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THE SPATIAL ECOLOGY OF PREDATOR-PREY INTERACTIONS: A CASE
STUDY OF YELLOWSTONE ELK, WOLVES, AND COUGARS

by

Michel T. Kohl

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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ABSTRACT

The Spatial Ecology of Predator-Prey Interactions: A Case Study of Yellowstone

Elk, Wolves, and Cougars

by

Michel T. Kohl, Doctor of Philosophy

Utah State University, 2019

Major Professor: Dr. Daniel MacNulty

Department: Wildland Resources

Predators can serve as an important top-down driver of ecosystems via their influence on prey behavior. Although predator effects on prey behavior (or traits) may be as strong as or stronger than predator effects on prey abundance in small-scale, experimental systems, it is unclear whether behavioral effects are as dominant in large-scale, free-living systems. The *objective* of this project was to improve our ecological understanding of the spatio-temporal interactions between large predators and their primary prey source in a free-living system. Specifically, I used data from northern Yellowstone to evaluate 1) the role of predator diel activity on prey habitat selection of risky places, 2) how prey operate in a landscape composed of multiple predators that occupy different spatial and temporal niches, and 3) how the density- and behaviorally-mediated effects of large predators influence the large-scale spatial distribution of a prey population. In Chapter 2, I show that the predictability of daily wolf (*Canis lupus*) hunting activity provided an opportunity for elk (*Cervus elaphus*) to use risky places

during safe times, which in essence, flattened (i.e., minimized) the landscape of fear in Yellowstone. In Chapter 3, I show that wolves and cougars (*Puma concolor*) hunt in different places, and at different times, which provided a refugia from these predators in time and space that likely minimized overall predation risk in an environment that was spatially saturated with wolves and cougars. In Chapter 4, I show that the current spatial distribution of elk across the northern range of Yellowstone is driven primarily by demographic rather than behavioral mechanisms. Overall, the results from chapters 2-4 suggest that any trophic cascade from predators, to prey, to deciduous woody plants in Yellowstone National Park is likely due to demographic mechanisms rather than a landscape of fear. More broadly, this research identifies a previously overlooked behavioral trait of predators, diel activity, which prey can use to minimize the effects of predators on sophisticated prey. Together, this study advances the field of ecology by quantifying the ecological importance of fear in a large-scale, free-living system.

(203 pages)

PUBLIC ABSTRACT

The Spatial Ecology of Predator-Prey Interactions: A Case Study of Yellowstone Elk,
Wolves, and Cougars

Michel T. Kohl

The loss of large apex predators, and their subsequent reintroduction, has been identified as a substantial driver on the structure and function of ecological communities through behavioral mediated trophic cascades (BMTCs). The reintroduction of wolves (*Canis lupus*) to Yellowstone National Park (YNP) has served as foundational case study of BMTCs. In our system, it has been suggested that wolves have established a ‘landscape of fear’ in which the primary prey, elk (*Cervus elaphus*), now avoid risky places, which ultimately led to the recovery of the vegetation community. Although this case is frequently cited as a well-understood example of a landscape of fear, researchers never quantified whether elk avoided risky places, a critical component of the BMT hypothesis. Thus, I employed numerous quantitative approaches to evaluate the role of wolves and cougars on elk habitat selection in northern Yellowstone. The results from this work suggest that the daily activity schedule of wolves provide a temporally predictable period of risk that allows elk to use risky places during safe times. As such, diel predator activity flattened (i.e., made less risky) the landscape of fear for 16 hours per day, 7 days a week, which permitted elk to forage on deciduous woody plants despite the presence of wolves. Thus, suggests that any trophic cascade in northern Yellowstone is likely driven by the consumptive effects of wolves on elk. In addition, my results suggest that daily activity patterns are an important component of predation risk, and as

such, provide a predictable avenue for elk to avoid predators despite residing in an environment spatially saturated with wolves and cougars. Thus, the ability of elk to avoid predators through fine-scale spatial decisions provides support for my findings that the current spatial distribution of prey is largely driven by the consumptive effects of predators on the prey population, rather than a landscape of fear. In combination, these results suggest that the landscape of fear, and more generally, fear effects, may be of less relevance to conservation and management than direct killing within free-living, large landscapes.

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Michel Thomas Kohl

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CHAPTER 1

INTRODUCTION

Predators are important top-down ecological drivers with examples documented in marine, freshwater, and terrestrial ecosystems (Estes et al. 2011). Across these systems, predators attempt to kill prey, prey respond, and the consequences of those interactions ripple throughout the ecosystem. Historically, ecologists have viewed these interactions through the lens of consumption; predators capture and consume their prey. Such density-mediated interactions (DMI) are the cornerstone of ecological theory (e.g., Lotka-Volterra models), and as such, have been subjected to extensive empirical and theoretical study (Preisser et al. 2005).

More recently, ecologists have shifted their focus toward understanding the role that nonconsumptive effects (NCEs) have on these systems. NCEs are predator-caused trait changes (e.g., behavioral, morphological, physiological) that lead to a fitness consequence (Werner and Peacor 2003). Importantly, recent meta-analyses have suggested that NCEs can be as strong as or stronger than a predator's consumptive effects. These effects become more pronounced as they cascade throughout the ecosystem (e.g., predator → prey → forage resource; Preisser et al. 2005) leading to suggestions that the non-consumptive interactions between predators and prey may be a critical driver of ecosystem structure and function that has until recently been overlooked.

Questions remain, however, about the influence of these nonconsumptive interactions in large-scale, free living systems. The vast majority of these studies have occurred in small-scale, experimental systems. Furthermore, Preisser et al.'s (2005) study also highlighted the strength of consumptive effects, rather than nonconsumptive

interactions as the primary driver of predator-prey interactions within terrestrial systems. Together, this demonstrates the need to quantify the role of consumptive and nonconsumptive interactions between predator and prey in large-scale, free-living terrestrial systems.

Anti-predator behavioral responses, or behaviorally-mediated interactions (BMI), have been of particular interest to the ecological community because they constitute a key mechanism by which predators affect prey populations (Preisser et al. 2005, Zanette et al. 2011), communities (Schmitz et al. 1997, Werner and Peacor 2003), and ecosystems (Schmitz 2008, Hawlena et al. 2012). Of broad interest to both the general public and scientific community is the role of anti-predator behaviors in shaping ecosystems. In such cases, predators may induce a behavioral shift in prey populations that ultimately facilitates changes (e.g., vegetation growth) within lower trophic levels. This process, termed a trophic cascade, can occur via density- and behaviorally-mediated pathways. Although the presence of density-mediated and behaviorally-mediated trophic cascades (BMTC) occurs across biological systems, our understanding of the relative contribution of these underlying mechanisms in directing a biological system is less clear (Schmitz et al. 1997).

The ‘landscape of fear’ [LOF] has been advanced as one such mechanism that drives the effects of fear that cascade from individuals to ecosystems (Brown and Kotler 2004, Schmitz 2005, Laundré et al. 2010), including changes in prey physiology (Zanette et al. 2014), and demography (Preisser et al. 2005), plant growth (Ford et al. 2014), and nutrient cycling (Hawlena et al. 2012). The LOF is defined as a map that describes the continuous change in predation risk that an animal perceives as it navigates the physical

landscape (Laundré et al. 2001, Brown and Kotler 2004, Laundré et al. 2010). As such, the fear of predation (perceived predation risk) caused by the mere presence of a predator and its subsequent mapping (i.e., LOF) within an ecosystem is an ecological force that can rival or exceed that of direct killing (Preisser et al. 2005). Despite this, little is known about the LOF and how it may fluctuate across the diel (24-hr) cycle. Rather, most ecologists have assumed that the LOF is a fixed spatial pattern of predation risk when the predator is present. This ignores, however, the daily activity patterns of predators which are often active at only certain times of the day.

The 24 hour activity pattern of predators and prey can be broken into two distinct periods: activity and rest. These periods represent fundamental differences in energy expenditure and uptake, as well as serving important biological functions (e.g., activity periods may include territorial defense or mating behaviors). Because environmental fluctuations are relatively consistent across the 24-hour cycle (e.g., temperature, humidity changes), intra-species variability in activity cycles has the potential to directly influence fitness and thus, over evolutionary timescales, produce predictable predator activity schedules (Enright 1970). As a result, predator activity schedules should produce a period of temporal predictability which prey can use to mitigate predation risk through appropriately timed anti-predator behaviors (e.g., use risky places at safe times). If prey can efficiently manage predation risk in time and space, it may suggest that the LOF concept may be of less importance to conservation and management than direct killing.

Although it is well known that prey utilize both space and time to manage predation risk (Creel et al. 2005, Latombe et al. 2013, Middleton et al. 2013), studies rarely examine predator-prey interactions according to both spatial and temporal axes

(Creel et al. 2008). Moreover, researchers have rarely accounted for the spatial and temporal risk imposed by the entire predator community (Halle 1993). This is an important knowledge gap because when prey are making decisions about acquiring forage or avoiding predation risk, they must account for both spatial and temporal risk that includes all sources of predation risk. Moreover, in systems consisting of multiple predators, quantifying the trade-off between the foraging activity of prey and avoidance of predation has seldom been examined within the 24-hour cycle (Halle 1993, Halle and Stenseth 2000). This is a significant oversight because time is a key niche axis that predators use to minimize interspecific competition across the diel (24-hour) cycle (Ross 1986, Cozzi et al. 2012, Monterroso et al. 2013). Thus, the combination of temporal and spatial niche axes increases the availability of predator-free space. For example, in a system with two spatial domains (e.g., forest and grassland), the addition of two diel domains (e.g., night and day) increases the number of potential predator-refugia from two to four. As such, it is possible that the contrasting spatial and temporal foraging niches within a multi-predator environment may provide an avenue within which prey can avoid predators in time and space. If prey do in fact use the diel activity schedules of multiple predators, it suggests that fear responses are not as significant a driver of these systems as predictions of predator facilitation would suggest.

Given that prey may be able to manage predation risk via the predictability of diel predator activity schedules at a fine scale, and as such, minimize any fear effects, it raises questions about whether we should expect to see fear effects at larger spatial scales. Despite this knowledge gap, we know very little about the mechanisms in which predators regulate prey spatial distributions at large spatial scales. Generally, this occurs

in two ways: 1) predators either reduce the local prey population through direct consumption, or 2) predators induce shifts in habitat use (Preisser et al. 2005). Although recent work has been extensive in examining the relative role of consumptive-interactions and behaviorally-mediated interactions on prey populations, research has largely overlooked how these consequences translate upward to the large-scale spatial distribution of prey, and as such, the ecological consequences of that spatial distribution on lower trophic levels.

Habitat selection provides an ideal framework for quantifying the relative role of density-mediated and behaviorally-mediated interactions in determining the fine-scale and large-scale patterns of prey species. This is because habitat selection represents a hierarchical process in which a species first uses general features of the landscape to broadly select from among different habitat characteristics, and subsequently responds to more fine-scale habitat characteristics (Johnson 1980). Because habitat selection is the result of behavioral trade-offs across multiple scales, it can be used to quantify how prey respond to periods and places of increased risk.

To evaluate the effect of fear on prey populations within a large-scale, free living system, I evaluated the role of wolf (*Canis lupus*) and cougar (*Puma concolor*) predation risk on elk (*Cervus elaphus*) habitat selection in Yellowstone National Park (YNP). Within this context, I examined how the daily activity schedules of both predators may provide a predictable source of predation that allowed elk to use risky places at safe times. After this, I examined large-scale demographic and behavioral processes to evaluate the relative role of density-mediated and behaviorally-mediated interactions on elk spatial distribution. I do this within the Yellowstone system because it serves as an

important case study in the ecological understanding of behaviorally-mediated interactions following the reintroduction of wolves (*Canis lupus*) with broad implications for predator conservation and restoration across both marine and terrestrial systems.

In the following chapters, I provide the first comprehensive assessment of shifts in elk habitat selection in response to spatial and temporal variation in predation risk in northern Yellowstone during winter. This work differs significantly from previous analyses of elk habitat selection in northern Yellowstone. Previous work has entailed cursory examinations of elk habitat selection prior and post-wolf reintroduction using VHF telemetry (Mao et al. 2005). In addition, four studies of elk habitat selection included elk GPS data for our population that examined of elk resource selection as it relates increasing spatial heterogeneity and extent (Boyce et al. 2003), the interaction between wolf density and aspen distribution during winter (Fortin et al. 2005), and the study of elk habitat selection during summer (Forester et al. 2007, Forester et al. 2009). All of these studies have employed wolf density as their metric of predation risk, despite its potential for bias (Moll et al. 2017; also see Chapter 2). Furthermore, I was able to acquire additional unpublished data that was not previously evaluated in any these previous studies, essentially doubling the number of individuals from which to make inferences.

I focus my research efforts during winter because this represents the period in which elk habitat use overlaps with the majority of browse species, and, as such, anti-predator responses during winter have the greatest potential for affecting browse recovery. This dissertation encompasses three distinct time-frames. The primary period of interest occurs during a time of peak predator abundance, 2001-2004, and when the

first GPS data for elk in northern Yellowstone were collected. I focus on this period in chapters 2 and 3 because this period represents the timeframe when wolf numbers peaked and coincides with relatively high elk numbers. Because the elk numbers remained large during this time period, some scientists have speculated that any apparent recovery of browse species during this period must be due to a behavioral rather than numerical effect of wolves (Ripple et al. 2001, Ripple and Beschta 2003, Beschta and Ripple 2007). Two additional periods of data are included in Chapter 4. This includes a period of no wolves in which VHF data was collected and serves as a baseline for understanding site-fidelity of elk prior to wolf reintroduction. The second period includes VHF and GPS data collected from 2011-2016 when both wolf and elk numbers were lower, and potentially stable.

The existence of a BMTC in and around YNP continues to be debated within the ecological community. A BMTC relies on the assumption that prey are capable of ascertaining predation risk and responding accordingly, yet there remains a lack of understanding on whether a perceived trophic cascade in the GYE is due to density-mediated or behaviorally-mediated interactions between wolves and elk. In particular, little is known about how predator activity cycles alter anti-predator responses, and how those predator activity cycles may interact with prey habitat selection to influence the behavioral response of elk to wolves. To help shed light on this subject, I examined the influence of predator daily activity of wolves (Chapter 2) and mountain lions (Chapter 3) on elk selection of risky sites. I then examine how large-scale prey spatial distributions may be influenced by the demographic and behavioral consequences of large-predator

recovery in northern Yellowstone (Chapter 4). I then conclude with a summary chapter on the results and their importance for the larger ecological community (Chapter 5).

