	-	-	5	-	-	2	-	-
	juvenile elk	4	-	-	10	1	112	6	-	-	8	-	4	2	-	-	4	-	44
	elk total	**16**	**-**	**27**	**13**	**2**	**153**	**19**	**-**	**17**	**13**	**2**	**23**	**22**	**5**	**68**	**10**	**-**	**127**
cattle	adult cow	-	-	-	1	6	13	1	3	8	1	4	1	-	-	-	-	1	-
	juvenile cow	-	1	-	4	1	2	-	-	-	3	7	-	-	-	-	-	-	-
	cattle total	**0**	**1**	**0**	**5**	**7**	**15**	**1**	**3**	**8**	**4**	**11**	**1**	**-**	**-**	**-**	**-**	**1**	**-**
alternate ungulates	adult deer	-	-	2	-	1	19	2	-	18	1	-	1	10	3	36	1	1	5
	yearling deer	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
	juvenile deer	-	-	-	5	-	8	-	-	-	-	1	1	6	-	-	2	-	6
	adult pronghorn	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-
	juvenile pronghorn	-	-	-	10	1	1	-	-	-	1	-	-	-	-	-	-	-	-
	adult moose	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
	juvenile moose	-	-	-		-	-	-	-	-	2	-	-	-	-	-	-	-	-
	adult bighorn	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
	unknown ungulate*	2	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	horse	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
	bison	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	alt.ung. total	**2**	**-**	**2**	**17**	**5**	**28**	**2**	**-**	**18**	**4**	**2**	**1**	**19**	**6**	**36**	**3**	**2**	**11**
alternate small prey*	small mammals[1]	-	-	4	1	-	45	-	-	-	-	-	5	-	-	-	-	-	31
	non-mammal prey[2]	-	-	-	2	-	1	-	-	--	-	-	-	-	-	-	-	-	14
	plants[3]	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	18

* not included in prey composition analysis
[1] mice, voles, squirrels, pocket gophers, prairie dogs, marmots
[2] birds, fish, insects (grasshoppers, ants, ground beetles, ticks)
[3] grass, berries, moss, leaves, pine needles

Supplementary Materials C Table 3. Percent frequency and percent biomass values for **kills** in winter and summer

pack	year	season	prey	metric	value
Long A	2020	winter	elk	percent frequency	0.38
Long A	2020	winter	elk	percent biomass	0.65
Long A	2020	winter	AltWildPrey	percent frequency	0.63
Long A	2020	winter	AltWildPrey	percent biomass	0.35
Long A	2020	summer	elk	percent frequency	0.75
Long A	2020	summer	elk	percent biomass	0.92
Long A	2020	summer	AltWildPrey	percent frequency	0.25
Long A	2020	summer	AltWildPrey	percent biomass	0.08
Long A	2021	winter	elk	percent frequency	0.36
Long A	2021	winter	elk	percent biomass	0.70
Long A	2021	winter	AltWildPrey	percent frequency	0.64
Long A	2021	winter	AltWildPrey	percent biomass	0.30
Long A	2021	summer	elk	percent frequency	0.50
Long A	2021	summer	elk	percent biomass	0.98
Long A	2021	summer	AltWildPrey	percent frequency	0.50
Long A	2021	summer	AltWildPrey	percent biomass	0.02
Long B	2020	winter	elk	percent frequency	0.63
Long B	2020	winter	elk	percent biomass	0.78
Long B	2020	winter	AltWildPrey	percent frequency	0.38
Long B	2020	winter	AltWildPrey	percent biomass	0.22
Long B	2020	summer	elk	percent frequency	1.00
Long B	2020	summer	elk	percent biomass	1.00
Long B	2020	summer	AltWildPrey	percent frequency	0.00
Long B	2020	summer	AltWildPrey	percent biomass	0.00
Long B	2021	winter	elk	percent frequency	0.71
Long B	2021	winter	elk	percent biomass	0.76
Long B	2021	winter	AltWildPrey	percent frequency	0.29
Long B	2021	winter	AltWildPrey	percent biomass	0.24
Long B	2021	summer	elk	percent frequency	NA
Long B	2021	summer	elk	percent biomass	NA
Long B	2021	summer	AltWildPrey	percent frequency	NA
Long B	2021	summer	AltWildPrey	percent biomass	NA
Short A	2019	winter	elk	percent frequency	0.78
Short A	2019	winter	elk	percent biomass	0.63
Short A	2019	winter	AltWildPrey	percent frequency	0.11
Short A	2019	winter	AltWildPrey	percent biomass	0.05
Short A	2019	winter	cattle	percent frequency	0.11
Short A	2019	winter	cattle	percent biomass	0.03
Short A	2019	summer	elk	percent frequency	0.78
Short A	2019	summer	elk	percent biomass	0.70

			AltWildPrey	percent frequency	0.11
				percent biomass	0.06
			cattle	percent frequency	0.11
				percent biomass	0.24
	2020	winter	elk	percent frequency	0.92
				percent biomass	0.97
			AltWildPrey	percent frequency	0.08
				percent biomass	0.03
			cattle	percent frequency	0.00
				percent biomass	0.00
		summer	elk	percent frequency	0.17
				percent biomass	0.10
			AltWildPrey	percent frequency	0.33
				percent biomass	0.12
			cattle	percent frequency	0.50
				percent biomass	0.77
Resident A	2021	winter	elk	percent frequency	1.00
				percent biomass	1.00
			AltWildPrey	percent frequency	0.00
				percent biomass	0.00
			cattle	percent frequency	0.00
				percent biomass	0.00
		summer	elk	percent frequency	0.64
				percent biomass	0.40
			AltWildPrey	percent frequency	0.09
				percent biomass	0.00
			cattle	percent frequency	0.27
				percent biomass	0.60
Resident B	2021	winter	elk	percent frequency	1.00
				percent biomass	1.00
			AltWildPrey	percent frequency	0.00
				percent biomass	0.00
			cattle	percent frequency	0.00
				percent biomass	0.00
		summer	elk	percent frequency	0.25
				percent biomass	0.58
			AltWildPrey	percent frequency	0.67
				percent biomass	0.17
			cattle	percent frequency	0.08
				percent biomass	0.25

Supplementary Materials C Table 4. Summary of Fisher's exact tests' p-values comparing winter vs summer prey composition. P-values <0.05 are highlighted in bold.

data	year	metric	winter vs summer	p-values of elk vs altPrey (AltWildPrey & cattle)
kills	2020	frequency	Long A	0.3
		biomass	Long A	0.60
		frequency	Long B	1
		biomass	Long B	1.00
	2021	frequency	Long A	0.5
		biomass	Long A	1.00
	2019	frequency	Short A	1
		biomass	Short A	1
	2020	frequency	Short A	**0.003**
		biomass	Short A	**0.0005**
	2021	frequency	Resident A	0.12
		biomass	Resident A	**0.013**
		frequency	Resident B	**0.0001**
		biomass	Resident B	**0.03**
scats	2020	frequency	Long A	**0.02**
		biomass	Long A	**0.00009**
		frequency	Long B	0.4
		biomass	Long B	**0.047**
	2021	frequency	Long A	0.6
		biomass	Long A	1
	2019	frequency	Short A	0.07
		biomass	Short A	**0.04**
	2020	frequency	Short A	0.5
		biomass	Short A	**0.04**
	2021	frequency	Resident B	1
		biomass	Resident B	0.18

Supplementary Materials C Table 5. Summary of Fisher's exact tests' p-values comparing kills vs scats prey composition in winter and summer. P-values < 0.05 are highlighted in bold.

season	year	metric	pack	p-values of elk vs altPrey (AltWildPrey & cattle)
winter	2019	frequency	Short A	0.11
		biomass	Short A	0.68
	2020	frequency	Short A	**0.01**
		biomass	Short A	**0.01**
	2021	frequency	Resident A	NA
		biomass	Resident A	NA
		frequency	Resident B	0.175
		biomass	Resident B	0.44
summer	2019	frequency	Short A	0.7
		biomass	Short A	0.07
	2020	frequency	Short A	1
		biomass	Short A	0.40
	2021	frequency	Resident A	NA
		biomass	Resident A	NA
		frequency	Resident B	**0.002**
		biomass	Resident B	0.11
winter	2020	frequency	Long A	1
		biomass	Long A	0.31
		frequency	Long B	1
		biomass	Long B	1
	2021	frequency	Long A	1
		biomass	Long A	0.6
		frequency	Long B	NA
		biomass	Long B	NA
summer	2020	frequency	Long A	1
		biomass	Long A	0.43
		frequency	Long B	1
		biomass	Long B	1.00
	2021	frequency	Long A	0.45

		biomass	Long A	1.00
		frequency	Long B	NA
		biomass	Long B	NA

Supplementary Materials Table 6. Summary of Fisher's exact tests' p-values comparing small prey (<96kg) vs large prey (>96kg) prey composition (frequency occurrence and percent biomass) for resident and migratory wolf packs in summer. No p-values were < 0.05.

year	metric	pack	small vs large prey p-value
2019	frequency	Short A	0.48
	biomass	Short A	0.6
2020	frequency	Short A	0.6
	biomass	Short A	1
2021	frequency	Resident A	NA
	biomass	Resident A	NA
	frequency	Resident B	0.58
	biomass	Resident B	0.64
2020	frequency	Long A	0.7
	biomass	Long A	1
	frequency	Long B	1
	biomass	Long B	0.5
2021	frequency	Long A	NA
	biomass	Long A	NA
	frequency	Long B	NA
	biomass	Long B	NA

Supplementary Materials C Table 7. Percent frequency and percent biomass values for **scats** in winter and summer

pack	year	season	prey	metric	value
Long A	2020	winter	elk	percent frequency	0.33
				percent biomass	0.28
			AltWildPrey	percent frequency	0.67
				percent biomass	0.72
		summer	elk	percent frequency	0.75
				percent biomass	0.96
			AltWildPrey	percent frequency	0.25
				percent biomass	0.04
	2021	winter	elk	percent frequency	0.76
				percent biomass	0.93

			AltWildPrey	percent frequency	0.24
				percent biomass	0.07
		summer	elk	percent frequency	0.83
				percent biomass	0.97
			AltWildPrey	percent frequency	0.17
				percent biomass	0.03
Long B	2020	winter	elk	percent frequency	0.44
				percent biomass	0.66
			AltWildPrey	percent frequency	0.56
				percent biomass	0.34
		summer	elk	percent frequency	0.68
				percent biomass	0.92
			AltWildPrey	percent frequency	0.32
				percent biomass	0.08
Short A	2019	winter	elk	percent frequency	0.41
				percent biomass	0.55
			AltWildPrey	percent frequency	0.38
				percent biomass	0.10
			cattle	percent frequency	0.22
				percent biomass	0.35
		summer	elk	percent frequency	0.74
				percent biomass	0.93
			AltWildPrey	percent frequency	0.23
				percent biomass	0.02
			cattle	percent frequency	0.03
				percent biomass	0.05
	2020	winter	elk	percent frequency	0.31
				percent biomass	0.44
			AltWildPrey	percent frequency	0.62
				percent biomass	0.32
			cattle	percent frequency	0.08
				percent biomass	0.24
		summer	elk	percent frequency	0.09
				percent biomass	0.01
			AltWildPrey	percent frequency	0.27
				percent biomass	0.06
			cattle	percent frequency	0.63
				percent biomass	0.93
Resident B	2021	winter	elk	percent frequency	0.71
				percent biomass	0.93
			AltWildPrey	percent frequency	0.29
				percent biomass	0.07
			cattle	percent frequency	0.00
				percent biomass	0.00
		summer	elk	percent frequency	0.63
				percent biomass	0.69
			AltWildPrey	percent frequency	0.32
				percent biomass	0.10

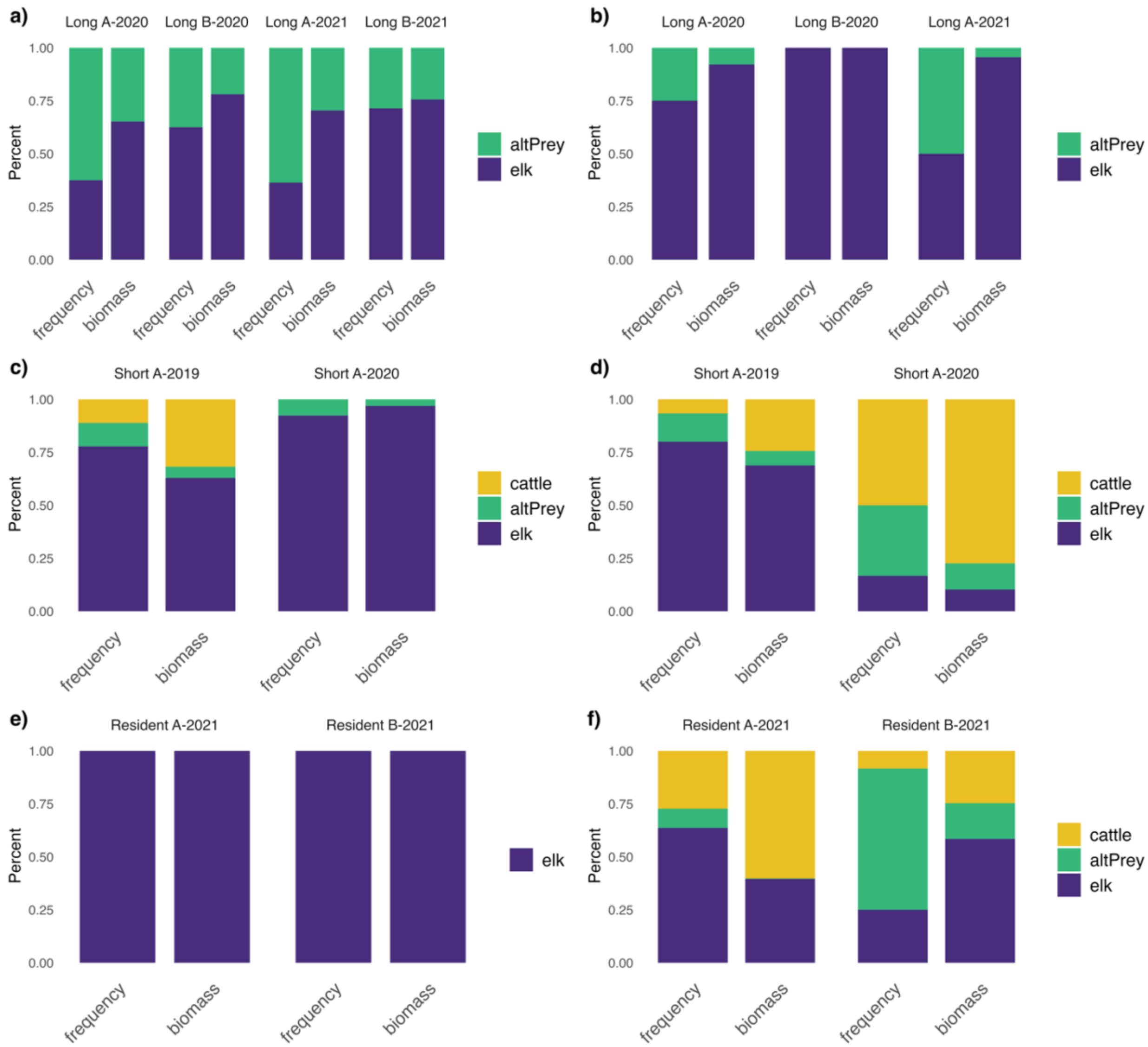
			cattle	percent frequency	0.05
				percent biomass	0.21

Supplementary Materials C Table 8. Percent frequency and percent biomass of summer wolf-killed elk age classes for Short and Resident wolf packs.

wolf-killed elk	percentages	Short A-2019	Short A-2020	Resident A-2021	Resident B-2021
% elk of all prey	percent frequency	0.8	0.17	0.64	0.25
	percent biomass	0.69	0.1	0.4	0.58
% neonate of all elk	percent frequency	0.58	1	0.86	0.67
	percent biomass	0.26	1	0.63	0.34
% adults & yearlings of all elk	percent frequency	0.42	0	0.14	0.33
	percent biomass	0.74	0	0.37	0.66

Supplementary Materials C Table 9. Percent biomass of early (end of June + July) vs late (August) summer resident wolf kills.

kills percent biomass					
pack	month	adult elk	neonate elk	alternate prey	cow
Short A-2019	June + July	0.47	0.37	0.16	0.00
	Aug	0.53	0.04	0.00	0.42
Resident B-2021	June + July	0.51	0.26	0.08	0.16
	Aug	0.00	0.00	0.47	0.53



Supplementary Materials C Figure 1. Prey composition (percent frequency and percent biomass) of kills in winter (column 1) and summer (column 2) for long-distance migratory packs (top row), short-distance migratory packs (middle row), and resident packs (bottom row) [a) long-distance migratory winter, b) long-distance migratory summer, c) short-distance migratory winter, d) short-distance migratory summer, e) resident winter, f) resident summer].

Supplementary Materials D - Cattle kill locations and elk distributions

Supplementary Materials D - Methods

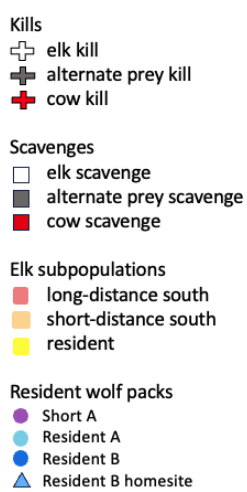
We compared cattle depredations location and timing with a combination of collared elk locations, confirmed elk kill locations, and elk migratory dates to evaluate whether wolves tended to kill cattle among co-occurring elk or in areas where most elk had recently vacated. To determine elk subpopulation summer distributions, we calculated summer range using dynamic Brownian Bridge movement models (dBBMMs) with 99% isopleths for each of the three elk subpopulations in the resident wolf area for every summer month with investigated kills. Additionally, we assumed that there are areas with elk not detected by our GPS collared elk, and so we also used our investigated elk kill locations as a proxy for areas with elk presence. If depredations occurred on or near the elk summer range or elk kills, they would be considered to be associated with migratory elk presence. If depredations were not spatiotemporally aligned with the summer range or kills, they were considered to be associated with elk absence.

Supplementary Materials D Results

We found a total of 10 wolf-killed cattle through our cluster investigations. All but one of these kills occurred in the summer (Short A pack killed an old dying cow in winter 2019) with summer kills distributed across June (n=3), July (n=4), and August (n=2) (Fig. 4). Most kills were on or near elk summer range dBBMMs and elk kills. The short-distance migratory pack (Short A) exclusively killed elk and cattle (n=1 in 2019; n=3 in 2020) on higher elevation USFS land in or near elk kills and elk summer range dBBMMs (Maps A-D below). The resident packs (Resident A and B) killed elk and cattle in lower elevation areas on private, BLM and state land (Maps E-I). Resident A pack's cattle kills (n=3) were among elk kills and elk summer range dBBMMs prior to when collared elk had vacated the area (Maps E & F). Whereas Resident B packs' cattle kills (1 in June & 1 in August) did not align spatially or temporally with their elk kills or elk summer range dBBMMs. Their depredations were closer to alternate prey kills than elk kills. Additionally, all of their elk kills occurred in July and occurred on short-distance migratory elk summer range dBBMMs near Resident B's den site (Map H).

Supplementary Materials D Maps

Legend for all maps:

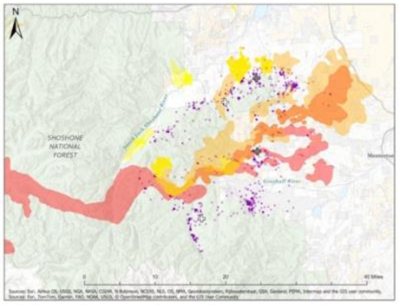


Supplementary Materials D Maps

June July August

2019 - Short A pack

A)



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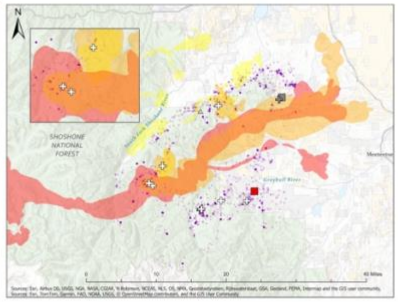
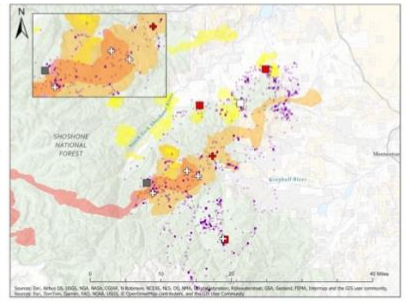
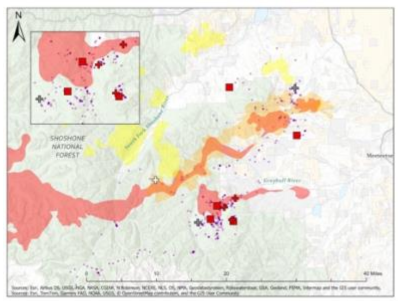


C)



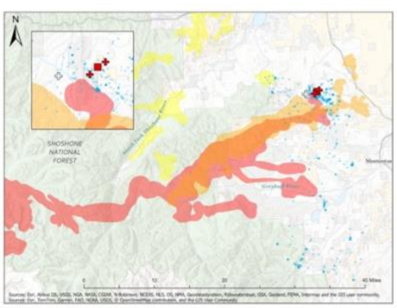
2020 - Short A pack

D)

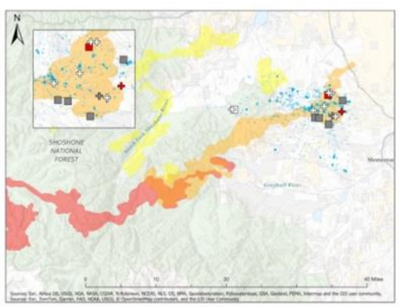


2021- Resident A pack

E)

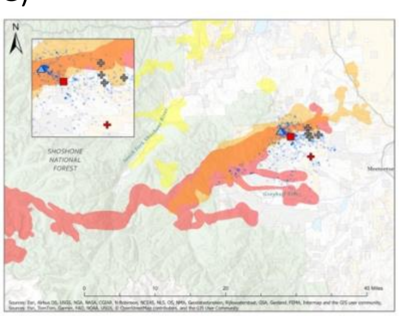


F)

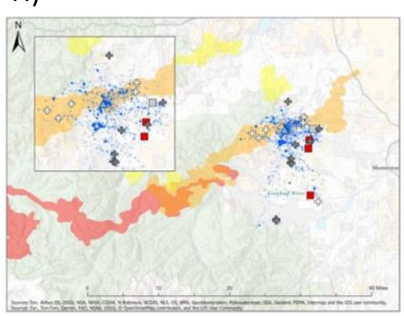


2021 - Resident B pack

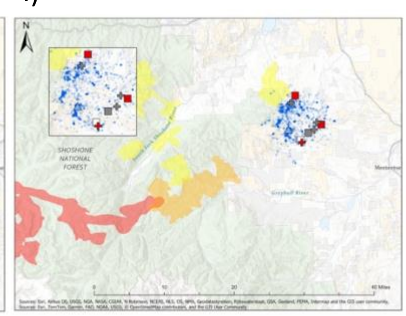
G)



H)



I)



CHAPTER 3. ADAPTATIONS BY RANCHERS AND WILDLIFE MANAGERS OVER TWO DECADES OF WOLF RECOVERY IN THE GREATER YELLOWSTONE ECOSYSTEM

Abstract

After decades of recovery efforts, the gray wolf (*Canis lupus*) is now one of the most widespread large carnivores and a major source of livestock depredation worldwide. Intolerance is often cited as the greatest threat to continued wolf recovery, with ranchers viewed as especially resistant to wolves due to depredations and threats to rural values and identity. Thus, many wolf conservation efforts have focused on ways to improve ranchers' attitudes towards wolves – from reducing economic costs with compensation programs, to promoting the use of nonlethal measures to reduce livestock depredations. However, few studies have investigated local perspectives of people who are at the heart of these wolf-livestock conflicts – ranchers and wildlife managers. In order to increase our understanding of the opportunities and challenges to mitigating conflict, we conducted semi-structured interviews in communities at the eastern frontier of the Greater Yellowstone Ecosystem, where ranchers and wildlife managers have two decades of experience with wolf-livestock conflict. Our findings reveal that ranchers view wolves as part of the landscape and are willing to try new approaches to conflict reduction, but that barriers persist and are related to logistical constraints. Ranchers in the area have tried numerous nonlethal measures and adapted their practices, yet these efforts often go unrecognized. We found that the main barriers to conflict mitigation were rooted in social conflict related to issues of inequity and constraints on autonomy of the reintroduction process, which fueled intolerance towards how wolves were being managed. Yet, early wolf recovery focused efforts on addressing intolerance directed towards wolves themselves. Only after delisting and transfer of management did Wyoming Game & Fish Department (WGFD) begin to gain local control of wolf populations and conflict, and wolf presence became more tolerable and normalized as wolves were allowed to be managed like other wildlife. This enabled trust-building between WGFD biologists and ranchers and resulted in heightened tolerance for sharing the landscape with wolves, while also potentially creating space for future wildlife conservation initiatives. Our research highlights the importance of addressing the social challenges of large carnivore recovery in other communities facing similar issues and the need for qualitative research to integrate local perspectives and experiences into conflict reduction strategies.

Introduction

As large carnivores continue to recover across the globe, they are increasingly ranging beyond protected areas into human-dominated landscapes, which can lead to conflict that fuels intolerance and threatens large carnivore conservation (Woodroffe et al. 2005; Chapron et al. 2014). In the Northern Hemisphere, one of the most prevalent sources of conflict is wolf predation on livestock, which can cause financial losses and emotional hardship for rural communities (Thirgood et al. 2005; van Eeden et al. 2018;). These conflicts predominantly unfold on working lands, pivotal for providing economic resources and ecosystem services while fostering landscape connectivity and resilience against more intensive land uses (Kremen & Merenlender 2018).

The perspectives of those who experience livestock losses to wolves are important for designing conflict reduction programs, particularly because the views of key actors such as livestock producers and wildlife managers can reveal opportunities and barriers to mitigating conflicts. Yet these perspectives are not always accessible or well understood by conservation scientists, policy makers, and practitioners. Further, despite extensive research about the ecological drivers and technical solutions to wolf depredation, identifying the best practices to reduce wolf depredations on livestock remains a challenge (Miller et al. 2016; Wilkinson et al. 2020). This is likely because livestock operations vary widely in scale, husbandry practices, wealth, environmental features, and assemblage of native wildlife, mitigation measures are highly context specific (DeCesare et al. 2018). While co-produced research on conflict reduction practices is increasing (McInturff et al. 2021a; Volski et al. 2021; Hyde et al. 2022), there is still a lack of direct information and input from producers with experience dealing with carnivore conflict.

Wolf conflict can be managed through lethal and nonlethal measures. Lethal measures include hunting, lethal take permits for producers, and/or lethal control actions by agencies. While the lethal removal of depredating wolves can be effective in halting conflict in the short-term, wolves often return to recolonize the vacated territory within one to two years (Bradley et al. 2015). Many also see lethal control as a threat to wolf recovery, which can lead to sociopolitical conflicts over how wolves should be managed (McManus et al. 2015). Thus, controversy over lethal control has increased interest in using nonlethal conflict mitigation measures to promote coexistence, a term with many interpretations (Carter & Linnell 2016; Martin et al. 2021).

Nonlethal mitigation measures include tools and practices such as increasing human presence around livestock using range riders, setting up temporary fencing such as electrified fladry ("turbofladry"), protecting livestock with livestock guardian animals, deploying audio and visual deterrents, and changing livestock husbandry practices (Wilkinson et al. 2020; Martin 2021). While there have been success stories of community-based collaboratives in the Northern Rockies (Stone et al. 2017; Wilson et al. 2017; Young et al. 2018), evidence of the effectiveness of nonlethal interventions is varied and limited (Miller et al. 2016; Eklund et al. 2017; van Eeden et al. 2018). Because nonlethal interventions are designed to prevent depredations by targeting ecological drivers of a predator-prey interaction (Wilkinson et al. 2020), studies of the efficacy of any given intervention are aimed at measuring biological and quantitative outcomes. This has resulted in calls in the scientific literature for more controlled experimental designs, which can be difficult in practice because of logistical and ethical reasons (Eklund et al. 2017; van Eeden et al. 2018).

Important as those research directions may be, a growing body of research illustrates that conflict mitigation tools can only be useful if livestock producers are aware of them, and able and willing to implement them. Social factors such as recommendations from a trusted producer, good relationships with scientists and conservation groups, and inclusion of producers in research efforts have all been found to positively influence willingness to try a nonlethal intervention (Bogezi et al. 2021; Volski et al. 2021; Hyde et al. 2022; Lucas et al. 2022). Ultimately, if ranchers perceive nonlethal methods to be less effective than lethal methods, they may be less likely to try them (Scasta et al. 2017), and some studies have also shown that livestock producers' perceptions of social acceptability are critical to their willingness to try a nonlethal intervention (Volski et al. 2021; Lucas et al. 2022). This body of research suggests that increased incorporation of social science research is crucial for understanding the adoption of nonlethal conflict mitigation measures (Dickman 2010; Niemiec et al. 2021).

Quantitative methods such as surveys are valuable for predicting trends across large datasets such as how identities shape attitudes towards wolves and factors influencing wolf conflict mitigation decision-making (Scasta et al. 2017; Manfredo et al. 2020). Qualitative approaches, such as in-depth interviews, are more effective for exploring the experiences and identities of decision-makers and offer more flexibility to uncover insights and context that might otherwise be overlooked (Sayre 2004; Drury et al. 2011). Qualitative methods are especially vital when investigating changes in ranch management, which often involve holistic considerations beyond economic reasoning (Sayre 2004; Volksi et al. 2021).