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CHAPTER 2

DIEL PREDATOR ACTIVITY DRIVES A DYNAMIC LANDSCAPE OF FEAR¹

ABSTRACT

A ‘landscape of fear’ (LOF) is a map that describes continuous spatial variation in an animal’s perception of predation risk. The relief on this map reflects, for example, places that an animal avoids to minimize risk. Although the LOF concept is a potential unifying theme in ecology that is often invoked to explain the ecological and conservation significance of fear, little is known about the daily dynamics of a LOF. Despite theory and data to the contrary, investigators often assume, implicitly or explicitly, that a LOF is a static consequence of a predator’s mere presence within an ecosystem. We tested the prediction that a LOF in a large-scale, free-living system is a highly-dynamic map with ‘peaks’ and ‘valleys’ that alternate across the diel (24-hour) cycle in response to daily lulls in predator activity. We did so with extensive data from the case study of Yellowstone elk (*Cervus elaphus*) and wolves (*Canis lupus*) that was the original basis for the LOF concept. We quantified the elk LOF, defined here as spatial allocation of time away from risky places and times, across nearly 1000-km² of northern Yellowstone National Park and found that it fluctuated with the crepuscular activity pattern of wolves, enabling elk to use risky places during wolf downtimes. This may help explain evidence that wolf predation risk has no effect on elk stress levels, body

¹ Kohl, M. T., D. R., Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88:638-652.

condition, pregnancy, or herbivory. The ability of free-living animals to adaptively allocate habitat use across periods of high and low predator activity within the diel cycle is an underappreciated aspect of animal behavior that helps explain why strong antipredator responses may trigger weak ecological effects, and why a LOF may have less conceptual and practical importance than direct killing.

INTRODUCTION

Fear of predation (perceived predation risk) caused by the mere presence of a predator within an ecosystem is increasingly regarded as an ecological force that rivals or exceeds that of direct killing (Preisser et al. 2005). The ‘landscape of fear’ (LOF) concept has been advanced as a general mechanism that drives the effects of fear that cascade from individuals to ecosystems (Brown and Kotler 2004, Schmitz 2005, Laundré et al. 2010), including changes in prey physiology (Zanette et al. 2014) and demography (Preisser et al. 2007), plant growth (Ford et al. 2014), and nutrient cycling (Hawlena et al. 2012). Operationally, a LOF is a map that describes the continuous change in predation risk that an animal perceives as it navigates the physical landscape (Brown and Kotler 2004, Laundré et al. 2001, 2010). This mental map of risk overlies the physical terrain like a map of soils, vegetation, or climate, and its ‘peaks’ and ‘valleys’ describe an animal’s perception of those locations as dangerous and safe, respectively (van der Merwe and Brown 2008). Risk perception is indexed by an animal’s measurable response to changes in predation risk (Lima and Steury 2005), and the continuous spatial patterning of this response approximates a LOF as originally defined by Laundré et al. (2001, 2010). Brown and Kotler (2004) defined the concept more narrowly as the spatial

distribution of the foraging cost of predation, which is fear measured as the energetic consequence of an animal's response, chiefly vigilance and (or) time allocation. No matter its definition, the LOF concept is often invoked to explain the ecological effects of fear.

Yet little is known about LOF dynamics across the diel (24-hr) cycle. To date, many ecologists have, implicitly or explicitly, assumed that a LOF is a fixed spatial pattern as long as the predator is present (but see Palmer et al. 2017). The underlying rationale is that a constant possibility of predation enforces a chronic state of apprehension in the prey (Schmitz et al. 1997, Brown et al. 1999). This 'fixed-risk' assumption of constant attack over time has been a conceptual mainstay in the study of behavioral predator-prey interactions for decades (Lima 2002). Yet it neglects how predator activity and hunting ability can vary across the diel cycle, and how this may foster a fluctuating acute state of apprehension in the prey and a dynamic LOF despite the constant presence of predators.

Many predators are only active at certain times of day, and visual predators active at night often cannot hunt in absolute darkness. These predatory constraints provide pulses of safety during the diel cycle that may temporarily relieve an animal's fear of predation and flatten its LOF. This hypothesis is broadly consistent with risk allocation theory, which predicts that animals constantly exposed to predators should respond to pulses of safety with intense feeding efforts (Lima and Bednekoff 1999). It also accords with numerous empirical studies that show how various animals (e.g., zooplankton, rodents, and ungulates) forage in risky places during periods of the diel cycle (e.g., day or night) associated with reduced predator activity and/or hunting ability (reviewed by Lima

and Dill 1990, Lima 1998, Brown and Kotler 2004, Caro 2005; see also Fischhoff et al. 2007, Tambling et al. 2012, Burkepile et al. 2013). However, these studies neither tested how animal response to spatial risk is linked to measured variation in diel predator behavior, nor showed how this linkage shapes the animal's LOF across the diel cycle. Dichotomizing continuous variation in diel predator behavior into periods of presumed safety and danger (e.g., day versus night) is potentially misleading if diel behavior does not conform to these simple categories or if animals assess predation risk as a continuous variable (Creel 2011).

This empirical gap in the LOF concept is exemplified by its founding case study of elk (*Cervus elaphus*) in northern Yellowstone National Park (YNP) following wolf (*Canis lupus*) reintroduction there in 1995-97 (Laundré et al. 2001). Although this case is frequently cited as a well-understood example of a LOF, and is one that has motivated the proposal that the LOF is a unifying concept in ecology (Laundré et al. 2010), researchers never quantified the elk LOF after wolf reintroduction, nor examined its temporal dynamics in relation to diel wolf behavior. Instead, the elk LOF was inferred from broad-scale, population-level data on vigilance behavior (Laundré et al. 2001), fecal pellets (Hernández and Laundré 2005), and herbivory (Ripple and Beschta 2004) that supported three predictions based on the LOF concept: (1) elk shifted habitat use in response to wolves, including abandonment of high-risk open areas, which (2) decreased diet quality and body fat, and (3) reduced browsing on woody deciduous plants in high risk areas (Laundré et al. 2001, 2010). Some researchers have argued that habitat shifts also reduced elk pregnancy rate (Creel et al. 2009, Christianson and Creel 2014). On the other hand, concurrent fine-scale, individual-level data on movement, body condition, and pregnancy

rate indicated elk selected for open areas (Fortin et al. 2005, Mao et al. 2005) and maintained body fat and pregnancy rate (Cook et al. 2004, White et al. 2011, Proffitt et al. 2014). And whereas one study suggested elk avoided aspen (*Populus tremuloides*) forests in response to wolves (Fortin et al. 2005), another found that elk browsed aspen irrespective of wolf predation risk (Kauffman et al. 2010). These divergent results have yet to be reconciled, and together they highlight an outstanding need to clarify the elk LOF that prevailed in YNP during the initial years after wolf reintroduction.

The overarching purpose of this study was to improve the empirical foundation of the LOF concept. Our objective was to determine how a large-scale LOF changes across the diel cycle in response to the daily activity pattern of a predator that is always present. Because the response of Yellowstone elk to wolf reintroduction is a seminal yet unresolved example of a LOF, we examined the elk LOF in northern YNP within the first decade after wolves were released.

We defined the elk LOF as spatial allocation of time away from risky places and times. This conforms to Laundré et al.'s (2001, 2010) broad definition and approximates Brown and Kotler's (2004) narrower definition. The latter is possible because research indicates that Yellowstone elk manage wolf predation risk mainly through time allocation, keeping vigilance levels constant across habitats that vary in predation risk (e.g., near versus far from forest cover) and increasing vigilance only when wolves are an immediate threat (Childress and Lung 2003; Lung and Childress 2007; Winnie and Creel 2007; Creel et al. 2008; Liley and Creel 2008; Gower et al. 2009; Middleton et al. 2013a).

To assess spatial time allocation, we conducted a retrospective habitat selection analysis of data collected during 2001-2004 from 27 female elk equipped with global

positioning system (GPS) radio collars. This included 13 unique elk from Fortin et al. (2005), 2 more from Boyce et al. (2003), 1 more from Forester et al. (2007, 2009), and 11 more whose data were never published. Together, these were the first elk GPS location data ever collected in YNP, and we used them to quantify the elk LOF across 995-km² of northern YNP. We tested how this large-scale LOF varied across the diel cycle in relation to the daily activity pattern of wolves which we estimated from direct observations of hunting behavior (1995-2003) and GPS location data (2004-2013). We predicted a dynamic LOF with peaks and valleys that alternated across the diel cycle in response to daily lulls in wolf activity.

METHODS

Study Area

Our study occurred in a 995-km² area of northern YNP (44° 56' N, 110° 24' W) where the climate is characterized by short, cool summers and long, cold winters (Houston 1982). Low elevations (1500-2000 m) in the area create the warmest and driest conditions in YNP, providing important winter range for ungulates, including elk. Vegetation includes montane forest (44%; e.g., lodgepole pine [*Pinus contorta*] and Douglas fir [*Pseudotsuga menziesii*]), open sagebrush–grassland (37%; e.g., Idaho fescue [*Festuca idahoensis*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], and big sagebrush [*Artemisia tridentata*]), upland grasslands, wet meadows, and non-vegetated areas (19%) (Despain 1990).

Study Population

We analyzed habitat selection behavior of 27 adult (> 1 year-old) female elk that spent winter in northern YNP and adjoining areas of the Yellowstone River valley outside YNP from about 15 October to 31 May, 2001-2004. These elk were from a migratory population that numbered from 8,300-13,400 individuals. Our sample of adult female elk was captured in February (2001-2003) via helicopter net-gunning (Hawkins and Powers, Greybull, Wyoming, USA; Leading Edge Aviation, Lewiston, Idaho, USA) and fitted with Telonics (Telonics, Mesa, Arizona, USA) or Advanced Telemetry Systems Inc. (Isanti, Minnesota, USA) GPS radio-collars ($\bar{x} \pm \text{SD}$ location error = 6.15 ± 5.24 m; Forester et al. 2007) programmed to collect locations at 4-6 hour intervals (5 hour intervals: $n = 23$; alternating between 4 and 6 hour intervals: $n = 4$). To control for movements associated with migratory behavior, we limited our analysis to winter locations collected from 1 November – 30 April. If individuals arrived on the winter range after 1 November, data were censored to the individual's arrival date (1-22 November). Location data for each individual were collected for 30-353 days ($\bar{x} \pm \text{SD} = 124.5 \pm 12.5$) across 1-3 winters until collar failure, collar removal, or animal death. We censored location data to include only high-quality locations following guidelines developed by Forester et al. (2009).

Elk age was estimated using cementum analysis of an extracted vestigial upper canine (Hamlin et al. 2000), and pregnancy was determined from a serum sample using the pregnancy-specific protein B assay (Sasser et al. 1986, Noyes et al. 1997, White et al. 2011). We evaluated elk nutritional condition with a rump body condition score developed for elk and maximum subcutaneous rump fat thickness measured using an

ultrasonograph (Cook et al. 2004). We estimated ingesta-free body fat percentage using the scaled LIVINDEX, which is an arithmetic combination of the rump body condition score and maximum rump fat thickness allometrically scaled using body mass estimated from chest girth measurements (Cook et al. 2004).

Wolves in this study were members or descendants of a population of 41 radio-collared wolves reintroduced to YNP in 1995-1997 (Bangs and Fritts 1996). The study occurred during a time of peak wolf abundance in YNP: wolf numbers in northern YNP ranged from 70-98 individuals in 4-8 packs (Cubaynes et al. 2014). Each winter, 20-30 wolves, including 30-50% of pups born the previous year, were captured and radio-collared (Smith et al. 2004). Wolves were fitted with very high frequency (VHF; Telonics Inc., Mesa, AZ, USA) or GPS (Televilt, Lindesberg, Sweden; Lotek, Newmarket, ON, Canada) radio-collars. Locations of VHF- and GPS-collared wolves were recorded approximately daily during two 30-day periods in early (mid-November to mid-December) and late (March) winter, when wolf packs were intensively monitored from the ground and fixed-wing aircraft, and approximately weekly during the rest of the year. Wolf GPS collars recorded locations every hour during the 30-day periods and at variable intervals outside these periods. The proportion of the Yellowstone wolf population that was radio-collared ranged from 35-40% and included all wolf packs in the study area. We captured and handled wolves and elk following protocols in accord with applicable guidelines from the American Society of Mammalogists (Sikes 2016) and approved by the National Park Service Institutional Animal Care and Use Committee.

Diel activity patterns

We used movement rate to index diel wolf activity given that speed of locomotion is a valid proxy for diel activity patterns in large mammals (Ensing et al. 2014). We estimated movement rate at each hour of the day from the hourly positions of 21 GPS-collared wolves recorded in northern YNP during early and late winter, 2004-2013. Wolf GPS data were unavailable prior to 2004. Movement rate equaled the average Euclidean distance of the preceding 1-hour or 5-hour time step. We used hourly movement rate (km/hr) to describe the diel pattern in wolf activity and 5-hour movement rate (km/5-hrs) to test how diel wolf activity influenced elk selection of safe and risky places. We used 5-hour movement rate in the habitat selection analysis to match the 5-hour time interval between consecutive elk locations. To generalize the 1-hour data to 5-hour data, we retained every fifth location beginning with the first 5-hour location available. We used only consecutive 1-hour or 5-hour locations to calculate movement rates.

We estimated the population-level pattern in diel movement rate with generalized additive mixed models (GAMMs) separately fitted to the 1-hour and 5-hour locations using the *mgcv* package (version 1.8.0) in R 3.2.3. Because movement data were heavily right skewed (e.g., Fortin et al. 2005), we fit the GAMM using the negative binomial family and incorporated performance iterations such that the scale parameter was as close to 1 as possible. We applied a cyclic cubic regression spline so that the first and last hour of the day matched in accordance with the diel cycle. We included a random intercept for individual identity to account for repeated measurements of individuals across the study.

Each wolf provided an independent measure of movement rate because it was solitary or the sole GPS-collared wolf in a pack, or rarely associated with other GPS-

collared pack members. The latter was limited to 3 pairs of GPS-collared wolves that were nominally in the same pack during a 30-day period. The proportion of simultaneous fixes that wolves in each pair were near each other (< 2 km) was low: 3%, 6%, and 22%. We could not distinguish between individual and annual variation in wolf diel activity patterns because the number of individuals sampled within years was too small (Appendix 1: Table S1). Thus, our estimate of diel activity is a population-level estimate calculated as a univariate function of time of day. It is also a seasonal average that subsumes an approximate 3-hour shift in the timing of dawn and dusk between 1 November and 30 April that may add variation to hourly measurements of activity. We used this same approach to model the average winter diel activity pattern of GPS-collared elk, which we did for illustrative purposes. All of our major inferences were based on analyses of elk habitat selection.

We used the estimated 5-hour wolf movement rate as the covariate for diel wolf activity in the habitat selection analysis. We checked that our estimate of diel wolf activity was a valid index of diel hunting pressure during the study period by comparing mean 1-hour diel movement rate to the hourly distribution of directly observed daylight (0700-2000) encounters between wolves and elk in winter from 1995-2003. These behavioral data were independent of the wolf GPS data we used to calculate diel activity. An encounter was defined as wolves approaching, harassing, chasing, and (or) grabbing elk. Details about how we observed and recorded wolf-elk encounters are described elsewhere (MacNulty et al. 2007).