In this study, we sought to better understand ranchers' orientations towards nonlethal and lethal conflict mitigation measures, with an emphasis on barriers to adopting nonlethal measures. We conducted in-depth interviews with ranchers and wildlife managers in northwest Wyoming, east of Yellowstone National Park near the towns of Cody and Meeteetse. Ranchers and wildlife managers in the study area have contended with wolf depredation on livestock conflict since 2001, with fluctuating rates of depredation and lethal control (Fig. 1 & 2). Studies in the U.S. have shown that ranchers are more likely to hold more negative views of wolves, and be more supportive of lethal measures, compared to the general public, who often favor nonlethal approaches (Needham et al. 2004; Bruskotter et al. 2019; Manfredo et al. 2020; van Eeden et al. 2021). Thus, we expected to find largely negative attitudes toward wolves directly associated with a strong preference for lethal control. We also expected to find hesitation to implement nonlethal conflict mitigation measures and little evidence of their adoption. Consequently, we focused our interviews on examining the socioeconomic factors influencing ranchers' willingness to adopt nonlethal measures. In contrast, we did not have specific expectations regarding wildlife managers' views, as their perspectives have been less studied in existing research.

We first provide background information on the history of wolf reintroduction and recovery in Wyoming. We then summarize the results of our interviews, encompassing interviewees' experiences with wolf conflict and mitigating conflict. Finally, we discuss key insights emerging from the totality of the interviews - particularly the evolution of tolerance for wolves and trust for wildlife managers from the days of federal reintroduction and protection to an era of local control. Finally, we draw on this case study to provide recommendations for practitioners grappling with these issues in other areas including how social science research can be used to identify and address the social conflict which underlies predator-livestock interactions. Our study contributes to the increasing body of recent research using qualitative methods to explore rancher and land manager perspectives on wolf conflict and coexistence (Anderson 2021; Bogezi et al. 2021; Martin 2021; Martin et al. 2021; Richardson 2022).

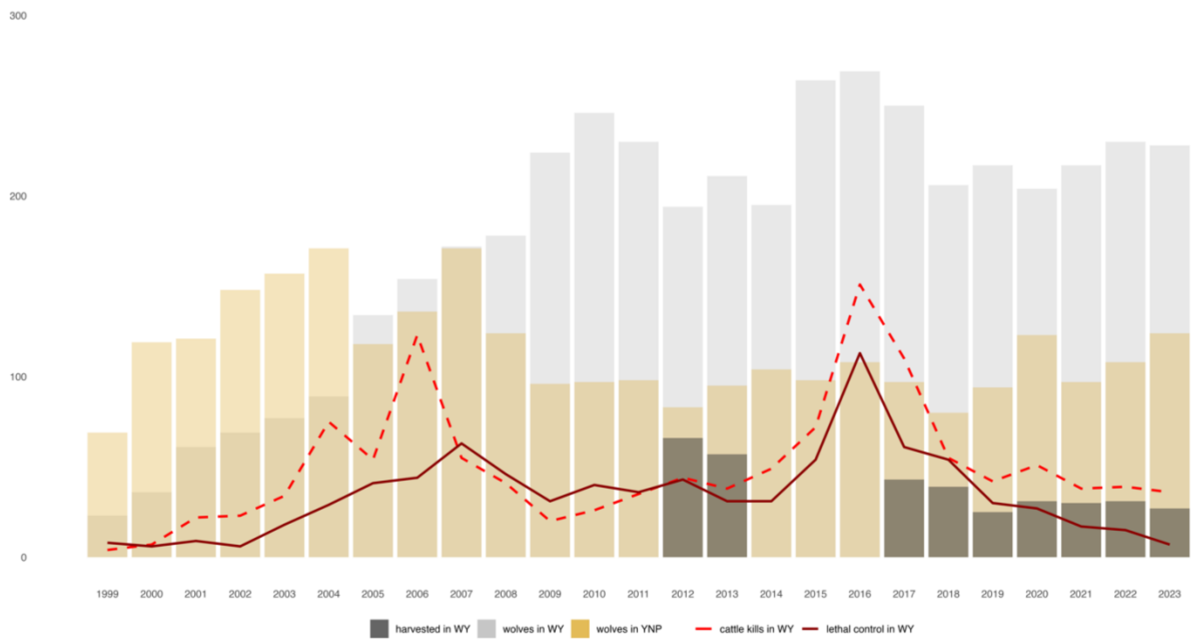


Figure 1. *Plot shows Wyoming wolf populations in light gray, Yellowstone wolf populations in yellow, and legally harvested wolves in dark gray. Confirmed wolf depredations on cattle are shown with light red dashed line and number of lethally controlled wolves shown with dark red solid line. Data is from WGFD Annual Wolf Reports from 1999 to 2024.*

Figure 2. *Plot shows study area wolf populations in light gray and legally harvested wolves in dark gray. Confirmed wolf depredations on cattle are shown with light red dashed line and number of lethally controlled wolves shown with dark red solid line. Data is from WGFD Annual Wolf Reports from 1999 to 2024.*

Background

Having been largely eradicated from the region by the 1930s, changing attitudes toward predators, the emergence of environmental activism, and the passage of the Endangered Species Act in 1974 paved the way for wolves to be listed as one of the first protected species. Following widespread public support and meticulous planning, wolves were translocated from Canada to Yellowstone National Park and central Idaho in 1995 and 1996. The Northern Rocky Mountains (NRM) minimum recovery criteria of ≥300 wolves and ≥30 breeding pairs for three consecutive years was met by 2002. Despite USFWS recommending delisting several times, there was disagreement on whether Idaho, Montana, and Wyoming wolf management plans, regulatory frameworks, and laws adequately met ESA protection requirements. This led to back and forth delisting and relisting as environmental non-governmental organizations (eNGO) groups litigated federal court rulings. While wolves in Idaho and Montana were delisted in 2008, 2009, and for the last time in 2011, delisting in Wyoming was delayed due to disagreement over what portions of Wyoming constituted a significant portion of the NRM's range. Wolves in Wyoming were first delisted for four months in 2008, 2012-2014, and for the last time in April 2017 (Fig. 3).

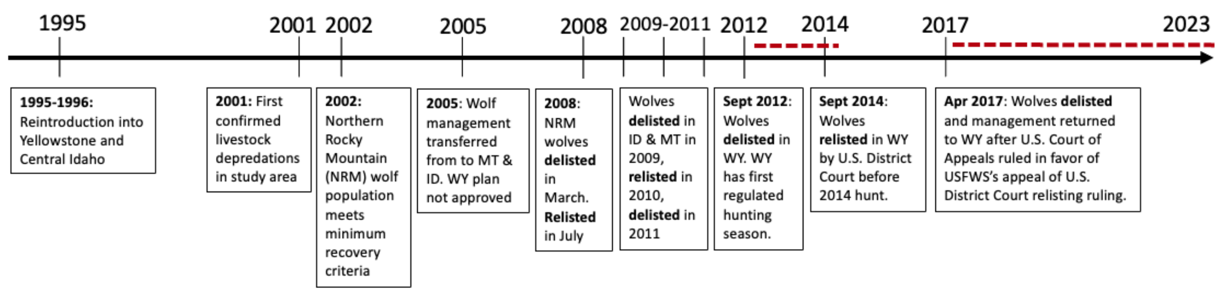


Figure 3. *Northern Rocky Mountains Wolf Management Timeline - red dashed line represents Wyoming wolf delisted period.*

Since the state of Wyoming took over wolf management post-delisting in 2017, Wyoming Game & Fish Department (WGFD) has managed wolves around a biological objective of 160 wolves (WGFD et al. 2024; Fig. 2). Wyoming has exceeded minimum recovery criteria for 22 consecutive years and has supported more wolves living in the Wolf Trophy Game Management Area (WTGMA) than within Yellowstone (n = 124 in 2023) since 2005 (Fig. 1). During the 2014-2017 period when wolves were listed, the WTMGA population peaked in 2016 at 269 wolves, resulting in 243 depredations and 113 lethal control actions (USFWS et al. 2017). Since delisting, wolf populations, depredations, and lethal control actions in Wyoming and in the study area have decreased (Fig. 1 & 2). In 2023, seven wolves were lethally controlled in response to 37 depredations (WGFD et al. 2024). Additionally, since wolves were delisted, compensation payments declined from >$300,000 from 2014-2017 to ~$200,000 or less from 2018-2022 (WGFD et al. 2024).

Methods

General Approach

This study takes a Grounded Theory approach to draw broader themes from observed patterns in interviewee responses. Grounded Theory is a qualitative data analysis method that uses systematic guidelines for collecting and analyzing empirical data such as interviews and is designed to discover patterns of human experience (Charmaz 2014; Glaser & Strauss 2017). We used semi-structured interviews under the assumption that our knowledge of conflict management and mitigation measures differs from the people who have lived experience working and sharing the landscape with wolves. This allows the interviewee to answer our questions while also allowing for the exploration of topics to come up that we would have otherwise missed. The semi-structured format also enabled us to gather data on topics such as the use of nonlethal measures directly through targeted questions and indirectly through our general discussion about the challenges of managing conflict with wolves, while allowing for the discovery of unanticipated factors (Sayre 2004).

Recruitment and Interviews

The first author conducted 34 semi-structured interviews from October 2021 to January 2023. Three of the interviews were conducted with two people (married couples) – for a total of 37 interviewees. Interviewees were identified using key informants and snowball sampling techniques (Bernard 2017), beginning with ranchers and wildlife managers we knew from a larger research effort on wolf-livestock conflict in the study area (Chapters 1 & 2). Most interviews were with people dealing with wolf-livestock conflict, such as ranchers experiencing depredations and wildlife managers responding to depredations. We also interviewed several retired wildlife managers to capture perspectives across time. We also interviewed a couple conservation NGO staff and local outfitters who didn't have direct experience dealing with wolf depredation on livestock but could provide a broader perspective on local attitudes towards wolves. Interviewees were contacted over email or phone and sent a Letter of Information (Appendix A) about the intent and voluntary nature of the study, the use of audio recording, as well as the measures being taken to ensure anonymity and confidentiality. All interviews were conducted in person, except for one conducted over a virtual video platform. All interviews were conducted by the same person, and all but two interviews were audio-recorded, totaling to 2,545 minutes (42.4 hours) of recordings. All recorded interviewees confirmed permission to be recorded with verbal consent. Interviews lasted from 45 minutes to 140 minutes, averaging between 60 and 90 minutes.

Interviews followed a structured guide created by the author team (Appendix B). The interview guide covered a range of topics related to our research question and questions aimed to gather information on experience with and perspectives on wolf-livestock conflict. Topics included: background and experience with wolf-livestock conflict, experience with conflict mitigation measures, pros/cons of non-lethal measures, lethal measures, compensation, funding and resource needs, conflict mitigation ideas, future of conflict, and what they wished people would know about sharing the landscape with wolves. We conducted pilot interviews and added, removed, or rephrased questions to reflect the feedback. During the interviews, the wording and order of questions varied depending on how the interviewee responded to allow for a more conversational interaction. However, we made sure to avoid using ambiguous words or phrases that could be interpreted differently by interviewees, for example “coexistence” (Martin et al. 2021; CRC 2022). This study was approved by the Institutional Review Board (IRB) at the University of California Berkeley (Federalwide Assurance #00006252/CPHS Protocol # 2020-04-13212).

Once people agreed to be interviewed, a time and place were set to meet in person. Prior to the start of the interview, we re-confirmed verbal consent with the interviewee to be audio recorded. To ensure confidentiality, interviewees were assigned codes without identifying information, which were used to name the audio recordings and transcripts. These codes, recordings and transcripts are kept in an online file that only the interviewer has access to. Interviews were conducted until we reached the theoretical point of saturation - when gathering more data reveals no new information or insights (Hennink & Kaiser 2022).

Data Analysis

All interview recordings were transcribed verbatim by the interviewer using Otter.Ai and MAXQDA (Otter.Ai 2021; VERBI Software 2022). The interviewer analyzed transcripts using MAXQDA, a qualitative data analysis software. We used thematic analysis in MAXQDA to identify and describe major themes and patterns in the interviews (Gizzi & Rädiker 2021; VERBI Software 2022). We used a six-phase procedure developed by Braun & Clark (2006, 2012): 1) familiarization, 2) coding, 3) generating themes, 4) reviewing themes, 5) defining and naming themes, and 6) reporting. This method is a systematic and iterative process that requires researchers to get deeply immersed in their data because it involves multiple rounds of analysis and refinement. We first used a deductive coding scheme based on conflict management and mitigation measures to identify, categorize, and describe practices employed by interviewees. We then went through the transcripts again using inductive coding (a.k.a. “open coding”), which is rooted in the Grounded Theory approach and requires the researcher to explore the data to determine themes.

Results

Interviewees summary

Seventeen of the interviewees identified as ranchers (owners, managers, or both), 14 identified as agency wildlife or land managers (WGFD, U.S. Forest Service (USFS), and U.S. Dept. of Agriculture (USDA) APHIS Wildlife Services), 3 identified as conservation NGO representatives, and 3 identified as hunting outfitters. Several interviewees identified with more than one of these categories either currently or previously; these were placed into the category where they had the most experience. Ranch operations varied in scale from a few hundred to several thousand cattle, and from hundreds of acres to hundreds of thousands of acres. Most used rotational grazing practices and many encompassed both deeded (i.e., private) land and leased public grazing allotments on USFS, Bureau of Land Management (BLM), and/or state land. Most of the ranches represented in the interviews run traditional cow/calf pairs, with a few ranches running yearlings. Cattle breeds from these ranches include purebred and crosses of Black Angus, Red Angus, Herefords, Charolais, Saler, Simmental, and Corriente. The majority of verified depredations (74%) in the study area between 2012 and 2020 occurred on private land (Atkinson 2023) and the remainder on public land. Figure 4 shows a map of the study area with ranches and jurisdictions represented by interviewees.

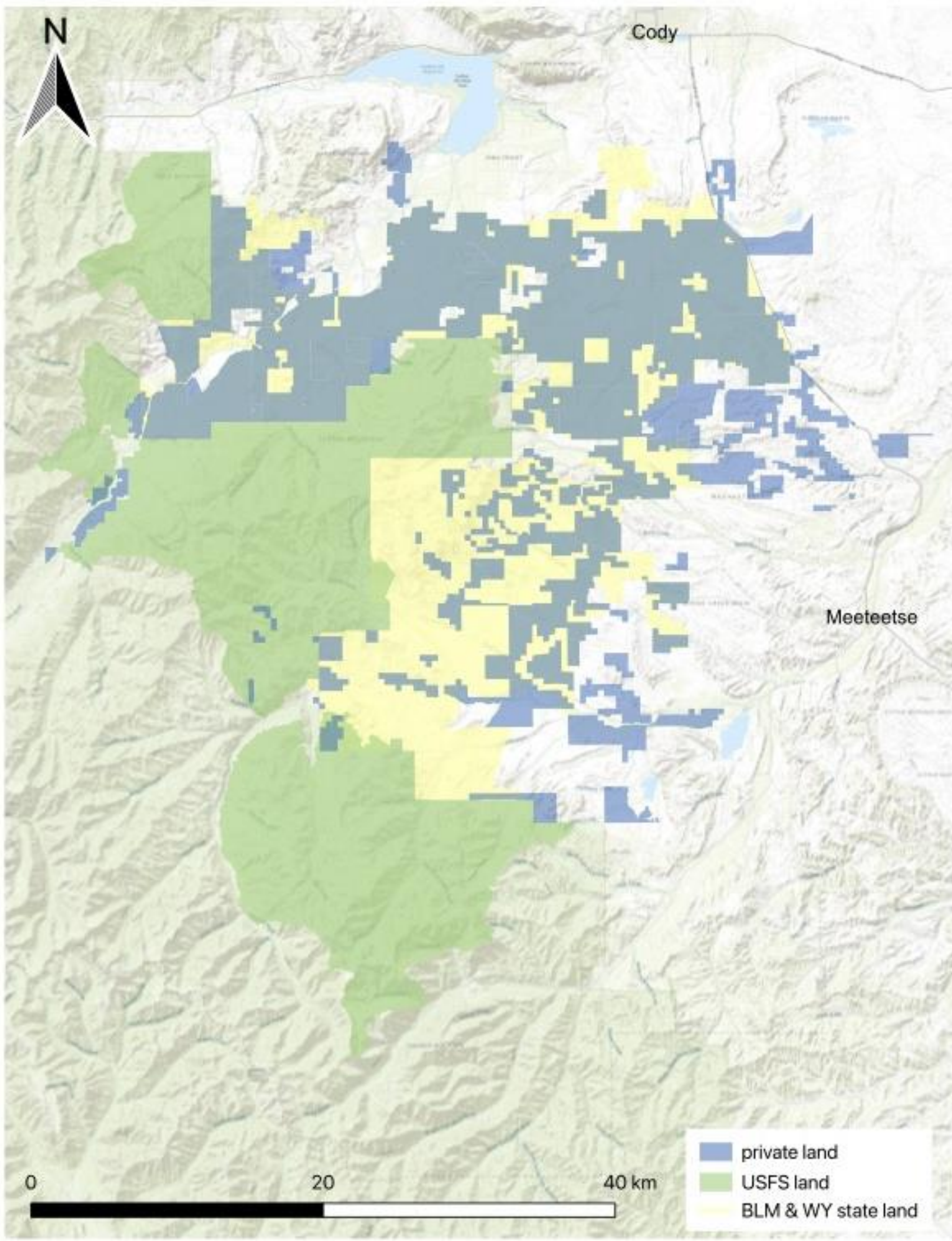


Figure 4. *Map of private and public land owned, grazed, and/or managed by interviewees within the study area.*

Reevaluating assumptions about wolf-livestock conflict mitigation

Our initial research objective was to characterize rancher and wildlife manager perspectives on wolf-livestock conflict management and mitigation with a focus on investigating the socioeconomic barriers to adopting nonlethal mitigation measures, similar to previous social science studies in other regions (Bogezi et al. 2021; Volski et al. 2021). However, interviews challenged our implicit assumptions about ranchers' willingness to try nonlethal measures and their attitudes towards wolves. Instead of finding fundamental socioeconomic barriers impacting willingness in our study area, we found ranchers and wildlife managers shared an unanticipated depth of experience implementing a range of nonlethal measures over the past two decades. Rather than a lack of willingness, we found that logistical constraints arising from the scale of ranch operations and complexity of the landscape, and in some cases, the financial outlay and risk associated with some interventions, were the main barriers to many nonlethal measures. Interview findings also challenged our assumption that lethal control was linked to negative attitudes towards wolves, as most interviewees shared neutral or positive sentiments towards wolves. Instead, our interviews revealed that wolf delisting and the ensuing increase in local control of wolf management, including lethal measures, may have played a role in reducing barriers to conflict mitigation by facilitating the resolution of social conflicts related to equity issues. Moreover, several interviewees suggested that local wolf management and conflict mitigation efforts, along with increased trust with WGFD on-the-ground personnel have fostered greater tolerance for wolves within the study area. Thus, we took the opportunity to dive more deeply into the shift from intolerance to tolerance.

Interview findings

Misconception about willingness to adapt nonlethal measures

Since the first depredations in the study area in 2001, interviewees have tried nearly all the nonlethal mitigation strategies cited in recent studies including increased human presence, temporary fencing, carcass removal, audio/visual deterrents, and changes to ranching practices (Supplementary Materials Table 1). For this reason, ranchers expressed frustration at being portrayed as resistant to change or adaptation. One multigenerational rancher summed up this feeling with the statement, *"you have to adapt to survive out here."* Many interviewees referenced how both people and wildlife have been exploring how to share the landscape, *"So adaptation just like an animal adapts. And we adapt with them"* - similar to Carter & Linnell's (2016) definition of "coexistence". Several participants emphasized that ranching inherently involves adaptive management, given the dynamic nature of wildlife populations, climate conditions (such as droughts or severe winters), and economic fluctuations. One rancher described a process of trial and error: "*We installed the electric fence around the calving pasture, and I was thinking that they could camp out there. But it didn't work. The wolves went through it".* This same rancher had also tried grazing horned cattle and moving calves to a different calving pasture and despite multiple failures, has kept trying new ideas.

Many wildlife managers described how the ranchers they work with are very open-minded and creative, *"...they just want their livestock to stay alive; they don't care what the technique* *is…they've always been very tolerant of a new idea, a new concept that could work…Something that could help. So, I think there's tolerance and in allowing new ideas and concepts, unless it's way out there."* One ranch manager described how ranchers are open to finding common ground despite being resistant to some things, *"I think for the most part, ranchers are willing to make compromises. I mean, we're pretty bullheaded, but I think I think we're all willing to make compromises to kind of make it work."*

However, some ranchers are limited in their ability to take the financial risk to try these new ideas, as described by one rancher, *"there's likely some really good solutions out there, but there's often risk in getting to those right solutions. And just because it might fail the first year, they might take something out of that and be able to tweak something and move on…There's a lot of different stuff that can be tried or done, but without these discussions, how do you get there? …it's something that's always pounded into agricultural producers' heads that it is their job to manage risk…Next year might be a drought or you know, the crop might fail or that you might get a disease in your cow herd…It's a lot easier to be risk averse in agriculture than it is to go take big risks. Because rarely is the reward worth the risk."* Thus, there is a constraint about being able to take the financial risk to test new tools, which would also take time away from other ranch duties.

Our findings indicated that ranchers have neutral or even positive attitudes towards wolves. Many described how increased experience and knowledge drove a shift in their attitude from negative to neutral or positive over time, as one rancher said, "*Growing up in this country, I wasn't a real big fan of wolves. But I grew up in a culture that didn't understand them very well…I think there's probably a lot more pushback 10 years ago on this than there is now. But now we've all realized that they're here to stay and so we all learned to live with it.*" As this wildlife manager and outfitter explains, *"...the closer you are to living day to day with wolves, the more tolerant, accepted, and normal it is"* and "*they just became a part of the landscape."* Some expressed positive sentiments, such as this wildlife manager, mentioning that "*when you spend as much time as we do monitoring wolves, you can't help but admire them".* Many even expressed a sense of pride, as described by one wildlife manager, *"It's fantastic to have them in the country…it's amazing to live in a place where there is room for bears and wolves".* Ranchers, wildlife managers, and professional outfitters in the area who are more knowledgeable about wolves tend to have moderate views, as described by wildlife managers, *"you can't help but work with them every day and have a more informed opinion*". Interviewees also distanced themselves from the "shoot, shovel, and shut up" attitude, which is only prevalent in *"a very fringe, .001%"* of people in the area and expressed how it is *"not a good way to accomplish anything*". In this context, unsurprisingly, interviewees voiced frustration over the assumption that supporting lethal control as a conflict mitigation strategy stems from hatred of wolves.

Human presence is the most commonly used nonlethal measure in the study area

Human presence was the most commonly cited adaptation in response to wolf conflict, with many interviewees noting a perception of increased effectiveness following the legalization of hunting as wolves grew more wary of humans. However, a clear pattern in the interviews was that human presence arises from many ranch activities other than nonlethal conflict mitigation, so as a result, some do not explicitly report using human presence as a nonlethal conflict mitigation measure. Ranchers routinely ride (or use ATVs) out to monitor cattle for various reasons including but not limited to conflict mitigation, including attending to sick or injured animals, repairing infrastructure, replenishing stock tanks and mineral blocks, and finding cow carcasses. Interviews also revealed that few ranchers in the study area use or recognize the term “range riding” that is widely used by scientists, NGOs, and agencies to describe increased human presence. One ranch manager, recalling a previous role as an official “range rider” for another ranch one summer, pointed out that the work was similar to the routine on their own ranch, without a special name. We found that people in our study area are more likely to use terms like “checking cows”, “permit riding”, “riding.” One rancher said, *“that’s just called good ranching.”* Indeed, some were offended by the insinuation in the term “range riding” that ranchers normally just turn their cows out for the summer and never see them. While the few smaller operations can account for every cow every day, larger operations, who can have up to 10 people out riding during the day during peak conflict season, will regularly check on groups of cattle. Ranches utilizing higher elevation USFS summer allotments often establish "cow camps" or cabins where ranch hands reside throughout the summer to closely monitor the cattle, and some even bring their families along. Riding or increased human presence for other ranch activities, along with the fact that many don’t use the term, “range riding”, may contribute to the fact that it’s not recognized as a conflict mitigation measure that is widely used in this study area.

Some NGOs have advocated for increasing the number of range riders to boost human presence and deploy deterrents (Stone et al. 2016). However, our interviewees cited a number of constraints on the feasibility and effectiveness of this approach which they feel are not widely recognized. One major challenge was finding people willing to undertake this isolating, dangerous, and physically demanding work, possessing the needed horsemanship and stockmanship skills - particularly given the seasonal nature of the work. Another was the financial burdens associated with hiring, housing, and insuring individuals. Some noted that proceeding with volunteer and/or underqualified riders lacking essential skills can create more work for ranchers and even take time away from mitigating conflict. Ranchers also emphasized the importance of being able to trust hired range riders, an important factor identified in other range riding programs across the West (Parks & Messmer 2016).

Successful interventions are mostly related to ranching and husbandry practices

Interviewees also reported changing several ranching or husbandry practices to reduce the vulnerability of livestock to predators. A recurring topic was the importance of harnessing cattle behavior, learning and experience. Ranchers emphasized the importance of having experienced mother cows that know the terrain, stick together, and stand their ground during attacks - with some interviewees having witnessed mother cows chasing off wolves or a grizzly bear. Several ranchers do not use dogs to work cattle in order to avoid their stock becoming habituated to canids. Interviewees also highlighted experimentation with cattle breed and age/sex class. Most ranchers opt for high-elevation adapted crosses to mitigate health issues like “brisket disease” (i.e., hypoxic pulmonary hypertension) that can weaken cattle and make them vulnerable to predation. Some prefer aggressive breeds like Saler crosses, while others prefer cattle that are easier to work such as Hereford crosses. While few actually use the term "low-stress stock handling", most ranchers in the study area employ this technique, finding it efficient and less taxing on the cattle and themselves. Because calves are the most common depredations, some have suggested switching from cow/calf pairs to yearlings due to their larger body size. But yearlings also have drawbacks: without mothers they are unfamiliar with the landscape and are curious, making them vulnerable. While a few ranches opt for yearlings, most stick to cow/calf operations, driven by various factors beyond just predator conflict mitigation. As with human presence, many of these trials and adaptations were implemented for a variety of reasons not limited to conflict mitigation, which may help explain why they are not commonly credited as nonlethal techniques in the study area.

Impracticality of many nonlethal measures due to scale mismatches

Many interviewees have tried other, common nonlethal measures such as temporary fencing, carcass removal, or deterrents and found them ineffective and impractical on a large, rugged landscape. Many have experienced frustration when met with skepticism from conservation practitioners who assume the technique was not applied correctly because it had been effective in another setting. As one wildlife manager noted, *"...we've tried some [nonlethal tools] in the past. It's not that they've never been willing to try it, it just hasn't worked very well."* The substantial maintenance necessary for some interventions compounds this issue. For instance, to ensure electrified fladry (i.e., "turbofladry") stays hot, vegetation must be continuously trimmed to prevent it from touching the wire. While some ranchers we interviewed have been able to maintain turbofladry in smaller pastures near the main ranch, doing this on a much larger scale in a rugged setting is considered infeasible, as other studies have also found (Martin 2021; Martin et al. 2021). Similarly, while producers and wildlife managers found that removing attractants such as carcasses reduced depredations near the main ranch, similar to other places in the Northern Rockies (Morehouse et al. 2021; Wilson 2023), this would be very difficult to do in a remote range setting inaccessible by road. Wildlife managers are very aware of what is a realistic option for ranchers to try, as one describes, *"I'm pretty careful in what I take to them as well. Because I don't want to waste my time or anybody's time. Unless I really feel like it's something that could be efficient, even a little bit".*

Interviewees highlighted two types of scale mismatch between nonlethal measures and the operational scale of ranching practices. The first was the spatial mismatch. While many nonlethal measures are tailored for smaller-scale settings, such as during calving when cows and calves are near the main ranch, the bulk of wolf conflicts arise in late summer, not during calving. During this period, cattle are dispersed across the landscape, rendering it infeasible to deploy nonlethal tools because, as one rancher noted, *"you can't be everywhere at once*". Wolves' ability to quickly traverse long distances presents an additional challenge to mitigating conflict on a large scale and some ranchers voiced concern about inadvertently driving wolves towards other groups of their own cattle or onto neighboring ranches. One rancher recounted an incident where he hazed wolves away from his cattle one night, only to learn the next day that the wolves had killed some of his neighbors' cows, saying *"Yeah, I remember feeling really bad about that."*

There is also a temporal mismatch between nonlethal measures and ranch operations, as many, if not most, depredations occur at night (Chavez & Gese 2006). As other research has found, most ranchers mentioned the impracticality of riding around or camping with cattle at night on this landscape (Bogezi et al. 2021). Even if a ranch could afford to hire a day crew and night crew, riding at night is ineffective due to limited visibility and, in our study area, hazardous due to rugged terrain and the high density of grizzly bears. Ranch managers emphasized the irresponsibility of sending employees into such conditions, regardless of their experience level. Additionally, some ranchers mentioned instances of depredations occurring at night at the main ranch, highlighting that even with human presence, nighttime depredations can be difficult to prevent.