A concurrent cause-specific mortality study established that wolves were the primary predator of our sample of adult female elk; only one case of cougar-caused

mortality was documented (Evans et al. 2006). Analyses of wolf-killed prey during our study period also revealed that elk comprised 90-96% of prey species killed by wolves during winter (Smith et al. 2004; Metz et al. 2012). Together, these studies indicate that the opportunity to kill elk was a key driver of wolf activity in our study area during the study period (2001-2004).

Spatial variation in wolf predation risk

We considered multiple indices of spatial variation in wolf predation risk because it is unclear how elk perceive spatial risk (Beschta and Ripple 2013, Kauffman et al. 2013, Moll et al. 2017). We calculated four indices of spatial risk: predicted occurrence of wolf-killed elk (Kauffman et al. 2007, 2010), density of wolf-killed elk (Gude et al. 2006), openness (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005), and wolf density (Fortin et al. 2005, Mao et al. 2005, Forester et al. 2007). Kill sites are a well-established metric of predation risk in wildlife systems (e.g., Hopcraft et al. 2005, Thaker et al. 2011, Gervasi et al. 2013, Lone et al. 2014). All spatial risk indices (30 x 30 m grid cell) were developed using the Geospatial Modelling Environment or ArcGIS 10.1.

Predicted kill occurrence - We used a previously published model to predict the spatial distribution of wolf-killed elk in northern YNP during each winter of our study (Fig. 2-1a). Kauffman et al. (2007) developed this model to understand elk response to wolf predation risk in northern YNP. It estimates the relative probability of a kill on the landscape compared to random locations based on the landscape attributes of 774 locations of wolf-killed elk. These kills included all age and sex classes and were documented in winter during a period (1996-2005) that encompassed the present study.

Landscape attributes included annual distribution of wolf packs (based on cumulative kernel densities weighted by pack size), relative elk density (from an elk habitat model; Mao et al. 2005), proximity to streams, proximity to roads, habitat openness (forest vs. grassland), slope, and snow depth. The model predicts kill occurrence with respect to the average value of each landscape attribute, such that a predicted kill occurrence of 1 equals no difference between the location of interest and the average landscape, whereas a predicted kill occurrence of 10 equals a kill probability 10 times greater than average for a given year. This produces a year-specific range of values that did not exceed 245 for any year. For example, the range in winter 2000-01 was 0 – 36.5 whereas the range in winter 2001-2002 was 0 – 245.

Kill density - We used a kernel density estimator (KDE) to estimate the spatial distribution of wolf-killed adult female and calf elk in northern YNP during each winter of our study (Fig. 2-1b). We excluded kills of adult males because their spatial distribution differed from that of adult females and calves (Pearson's correlation coefficient, $r = 0.39$; Appendix 1: Fig. S1), and we sought to control for possible behavioral responses of adult female elk to sex-specific kill distributions. A total of 235 wolf-killed adult female and calf elk were recorded across the 4 winters (Nov. 2000 – Apr. 2004) following established protocols (Smith et al. 2004). The number of kills included in each annual kill density KDE ranged from 44-84. Following previous studies, we used a fixed bandwidth of 3 km (Fortin et al. 2005). Annual kill density KDEs were standardized from 0 – 1.

Openness - We calculated openness (Fig. 2-1c) as the sum of non-forested cells within a 500 x 500 m moving window centered on each grid cell (range 0 [deep forest] – 289 [open grassland]) following Boyce et al. (2003). We obtained information on the spatial distribution of vegetation types in northern YNP from databases provided by the YNP Spatial Analysis Center. Non-forested pixels were identified from a 1991 vegetation layer which accounted for vegetative changes following the 1988 fires in and near YNP (Mattson et al. 1998). We used this layer to calculate openness because it permitted direct comparison with contemporaneous northern Yellowstone elk habitat selection studies that also utilized the 1991 vegetation layer (e.g., Boyce et al. 2003, Fortin et al. 2005, Mao et al. 2005). We verified that our map of openness was representative of conditions during the study period by comparing it to one calculated from a 2001 LANDFIRE vegetation layer (landfire.gov). We developed and analyzed a single map of openness because there was no inter-annual variation in openness during the study.

Wolf density - We estimated wolf density (Fig. 2-1d) from winter aerial wolf telemetry locations that were randomly filtered to obtain a single location per pack per day given that packs often included more than one radio-collared wolf. We calculated a least-squares cross-validation fixed smoothing factor (H) for each pack with at least 25 locations per winter using Animal Space Use 1.3. Using all non-redundant locations, we used mean H (1 km) to calculate annual winter bi-weight kernel densities weighted by pack size (Forester et al. 2007). Annual wolf density KDEs were standardized from 0 – 1.

Elk habitat selection

We analyzed elk habitat selection using matched case-control logistic regression (CCLR). We used a 1:3 empirical sampling design (Fortin et al. 2005, Forester et al. 2009) where, for each end location of a movement step, 3 available locations were sampled with replacement from each individual's respective step-length and turning-angle distributions. Each set of 4 locations defines a unique stratum (k). Successive strata ($k = 10,199$) were not independent. Although this autocorrelation does not affect estimated coefficients it does bias the associated standard errors (Fortin et al. 2005). We calculated robust standard errors by specifying an intragroup correlation in our model (Craiu et al. 2008). Groups were clusters of strata ($n = 1,080$ clusters) assigned sequentially to each individual each winter and defined by a step-lag at which the autocorrelation was nearly zero. Autocorrelation analysis indicated that this step-lag was 15 steps, such that steps separated by 75 hours were independent.

We used a CCLR (where each observed step was compared to a sample of available steps that originated from the same starting location) to estimate the parameters of a resource selection function, $\exp(Z' \beta)$, where Z is a vector of environmental covariates, and β is a vector of selection coefficients (Forester et al. 2009, Merkle et al. 2017). The CCLR model describes the relative probability of a movement step, p , which is the straight-line segment between successive locations at 5-hour intervals. Movement steps with a higher score relative to the set of possible steps have higher odds of being chosen by an animal (Fortin et al. 2005). The sign of the relationship between p and spatial risk indicates steps toward or away from risky places: a positive relationship indicates steps toward risky places whereas a negative relationship indicates steps away

from risky places. Values of p that depict these relationships reflect different levels of perceived predation risk that correspond to the ‘peaks’ and ‘valleys’ in a LOF: minimum values identify peaks (high perceived predation risk) and maximum values identify valleys (low perceived predation risk). We rescaled predicted values of p to present an intuitive visualization of the elk LOF (see below).

Our step selection model does not estimate behavioral state per se (e.g., rest, forage, and travel) because our data derive from first generation GPS radio-collars which provided only location data. We assume elk were foraging when they selected for open areas because in our system elk are mainly grazers that feed in open grasslands and rest in wooded areas (Houston 1982, Creel et al. 2005, Mao et al. 2005, Christianson and Creel 2007, 2009). Current GPS radio-collars that also provide accelerometer data will allow future studies to link step selection with direct estimates of behavioral state (Mosser et al. 2014, Collins et al. 2015)

We could not estimate the main effect of mean 5-hour wolf movement rate because it did not vary within a stratum owing to how used and available locations within a stratum share the same point in time. Within the case-control design of our model, spatial risk variables assigned to each of the three control locations came from the same year in which the use location occurred. Because results did not differ between models fitted to all clusters and models fitted to every other independent cluster ($n = 2$ independent datasets), we present results from the analysis of all the clusters.

For each spatial risk index, we developed a ‘space-only’ habitat selection model and compared it to a ‘space \times activity’ model that included terms for the interaction between spatial risk and mean 5-hr wolf movement rate. The space \times activity model

evaluated how elk selection for risky places at the end of a 5-hour movement step was affected by the mean wolf movement rate during that step. Because prey may not respond instantaneously to predator activity due to imperfect knowledge (Brown et al. 1999), optimal foraging strategies (Kie 1999), shell games (Mitchell and Lima 2002), large landscapes (Middleton et al. 2013a), or a combination thereof, we evaluated the potential for a behavioral lag in habitat selection up to the preceding behavioral step (i.e., 5 hours). We tested different forms of the relationship between habitat selection and spatial risk in the space-only analysis and compared the best-fit space-only model to the best-fit forms in the space \times activity analysis. This was necessary to account for how elk in northern YNP may tolerate low levels of spatial risk (Fortin et al. 2005, Mao et al. 2005). We tested for a response threshold by comparing models with a linear effect for spatial risk to models with a threshold effect specified by two linear splines. We performed a grid search of candidate CCLR models to determine the presence and position of thresholds. To control for outliers, we imposed constraints such that the threshold occurred within 1 – 99% of all used data points for a given spatial risk index. This resulted in a range of candidate models ($n = 41$ -288) depending on the precision (i.e., decimal units) and scale (i.e., difference in minimum/maximum values) of the spatial risk index. We compared models using the quasi-likelihood under independence criteria (QIC, Pan 2001), which considers independent clusters of observations while also accounting for non-independence between subsequent observations (Craiu et al. 2008).

We performed 1,000 iterations of a 5-fold cross validation for case-control design to evaluate the predictive accuracy of each best-fit model (Boyce et al. 2002, Merkle et al. 2017). Location data were partitioned into five equal sets and models were fitted to

each 80% partition of the data, while the remaining 20% of the data were withheld for model evaluation. Within a cross-validation, the estimated probabilities were binned into 10 equal bins and correlated with the observed proportion of movement steps within the evaluation set. This yielded an average Spearman rank correlation (r_s). Correlations > 0.70 indicate satisfactory fit of models to data (Boyce et al. 2002). CCLR analyses and k -folds cross validations were performed in R 3.0.2 using the SURVIVAL and HAB packages, respectively.

Visualizing the landscape of fear

We used predicted values from our best-fit space \times activity step-selection model to visualize the elk LOF in a region of northern YNP that we sampled as available. For simplicity, we focused on a single index of spatial risk: kill density. We calculated the predicted relative probability of a movement step, p , at each level of kill density at each hour of diel wolf activity. We rescaled these values ($1 - p$) and used the results to elevate the 2-dimensional kill density layer in ArcScene 10.2. Rescaling was necessary so that higher elevations indicated increasing levels of perceived predation risk as per the LOF concept. We constructed a static visualization at two hours when wolf activity was highest (1100: 2.80 km/5-hour) and lowest (1600: 1.42 km/5-hours), and an animated visualization that showed perceived predation risk at each hour of the diel cycle (0000-2300).

RESULTS

Most GPS-collared wolves (19 of 21) were crepuscular such that their hourly movement rates followed: morning > evening > night > day (Fig. 2-2a). There was less individual-level variation during peak morning hours than during peak evening hours, indicating that morning was a more reliably active period. The population-average pattern in hourly movement rate during 2004-2013 matched the hourly distribution of directly-observed daylight wolf encounters with elk ($r = 0.79$; $N = 502$ encounters; Fig. 2-2a) during 1995-2003. A similar and slightly stronger association was evident when we limited the encounter data to actual kills ($r = 0.87$, $N = 89$ kills). This suggests that diel variation in wolf movement rate was a meaningful index of diel variation in wolf predation risk. It also suggests, together with evidence that the crepuscular pattern in Fig. 2-2a was consistent across years (Appendix 1: Fig. S2), that the crepuscular pattern during 2004-2013 was representative of the crepuscular pattern during 2001-2004 when elk location data were recorded.

We estimated wolf movement rate as distance travelled per 5 hours to match the time interval between consecutive elk locations. This shifted the timing of wolf activity to later in the day but it did not alter the crepuscular pattern (Fig. 2-2b). The mean diel movement rate (km/5-hrs) of elk was similarly crepuscular except that the timing of high and low movement rates was opposite that of wolves: elk movement was greatest at dusk and less at dawn (Fig. 2-2b). Correlation between wolf and elk movement rates was moderate ($r = 0.58$).

Irrespective of diel wolf movement, the influence of spatial risk on elk habitat selection was inescapably nonlinear. For each spatial risk index, the best-fit space-only

model included a linear spline for spatial risk (Appendix 1: Table S2), indicating a threshold at which the effect of spatial risk on habitat selection changed. Evidence against a model describing a simple linear relationship between spatial risk and habitat selection was strong for predicted kill occurrence ($\Delta\text{QIC} = 347.13$), kill density ($\Delta\text{QIC} = 78.72$), openness ($\Delta\text{QIC} = 16.35$), and wolf density ($\Delta\text{QIC} = 9.98$; Appendix 1: Table S2). The best-fit models indicated that elk preferred increasingly risky places at low levels of spatial risk ($P < 0.01$; Appendix 1: Table S3) perhaps due to more food in these areas. At high levels of spatial risk, the effect of risk on habitat selection was negative (wolf density; $P = 0.02$), positive (kill density, $P < 0.01$; openness, $P < 0.001$), or nil (predicted kill occurrence; $P = 0.76$; Appendix 1: Table S3).

Support for the best-fit space-only models was substantially weaker compared to models that included space \times activity interactions between mean diel movement rate (km/5-hrs) of wolves (Fig. 2-2b) and linear splines for predicted kill occurrence ($\Delta\text{QIC} = 126.73$), kill density ($\Delta\text{QIC} = 95.28$), openness ($\Delta\text{QIC} = 200.98$), and wolf density ($\Delta\text{QIC} = 35.28$; Appendix 1: Table S4). The best-fit space \times activity model included a time lag of 2 hour (kill density, openness, wolf density) or 3 hours (predicted kill occurrence; Appendix 1: Table S4). Five-fold cross validation revealed strong correlations between observed and predicted values for the best-fit space \times activity models that included predicted kill occurrence (mean Spearman-rank correlation, $r_s = 0.99$), openness ($r_s = 0.99$), and kill density ($r_s = 0.97$). Correlations of this magnitude indicate that these models are reliable. By contrast, the reliability of the model that included wolf density was poorer ($r_s = 0.67$), consistent with earlier findings that wolf density is an inaccurate index of spatial risk in northern YNP due to wolf packs

displacing one another from the best hunting grounds where they kill elk (Kauffman et al. 2007). We therefore excluded the wolf density model from further consideration.

Negative space \times activity interactions before or after thresholds in predicted kill occurrence ($P < 0.001$; before threshold), kill density ($P < 0.001$; after threshold), and openness ($P < 0.001$; before and after threshold; Appendix 1: Table S5) showed that elk avoided open grasslands and places where kills occurred when wolf activity was high, but selected for these places when wolf activity was low (Fig. 2-3a-c). Habitat selection probably did not vary beyond a predicted kill occurrence of 4.5 (Fig. 2-3a; $P = 0.87$; Appendix 1: Table S5) because there were few places where the predicted kill occurrence was more than 4.5 times the average kill probability; together, these places comprised only 7% of the study area.