A second type of temporal mismatch is mediated by animal behavior. Many interviewees have observed that wolves can quickly habituate to nonlethal tools, even when rotated frequently. One wildlife manager who has applied visual and audio deterrents for coyotes and wolves said, *"they both reason really well. And when something's different, they stop, sit down, and think…and half hour, 45 minutes, they realize that is not really giving some sort of adverse reaction to them, then they come and investigate. And then, boom, that switch hits, and then they're back to normal. It's not a threat anymore."* Several people emphasized how the lack of physical harm makes most deterrents ineffective, as another wildlife manager notes, *"when there's no physical pain with it, it doesn't take them very long to get the idea".*

Ranchers have to factor many other variables besides reducing conflict

Ranching practices are dependent on many factors as ranchers employ a holistic approach. Thus, one change can limit future options. For example, some wildlife advocates and academics have suggested that ranchers simply move their cattle to reduce spatial overlap with wolves. Besides the fact that wolves can easily move between pastures and operations, many smaller operations may not own other pastures and public grazing allotments have to stick to a strict schedule for range health. This is often even infeasible for large ranches who own a lot of land, as one ranch manager who runs cattle on private lands explains, *"If we know that there's an active pack or grizzlies around, does that influence my grazing rotation? It really can't because there's so many constraints on that already. And so many variables have been accounted for… I mean it's just an endless dissertation as to why we graze the way we do, and why we rest the pastures when we rest them. It's really difficult in the middle of that, with four or five different cattle herds to say, "Oh, well, we can't go into this pasture now because of this", when there may not be any other pastures available or that's the one you've been resting for two years. To have another variable like that to throw into that grazing plan equation, it's really difficult."*

Interviewees indicated that having flexible options that account for some of those limitations would be helpful for conflict mitigation. For instance, one wildlife manager mentioned utilizing USFS forage reserves, which are saved for when an allotment is burned in a wildfire. Yet, they recognized that deciding who has priority amid multiple conflict-ridden ranches poses challenges. Another wildlife manager gave the example of a ranch that puts young calves on the range earlier than they would like because they run out of grass in the calving pasture. Thus, providing winter feed could be a mitigation measure for that ranch. People without ranching experience would find it difficult to know how assistance that seems unrelated to reducing depredations can actually help mitigate conflict. Embracing flexibility and leveraging local expertise can foster adaptive and tailored conflict mitigation approaches beyond well-known nonlethal measures.

Lethal control is the most effective way to stop chronic depredation

Many interviewees referred to lethal control as one of the tools in the toolbox and many see it as the most effective conflict reduction measure in our study area when addressing chronic conflict situations when multiple depredations occur in a short span of time. This view was related to the notion that depredation will never be completely eliminated where wolves and cattle overlap in the vast rugged terrain of our study area. Currently, WGFD and, in some cases, producers, can use several forms of lethal control. Limited public hunting is used to proactively decrease wolf densities in areas with consistent depredation. In response to repeated depredations, the agency can also issue lethal take permits to ranchers or their designees. Finally, the agency can mount focused lethal control actions to address chronic depredations. For many interviewees, the goal is to delay conflict for as long as possible because it will inevitably occur. This sentiment stems from decades of grappling with wolf-livestock conflict, during which ranchers and wildlife managers have honed strategies to minimize conflict on this specific landscape. Initially lethal control was used very conservatively because there was uncertainty of its impact on recovery goals and ranchers recall being particularly frustrated during this time period. After almost a decade of learning how to identify chronic conflict situations, according to one wildlife manager, *"They [USFWS + WGFD] switched approaches to how they were dealing with depredation, and they would kill larger numbers of wolves faster",* leading to less depredations and lethal control actions (Fig. 1 & 2). Wildlife managers have observed factors that increase the likelihood of depredations in this study area, such as packs with a higher proportion of non-capable hunters (e.g., young, old, or injured wolves). However, because depredations are very context-dependent, wildlife managers have adopted a case-by-case approach and never proactively use lethal control. For example, conflicts in spring and early summer tend to be isolated events, where lethal control is not needed. However, later in the summer and early fall chronic depredation is more likely. This peak conflict period coincides with when many elk have migrated to their summer ranges and the available elk are more difficult to kill because they are in peak nutritional condition.

While not perfect, compensation for depredations is appreciated & important for tolerance

Compensation for verified losses was one of the earliest initiatives for wolf reintroduction aimed at fostering tolerance. Wyoming's compensation program employs a 7:1 multiplier for verified losses to wolves based on studies of producer depredation detection rates and is unique compared to other states (Oakleaf et al. 2003; Bruscino & Cleveland 2004). Interviewees had varied opinions on Wyoming's compensation program. Most interviewees agreed that it has contributed to increased tolerance and emphasized its importance for keeping ranchers in business, as one wildlife manager explained, "*They don't raise these animals to have them killed by wolves and do it 24/7 and lead that hard life where if they make money two years out of five, they're ahead of the curve. It's not an easy existence. So, they need to have a way to live with these animals and not have them cause financial ruin to where the ranch has to be sold*."

Ranchers expressed several concerns about compensation as a conflict mitigation tool. It can be very difficult to find carcasses or enough evidence to confirm kills and navigating the compensation payment process can be frustrating. Finally, the payment does not account for potential impacts of wolves on the fat gain and pregnancy rates of cattle, also known as "indirect losses." Interviewees were split on the multiplier numbers - some felt it wasn't enough and others said it was *"about where it should be"*. Despite these shortcomings, many interviewees mentioned a reluctance to complain about Wyoming's compensation scheme because they appreciate the multiplier and know that the program is more generous than those of other states.

Ranchers cited another set of concerns with how the compensation program is funded. Rather than relying on revenue from the state's hunters and anglers, who were mostly opposed to wolf reintroduction, many felt that compensation should be funded by out-of-state wolf supporters. As this rancher said, **"***Our society and culture have imposed this regional cost. And so, if our country and everybody in it deems that this is an important thing, and something worth spending money on, I think that burden should be shared by the rest of the country honestly.*" Another rancher seconded this view, *"If there's all this money out there in the world, why can't everybody who is gung-ho about these predators pay for some of those damages?"* A third rancher lamented that agricultural landowners don't receive economic benefits of harboring wildlife that move beyond Yellowstone's boundaries, *"The reason we have wolves and bears here is because of Yellowstone National Park. They don't pay a cent to the ranchers who are losing cattle because of these predators."* Though concerned about this apparent inequity, interviewees were also wary that external funding may be inflexible or come with strings attached.

Discussion

Interviewees presented an understanding of wolf-livestock conflict mitigation that contrasts with the common perspectives of many conservation biologists and eNGOs focused on promoting nonlethal measures. While the latter typically prioritize reducing tangible costs like livestock depredations and financial burdens, interviewees underscored the importance of also addressing intangible costs embedded within the social context of the wolf reintroduction and recovery process. People engage in conflict mitigation for different reasons – some prioritize reducing wolf deaths and other prioritize reducing the burdens of sharing the landscape with wolves. Our interviews reveal that while there is the common goal of reducing the tangible costs of livestock depredation, conflict with wolves cannot be fully addressed without actions that alleviate the underlying social conflict. Investigating how people who are directly impacted by wolf depredations on livestock define conflict mitigation is essential for comprehending the specific actions that have fostered increased tolerance for wolves in the study area.

Where does intolerance stem from?

Intolerance is more about how wolves are managed than wolves themselves

Intolerance remains a significant threat to wolf and other large carnivore conservation efforts. A 2009 analysis by the USFWS identified negative attitudes towards wolves as a primary threat to their recovery in the Northern Rocky Mountains (Endangered and Threatened Wildlife 2009, 74 F.R. 15175). Previous studies have linked ranchers' traditional values and negative wolf experiences to lower tolerance levels (Needham et al. 2004; Bruskotter et al. 2019; Manfredo et al. 2020), but our findings were not consistent with this work. Although interviewees supported hunting and lethal control as conflict management measures, they appreciate the intrinsic and ecological value of wolves. An emergent theme from interviews is that many view lethal control as an unavoidable necessity for chronic depredation situations.

As evidenced by prior research (Skogen 2017; von Essen & Adams 2020; Anderson 2021), opposition to wolves typically arises from dissatisfaction with the recovery process and perceptions of inadequate governance, rather than animosity towards the animals themselves, underscoring that human-wildlife conflict often emerges from disagreements over wildlife management strategies (Dickman 2010; Madden & McQuinn 2014; Skogen 2017). They don't blame them for killing cattle, as a rancher and wildlife manager described, *"it's just a wolf being a wolf"* and *"it's just trying to survive like the rest of us"*. Several people also expressed sympathy for wolves because they are on the edges of suitable habitat, as one rancher said, *"I don't think it's fair to them."* There was considerable frustration towards wildlife advocates that think the area needs more wolves (as well as grizzly bears). Some, like this wildlife manager, even challenged whether people advocating for more wolves and grizzlies genuinely care for the ones already inhabiting the landscape, *"It seems like the conversation is always "what are we going to do to mitigate that stuff so that we can have more bears on the landscape?" instead of saying, "we've got this magic little jewel right here. Why do you continue to push for more if the ones that were here would lead a better life?". I mean, you really can't say that you care a lot about bears and wolves, if they don't have the basic things that they need to make a living without getting into conflict with people."*

Interviewees consistently mentioned the importance of socially suitable areas, as one wildlife manager describes, *"People just want to keep this thing very simple, but it's just really complex. You can't just say, "we need more bears and wolves in this because we have all this habitat that's biologically suitable"- but it's not socially suitable, right?".* One wildlife manager even made the case for ensuring the social suitability of a landscape before reintroducing large carnivores, *"It's irresponsible for managers and advocates to force a collision…I think it's irresponsible for anyone advocating to have these animals around to force a conflict and see who comes out the winner? We should make the landscape suitable for recolonization and then advocate for recolonization."* The observed increase in tolerance after delisting and transfer to state management suggests that resolving social conflicts played a pivotal role in increasing tolerance for how wolves are managed.

Wolf-livestock conflict represents a broader underlying social conflict

Conservation social scientists have increasingly borrowed concepts from the fields of psychology, environmental justice, and peace studies by incorporating psychological theory to explore relationships between conservation initiatives and perceptions of risk linked to unmet psychological needs of local people (McDermott et al. 2013; Madden & McQuinn 2017; Akers & Yasué 2019). Suggesting specific measures based on conflict mitigation goals that limit autonomy and don't include local perspectives can inadvertently trigger "psychological reactance," to reclaim autonomy through illegal pathways (e.g., "shoot, shovel, & shut up") (Brehm 1966; Jones 2024). Wolf-livestock conflict represents the surface of deeper layers of social discontent. While wolf reintroduction was driven by a sense of environmental justice and seen by wildlife advocates as a morally necessary step to rectify historical wrongs against wolves, our interviews reveal that the reintroduction process and ensuing conflicts also represent a social injustice for people living in wolf country. Like other communities where large carnivores have been reintroduced, locals experienced impacts on their well-being and perceived risks (Lederach 2015; von Essen & Allen 2020; McInturff et al. 2021b; Richardson 2022; Lamar et al. 2024). These impacts are due to the diminishment of multiple dimensions of equity and justice, including distributive, procedural, recognitional, and contextual equity and justice (McDermott et al. 2013; Olive 2016; McInturff et al. 2021b). Examining these dimensions of inequity can shed light on the factors contributing to intolerance.

Distributive inequity – local communities bear a disproportionate amount of costs

Conservationists increasingly acknowledge that local communities making a living near protected areas often bear negative impacts of sharing the landscape with wildlife without reaping the benefits (Jordan et al. 2020; Middleton et al. 2021). Consequently, many community-based conservation efforts have aimed to enhance fairness by redistributing costs and benefits, or distributional equity (McDermott et al. 2013). While some redistribution occurred through compensation programs, it was limited in scope with funds coming from the state of Wyoming. Additionally, compensation does not cover all costs associated with depredations because it does not reduce exposure to risks, alter outcomes from encounters, or deal with emotional toll or psychological effects (McDermott et al. 2013; Harris et al. 2023; Lamar et al. 2024). Interviewees strongly advocate for out-of-state supporters of wolf reintroduction to contribute to compensation efforts and suggest economic benefits from Yellowstone be distributed to people that harbor Yellowstone's wildlife. And though there have been efforts to investigate pathways to direct tourism revenue from Yellowstone to local communities, none have been implemented (Middleton et al. 2021).

Procedural inequity - wolf reintroduction and recovery process excluded locals

Procedural inequity pertains to unfairness in political processes and participation in decision-making and played a major role in the wolf reintroduction process (McDermott et al. 2013). External entities wielded significant power in both the decision-making process and subsequent litigation and interviewees felt there was little consideration of local communities. As one rancher described reintroduction, *"as a rancher you have so many things working against you… then throw in something that wasn't there before. That was brought back, it wasn't your idea.*

And it's making a dent in your livelihood. You lose a lot of sleep over it.” Ranchers recall during the wolf reintroduction process feeling that their voices were drowned out by outsiders, as well as anger that USFWS was lying about being able to contain wolf populations. The prolonged 15 years between meeting recovery criteria and delisting confirmed fears and eroded trust in governance, democratic processes, and legislation such as the ESA, as one wildlife manager described, *“... the ESA is a great idea, but it has been hijacked and moving the goalposts is making it lose its credibility.”* Interviewees describe feeling helpless saying how they “*just had to take it back then”* and feeling that they were at the mercy of federal wildlife managers and litigating eNGOs.

Recognitional inequity - wolf recovery minimized peoples’ identities and way of life
During wolf recovery, ranchers not only perceived loss of autonomy, but also a disregard for their identities, knowledge, values, and way of life - or recognitional inequity (Olive 2016). Many conservation issues represent deeper threats to cultural identities of rural communities making a living on working lands (Bonnie et al. 2020; Gentner & Tanaka 2002), as one wildlife manager described, *“Maintaining beef production in Wyoming, especially on public land grazing, is about tradition. And it's about maintaining family, heritage, and opportunity. In other words, if you shut that down, you shut down the ranch, you shut the opportunity for someone who's always ranched to do that. And so, it's about people and their values. It's not about beef production”*. Similarly, the belief that receiving compensation adequately addresses all forms of loss overlooks risk perception, disempowerment, and loss of identity. And as one wildlife manager mentioned, *“it’s still an insult on their way of life”.* They also experienced moral devaluation as people from other parts of the country deemed lethal measures as immoral. Additionally, heated debates over ranchers' rights to use public grazing allotments have led many environmentalists to argue that ranching harms conservation efforts, with many advocating to ban grazing on public lands (Merrill 2002). One rancher summarizes this sentiment, *“Because for so long people want to come in and ban grazing. It's no grazing, no working lands. Like cows are the problem. Your way of life is the problem*”.

Contextual equity - differences in ranch wealth can lead to uneven costs and benefits
Contextual inequity refers to an uneven playing field and accounts for pre-existing political, economic, and social conditions influencing people’s access to resources and power (McDermott et al. 2013). In our study area, contextual equity hinges largely on the type of ranch ownership, as wealthier ranchers have greater financial stability. Many smaller "land rich, cash poor" family ranches face greater constraints and are more susceptible to risk. Many also rely on ranching as their primary source of income, with many ranchers having to take on additional jobs to make ends meet. Larger wealthier ranches have more flexibility, as one ranch manager describes, *“We can withstand the inherent risks of ranching in this environment… better than a smaller producer. Whether that risk comes from large carnivores, or drought or fire or bug infestation, we can shift cows over here from there if we absolutely have to. We have some options that smaller producers don't have.”* Additionally, wealthier ranches have greater access to power through their connections to agencies, NGOs, and policymakers and have greater capacity to engage in collaborative conservation initiatives. They are also able to make conservation plans further into the future, such as placing conservation easements, and are

often more tolerant of wildlife, which many consider to be an amenity (Gosnell et al. 2006). The influx of wealthier ranch ownership in the study area and the rest of the GYE has profound implications for shaping the landscape of conservation priorities and conflict tolerance (Gosnell et al. 2006; Gude et al. 2006; Epstein et al. 2022).