To assess the time of day that elk selected for risky places, we calculated the bi-hourly frequency that elk steps ended in these places. A place was ‘risky’ if it exceeded the average value of a spatial risk index measured across all available locations in the study area. For example, 10.5% of 4084 elk steps ending in places that exceeded the study area’s mean predicted kill occurrence (4.5) happened at 0400-0500, whereas 5.5% of these steps happened at 1200-1300 (Fig. 2-3d). Steps ending in risky places were most frequent from 2200-0500, which corresponded to the nightly lull in wolf activity (Fig. 2-3d-f).

To illustrate the effects of diel wolf activity on the elk LOF, we focused on kill density in a portion of our study area (Fig. 2-4a). Using our best-fit space \times activity model for this index (Fig. 2-4b), we show that places where kills were densely concentrated were valleys (low perceived predation risk) when wolf activity was low

(Fig. 2-4c) and peaks (high perceived predation risk) when wolf activity was high (Fig. 2-4d). Wolf downtime allowed elk to use places where wolves were more likely to kill them, flattening the LOF every night for about 12 hours (Fig. 2-3d-f, Appendix 1. Fig. S4). This may explain why prime-aged (2-11 years-old) elk in our sample were in excellent body condition (% ingesta-free body fat; $\bar{x} \pm \text{SE} = 10.12 \pm 0.18$, $n = 13$) with high pregnancy rate (0.89 ± 0.11 , $n = 15$) when radio-collared at midwinter.

DISCUSSION

The landscape of fear (LOF) has been proposed as a possible unifying concept in ecology that explains animal behavior, population dynamics, and trophic interactions across diverse ecosystems (Brown and Kotler 2004, Schmitz 2005, Heithaus et al. 2009, Laundré et al. 2010, Catano et al. 2016). It has also been argued that effective ecological restoration may depend on reestablishing landscapes of fear because fear may be as or more important than direct killing in structuring food webs and modifying ecosystem function (Manning et al. 2009, Suraci et al. 2016). Doubts about the conceptual and practical importance of the LOF stem from a dearth of information about it how it operates across large spatial scales in free-living systems involving apex predators and highly mobile prey (Hammerschlag et al. 2015). We addressed this gap with extensive data from the Yellowstone elk-wolf case study that was the original basis for the LOF concept.

An important aspect of our study is that we measured the LOF as a spatial mapping of time allocation (avoiding risky places and times). This approach accords with the original and widely applied definition of a LOF as a spatial mapping of “any measure

of fear” (Laundré et al. 2001, 2010), but differs from the definition of a LOF as a spatial mapping of an animal’s foraging cost of predation (Brown and Kotler 2004). The latter is calculated from giving-up densities which are difficult to measure across vast landscapes like the one we studied (see Bedoya-Perez et al. 2013 for details about the practical uses of giving-up densities). Reconciling the two definitions is important because analyses of a single fear response may describe a landscape that is qualitatively different from a landscape of predation foraging cost, which is an integrative measure of fear that accounts for potential differences in how animal vigilance and time allocation vary with predation risk. For example, if an animal increases its vigilance while foraging in risky places, these places will appear as valleys in a map of time allocation and as peaks in a map of predation foraging cost, thus masking potential ecological effects of fear. Alternatively, if an animal manages risk mainly with time allocation (keeping vigilance constant across safe and risky places), or if vigilance and time allocation respond similarly to temporal variation in risk (decreasing vigilance while foraging in risky places at safe times; Lima and Bednekoff 1999), then the two maps will agree. Constant vigilance provides perfect agreement (Brown 1999), whereas vigilance that covaries with time allocation may provide relatively less relief (lower peaks, shallower valleys) in the map of time allocation, thus underestimating the foraging cost of predation.

Evidence that adult female elk in northern Yellowstone (and adjacent areas) maintain constant vigilance levels across habitats that vary in wolf predation risk (high vs. low wolf densities, near vs. far from forest cover: Childress and Lung 2003, Lung and Childress 2007, Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008) suggests our map of time allocation (Fig. 2-4c-d) matches a map of predation foraging cost. These

elk increase vigilance levels only when wolves are an immediate threat (Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008, Gower et al. 2009, Middleton et al. 2013a) because they can simultaneously process their food and scan their surroundings (Fortin et al. 2004, Gower et al. 2009) as well as escape wolves that attack them (MacNulty et al. 2012, Mech et al. 2015). In general, animals, especially food-limited ones, are expected to use little or no vigilance when they can escape predators in the absence of vigilance (Brown 1999).

On the other hand, if elk vigilance is sensitive to short-term (≤ 24 hours) temporal variation in wolf predation risk as many studies report (Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008, Gower et al. 2009, Middleton et al. 2013a), then elk may increase vigilance in risky places during periods of the diel cycle when wolves are most active. This is an open question because studies have yet to test how spatial variation in elk vigilance changes across the diel cycle. Nevertheless, theory predicts that an animal's vigilance level (and its predation foraging cost) should track its predator encounter rate which is itself a function of predator activity level (Houston et al. 1993, Brown 1999, Lima and Bednekoff 1999). If so, elk should reduce vigilance when foraging in risky places during lulls in wolf activity when encounters are infrequent (Fig. 2-2a) leading to a map of predation foraging cost with more relief than is evident in our map of time allocation (Fig. 2-4c-d).

The large scale of our estimated LOF is also notable. Among studies that have mapped animal response to spatial variation in predation risk in accord with the LOF concept, none mapped areas much larger than 1-km² (Shrader et al. 2008, van der Merwe and Brown 2008, Druce et al. 2009, Willems and Hill 2009, Abu Baker and Brown 2010,

Emerson et al. 2011, Matassa and Trussell 2011, Iribarren and Kotler 2012, Coleman and Hill 2014). Many maps purported to describe a LOF are not based on measurements of animal response to spatial risk (e.g., Kauffman et al. 2010, Madin et al. 2011, Catano et al. 2016). A common misconception is that spatial risk by itself defines a LOF.

The role of diel predator activity

We make two important advances with our results. First, we demonstrate that diel predator activity is a crucial driver of a LOF. In the large-scale, free-living system we studied, the mere presence of a predator was a necessary but insufficient condition to stimulate a LOF. Had we adopted the classic fixed risk assumption of constant attack over time (Lima 2002) by ignoring diel predator activity, we would have concluded, incorrectly, that our focal prey population had little fear of risky places (Appendix 1: Table S3). Instead, our consideration of diel predator activity revealed a LOF with peaks and valleys that oscillated across the diel cycle according to the predator's activity rhythm (Fig. 2-4, Appendix 1: Fig. S4). This temporally-sensitive response aligns with the 'risk allocation hypothesis' (Lima and Bednekoff 1999) which predicts that animals in high-risk environments take maximal advantage of safe times to forage in risky places, and with numerous day-night and light-dark comparisons that show how many taxa (e.g., zooplankton, rodents, and ungulates) use risky places at times of the day when predator activity or hunting ability is minimal (Lima and Dill 1990, Lima 1998, Brown and Kotler 2004, Caro 2005, Fischhoff et al. 2007, Tambling et al. 2012, Burkepile et al. 2013, Palmer et al. 2017).

However, previous studies of diel predator effects on prey habitat use neither quantified a LOF nor linked it to measured variation in diel predator activity as we did.

These studies only compared habitat use between day and night, or light and dark periods. This approach would have obscured our results because wolf activity was a complex function of time of day that did not neatly fit the conventional dichotomy of safe and dangerous periods (Fig. 2-2). As far as we know, our study is the first to quantify how continuous variation in spatial predation risk (Fig. 2-1) and diel predator activity (Fig. 2-2) interact with one another to affect an animal's habitat selection (Fig. 2-3, Appendix 1: Table S5) and, ultimately, its LOF (Fig. 2-4, Appendix 1: Fig. S4).

Ecologists have only recently started to investigate the influence of diel predator activity on animal habitat selection (Fischhoff et al. 2007, Tambling et al. 2012, Burkepile et al. 2013). Many of the classic studies of diel predator effects, including zooplankton diel vertical migration (Iwasa 1982) and rodent response to moonlight (Kotler et al. 1991), considered diel changes in the ocular capability of visual predators (Gibson et al. 2009, Upham and Hafner 2013) rather than diel predator activity per se. This aspect of predator-prey interactions deserves more attention because the prevalence of diel activity patterns in apex predators across diverse ecosystems (e.g., Theuerkauf et al. 2003, Roth and Lima 2007, Whitney et al. 2007, Andrews et al. 2009, Cozzi et al. 2012) suggests that it is a potentially common driver of landscapes of fear.

Diel predator activity was an important driver of the landscape of fear in the system we studied because it was a valid source of risk that prey could evidently perceive. Wolves are cursorial hunters that find and select prey by actively searching the environment and visually identifying vulnerable prey that are safe to kill (MacNulty et al. 2007, Mech et al. 2015). The risk of wolf predation is therefore low when wolves are not highly active. This is illustrated in our data by how the frequency at which wolves

encountered, attacked, and killed elk mirrored changes in wolf activity levels (Fig. 2-2a). The low levels of nighttime activity that we documented is consistent with the hypothesis that wolves avoid hunting at night because their vision is best adapted to crepuscular light (Kavanau and Ramos 1975, Roper and Ryan 1977, Theurerkauf 2009). This may explain why wolves in Yellowstone and most other regions exhibit a crepuscular activity pattern (Theurerkauf et al. 2003, Theurerkauf 2009).

The strong statistical association between elk habitat selection and diel wolf activity across three different measures of spatial risk (Fig. 2-3, Appendix 1: Table S5) implies that elk perceived diel variation in wolf activity. How elk did this is not obvious from our data. The lagged influence of wolf activity on elk habitat selection (Fig. 2-3d-f, Appendix 1: Table S5) suggests that elk did not perfectly perceive changes in wolf activity. Or it could reflect a deliberate tradeoff between safety and food in which elk accepted a higher likelihood of wolf encounter in exchange for more time in preferred foraging habitats. Support for this hypothesis is given by the temporal distribution of elk steps in risky places, which shows that elk minimized their steps in risky places after wolf activity peaked in the morning and started increasing their steps back into these places before wolf activity dipped in the afternoon (Fig. 2-3d-f). Elk probably tolerate a modest likelihood of wolf encounter because they often survive encounters (MacNulty et al. 2007, Mech et al. 2015). The success of wolves hunting elk in northern YNP during the study period rarely exceeded 20% (Smith et al. 2000, Mech et al. 2001) and dropped below 10% when wolves hunted adult elk (MacNulty et al. 2012). After accounting for herd size, success rate per elk was as low as 1-3% (Mech et al. 2001).

The landscape of fear in northern Yellowstone

Our second key advance is that we provide the first approximation of the elk LOF that prevailed in northern YNP following wolf reintroduction in 1995-1997. This matters to the discipline of ecology and the practice of conservation because this particular case study is an empirical cornerstone in the LOF concept (Laundré et al. 2001, 2010). Moreover, this case study is a seminal example in broader debates about the ecological consequences of fear (Ripple and Beschta 2004, Zanette et al. 2011) and the importance of apex predators to the structure and function of ecosystems (Terborgh and Estes 2010, Dobson 2014). Our central finding is that wolves established an elk LOF that was not as relentlessly intimidating as originally proposed and subsequently argued. On the contrary, our results indicate that wolves established a dynamic LOF that shifted hourly with the ebb and flow of wolf activity. Whereas previous studies reported that elk behaviorally abandoned risky places in response to the mere presence of wolves, our research reveals that elk maintained regular use of these areas during nightly lulls in wolf activity. This finding is important because many hypotheses about the ecological effects of the elk LOF in the Greater Yellowstone Ecosystem (GYE) assume that elk abandon risky places when wolves are present.

For example, the ‘predator-sensitive food hypothesis’ that fear of wolves decreases elk pregnancy rate via increased over-winter fat loss assumes that females move into the protective cover of nutritionally-improverished forests when wolves are present, reducing their use of preferred grassland foraging habitats that have high predation risk (Creel et al. 2009). Although our study is the first to show how female elk can safely use grasslands when wolves are present, prior studies of 243 females across

four GYE elk populations (northern Yellowstone, Madison headwaters, Lower Madison, Clarks Fork) have shown that wolf presence does not exclude female elk from grasslands (Fortin et al. 2005, Mao et al. 2005, Proffitt et al. 2009, White et al. 2009a, Middleton et al. 2013a). Counter evidence is limited to one study of fewer than 14 females in one GYE elk population (Gallatin Canyon; Creel et al. 2005), and a gender-blind study of fecal pellet distributions in northern Yellowstone during summer (Hernandez and Laundré 2005) when predator-sensitive food effects are not expected (Creel et al. 2009).

Fortin et al.'s (2005) study is frequently cited as evidence that wolves exclude elk from grasslands (e.g., Schmitz et al. 2008, Creel et al. 2009, Creel and Christianson 2009, Creel et al. 2011). However, its results are more ambiguous than often acknowledged. Elk were found to prefer conifer forests to grasslands where wolves were numerous, but they were also *more* likely to use grasslands as local wolf densities increased (Fortin et al. 2005: Fig. 2-3). Confusing matters further, our study, which included the elk studied in Fortin et al. (2005), indicated that wolf density was an unreliable predictor of elk habitat selection (Appendix 1: Table S4) likely because wolf density was itself an inaccurate gauge of wolf predation risk (Kauffman et al. 2007). These issues highlight the preliminary quality of the results from Fortin et al. (2005).

In winter, the female elk we analyzed used grasslands at night when wolves were relatively inactive (Fig. 2-3c, 2-3f). Body fat and blood serum data taken from these elk when assayed at mid-winter were consistent with the hypothesis that nocturnal use of preferred grassland foraging habitats was sufficient to offset the effects of wolf presence on elk over-winter fat loss and pregnancy rate. Prime-aged (2-11 yrs-old) females carried enough body fat (10%) in February to maintain a high rate of pregnancy (89%) contrary

to the predator-sensitive food hypothesis. These results agree with those from a larger sample of elk (>90) from the same population and time period that included the sample we analyzed (Cook et al. 2004, White et al. 2011). They also agree with fetal data from thousands of females in this population that indicated pregnancy rate was independent of wolf predation pressure (Proffitt et al. 2014). Nocturnal use may explain how females from other elk populations maintained access to grasslands, and why they too maintained relatively high levels of over-winter nutrition and/or pregnancy rate despite wolf presence (Hamlin et al. 2009, White et al. 2009b, Middleton et al. 2013a, b). Finally, the consistently crepuscular pattern of wolf activity (Fig. 2-2, Appendix 1: Fig. S2; Theurerkauf 2009) suggests a degree of predictability in wolf predation risk that may explain why wolves have no effect on elk reproduction via chronic stress (Creel et al. 2009, Boonstra 2013).