Inequity and loss of autonomy decreases ability to control and erodes institutional trust

Human-wildlife conflict literature emphasizes the importance of empowering local communities (Madden & McQuinn 2017; Pittman 2019; Ryan et al. 2019). In our study, focusing solely on mitigating physical and economic losses overlooks the deeper opposition rooted in how the wolf reintroduction and recovery process was conceived and implemented. Ignoring the intangible costs that lead to disempowerment negatively impacted local communities' well-being and significantly undermined trust in federal conservation efforts (Madden & McQuinn 2017). Promoting equity in decision-making and access to resources and assistance can bolster local acceptance of governing institutions and conservation policies by fostering participation, knowledge integration, and collective action in wildlife management (Olive, 2016; Salvatori et al. 2021; Ayambire et al. 2022). In our study, increased local control of wolf populations and conflict after delisting, as well as institutional trust between ranchers and state wildlife managers played a major role in increasing perceptions of fairness and empowerment, as well as tolerance for wolves.

How local control and trust in wildlife agencies increased tolerance

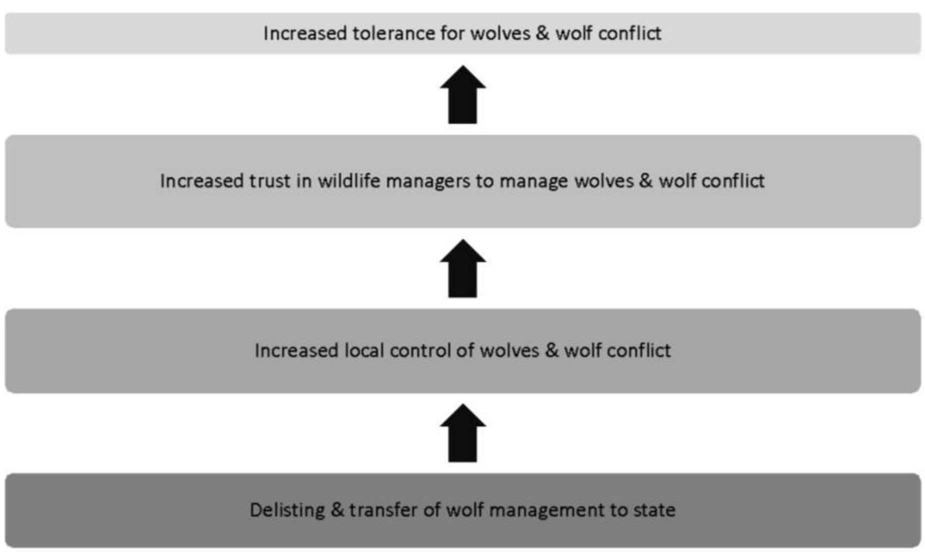


Figure 5. *Addressing the underlying social conflicts related to wolf recovery process led to increased local control of wolf populations & conflict, which allowed for trust in wildlife agency to manage wolves and increased tolerance.*

Allowing access to all management options enabled local control

Interviewees linked increased tolerance to the delisting and transfer of management to the state (Fig. 5). This allowed for local control over wolf populations and access to all management options, including lethal measures, which is perceived to be the most effective measure for mitigating chronic depredations. This finding corresponds with recent research in Montana and Washington, where increased tolerance for wolves was observed following the legalization of lethal control and hunting (Anderson 2021; Richardson 2022). Ranchers often mentioned how having management options for wolves made them in some ways more tolerable than wildlife with fewer options, as this rancher describes *"the nice part about wolves is that you can do something about them. There are some options, there's seasons on them. There are lethal take permits, these guys will come up and take out a pack if they really feel like it's necessary. So, there are some controls."* Grizzly bears are still protected under ESA, and population densities have grown in the last decade as one wildlife manager described, *"we're beginning to have degraded tolerance for grizzly bears…And we're seeing tolerance for wolves increase, and it's because of management. The ability to manage locally and the ability to have some local control, defend your livestock or whatever it may be. To have more moderate population densities, it changes a lot*." Interviewees see a parallel between the grizzly delisting process and the wolf delisting process, feeling that once again, external actors are wielding political influence to maintain protections for grizzlies, which limits conflict mitigation options. This sentiment arises as communities grapple with higher grizzly densities and increased property damage, maulings, and livestock depredation. Limited management options for elk, which are aggregating in larger numbers on private land, is decreasing tolerance for them as well, as one rancher noted, "*There's way too many elk. They're just tearing down fences, they go through a ton of grass. But the brucellosis just worries me more than anything else. Especially when you have a population that seems to be out of control. And WGFD is having a hard time getting a handle on it."*

Access to lethal control fosters tolerance for non-depredating wild wolves

Interviewees differentiated chronically depredating wolves from other wolves and believe that removing "problem wolves" increases social tolerance for "wild" wolf populations, as one wildlife manager summarized, "*you gotta kill some to keep some"*. One wildlife manager described it this way, *"...we're going in and removing those wolves and maintaining some sort of tolerance for wolves on the landscape - you're building a better setup for the ones that live away from cattle and conflict."* Other wolves can also include members of the same pack, as another wildlife manager explains, *".... we've seen it in certain packs where there's a couple individuals that go off to kill. And when we're able to figure those out and we get rid of those and then it [conflict] goes away".* Our findings align with research in Washington that describes lethal control as a biopolitical intervention to a socially produced issue (Anderson 2021). Social tolerance for lethal removal, particularly among wolf advocates, is crucial to fostering social tolerance among the people living with wolves (Anderson 2021). Allowing the removal of "problem" wolves signifies a willingness to allow access to all options to reduce risk. Conversely, during the period when wolves were protected under the ESA and restrictions on lethal control were in place, intolerance increased across the state, as noted by one wildlife manager, *"They pull wolves out of the wildlife category, and that's how they are allowed to hate them. But if you can put wolves in the normal category of wildlife, it's a lot harder to hate them."*

Trust between wildlife managers and ranchers increased tolerance of wolf management

Delisting and transfer of state management, coupled with local control and consistent positive interactions, enabled wildlife managers in the study area to cultivate trust with ranchers (Fig. 5). Trust between ranchers and wildlife managers can be challenging when addressing conflict with wildlife but is essential for strengthening relationships that allow people to work through conflict, and garner support for other wildlife management decisions (Ford et al. 2020; Salvatori et al. 2020; Jones 2024). Identifying the key factors that contributed to trust building is imperative for understanding what decreases risk perception and increases tolerance. Interviewees emphasized the importance of credibility, dependability, and communication as pivotal elements in fostering trust between ranchers and wildlife managers. Credibility refers to the perceived capability of wildlife managers to manage wolves and conflict, as one rancher describes, "*They [WGFD} seem to have a good handle on the local wolf population*s". WGFD's proactive approach to tracking and monitoring wolves, as well as its responsive measures to conflict situations, were widely acknowledged by ranchers in interviews. Dependability is characterized by the assurances that wildlife managers will intervene promptly and effectively to conflict. Local WGFD biologists in the study area are on-call 24/7, which is reassuring as one rancher puts it, "*I know they'll always show up when I call*". One wildlife manager describes how dependability facilitates trust, *"The reason that we have a fairly positive working relationship with the people who live, work, and recreate, especially in grizzly bear country, is the fact that they know that we're available 24/7. If they call us - we will respond. That's the key to having a high density of large carnivores and people in the landscape. Somebody has to be available to deal with that. I think that plays into the mindset too, that, you know, "I don't have control over this, but I have outlets and I have other professionals that I can call when I need help." And that's a big deal."*

Communication is important because the exchange of knowledge and information enhances credibility and dependability, as well as trust that wildlife managers are being transparent. One wildlife manager describes how they build relationships through good communication, "*I'll be out doing something, and I'll stop and talk to those guys for an hour…It's just getting stuff out there so you're not hiding things. We'll deal with this stuff together. That's where I see it being really positive.*" Another wildlife manager emphasized the importance of transparency in decision-making, *"...they're pretty in the loop. We're telling them, "We removed some" or "we're letting these hang out". And that way, they actually understand it, so they're not just reacting without any facts."* Some interviewees also mentioned how having a similar background, either experience living in the area and/or experience working on a ranch, can facilitate connections and trust. Interviewed ranchers appreciated that several WGFD personnel had worked on ranches and could understand ranching life, cultural identities, and the intangible losses associated with wolf-livestock conflicts. These shared experiences and familiarity facilitate stronger rapport between ranchers and wildlife managers allowing them to build connections and trust more quickly. Additionally, wildlife managers with similar backgrounds are equipped with insights into the challenges of conflict mitigation within this landscape, allowing them to discern practical and realistic expectations for ranchers.

Recommendations

Qualitative research, incorporating local perspectives, and co-producing knowledge

Qualitative methods can help us investigate the social context of wolf conflict, which is often deeply rooted in broader sociopolitical conflict that can threaten rural inhabitants on working lands (Nie 2003; Skogen 2017; Bennett et al. 2022). Conservation efforts focused solely on technical solutions and the physical, economic, and ecological components of conflicts risks overlooking underlying social conflict (Madison & McQuinn 2017). Prioritizing only tangible outcomes, like maximizing wolf populations, minimizing livestock depredations, and compensating economic losses, oversimplifies a complex situation and leaves little room for compromise or exploration of other solutions. It can also promote a binary mindset, where success or failure is judged solely by numerical changes. Moreover, trying to change ranchers' attitudes and increase their tolerance for wolves assumes that the ultimate goal of conflict mitigation is to reduce wolf deaths, which frames local people as barriers if they don't use nonlethal measures. Qualitative methods such as interviews can uncover different perceptions of conflict mitigation success (Lucas et al. 2022). We found that most interviewees perceive conflict mitigation to be successful and much better than before delisting because they have access to all management options and can trust WGFD to have local control of wolf populations and conflict levels. Using qualitative methods can yield more effective interventions aimed at promoting equity and fostering environments conducive to increased tolerance.

While qualitative methods such as interviews allow us to explore peoples' motivations and perceptions, they also have limitations. Despite precautions to ensure confidentiality, interviewees may have chosen their words carefully, withheld true feelings, or concealed information because interviews were recorded. However, we chose to analyze the interview data without assumptions about their underlying intentions. When possible, we also fact-checked information such as wolf pack size numbers or depredations and found them to be accurate. Our pre-existing relationships with some interviewees, developed over the course of other studies (Middleton et al. 2013; Chapters 1 & 2) built through earlier research, may have fostered honest sharing. Many also expressed appreciation that someone wanted to hear and share their perspective, suggesting a level of sincerity in their responses.

Conducting co-produced research that incorporates local experience and knowledge enhances equity, which can facilitate increased effectiveness of site-specific solutions and trust in scientists (McInturff et al. 2021a; Volski et al. 2021; Hyde et al. 2022). Co-production ensures that researchers prioritize strategies relevant to ranchers' holistic decision-making approach (Sayre 2004; Volski et al. 2021; Hyde et al. 2022). Additionally, co-produced research enhances the credibility of scientific findings by fostering trust and can increase the likelihood of the adoption of a conflict mitigation measure, regardless of its technical effectiveness (Martin et al. 2021; Volski et al. 2021; Hyde et al. 2022). Co-production can also facilitate knowledge transfer among peers since ranchers consider other ranchers to be the most trusted messengers for information sharing (Bogezi et al. 2021; Volski et al. 2021; Bennett et al. 2022; Hyde et al. 2022). Interviewed ranchers were more likely to try a new conflict mitigation measure if recommended by a respected rancher in the area. The importance of on-the-ground knowledge was emphasized, as this rancher explains, *"it's got to come from a person that has experience, it can't come from a person in education".* Although there is low overall trust between producers and scientists in the American West (Bonnie et al. 2020), some ranchers in our study area trust specific scientists whom they've closely worked with on past research projects. One ranch manager noted how collaboration with scientists is empowering because, *"Being able to manage issues entails having a good working relationship with the people that can influence or have a role in being able to help us manage it."*

Increased recognition and support for ranchers

Misrepresentation of individuals' identities and values can breed a sense of unfairness (McDermott et al. 2013; Ayambire et al. 2022). Ranchers, whose livelihood relies on sustainable stewardship of the land and who are committed to conservation, often feel their identities are misrepresented (Lien et al. 2017). They expressed frustration with the public's perception that ranchers are detrimental to conservation efforts. As one ranch manager explains, *"I'm here proactively saying, what I'm doing is helping the range. We're doing this to minimize the damage. What I'm doing here - water filtration, carbon sequestration, fire suppression, nutrient cycling, increases the quantity and quality of forage for all grazing animals, livestock, and wildlife. If you ask the general public, they are probably gonna say grazing on public land is bad."* For many ranchers in the study area, conservation is an inherent part of ranching here as this ranch manager summarized, *"I think conservation efforts are just a part of managing a larger ranch. That's not a set aside "thing". I think all land managers (including ranchers and agency natural resource managers) have an inherent obligation to maintain or enhance choices for future generations. So, within that is conservation, right? Cause if you don't manage in a way that enhances your resources, it's not sustainable. Period. We manage this ranch in a way that can produce economic benefits and still conserve it for future generations. And so, for me, it's one and the same."* Most interviewed ranchers have also actively engaged in conservation projects and have collaborated with wildlife managers and researchers. Many interviewees described the sense of pride they have for the land and their concerns for the future, as this rancher explains, *"We have a great respect for the land. We're just a blip in time. And we just hope that we can pass it on to my son and his family and his children, and that they will have this and have the same appreciation that we do for it. We just hope that we'll be able to have that go on for as long as it can. We hope that it's never subdivided - that we're whole."* Others, such as this wildlife manager, described a deep feeling of responsibility, *"We're as much a part of the natural world as an animal is, but we are tasked with this responsibility."*

To address misconceptions about ranchers and their role in land and wildlife conservation, close collaborators such as wildlife agencies and NGOs can provide support through public outreach. Expressing respect and gratitude for ranchers' stewardship of wildlife habitat on working lands can raise public awareness and appreciation. Positive meaningful events, such as being recognized and appreciated publicly, offer intangible benefits that can increase tolerance in the same way intangible costs can decrease tolerance (Kansky et al. 2016). In our study area, several ranches have received WGFD's Landowner of the Year Award, highlighting their conservation contributions. Additionally, several conservation NGOs that work closely with ranchers have been conducting outreach to the general public to share ranchers' stories and conservation efforts through various channels such as publications, podcasts, and social media (Middleton et al. 2022). This outreach helps ranchers feel acknowledged and valued as stewards of the land. Public recognition serves as a non-monetary social incentive for further engagement in conservation initiatives, offering an underutilized avenue for increasing intangible benefits associated with coexisting with wolves and other wildlife.

A number of recent federal funding commitments have increased recognition and support for agriculture producers or working lands, and for conflict mitigation specifically, in and around our study area. In 2022, the US Department of Agriculture and the state of Wyoming partners to pilot a Migratory Big Game Initiative to provide for agricultural land protection, habitat leasing, and habitat restoration. This program was expanded across Montana and Idaho in 2023 and has resulted in $40 million from the ACEP and EQIP programs and expansive enrollment in the Grasslands Conservation Reserve Program (CRP), a voluntary working lands program that provides annual rental payments to landowners to conserve grasslands while continuing to graze and hay (WLA, 2023a). Also in 2023, USDA's Natural Resources Conservation Service finalized new technical standards and payment scenarios to facilitate Environmental Quality Incentive Payment funding for conflict reduction and allocated $22 million through Regional Conservation Partnership Program (RCPP) projects in Montana, Oregon, Colorado, Arizona, and New Mexico. These resources support cost-sharing to assist ranchers with range riding, electric fencing and turbofladry, and livestock carcass removal (WLA, 2023b), which may alleviate at least some of the costs and labor constraints we heard from interviewees. There is also growing acknowledgment of the importance of compensation programs beyond payment for confirmed depredations (Macon 2020). These initiatives recognize the benefits ranchers provide, regardless of wildlife conflict levels, and emphasize positive outcomes over solely compensating negative ones. These funding commitments emerged through collaborative efforts among ranchers from across the western U.S., working in partnership with NGOs and agencies to secure funding from the USDA. By involving ranchers in both the planning and implementation phases, while also reducing costs and emphasizing their crucial role in supporting wildlife, these initiatives are fostering distributive, procedural, and recognitional equity.

Increased recognition and support for wildlife managers

Our study highlights the role of wildlife managers in alleviating physical and social conflict. Wildlife managers in the study area have gained more local control of wolf populations and conflict while building trust with ranchers – especially in the years since delisting in 2017. Interviewees emphasized how Wyoming's wolf management plan allowed for WGFD to build credibility by accounting for the needs of local people, cultivating social tolerance across many areas of the state. WGFD also put a lot of money into dedicating hiring on-the-ground personnel, tracking and monitoring wolves, compensating verified losses, and mitigating conflict. Having the capacity to monitor and manage wolves and wolf-livestock conflict has been essential for increasing credibility, dependability, and communication with ranchers. Increasing recognition and support for wildlife managers will help address the many challenges they face when dealing with wildlife conflict including burnout and feeling mischaracterized and underappreciated by the general public. Recognizing the work of wildlife managers who deal with social conflict related to wolves is important for understanding how trust can be built in other communities when working through wolf-livestock conflict. We recommend state wildlife agencies hire more on-the-ground personnel, including local people who are trusted in the community, and also provide training in conflict resolution to strengthen stakeholder engagement skills needed for mitigating depredations and social conflict that comes with wolf recovery.

Conclusion

While it's challenging to encapsulate the full range of insights from 37 interviews, this wildlife manager's perspective captures the sentiments of most interviewees, *"I think what we've seen is a growing tolerance for wolves, a growing normalization of wolves in the landscape. That's in response to local control, having a wolf management program, having hunting seasons, and moderating wolf densities. That's given people the slack they need mentally, emotionally, psychologically, to actually turn the corner. We give people the space to change their mind. We provide an opportunity for people to grow and tolerate. And I think that's the first step. I think as time goes on through, and we have stability and normalcy in wolf management in Wyoming, we have the potential to shift to a much better place, not just tolerance, not just "it's okay", but "can you imagine Wyoming without wolves?" - that's a whole different mindset."* Our findings reveal that failing to integrate local perspectives into conflict mitigation goals posed a significant barrier to developing effective mitigation interventions that benefit local communities. The social conflict stemming from the wolf reintroduction and recovery process undermined local autonomy and contributed to feelings of injustice, thereby prolonging intolerance for wolf management. It was only after the delisting and transfer of management that WGFD began to gain local control of wolf populations and conflicts. This along with trust building between wildlife managers and ranchers resulted in heightened tolerance for sharing the landscape with wolves, while also potentially creating space for future wildlife conservation initiatives.

Lessons learned from this study in the GYE, where stakeholders have been grappling with wolf-livestock conflict for over two decades, offer valuable insights for other states facing wolf recovery. While technical knowledge on nonlethal measures and compensation programs have been shared with those encountering conflict anew, we recommend focusing on alleviating social conflict to allow space for tolerance to grow. This includes incorporating ranchers' perspectives when identifying conflict mitigation goals, along with increasing recognition and support for existing efforts. Additionally, appreciation for the skills and expertise needed to mitigate conflict, as well as enhanced capacity to address social challenges is especially needed for state wildlife agencies that play a critical role in fostering tolerance. However, we recognize that this study explored the barriers and successes in one region in one state. Other states with recovering wolf populations such as Oregon, Washington, Colorado, and California that have different demographics and deeper urban-rural divides will vary significantly in their challenges. Our findings emphasize the need to incorporate qualitative research and empower local communities in conservation intervention decision-making processes. Only then, can effective strategies be devised that cultivate local tolerance for wolves and deepen understanding and empathy for the people sharing the landscape with them.

Supplementary Materials Table 1

Table 1. Conflict mitigation strategies pros and cons based on interview findings

Measure	What works?	Challenges/barriers
Human presence/ "range riding" ("checking/moving cows"; "riding"; "permit riding"; "low-stress handling/herding"); "just good ranching"	Will increase human presence when they know wolves are around; Already doing this for many ranch tasks: checking fences/infrastructure, water features, salt licks; checking cattle and doctoring if injured or ill; moving cows to better forage and into bigger groups; looking for dead cattle	Can't do at night (when most conflict occurs) because it's ineffective and dangerous; chances of always being at the right place at the right time to deter wolves is unlikely (e.g., "a wolf can be there 5 minutes after you've been there"); costly (pay, housing, insurance); hard to find qualified willing people (requires a wide range of skills, dangerous work, seasonal work); more people to manage; having employees with different workloads isn't good for ranch morale; hard to find people ranchers trust; some may just ride to look for dead cattle to get compensated
Reducing spatiotemporal overlap of cows and wildlife (by changing spring turnout, calving, or grazing rotation timing and/or location)	Can be useful for larger operations with multiple deeded pastures (on private land)	most wolf depredation does not occur during calving (although grizzly conflicts are bad then); smaller operations don't have as much flexibility - don't have as much deeded land and don't grow as much hay; Grazing allotments and pastures are on a strict schedule because they need to be rested - changing the grazing rotation can limit options in the long-term; Several ranches have delayed calving and/or turnout (often there are also economic reasons too)
Cattle type – breed; experience; cow/calf vs yearlings	Most ranchers emphasized the importance of experienced mother cows who know how to deal with predators because they know the landscape well and how to stay together and stand their ground - and to a lesser extent cattle breeds that are better adapted to high-altitude rugged environments	Have tried different breeds – aggressive cattle (e.g., Saler) make moving and handling cattle dangerous; one ranch tried longhorns and they ended up all over the place and were killed by predators because they were not familiar with the landscape; yearlings are inexperienced and curious and not good at defending against predators; while young calves are vulnerable, they are usually with their moms all the time - it is usually older calves that get killed because by late summer they tend to stray further from their mothers
Carcass removal	Easier in winter when cows are closer to main ranch; also good for reducing grizzly risk	Hard to detect all dead cattle; how to remove carcasses in rugged terrain far from roads; doesn't take long for grizzlies to get to and consume most of carcass
Temporary fencing fladry/turbofladry (electric fencing; hot wire; night penning)	On small scale ranches when cattle are near main ranch; Control grazing areas; bringing cows in for branding/pregnancy checks/brucellosis testing/shipping	Unfeasible on larger scale, cows don't band like sheep; rugged remote terrain; requires constant maintenance (e.g., need to keep vegetation cut if electrified); wolves eventually habituate; not great at deterring grizzlies
Noise and visual deterrents (e.g. cracker shells, zon guns (propane cannons), Foxlights, WS new trailer	Keeps wolves & other predators away in short-term; some also used to haze elk	Works in short-term but wolves eventually habituate; chances of always being at the right place at the right time to deter wolves is unlikely
Livestock guardian animals/dogs	N/A	Not used in study area - just bear dogs for human safety and some use dogs to work cattle. Several ranchers don't even use dogs at

		all so that the cattle don't get desensitized to canids. Works for sheep but doesn't work for cattle.
translocation/ relocation	removal of problem animals temporarily	used in the past for wolves, but not effective long-term solution and brings conflict to other areas; used for some grizzlies "playing musical bears between us and Dubois"
Monitoring/ Reconnaissance (wildlife managers)	WGFD has a good handle of wolf packs in the area and put a lot of effort into monitoring; VHF or GPS collars; regular aerial surveys from fixed-wing plane; tracking & looking for wolf sign; camera traps; den checks; monitoring climate and other food sources (mostly for grizzlies); coordinating with NPS for co-managed packs; communicating with ranchers; ranchers appreciate the 24/7 availability of WGFD large carnivore biologists	impossible to know of every wolf or bear in the area, so sometimes they are blindsided by conflict from unknown individual or pair; only have GPS collars when researchers are conducting research; can't share collar data with ranchers; a few ranchers said there were times in the past when they weren't informed of wolf pack presence; during conflict period WGFD biologists go months without days off and are on call 24/7
Lethal control (via Lethal Take Permits or removal by WS or WGFD)	Most effective and quick way to delay conflict for at least another year; some ranchers have people they hire to use lethal control permit; Most effective when WS does aerial gunning; give some sense of control to have the option	Lethal take permits issued first but difficult for ranches to find and shoot wolves while doing other ranch duties; new wolves eventually fill territory; sometimes better to have wolves you know around; least favorite part of their job (wildlife managers); public scrutiny
Public hunting/harvest	Keeps wolves in the area wary of humans; reduce overall number of wolves in area	Not killing target individuals; wolves are difficult to hunt; issues with allowing hunters to access private land - more work than it's worth
Compensation	Better than nothing; appreciate multiplier and recognize they have it way better than other states; "takes some of the sting out of the bite"; seen as the bare minimum	Depends on finding dead cow and what is left of the carcass to confirm depredation; doesn't cover indirect costs or all types of cattle; issues with source of funding (WY hunters and anglers); doesn't actually solve the problem - "not raising cows to feed wolves"; process to get compensated can be cumbersome; if a wolf injures livestock, have to kill it to get compensated
Habitat leasing programs (note that these interviews were conducted before announcement of USDA EQIP/ACEP and NRCS RCPP programs, but some interviewees were aware that something was in the works)	it would be nice to have some acknowledgement of land and wildlife stewardship; some liked the idea of sustainable federal funding	Previous habitat leasing program was very small monetary amount; Relatively new, so they didn't know much about it during the time of the interview; some wary of anything from federal government
New technology: virtual fencing, flashing ear tags, GPS eartags with mortality signal, drones with heat sensors	Willing to try if trusted rancher or researcher recommends, and it doesn't negatively affect their operation and they got some assistance in implementing	Worried about additional costs and labor; might be accused of "doing it wrong" if it doesn't work, which has happened in the past; skeptical there will be a "silver bullet" tool or technique that will drastically reduce conflict; wouldn't be surprised if wolves eventually habituated

Appendix A - Letter of Information

Carnivore-livestock conflict in the Cody area

Project Description

The purpose of this research study is to better understand the socioeconomic limitations of mitigating carnivore depredation on livestock. Since 2019, I have led winter and summer fieldwork to collect data on wolf predation patterns. Understanding the ecological dynamics can and has informed management strategies addressing conflict. What remains unknown are the often-overlooked socioeconomic dimensions of carnivore-livestock conflict and its impact on ranchers.

Reducing carnivore-livestock conflict in the West is a conservation priority. Less well appreciated, however, is the **indirect influence of these conflicts on conservation via impacts on agricultural economics and the rural communities**. Private landowners are stewards of critical wildlife habitat; yet their stewardship rests on their ability to maintain open space via range-based livelihoods. Declining cattle prices and the increase in land price (especially in rural areas where a high demand for natural amenities exists) makes the cost of owning and operating ranches prohibitive and could induce conversion of agricultural land to rural-residential developments. Therefore, **reducing livestock losses to large carnivores is not only important for wildlife conservation, but also the persistence of rural communities.**

We are inviting you to participate in this study because of **your experience with carnivore-livestock conflict in the Cody region** of the eastern Greater Yellowstone Ecosystem. Learning about these constraints will help wildlife managers and those advocating for nonlethal interventions avoid recommending strategies that ranchers are unable to employ and promote collaboration to find meaningful and site-specific solutions.

Interview Topics

- Experience with carnivore-livestock conflict
- Your observations of wolf/elk behavior and wolf-elk interactions
- Attitudes towards conflict management measures
- Wyoming's compensation program for carnivore depredations
- The future of carnivore-livestock conflict

Research Approach

Research will be carried out by conducting interviews with ranchers and wildlife managers who have direct experience with carnivore-livestock conflict in the Cody area. Interviews will take place fall 2021 with potential follow-up interviews in summer 2022. Products including presentations, reports, and publications will be prepared mid-late 2022/early 2023.

Research Team

Avery Shawler, University of California Berkeley
Dr. Arthur Middleton, University of California Berkeley

Interview Participant Information

Overview and procedures
By granting an interview, you agree to participate in our research study. Interview questions will focus on gaining your insights, knowledge, and opinions on issues related to carnivore-livestock conflict. These interviews will take place in-person (however, phone or Zoom interviews are also possible), and typically last between 1-2 hours. **With your permission, I will record and transcribe interviews to help me accurately represent your answers in our analysis**. If you prefer not to have your interview recorded, I will ask your permission to take notes.

Voluntary nature of participation and right to withdraw without consequence
Participation in this research is entirely voluntary. You may refuse to participate or withdraw at any time without consequence. Some of the research questions may make you uncomfortable or upset. You are free to decline to answer any questions you don't wish to, or to stop the interview at any time.

Benefits and risks
Your participation in this project will provide important information about issues concerning carnivore-livestock conflict. We hope that the information gained from the study will help inform carnivore-livestock conflict management in the region, as well as support ranchers and wildlife managers. We also hope, through this research, to produce concrete products of use to ranchers, wildlife managers, policy makers and other stakeholders. We do not anticipate that participating in this study will cause any harm; however, there is a minimal risk of loss of confidentiality. This study takes several steps to reduce this risk and maintain participant anonymity (described below).

Confidentiality
Research records will be kept confidential, consistent with federal and state regulations. Only I (Avery Shawler) will have access to data from the interviews (including recordings). In order to protect your privacy, personal identifiable information will be removed from study documents and replaced with an anonymous identifier (such as a number). Identifying information will be stored separately from the interview transcription and notes. Interview notes and any recordings and transcripts will be destroyed within 2 years or as soon as analysis is completed. Reports, publications, and academic dissertations resulting from this research project will synthesize findings, including qualitative summaries of information obtained from interviews. These may include direct quotations from interviews (unless you decline to be quoted), but any quotations used will be anonymous (unless you prefer and expressly grant permission to be quoted by name).

Questions
If you have any questions or concerns about this study, you may contact Avery Shawler.

Appendix B - Interview guides

Interview Guide – ranchers

Introduction

- Thank you for participating! You have been asked to participate in this study because of **your direct experience with carnivore-livestock conflict in the Cody area**. By participating in this study, you will contribute to research that will use local knowledge and direct experience of dealing with carnivore-livestock conflict to better inform management practices.
- You are **not obliged to participate** at all or answer any questions you do not want to answer, **we**
  will not share your name with anyone, and we will not associate your answers with your name.
- This interview process is completely **voluntary** and **confidential**.
- We would like **your permission to record** this interview. **The purpose of recording is to maintain the integrity of what you say**. Recording allows us to confirm that our notes are correct and be sure we represent your comments exactly as you say them – **they are for backup purposes only**. If we use a quotation in any publications, it will not be attributable to you. We will keep the recordings until the **end of the project and then destroy them**. Here is an Informed Consent document that you can read and sign. Do you mind if we record this conversation?