Elk behavioral abandonment of risky places is also a key mechanism in the behaviorally mediated trophic cascade hypothesis, which asserts that fear of wolves increases productivity of palatable woody deciduous plants in risky places via reductions in elk browsing (Ripple and Beschta 2004, Beyer et al. 2007, Kauffman et al. 2010, Winnie 2012, Peterson et al. 2014). Although population reduction via direct killing could also reduce elk browsing, evidence of an apparent trophic cascade in northern YNP in the decade after wolf reintroduction has been attributed to behavioral mechanisms in part because elk numbers remained high during that period (Ripple et al. 2001, Ripple and Beschta 2004, Ripple and Beschta 2006, Beyer et al. 2007, Ripple and Beschta 2012). Our results suggest that elk maintained access to aspen and willow (*Salix* spp.) within risky places during daily wolf downtimes. This inference contradicts initial reports

that elk avoided aspen where wolves were numerous (Ripple et al. 2001, Fortin et al. 2005). However, it agrees with a winter habitat selection analysis of 80 VHF-collared elk followed in 2000-2002, concurrent to the elk tracked by Fortin et al. (2005), and compared with 94 VHF-collared elk followed before wolf reintroduction (Mao et al. 2005). This study found that elk *preferred* aspen where wolves were numerous depending on slope and snow levels, and that “elk showed no significant change in selection of aspen, which was highly preferred during winter in both pre- and post-wolf reintroduction periods” (Mao et al. 2005: Table 6). Assessing results from Fortin et al. (2005) and Mao et al. (2005) is difficult, however, because both studies relied on an unreliable index of spatial risk (wolf density; Appendix 1: Table S4) and an unvalidated GIS layer for aspen.

Nevertheless, elk nocturnal use of areas of high predicted kill occurrence (Fig. 2-3d) aligns with how aspen in these same areas did not escape browsing (Kauffman et al. 2010). Evidence that our collared elk selected for willow riparian areas at night (Beyer 2006) may also explain why many willow also did not escape browsing (Bilyeu et al. 2008, Marshall et al. 2013, 2014; but see Beyer et al. 2007). Persistent browsing on aspen and willow was probably also related to how many of these plants existed outside of high-risk areas as defined by our indices of spatial risk (Appendix 1: Fig. S3). These results, together with evidence that wolf-caused changes in elk distribution arise from wolves removing individuals rather than elk redistributing themselves (White et al. 2009a, 2010, 2012), support the hypothesis that any indirect effect of wolves on woody deciduous plants is mainly the result of a density-mediated trophic cascade (Creel and

Christianson 2009, Kauffman et al. 2010, Winnie 2012, Marshall et al. 2014, Painter et al. 2015).

Data limitations

Although our data are the best available information about the role of wolves in shaping the elk LOF in northern YNP during the first decade of wolf recovery, they are limited in at least four ways. First, the 5-hour interval between consecutive elk locations was coarse and a potential source of bias. This possibility is minimized by the fact that several studies have analyzed subsets of our data and established that the 5-hour interval provides a valid basis for understanding elk movement and habitat selection (Boyce et al. 2003, Fortin et al. 2005, Forester et al. 2007, 2009). Second, our estimated diel wolf activity pattern (Fig. 2-2) was derived from wolf GPS data collected over a 10-year period (2004-2013) that only partially overlapped our elk study period (2001-2004). This was necessary because GPS data for wolves in YNP were not available until 2004, and the number of wolves equipped with GPS collars each year was small (2-5 animals; Appendix 1: Table S1). Nevertheless, our estimated diel pattern was most likely representative of the diel pattern during the non-overlapping years because it was: (1) correlated with the time of day that we directly observed wolves encountering ($r = 0.79$) and killing ($r = 0.87$) elk during the non-overlapping years (Fig. 2-2a); (2) consistent across the years in which it was measured (Appendix 1: Fig. S2); and (3) similar to diel patterns described for other wolf populations (Theuerkauf et al. 2003, Eggermann et al. 2009, Theuerkauf 2009, Vander Vennen et al. 2016).

Although wolves were the primary source of mortality for our study population (Evans et al. 2006), our study, like others before it, ignored the possibility that the elk

LOF was shaped by multiple predator species (e.g., wolves and cougars). One reason this may be important is if different predator-specific activity schedules (crepuscular versus nocturnal) create conflicting spatiotemporal patterns of predation risk that require prey to prioritize their response to one predator at the expense of increasing their risk to another. In addition, our analysis did not address the long-term dynamics of the elk LOF. Our results could be an artifact of the potentially unique conditions that prevailed during our study period including a large and growing wolf population, a large but shrinking elk population, and moderate to severe drought conditions. Further research is necessary to determine if and how our estimate of the elk LOF may have changed during the second decade of wolves in northern YNP.

Conclusions

In summary, our major insight is that an animal's spatially-explicit perception of predation risk (i.e., its 'landscape of fear') over a large physical landscape tracks the daily activity pattern of its primary predator, enabling the animal to utilize risky places during predator downtimes, which in turn mitigates the impact of fear on animal resource use, nutritional condition, and reproduction. Our results highlight how a LOF in a large scale, behaviorally-sophisticated system like northern YNP is not a simple, unconditional function of a predator's mere presence. To assume so may overestimate the threat of predation, underestimate the ability of prey to efficiently manage this threat, and exaggerate the ecological effects of fear. We encourage investigators to recognize the potential for free-living animals to adaptively allocate habitat use across periods of high and low predator activity within the diel cycle. This underappreciated aspect of animal behavior can help explain why strong antipredator responses (e.g., movement, vigilance)

may have weak ecological effects, and why these effects may not rival those of direct killing. It also provides a basis for understanding why a LOF may have less relevance to conservation and management than direct killing.

Data availability

GPS data associated with this research have been deposited in Dryad:

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FIGURES

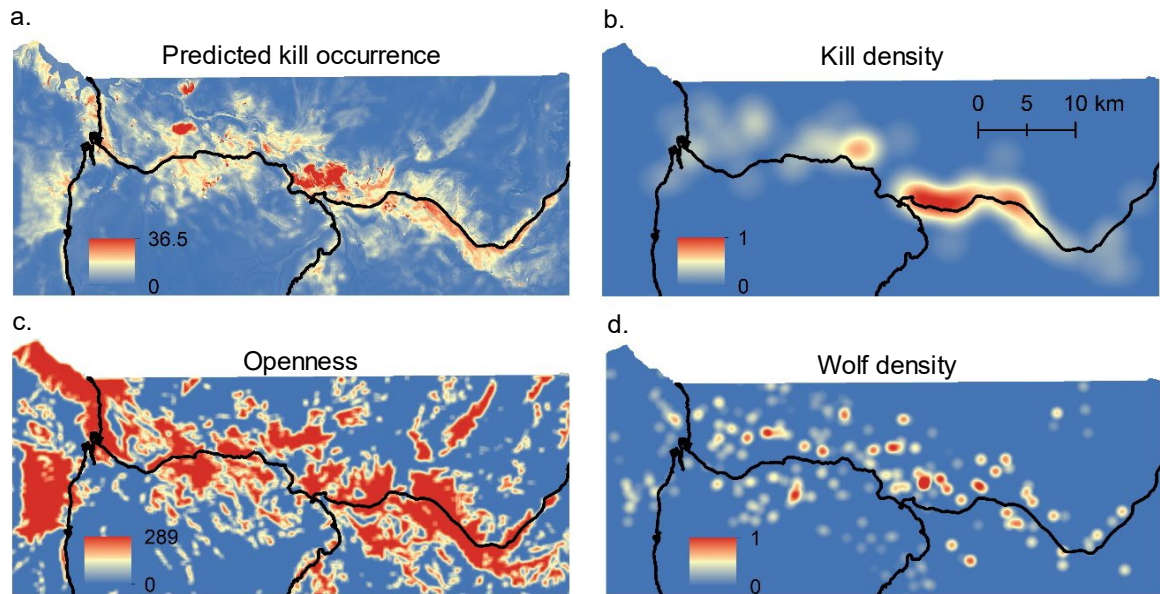


FIG. 2-1. Spatial variation in wolf predation risk during winter in northern Yellowstone National Park. Predation risk was indexed as (a) predicted occurrence of wolf-killed adult male, adult female, and calf elk, (b) density of wolf-killed adult female and calf elk, (c) openness, and (d) density of wolves. (a, b, and d) illustrate conditions during the first year of the study (2001). Openness was consistent across years. Black lines denote roads.

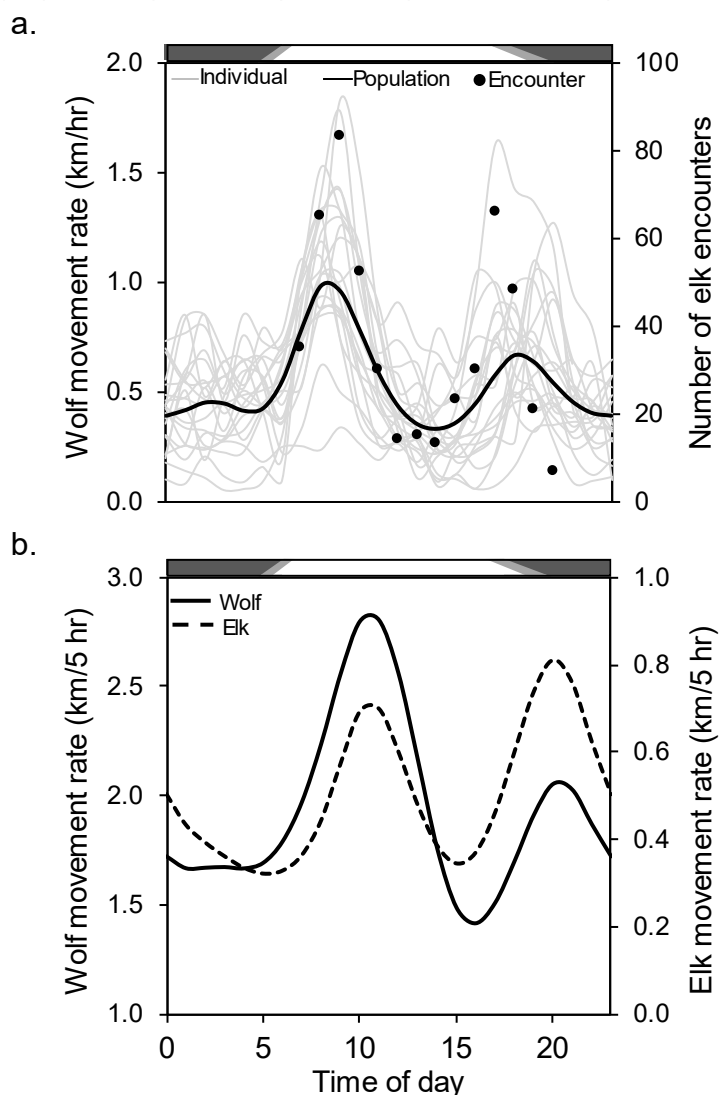


FIG. 2-2. Diel activity patterns of wolves and elk during winter in northern Yellowstone National Park. (a) Mean hourly movement rates for 21 GPS-collared wolves and predicted population mean from a general additive mixed model (left ordinate), and hourly number of directly-observed daylight encounters between wolves and elk (right ordinate). (b) Predicted 5-hr movement rates across 21 GPS-collared wolves (left ordinate) and 27 GPS-collared elk (right ordinate). Bars represent day (white), night (black), and variation in dawn/dusk periods (grey) from 15 Oct. – 31 May.

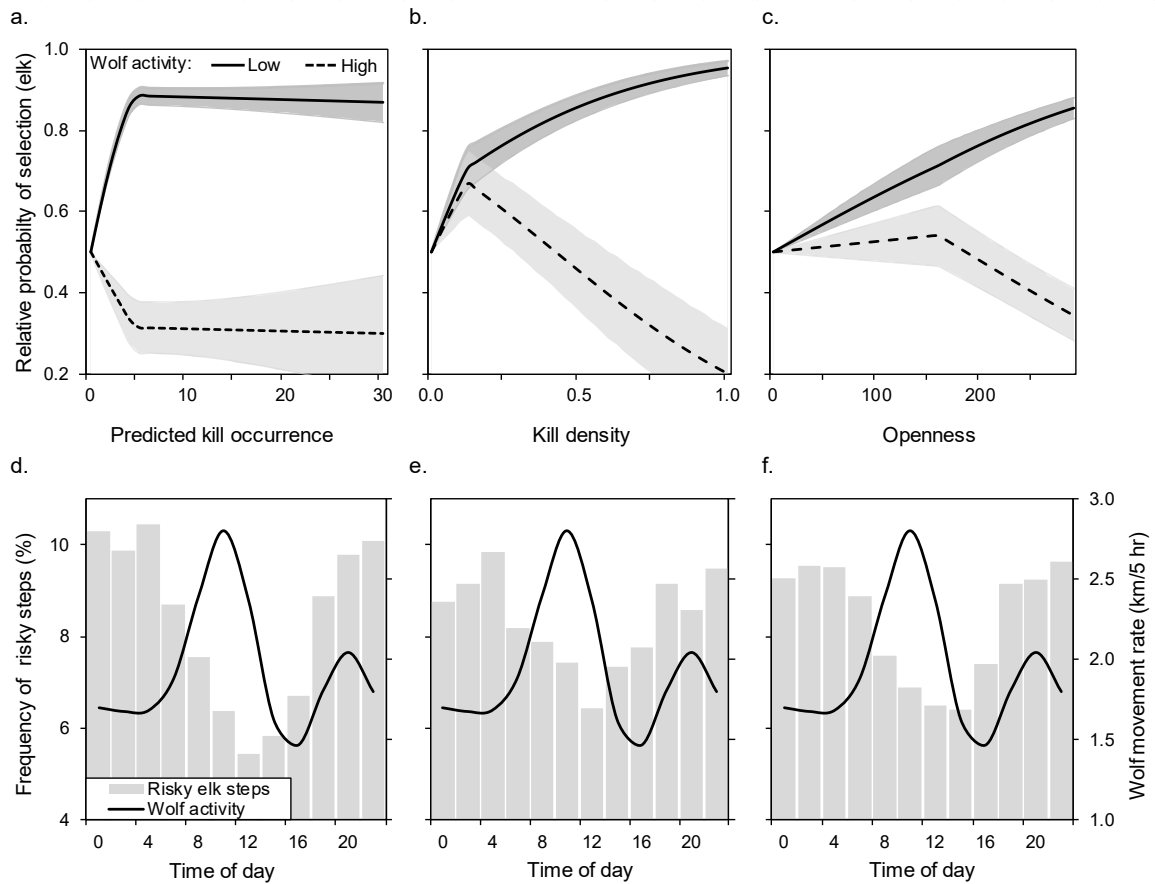


FIG. 2-3. Effects of diel wolf activity (predicted 5-hr wolf movement rate) on elk habitat selection in northern Yellowstone National Park, 2001-2004. (a-c) Elk were more likely to select risky places (areas where kills occurred and open grasslands) when wolf activity was low (1.42 km/5-hrs) than when it was high (2.80 km/5-hrs); lines are population-averaged fitted values with 95% confidence intervals (shaded areas) from the best-fit space \times activity models (Appendix 1: Table S5). (d-f) Frequency of elk steps ending in risky places (locations $>$ mean spatial risk: predicted kill occurrence = 4.5; kill density = 0.22; openness = 194; left ordinate) was greatest at night when wolf activity (mean 5-hr movement rate at 2-hr intervals; right ordinate) was low.

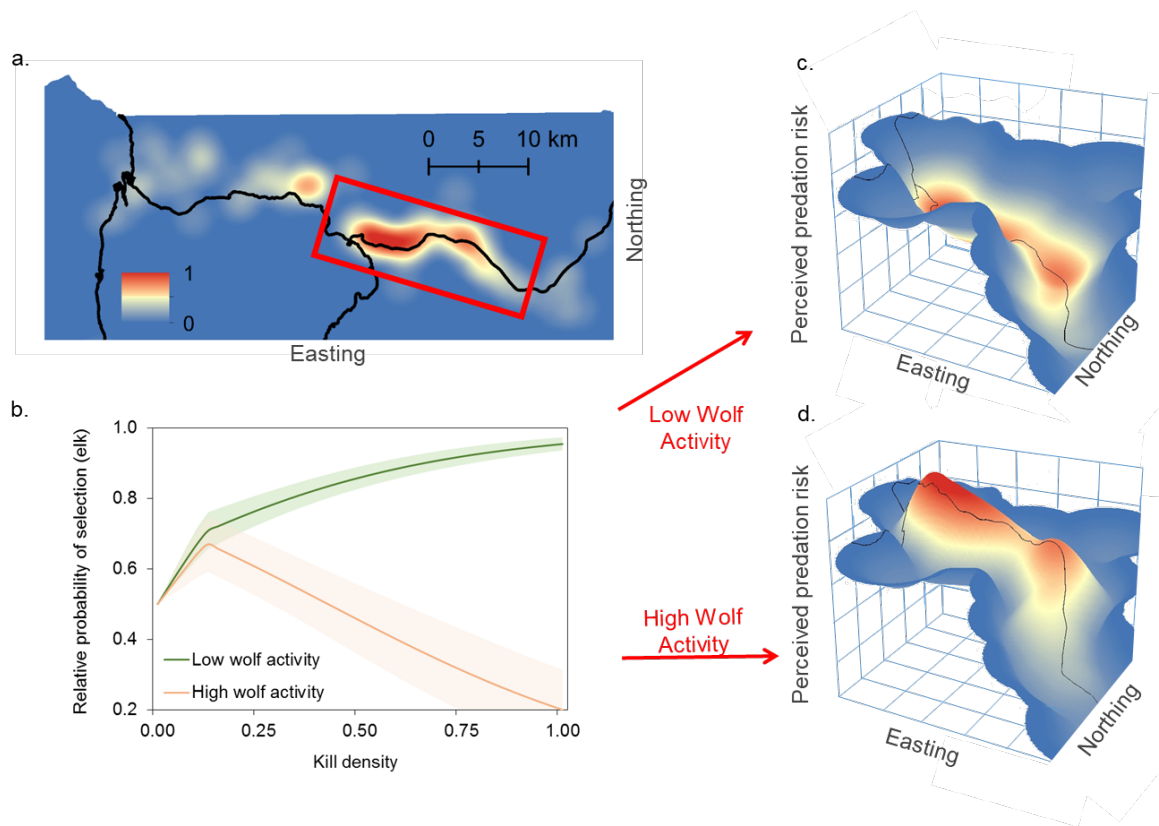


FIG. 2-4. Visualization of how diel wolf activity shaped the landscape of fear for adult female elk in northern Yellowstone National Park, 2001-2004. We examined kill density in one part of our study area, (a), and used the corresponding best-fit space \times activity step-selection model, (b), to calculate elk perception of wolf predation risk across this area when wolf activity was low (1.42 km/5-hrs) and high (2.80 km/5-hrs). Risky places where kills were densely concentrated were valleys when wolf activity was low, (c), and peaks when wolf activity was high, (d). Black lines in (a,c, and d) denote roads.

CHAPTER 3

ELK SELECTION FOR VACANT HUNTING DOMAINS MAY MINIMIZE A
MULTI-PREDATOR THREAT²**Abstract**

Many ecosystems contain sympatric predator species that hunt in different places and times. We tested whether this created vacant hunting domains, places and times where and when predators are least active, that prey use to minimize predation. We did this by measuring how Yellowstone elk (*Cervus elaphus*) responded to wolf (*Canis lupus*) and cougar (*Puma concolor*) predation risk during winter. Our data provided mixed support for this vacant domain hypothesis. Whereas elk did select for risky places during safe times in accordance with the hypothesis, there was also support for predator lethality and hunting mode hypotheses. Regardless, our results highlight predator activity as a key axis of the predator hunting domain that prey exploit to minimize predation risk in multi-predator environments. Ignoring the role of time may underestimate the capacity of prey to coexist with multiple predators and overestimate the total effect of multiple predators on prey populations and ecosystems.

INTRODUCTION

The influence of predators on prey space use is a key mechanism by which predators structure food webs and modify ecosystem function. Much of what is known about how prey spatially respond to predators, however, stems from studies that consider

² Kohl, M. T., T. K. Ruth, M. C. Metz, D. R. Stahler, D. W. Smith, P. J. White, D. R. MacNulty. *In Review*. Elk selection for vacant hunting domains may minimize a multi-predator threat. Ecology Letters.

the effects of a single predator species. A common finding is that prey avoid places where the predator is most abundant or lethal (Fig. 3-1a) (Lima & Dill 1990; Lima 1998; Brown *et al.* 1999). Less is known about the effects of multiple predator species on prey habitat selection despite the ubiquity of multi-predator environments in nature (Relyea 2003; Schmitz 2007). This is a significant knowledge gap because how prey spatially respond to multiple predators can influence the total impact of predators on prey distribution and potentially abundance. For example, if a prey species prioritizes its response to one predator at the expense of increasing its risk to another (Charnov 1976; Kotler *et al.* 1992), overall prey mortality may exceed the sum of all predator-specific mortality rates (i.e., synergistic predation; Sih *et al.* 1998). Understanding how prey manage threats from multiple predators is therefore a key step toward revealing the ecological effects of predators.

Current hypotheses about how prey navigate multi-predator environments primarily focus on prey use of predator spatial domains that result from interspecific competition and niche partitioning between predators (MacArthur 1958; MacArthur & Levins 1967). Prey may select for: (1) areas between predator spatial domains where both predator species are less lethal (i.e., low instantaneous probability of predator-caused mortality; Fig. 3-1b) (Fraser *et al.* 2004; Cresswell & Quinn 2013); (2) the spatial domain of the less lethal predator species (Fig. 3-1c) (Relyea 2003; Morosinotto *et al.* 2010); or (3) the spatial domain of cursorial predators assuming they leave too few reliable environmental cues to warrant avoidance (Fig. 3-1d) (Schmitz *et al.* 2004; Preisser *et al.* 2007; Thaker *et al.* 2011). We refer to these hereafter as the ‘gap’, ‘lethality’ and ‘*hunting mode*’ hypotheses, respectively. These hypotheses have provided

a productive framework for exploring prey spatial response to predators, but they overlook how the temporal dimension of the predator hunting domain and how it may provide prey with refuge from multiple predator species (Kronfeld-Schor & Dayan 2003). We define ‘predator hunting domain’ as the place(s) and time(s) where and when the predator kills its prey.

Time is a key niche axis that predators use to minimize interspecific competition across the diel (24-hour) cycle (Ross 1986; Cozzi *et al.* 2012; Monterroso *et al.* 2013). Segregation of predator species over space and across the diel cycle increases the number of potential hunting domains. For example, in a system with two spatial domains (e.g., forest and grassland), the addition of two temporal domains (e.g., night and day) doubles the number of potential hunting domains available to competitively-interacting predator species. This also doubles opportunities for prey to avoid predators. Specifically, any unfilled hunting domain provides a predictable refuge from predation in environments spatially-saturated with multiple predator species. Prey species living in such environments may therefore select for vacant hunting domains as a strategy to minimize the risk of predation (Fig. 3-2).

We tested the vacant-hunting domain hypothesis in a free-living, large mammal system in northern Yellowstone National Park (YNP). We did so by measuring how elk (*Cervus elaphus*) responded to predation risk from wolves (*Canis lupus*) and cougars (*Puma concolor*) during winter, 2001-2004. We focus on these years because it is when wolf and cougar numbers were known to be at recent historic highs (Cubaynes *et al.* 2014; Ruth *et al.* In press). Also, wolves and cougars are the only major predators of elk during winter (Evans *et al.* 2006). Wolves are cursorial predators that kill mainly in flat,

open areas (Kauffman *et al.* 2007) at dawn and dusk (Kohl *et al.* 2018), whereas cougars are spot-and-stalk/ambush predators that primarily kill in topographically rugged, forested areas at night (Murphy *et al.* 1998; Ruth *et al.* In press). We predicted that elk would select for flat, open areas at night (nighttime flat and open domain) and for rugged, forest areas during daylight (daytime rugged and forested domain). Our results highlight how prey can minimize predation risk in a multi-predator environment and diminish the potential for synergistic predation.

MATERIALS AND METHODS

Study area

Our study occurred within the northern Yellowstone elk winter range. This 1520-km² area is defined by the low-elevation (1500–2600 m) grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries along the northern border of Yellowstone National Park and adjacent areas in Montana (Lemke, Mack & Houston 1998). Approximately 65% (995-km²) of the winter range is located within the park. Most of the data in this study were collected in the park portion of the winter range (i.e., northern YNP; Appendix 2: Fig. S1; Fig. S2) because wolves were concentrated there (Stahler *et al.* 2016). See Kohl *et al.* (2018) for additional study details.

Study population

We analyzed habitat selection behavior of 27 adult (> 1 year-old) female elk from the northern Yellowstone population, which annually occupies the winter range from about 15 October to 31 May. This population ranged from approximately 10,700-17,600 individuals during the study (Tallian *et al.* 2017). Adult female elk were fitted with GPS

radio-collars programmed to collect locations at 4-6 hour intervals. We limited our analysis to winter locations collected from 1 November – 30 April. Appendix 2: Fig. S1 illustrates the spatial distribution of these data. Appendix 3 provides additional details about GPS data protocols.

Wolf numbers in northern YNP ranged between 70-98 individuals per 1000 km² in 4-8 packs (mean= 8.36; SE = 0.90 individuals / pack) during the study. Each winter, 20-30 wolves (35-40% of northern YNP wolf population), including 30-50% of pups born the previous year were captured and radio-collared with VHF ($n = 72$ wolves [11 unique packs], 2000-2004) or GPS collars ($n = 21$, 2004-2013; Smith *et al.* 2004). We maintained at least two radio-collars in all northern YNP wolf packs and recorded their locations approximately daily during two 30-day periods in early (mid-November to mid-December) and late (March) winter, when wolf packs were intensively monitored from the ground and fixed-wing aircraft, and approximately weekly during the rest of the year. GPS collars recorded locations every hour during the 30-day periods and at variable intervals outside these periods.

We monitored 54 (27 F, 27 M; Ruth *et al.* 2011) adult and independent, predispersal cougars (68-93% of estimated adult cougar population) in northern YNP using either VHF ($n = 83$) or GPS ($n = 10$) collars. The density of cougars in the study area ranged between 13-19 adults per 1000 km² (Ruth *et al.* In press). GPS collars recorded locations at either 3-hour fix intervals or recorded 8 locations per day skewed toward night and crepuscular hours (Ruth *et al.* 2010). See Appendix 3 for additional information.

Predation sampling

We searched for wolf-killed (Appendix 2: Fig. S-2a) and cougar-killed (Appendix 2: Fig. S-2b) elk from 1 November – 31 May by radio-tracking VHF and GPS-collared wolves and cougars (Appendix S3: Table S1). We excluded adult male elk from our predation sampling dataset because wolves killed males in different areas than they did females (Kohl *et al.* 2018) and because GPS data were unavailable to assess adult male habitat selection. All winter wolf kills ($n = 400$) that were located within the northern elk winter range were collected from 01 November 2000 to 31 May 2004 to correspond with the winters in which elk were monitored. All winter cougar kills ($n = 257$) that were collected from April 1998 to May 2005 were included to maximize sample size. See Appendix 3 for additional details.

Spatial variation in predation risk

We used vegetation openness (Appendix 2: Fig. S-3a) and topographic roughness (Appendix 2: Fig. S-3b) as separate indices of spatial variation in elk predation risk from wolves (Creel *et al.* 2005; Fortin *et al.* 2005; Mao *et al.* 2005; Kohl *et al.* 2018) and cougars (Atwood *et al.* 2009; Bartnick *et al.* 2013). We developed and analyzed single maps of openness and roughness because these landscape features did not vary during the study period (2001-2004). Both spatial risk indices (30 x 30 m grid cell) were developed using the Focal tool within the *raster* package in R 3.2.3. Openness and roughness were not highly correlated (Pearson's correlation coefficient, $r = -0.18$).

We calculated openness (range 0 [dense forest] – 289 [open grassland]) as the sum of non-forested cells within a 500 x 500 m moving window centered on each grid cell following Boyce *et al.* (2003) using data from the LANDFIRE program in 2001

(Appendix 2: Fig. S-4). We calculated roughness (range 0 [flat] – 1,114 [sheer cliff]) as the sum of the absolute value of the difference in elevation between each grid cell and surrounding eight neighbors (3 x 3 window) following the criteria previously developed for cougars in northern Yellowstone (Ruth *et al.* In press).

To determine if openness and roughness were valid indices of predation risk, we separately modeled the relative probability of a wolf or cougar killed elk (adult females and calves only) as a function of openness or roughness using a resource selection function framework (RSF; Manly *et al.* 2002). We analyzed wolf and cougar kill RSFs with a generalized additive model (GAM) to account for potential nonlinear relationships between kill locations and these spatial metrics. We used the *mgcv* package (version 1.8.0) in R 3.2.3 to estimate the GAM. See Appendix 3 for additional details.

Diel activity patterns

We used movement rate to index the diel activity patterns of wolves and cougars because speed of locomotion is a valid proxy for diel activity patterns in large mammals (Ensing *et al.* 2014; Vander Vennen *et al.* 2016). In addition, ungulates, including elk, are sensitive to temporal variation in predator locomotion (Fröhlich *et al.* 2012; Kohl *et al.* 2018). For wolves, we estimated movement rate at each hour of the day from the hourly winter positions of 21 GPS-collared animals recorded in northern Yellowstone during 2004-2013.