Background questions

1. How long have you been ranching?
2. How long have you been ranching here?
3. How long have you been ranching here with carnivores on the landscape?

a. How have your approaches to mitigate conflict changed over time?

Experience with carnivore-livestock conflict

4. What **types of wildlife conflict** you have experienced and for how long?

a. Elk, coyotes, wolves, grizzlies, lions etc.

b. Follow-up: eating crops, breaking fences, disease transmission risk, increasing stress on livestock, direct depredation from carnivores, etc.)

5. From your experience, what **factors seem to lead to cattle depredation**?
    - Number and distribution of wildlife (ungulates and carnivores)
    - Types of cattle (e.g., older experienced cows vs younger inexperienced cows, different breeds/crosses, etc.)
    - Time of year/ location of cattle? (e.g., calving season, when livestock are far from main ranch and difficult to monitor frequently, etc.)
    - Are there any hotspots where chronic depredation typically occurs or is it difficult to predict where conflict will occur in any given year?
6. Describe **a year where conflict was particularly bad**. What made it a bad conflict year?
    - Have you noticed a pattern?

- How much of your time and labor go into addressing these conflicts in a bad conflict year?

Questions about wolf-elk interactions

6. Have you ever had **wolves den near your cattle**?
    - Were you notified of denning wolves or did you find out yourself?
    - When wolves den near your cattle, do there seem to be more conflicts?
7. Have you noticed **any changes in elk populations** on your ranch and grazing allotments?

a. How have elk numbers on your operation changed over time?

b. How have elk numbers on your operation related to conflict with wolves and other carnivores?

i. Do you think keeping the elk away from cattle would lessen conflict with carnivores?

Attitudes towards conflict management measures

8. Do you think **management measures can mitigate conflicts** with wolves?

a. If no – why not?

b. If yes – which ones have you tried? *(open-ended question, then proceed to the below options in 8c not mentioned by interviewee)*

c. Have you tried _(method)_? Why or why not?

i. increasing human presence (i.e., range riders/cowboys monitoring cattle)

1. follow up: If you had the capacity to increase human presence on your operation, do you think most conflict could be mitigated?

ii. Fencing – e.g., temp fencing, fladry, permanent fencing

iii. Noise or light deterrents (e.g., cracker shells, airhorns, Foxlights)

iv. Livestock guardian animals

v. Direct hazing of carnivores when encountered

vi. Anything else I have not listed?

d. What would make you **more likely to try a nonlethal mitigation** measure? *(open-ended question, then proceed to the below options not mentioned by interviewee)*

- Follow-ups:
    - costs and labor were covered
    - scientific research proved the method was effective in other operations with similar scale and landscape as yours
    - a trusted and respected rancher in your community has tried it and recommends it to you
    - nonlethal measures were just called proactive management practices rather than placing an emphasis on "nonlethal" because "nonlethal" is a loaded word
    - There are other factors that would make me willing to use nonlethal measures not listed here

9. What makes **implementing nonlethal measures difficult** on your operation? *(open-ended question, then proceed to the below options not mentioned by interviewee)*

- Follow-ups
    - Size of the operation

- Difficulty of predicting where conflicts will occur and where to focus efforts
- Money/Labor
- Access to information on where wildlife are located
- Difficult to justify spending time and money on nonlethal measures when lethal control is an effective option
- social stigma
- Other – please list

10. What conflict management measures **would you like to see tested**? Or what conflict management measures are you **most curious about and/or interested in?**

- If you could design your own research experiment to test conflict management tools or techniques, what would you want to test?

11. Have you ever **requested a lethal control permit**?

- If yes, can you tell me about what circumstances led to that point?
- If not, what do you feel like would have to happen in order to motivate one?
- Do you think lethal control is the most effective conflict mitigation measure?
- Do you have any reason to stop using lethal control actions or is it working pretty well for you?

Carnivore-livestock depredation compensation in Wyoming

12. Now, I'd like to switch gears slightly and talk about **WY's compensation program**. Have you used this program?

a. How does this program affect your operation?

b. What aspects of the program do you like? Or what aspects of the program do you find effective?

c. What aspects of the program would you change?

d. How transferable do you think this program might be to other ranching contexts (for example in other states)?

The future of carnivore-livestock conflict and its effect on ranching livelihoods

13. Looking ahead, what do you think is the **future of wildlife-livestock dynamics** in this place? What are the **big changes that you *want* to see happen**?

14. Have your **views on wildlife/carnivores changed over time**? If yes, how, and what factors do you think affected your perspectives?

15. How does wildlife conflict factor **into how you run this operation long term**?

16. In your opinion, where would be the **best use of funds and resources to reduce conflict with carnivores**?

17. Who would you **be most willing to receive funding and resources from to reduce carnivore-livestock conflict**? Are there any sources you would not accept funding or resources from?

18. Is there anything **you wished the public would know** about what it's like to deal with carnivore-livestock conflict?

Interview Guide - wildlife managers

Introduction

- Thank you for participating! You have been asked to participate in this study because of **your direct experience with carnivore-livestock conflict in the Cody area**. By participating in this study, you will contribute to research that will use local knowledge and direct experience of dealing with carnivore-livestock conflict to better inform management practices.
- You are **not obliged to participate** at all or answer any questions you do not want to answer, **we**
  will not share your name with anyone, and we will not associate your answers with your name.
- This interview process is completely **voluntary** and **confidential**.
- We would like **your permission to record** this interview. **The purpose of recording is to maintain the integrity of what you say**. Recording allows us to confirm that our notes are correct and be sure we represent your comments exactly as you say them – **they are for backup purposes only**. If we use a quotation in any publications, it will not be attributable to you. We will keep the recordings until the **end of the project and then destroy them**. Here is an Informed Consent document that you can read and sign. Do you mind if we record this conversation?

Background

1. Can you describe your experience with carnivore-livestock conflict?
    - What were you doing prior to working in the wildlife job?
    - How long have you been working in the region?

Experience with carnivore-livestock conflict

2. Can you describe what **types of direct and indirect wildlife conflict** you have experience working with and for how long?

a. (e.g., eating crops, breaking fences, disease transmission risk, increasing stress on livestock, direct depredation from carnivores, etc.)

3. From your experience, what **factors seem to lead to cattle depredation**?
    - Number and distribution of wildlife (ungulates and carnivores)
    - Types of cattle (e.g., older experienced cows vs younger inexperienced cows, different breeds/crosses, etc.)
    - Time of year/ location of cattle? (e.g., calving season, when livestock are far from main ranch and difficult to monitor frequently, etc.)
    - Are there any hotspots where chronic depredation typically occurs or is it difficult to predict where conflict will occur in any given year?
4. Describe **a year where conflict was particularly bad**. What made it a bad conflict year?
    - Have you noticed a pattern?
    - How much of your time and labor go into addressing these conflicts in a bad conflict year?

Questions about wolf-elk interactions

20. Have you ever had **wolves den near cattle of ranches you work with**?
    - Did you or someone in your agency notify the ranchers of the den?
    - When wolves den near ranches you work with, do there seem to be more conflicts?

4. Have you noticed **any changes in elk populations** on ranch and grazing allotments in the area?

a. How have elk numbers on ranches you work with changed over time?

b. How have elk numbers on ranches you work with related to conflict with wolves and other carnivores?

   i. Do you think keeping the elk away from cattle would lessen conflict with carnivores?

Attitudes towards nonlethal and lethal measures

5. Do you think **management measures can mitigate conflicts** with wolves?

a. If no – why not?

b. If yes – which ones have you tried? *(open-ended question, then proceed to the below options in 8c not mentioned by interviewee)*

c. Have you tried _(method)_? Why or why not?

   i. increasing human presence (i.e., range riders/cowboys monitoring cattle)
      1. follow up: If you had the capacity to increase human presence on your operation, do you think most conflict could be mitigated?

   ii. Fencing – e.g., temp fencing, fladry, permanent fencing
   iii. Noise or light deterrents (e.g., cracker shells, airhorns, Foxlights)
   iv. Livestock guardian animals
   v. Direct hazing of carnivores when encountered
   vi. Anything else I have not listed?

6. How has your **approach to nonlethal measures changed over time**?

7. What factors do you think would make ranchers **more willing to try nonlethal measures**?

a. Possible options:
   - costs and labor were covered
   - scientific research proved the method was effective in other operations with similar scale and landscape
   - a trusted and respected rancher in the community has tried it and recommends it
   - nonlethal measures were just called proactive management practices rather than placing an emphasis on “nonlethal” because “nonlethal” is a loaded word
   - There are other factors that would make ranchers more willing to use nonlethal measures not listed here
   - Nothing would make ranchers more willing to use nonlethal measures
     - If this is the case, can you explain why?

8. What do you think makes **implementing nonlethal measures difficult** on different ranching operations?

- Size of the operation
- Difficulty of predicting where conflicts will occur and where to focus efforts
- Money
- Labor
- Access to information on where wildlife is located
- Difficult to justify spending time and money on nonlethal measures when lethal control is an effective option
- social stigma
- Other – please list

9. What conflict management **measures would you like to see tested**? Or what nonlethal measures are you most curious about and/or interested in?

- If you could design your own research experiment to test nonlethal tools, what would you want to test?

10. From your experience, what **factors motivate ranchers in the area to use a lethal control permit**? What factors seem to **prevent** them from using one?

Carnivore-livestock depredation compensation in Wyoming

11. Now, I'd like to switch gears slightly and ask about **WY's compensation program.**

a. What aspects of the program do you like? Or what aspects of the program do you find effective?

b. What aspects feel challenging? Or what aspects of the program would you change?

c. How transferable do you think this program might be to other ranching contexts (for example in other states)?

The future of carnivore-livestock conflict and its effect on ranching livelihoods

12. Looking ahead to the future, what do you think is the **future of wildlife-livestock dynamics in this place**? What are the **big changes that you want to see happen**?

13. Have your **views on wildlife/predators changed over time**? If yes, how, and what factors do you think affected your perspectives?

14. In your opinion, where would be the **best use of funds and resources to reduce conflict with carnivores?**

15. Is there anything you **wished the public would know** about what it's like to deal with carnivore-livestock conflict?

CONCLUDING REMARKS

The research laid out in this dissertation examines how wolves and people have adapted following two decades of wolf recovery. Wolves did not occur in the study area until the late 1990s, hence, their relationships to local prey have developed over the last two decades. We highlight wolves' responses to the movements of a partially migratory elk herd and how that fundamental ecological dynamic may relate to patterns of conflict. Additionally, we describe how ranchers and wildlife managers adapted to mitigate wolf depredation on livestock and built relationships to work through social challenges of sharing the landscape with wolves. By shedding light on both the ecological and social dimensions of wolf conflict, this research provides insights into wildlife and local communities in the later stages of wolf recovery.

In Chapters 1 and 2, we investigated interactions between multiple wolf packs and a partially migratory elk herd to characterize the movement and diet patterns of wolves living beyond protected areas. Chapter 1 reveals that wolves employed different strategies to track various elk subpopulations with several wolf packs engaged in migratory coupling, challenging the assumption that wolves outside of Yellowstone are spatially separated from migratory elk in the summer. Wolves that track long-distance migratory elk have distinct seasonal ranges and move young pups to multiple homesites along elk migratory routes into elk summer range. Meanwhile, some wolves track elk that migrate short distances, while other wolves remain resident and rely on elk that migrate later as well as alternate wild ungulates. To evaluate how movement strategy influences wolf prey composition, we investigated the predation and diet ecology of migratory and resident wolves in Chapter 2. We found that despite variability in movement strategies, wolf packs across a wilderness to working lands gradient maintained elk as their primary prey from winter to summer. Long-distance migratory wolves increased predation on elk while decreasing predation on alternate ungulate prey. While short-distance migratory wolves maintained elk as their primary prey in one year, they switched to cattle in the next year. Resident wolves decreased predation on elk and increased predation on alternate prey. However, despite increasing predation on other wild ungulates, the larger resident pack maintained elk as their primary prey. Meanwhile, the smaller resident pack switched to mainly consuming cattle. We learned that wolves outside of protected areas can employ a range of movement and predation strategies on a working lands frontier. In this sense, wolves have in only two decades adopted a complex set of behaviors aligned with the movement tactics of their primary prey.

What we learned in the first two chapters provides insight into the relationship between wolf-elk interactions and depredations. None of the packs tracking long-distance migratory elk killed cattle. Meanwhile, the short-distance migratory and resident wolves that maintained elk as their primary prey year-round killed fewer cattle than packs that did not. Additionally, we found that resident wolf packs increased predation on alternate wild ungulates such as deer and pronghorn to cope with the departure of elk, which may mediate depredations on livestock – supporting other research findings in the area (Nelson et al. 2016). Our research underscores wolves' reliance on elk and other wild ungulates on working landscapes while highlighting other factors that may impact conflict levels.

While our findings challenge common assumptions about conditions conducive to conflict, our study took place during a period of few cattle depredations. Investigating the drivers of wolf-livestock conflict is essential for improving mitigation strategies, but conflict levels are also shaped by management decisions. Thus, in Chapters 3, we used in-depth interviews to explore rancher and wildlife manager perspectives on conflict mitigation challenges and successes. Our findings reveal that people in the study area have employed a range of nonlethal and lethal conflict mitigation practices to reduce depredations and have built relationships to mitigate social conflict. Interviewees emphasized the importance of delisting for local control for not only decreasing physical depredations, but for also increasing tolerance for wolves and their management. This allowed for trust to be built between ranchers and on-the-ground personnel at WGFD responding to these conflicts. We recommend increased recognition, training, and support for state wildlife managers to enhance their capacity to manage and mitigate depredations, as well as address social conflict associated with managing a recovering species.

As long as there is a healthy assemblage of predators and prey in the Greater Yellowstone Ecosystem, wolf-livestock conflict in the study area will persist. However, people have found ways to adapt using a combination of nonlethal and lethal measures, resulting in reduced depredations and fewer lethal control actions. Notably, our study occurred during a period with the lowest conflict levels in the past 15 years, which may represent a new norm here. The evolving landscape of carnivore recovery is now significantly more optimistic than it was a decade ago. Previously, the recovery of large carnivores was confined to national parks and protected areas. Today, there are numerous examples of large carnivores living in working landscapes among people and livestock. Attributing this shift merely to the passage of time overlooks the decades of dedicated efforts that have made it possible. The arc of these developments illuminates a transition from an era in which compensation was the sole strategy for fostering tolerance of wolves, to an era in which a richer array of relationships and tools has begun to provide people with the resources, support, and flexibility they need to adapt. This transition accompanies a growing recognition that the people living on working lands, who are most impacted by the presence of large carnivores and other wildlife, are not barriers to their recovery and conservation, but rather stewards facilitating their expansion beyond protected areas. These research findings offer insights into how wolf recovery may unfold in other places where wolves inhabit working landscapes. We hope the lessons learned from this study can help other communities adapt more swiftly and effectively.

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