For cougars, we estimated movement rate at each hour of the day from winter locations collected at 3-hour intervals from 6 GPS-collared individuals (2 F, 4 M) in northern Yellowstone during 2001-2006. Four additional GPS-collared individuals were not monitored long enough to accurately assess movement rates. Movement rate equaled

the average Euclidean distance of the preceding 5-hour time step for wolves and 6-hour time step for cougars as these most closely matched the 5-hour interval between consecutive elk locations. We subsampled the wolf and cougar data to match the elk data by retaining every fifth wolf location or second cougar location. We used only consecutive 5- or 6-hour locations to calculate movement rates.

We modeled the population-level diel movement rate by applying a generalized additive mixed model to the 5-hour wolf and 6-hour cougar locations using the *mgcv* package (version 1.8.0) in R 3.2.3. For wolves, we could not distinguish between individual and annual variation in diel activity due to small sample sizes within years (Kohl *et al.* 2018). For cougars, we separately modeled male and female activity to account for potential sex-specific differences in activity patterns (Wang *et al.* 2015). See Appendix 3 for additional details.

Elk habitat selection

For each spatial risk index (openness and roughness), we evaluated models that tested whether elk selection for risky or safe places was (1) independent of wolf and cougar activity ('space-only' model), (2) dependent on the activity of wolves *or* cougars ('single-predator space \times activity' model), or (3) dependent on the activity of wolves *and* cougars ('multi-predator space \times activity' model). Space \times activity models included terms for the interaction between spatial risk and mean movement rate of wolves and/or cougars. These models therefore evaluated how elk selection for risky and safe places at the end of a 5-hr movement step was affected by the mean movement rate of predators during that step. Because male and female cougars exhibited different diel activity patterns (see *Results*), we specified separate models for the effects of male and female

cougars. We did not consider models that included female cougar and wolf activity due to multicollinearity between these interactions (Appendix 3: Table S2).

For each model, we tested different forms of the relationship between habitat selection and spatial risk to account for how elk tolerate low levels of spatial risk (Kohl *et al.* 2018). Specifically, we tested for a response threshold in elk habitat selection by comparing models with a linear effect for spatial risk to models with a threshold effect specified by two linear splines. We performed a grid search of candidate models to determine the presence and position of thresholds (see Appendix 3). We identified the best-fitting model using the quasi-likelihood under independence criteria (QIC; Pan 2001). We performed 5-fold cross validation ($n = 1,000$) for SSF design to evaluate the predictive accuracy of each best-fit model (Boyce *et al.* 2002). Average Spearman rank correlations > 0.70 indicated satisfactory fit of models to data (Boyce *et al.* 2002). We performed SSF analyses and k -folds cross validations in R 3.0.2 using the SURVIVAL and HAB packages, respectively. See Kohl *et al.* (2018) for additional details.

Visualizing elk selection for vacant hunting domains

To visualize elk selection of vacant hunting domains, we combined our predator activity and kill distribution models to delineate cougar and wolf hunting domains. The cougar hunting domain was based on the activity of males and the kills of males and females. We excluded female activity because it was a poor predictor of elk habitat selection (see *Results*), and included kills by both sexes because their spatial distributions were similar (Appendix 4: Fig. S1). Using predator activity and kill locations, we calculated quantile-specific ellipses to estimate predator-specific hunting domains. We then overlaid these hunting domains on a contour plot of elk habitat selection with respect

to a continuum of low to high spatial risk and time of day to reveal the extent that elk selected for vacant hunting domains. See Appendix 4 for additional details.

RESULTS

Hunting domains

Wolves and cougars hunted adult female and calf elk in different places and at different times in northern Yellowstone. Specifically, cougars mainly killed elk in moderately-forested, rugged areas while wolves killed elk in open, flat, areas (Fig. 3-3). And whereas cougars, especially males, hunted mainly at night, wolves hunted mainly during morning and at dusk (Fig. 3-4). The diel activity pattern of male cougars was unimodal with a single peak in activity at 0300-hrs (Fig. 3-4a). Female cougars exhibited a bimodal pattern, with comparatively lower activity peaks at about 0400-hrs and 2000-hrs. The activity pattern of wolves was also bimodal with activity peaks at 1000-hrs and 2000-hrs (Fig. 3-4b). Together, cougars hunting at night in rugged forests, and wolves hunting in daylight (morning/dusk) in flat grasslands indicate four vacant hunting: ‘nighttime grassland’, ‘nighttime flat area’, ‘daytime rough area’, and ‘daytime forest’.

Elk habitat selection

The effect of spatial risk on elk habitat selection was nonlinear. For each spatial risk index (openness and roughness), a space-only model that included a linear spline for spatial risk (Appendix 4: Tables S1, S2) was a better fit to the data than a model that only included a linear relationship between elk habitat selection and risk for openness ($\Delta\text{QIC} = 37.2$; Appendix 4: Table S1) and roughness ($\Delta\text{QIC} = 89.2$; Appendix 4: Table S2).

However, a single predator model that included space \times activity interactions between mean diel movement rate of male cougars or wolves ($\Delta\text{QIC} = 342.4 - 360.6$; Appendix 4: Table S1) and linear splines for openness and roughness ($\Delta\text{QIC} = 34.5 - 111.3$; Appendix 4: Table S2) was a better fit to the data than the space-only models. A similar model including mean diel movement rate of female cougars differed little from the best-fit space-only model ($\Delta\text{QIC} = -0.7 - 2.6$), indicating little or no effect of female cougar activity on elk habitat selection. Support for the single-predator wolf model was also notably weaker compared to the single-predator male cougar model (openness: $\Delta\text{QIC} = 18.3$, roughness: $\Delta\text{QIC} = 76.8$, Appendix 4: Tables S1, S2). This suggests the singular effect of male cougar activity on elk habitat selection was greater than that of wolf activity.

However, support for the single-predator male cougar model was much weaker compared to multi-predator models that included the activity of male cougars and wolves (openness: $\Delta\text{QIC} = 38.7$; roughness: $\Delta\text{QIC} = 10.9$; Appendix 4: Tables S1, S2), indicating that elk responded simultaneously to both predators. The alternative multi-predator space \times activity model that include male and female cougar activity was also weaker than a model that included male cougar activity and wolves (openness: $\Delta\text{QIC} = 13.5$; roughness: $\Delta\text{QIC} = 1.9$, Appendix 4: Tables S1, S2) further suggesting a minimal effect of female cougar activity on elk habitat selection. Five-fold cross validation revealed a strong correlation between observed and predicted values for the best-fit multiplicative multi-predator space \times activity models that included openness (mean Spearman-rank correlation, $r_s = 0.98$ and roughness ($r_s = 0.95$). Correlations of this magnitude indicate that these models are reliable.

Positive (openness: $\beta = 0.007$, $P < 0.01$ before threshold; $\beta = 0.013$, $P < 0.01$ after threshold) and negative (roughness: $\beta = -0.024$, $P < 0.01$ before threshold; $\beta = -0.009$, $P < 0.01$ after threshold) space \times activity interactions indicated that elk selected for open and flat areas when cougar activity was high and wolf activity was low (red line in Fig. 3-5; Appendix 4: Table S3). Negative (openness: $\beta = -0.003$, $P < 0.01$ before threshold; $\beta = -0.007$, $P < 0.01$ after threshold) and positive (roughness: $\beta = 0.015$, $P < 0.01$ before threshold) space \times activity interactions indicated that elk avoided open and flat areas when wolf activity was high and cougar activity was low (purple lines in Fig. 3-5; Appendix 4: Table S3). It is unclear from our data why elk avoided rougher areas beyond the threshold (Fig. 3-5b) when wolves were active. It could be in part due to lack of food in rougher places or because extremely rough areas were inaccessible (e.g., cliffs).

Visualizing selection for vacant predator hunting domains

Our visualizations suggested that four vacant hunting domains occurred in our system (Fig. 3-6): ‘daytime forest (< 175 openness)’, ‘nighttime grassland (>200 openness)’, ‘daytime rough area (> 75 roughness)’, and ‘nighttime flat area (< 85 roughness)’. Using our best-fit space \times activity model for openness (Appendix 4: Tables S1, S3), we found that elk strongly selected for the nighttime grassland domain, thereby avoiding the morning peak in wolf activity, but not wolves’ dusk activity period. Elk selection for the nighttime grassland domain also greatly reduced their exposure to cougar predation during the night. For roughness, our best-fit model (Appendix 4: Tables S2, S3) showed that elk selected for flat areas that overlapped with the wolf hunting domains but that they avoided the cougar hunting domain.

DISCUSSION

Despite the ubiquity of multi-predator environments, studies rarely consider the effects that multiple predator species have on prey spatial responses. We addressed this gap with extensive data from the elk–wolf–cougar system of northern Yellowstone. Specifically, we evaluated elk habitat selection relative to the spatial and temporal risk of wolves and cougars. From this, our results demonstrated how a single-predator focus within a multi-predator environment can generate misleading conclusions about prey spatial response to predation risk, including assessments about the principle predator affecting prey movement.

In northern Yellowstone, we found clear evidence that elk habitat selection was shaped by the risk of predation from wolves and cougars. Support for a multi-predator model that included wolves and cougars far exceeded that of any single-predator model (Appendix 4: Tables S1, S2). This differs from previous studies of elk in the Greater Yellowstone Ecosystem which have assumed, implicitly or explicitly, that elk respond primarily (or exclusively) to wolf predation risk (e.g., Mao *et al.* 2005; Fortin *et al.* 2005; Creel *et al.* 2005; Kohl *et al.* 2018). This ‘wolf-only’ perspective is also at odds with our finding that elk responded more strongly to cougars (males) than to wolves. This was evidenced by how elk selection for open grasslands that are safe from cougar predation (identified as O2 in Appendix 8) when cougars were highly active ($\beta = 0.013$) was stronger than the avoidance of those open grasslands when wolves were highly actively ($\beta = -0.007$; Appendix 4: Table S3). Together, these results suggest that previous elk studies that ignored cougars may have overlooked the primary predator responsible for influencing elk habitat selection in northern Yellowstone.

Interestingly, elk responded less strongly to female cougars than either wolves or male cougars. We are uncertain why elk responded weakly to female cougars (Appendix 4: Tables S1, S2). In northern Yellowstone, the sex ratio of adult resident male to female cougars was 1:3.2 (Ruth *et al.*; *In press*) during our study, suggesting that females represent an important component of the predation landscape. Moreover, females with kittens have a higher per capita kill rate than male cougars (Clark *et al.* 2014; Ruth *et al.*; *In press*), and at least one of the females was supporting kittens during our study. This may suggest our measure of diel female cougar activity was inaccurate. On the other hand, the cougar activity patterns we observed in our system were consistent with those described in other systems (Wang *et al.* 2015). Thus, our sample of adult female elk may have been less sensitive to female cougars because they were rarely killed by cougars (Evans *et al.* 2006) and lacked calves. Cougars are size-selective predators such that female cougars primarily killed calves (relative to adult elk) in northern Yellowstone during our study (Murphy *et al.* 1998; Ruth *et al.* *In press*), and it is possible that most of our sampled elk lacked calves during winter given the low cow-calf ratio observed in northern Yellowstone during our study (< 16 calves per 100 cows [2001-2004]; Proffitt *et al.* 2014). Thus, the weak response of our monitored elk to female cougar activity suggests a less predictable or realized risk of predation from female cougars. If so, this may mean that female cougars should be functionally treated as a separate predator species in these wolf-cougar-elk systems.

Our results also highlight how prey navigate multi-predator environments in time and space. In our system, models that contained both spatial risk and predator activity outperformed space-only models (Appendix 4: Tables S1, S2). Had we ignored predator

activity, we would have concluded, incorrectly, that elk were at risk of synergistic predation due to a landscape saturated with spatial risk (Fig. 3-3). Instead, wolves and cougars partitioned their prey resource across space and time (Fig. 3-3; Fig. 3-4). This provided ample opportunity for elk to minimize predation risk by using risky places during safe times as predicted by the vacant domain hypothesis (Fig. 3-2).

Evidence in support of the vacant hunting domain hypothesis was contingent on our definition of the vacant hunting domain. When it was defined according to the most lethal places and times (i.e., 90th quantile in Fig. 3-6), we identified four domain vacancies (night-open, night-flat, day-forest, day-rough). Of these, elk selected for one strongly (night-open), two moderately (night-flat, day-rough), and one weakly (day-forest). For openness, elk strongly selected (bright green) for the vacant night-time grassland hunting domain, and mildly selected (light blue to light green) for intermediately forested areas (~ 150 – 225 openness) during the peak hunting times of wolves (~ 1000-hrs; Fig. 3-6a), both of which accord with the vacant hunting domain hypothesis. For roughness, elk selected moderately selected (light green) for the night-flat domain (Fig. 3-6b). In addition, elk selected strongly for slightly rougher areas (~ 25-40 roughness) during peak wolf hunting times (~ 1000-hrs). Although this selection nearly overlapped with the core morning hunting domain of wolves, the relative probability of a wolf kill dropped significantly at ~ 25 roughness (Fig. 3-3b) suggesting that this area may be safer than it appears from Figure 3-6a, and thus, taken together with the clear lack of overlap with the cougar roughness hunting domain, provided evidence that elk were also selecting for a vacant hunting domain across our roughness metric. This suggests that the selection of vacant predator hunting domains was an important predator

avoidance mechanism. On the other hand, if we use a broader definition of a hunting domain (i.e., 50th quantile; Fig. 3-6), we identify only three vacant domains (night-open, day-forest, night-flat), of which elk selected for one strongly (night-open), one moderately (night-flat), and one weakly (day-forest). This definition provided less support for the vacant hunting domain hypothesis.

Although the space-only models (Fig. 3-1) did not explain elk habitat selection in our system they did offer some insight into how elk may manage multi-predator landscapes in the context of the prevailing space-only hypotheses. For example, we can reject the gap hypothesis (Fig. 3-1b) because elk overlapped with at least one hunting domain for both openness and roughness (Fig. 3-6). In contrast, our results provided support for the lethality hypothesis (Fig. 3-1c), but which predators elk perceived to be the most lethal was unclear. In relation to openness, elk strongly avoided (dark blue) the wolf morning domain, but only moderately selected (green) for the cougar domain, thereby suggesting wolves may be the more lethal predator (Fig. 3-6a). Elk may have avoided wolves because wolves were the primary predator of adult female elk in this system (Evans *et al.* 2006). It also may be because wolf densities (~ 85 wolves / 1000 km²) were higher than cougar densities (~ 16 adult resident cougars / 1000 km²) during our study. However, elk clearly avoided cougars, but strongly overlapped with wolves, when we evaluated elk habitat selection as a function of roughness (Fig. 3-6b). In this case, elk may have been responding to hunting efficiency rather than predator density since cougar hunting success can exceed 80% (Hornocker 1970). In comparison, the success of wolves hunting elk rarely exceeded 20% (Smith *et al.* 2000; Mech *et al.* 2001) and dropped below 10% when wolves hunted adult elk (MacNulty *et al.* 2012).

There was also support for the hunting mode hypothesis (Fig. 3-1d) but, similar to the lethality hypothesis, it was unclear which predator elk were responding too. For example, elk avoided the cursorial hunter (i.e., wolves) when evaluating the openness metric, but avoided the ambush predator (i.e., cougar) when evaluating the roughness metric (Fig. 3-6). This discrepancy may be because it is unclear in our system how predictable wolves and cougars were. Whereas cougars are commonly thought of as the spatially predictable predator due to their ‘ambush’ hunting mode, previous work has shown that wolves are also spatially (Uboni *et al.* 2015) and temporally (Kohl *et al.* 2018) predictable calling into question the hunting mode hypothesis in wolf-cougar systems.

The combination of all our results represents one of the first comprehensive evaluations of how prey minimize predation risk from multiple predators in a large-scale, free-living terrestrial system. This is significant advancement in ecology because understanding how prey respond to variation in predation risk is critical for understanding how prey can coexist with multiple predators. If prey employ the incorrect anti-predator behavior, prey populations may decline. For example, if prey respond to predator lethality in a system where the secondary predator (i.e., less lethal predator) is still highly capable of killing prey, then the prey population may experience high levels of synergistic predation. But synergistic predation is rare in natural systems (Schmitz 2007) and our finding that prey can use space and time to avoid predation may provide an explanation why.

Although these results suggest that changes in behavior may minimize direct mortality, it does not preclude significant demographic costs due to the nonconsumptive

effects imposed by multiple predators (Preisser *et al.* 2005). For example, we might expect elk to demonstrate high levels of vigilance due to a landscape saturated with spatial risk (Fig. 3-3). If true, we would predict a reduction in elk foraging opportunities (Lima 1992) that could contribute to a decline in body condition and pregnancy rates. However, neither elk vigilance, nor body condition or pregnancy rates varied by predation risk in our system suggesting that elk habitat selection behaviors likely mitigated any nonconsumptive effects (see Kohl *et al.* 2018). More generally, these spatio-temporal behaviors could provide a mechanistic explanation for why nonconsumptive effects may not exceed consumptive effects in some biological systems (Preisser *et al.* 2005).

Alternatively, the movements of elk between high cougar and high wolf risk areas could influence ecosystem structure and function through changes in herbivory. In northern Yellowstone, some ecologists have suggested that wolf recovery established a landscape of fear that reduced browsing on woody deciduous plants in high wolf risk areas (Laundré *et al.*; 2001, 2010). However, the magnitude of browse recovery has varied across northern Yellowstone (Kauffman *et al.* 2010) leading to significant debate regarding the impacts of wolf restoration on lower trophic levels (e.g., Beschta & Ripple 2013 vs. Kauffman *et al.* 2013). This may be due in part to abiotic factors (Marshall *et al.* 2013), however, our results suggest that previous wolf-elk-browse research overlooked the primary predator that drives elk spatial behavior in our system (i.e., cougars), and as such, may explain why it has been difficult to associate wolf predation risk with browse recovery. Alternatively, the ability of elk to use risky places during safe times, irrespective of either wolf or cougar predation, may help explain why riparian

browse species may not have escaped browsing (Kohl *et al.* 2018). Either way, this provides another example of why strong anti-predator behaviors may produce weak ecological effects (Kohl *et al.* 2018).

In summary, a prey's response to predation risk must account for multiple sources of risk within multi-predator systems. Most biological systems are composed of multiple predators, and as such, ecologists should move beyond the single-predator paradigm to better understand prey spatial behavior. With that context, our work also demonstrates the need to evaluate prey response to the spatial and temporal risk imposed by multiple predators. If we continue to ignore the ability of prey to manage predation risk in both space and time, we are in danger of making inappropriate conclusions that may overestimate the effects predators on prey space use and demography.

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FIGURES

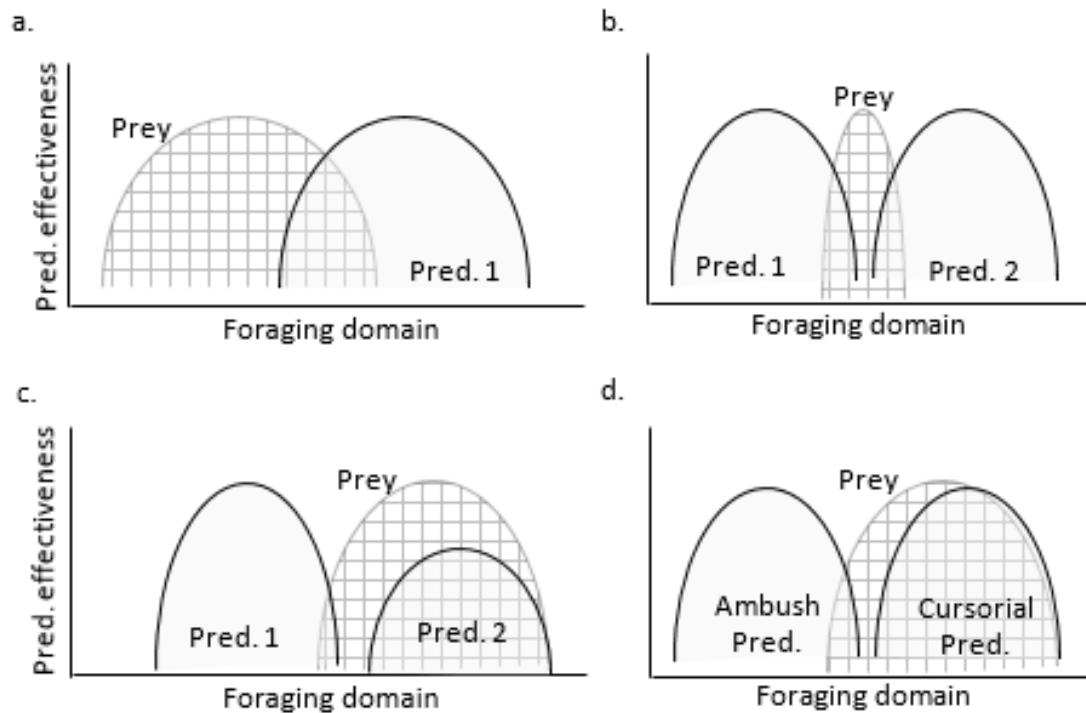


Figure 3-1. Hypotheses about how prey avoid predators. In single-predator systems, prey avoid the spatial domain where predators are most lethal (a). In multi-predator systems, prey avoid the spatial domains where both predators are most lethal (b), the spatial domain occupied by the most lethal predator (c), or the spatial domain occupied by the most spatially-predictable predator, e.g., ambush predators (d). These are referred to, in order, as the 'gap', 'lethality', and 'hunting mode' hypotheses within the text. Shaded and hatched areas identify predator and prey, respectively.

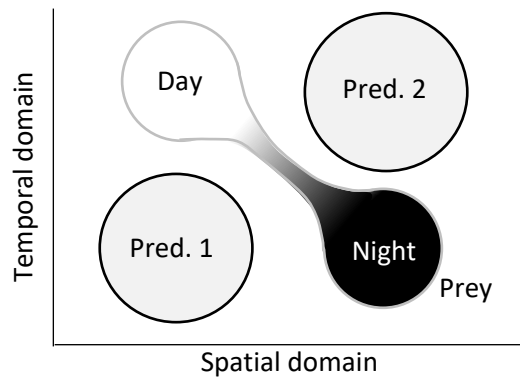


Figure 3-2. The vacant hunting domain hypothesis considers both spatial and temporal axes of predation risk. Prey may exploit unused hunting domains (i.e., low risk of predation in space and time) to minimize predation from multiple predators. Grey shaded circles represent predator hunting domains. White-to-black transition vacant hunting domains.

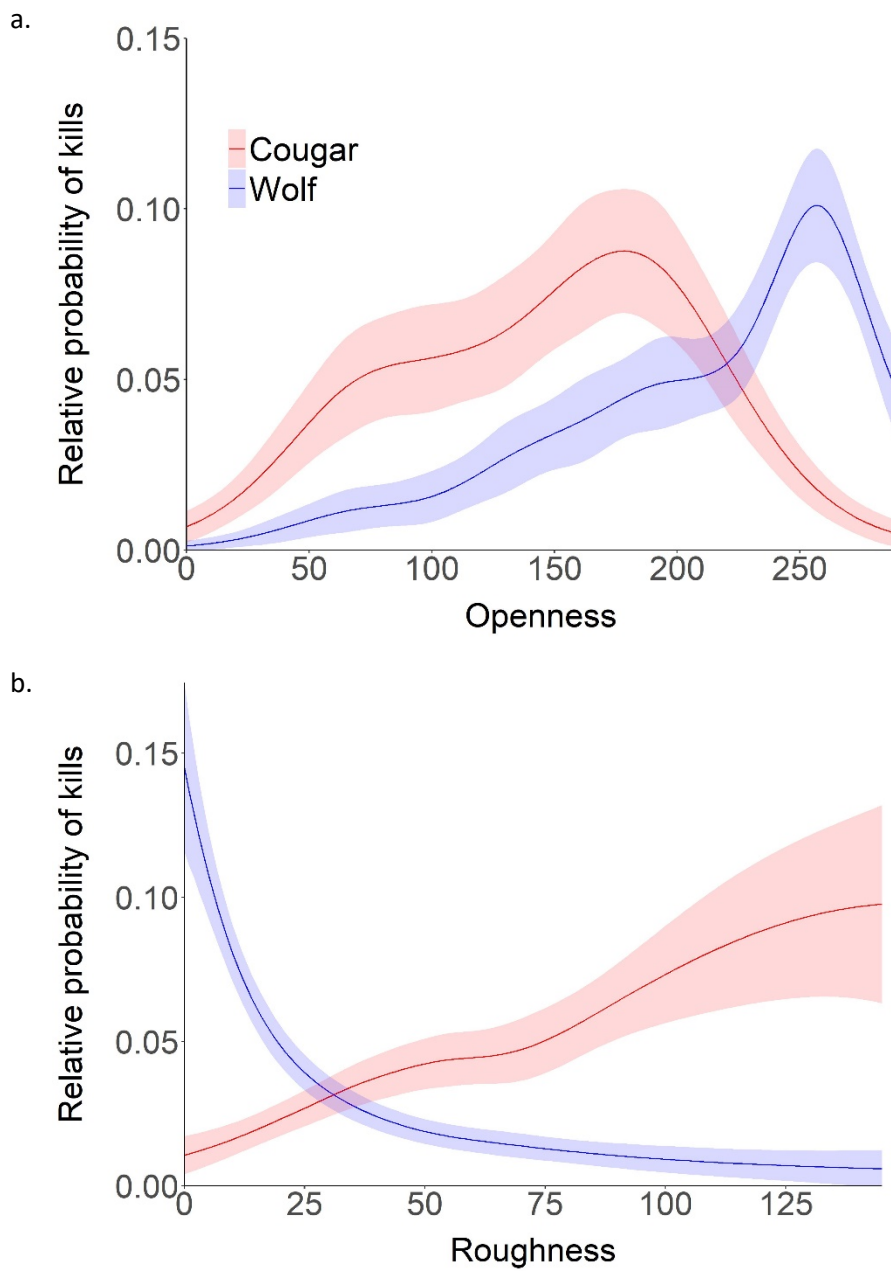


Figure 3-3. Predicted kill distribution of wolves (2000-2004) and cougars (1998-2006) relative to openness (a) and topographic roughness (b) in northern Yellowstone during winter.

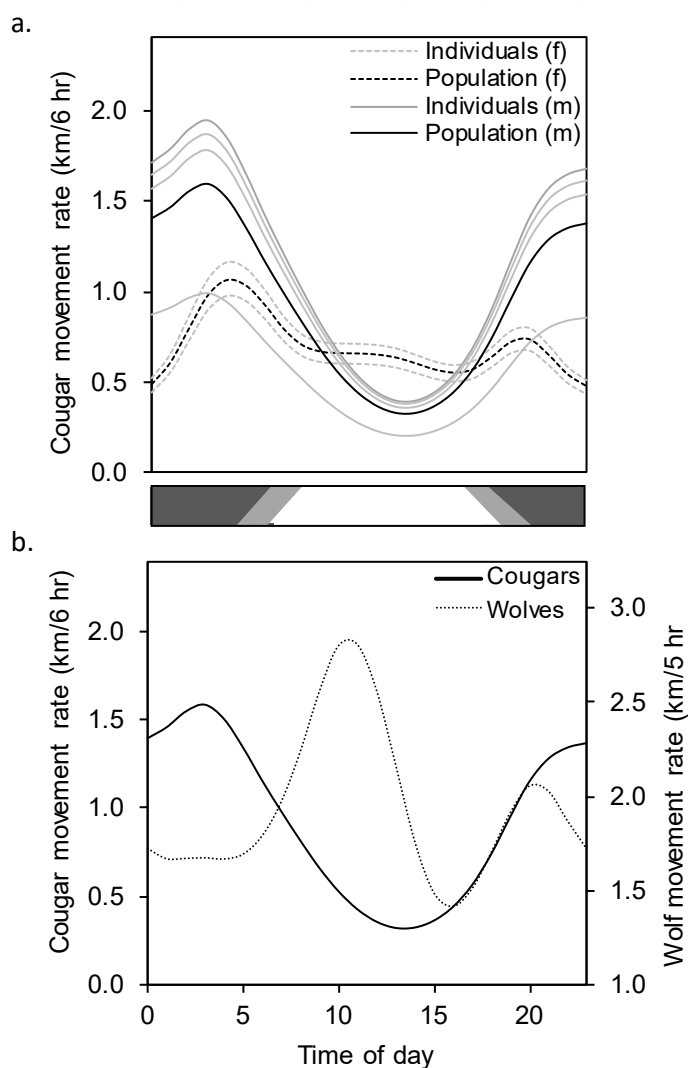


Figure 3-4. Diel activity pattern of cougars and wolves in northern Yellowstone during winter. (a) Mean 6-hr movement rate for 6 GPS-collared cougars (2 F, 4 M) and the sex-specific population-averaged response. (b) Modeled 6-hr movement rates across 4 male GPS-collared cougars (left ordinate) and 21 GPS-collared wolves (right ordinate). Only males are displayed because they best explained elk habitat selection (Appendix 7). Bars represent day (white), night (black), and variation in dawn/dusk periods (grey) from 15 Nov – 15 April.

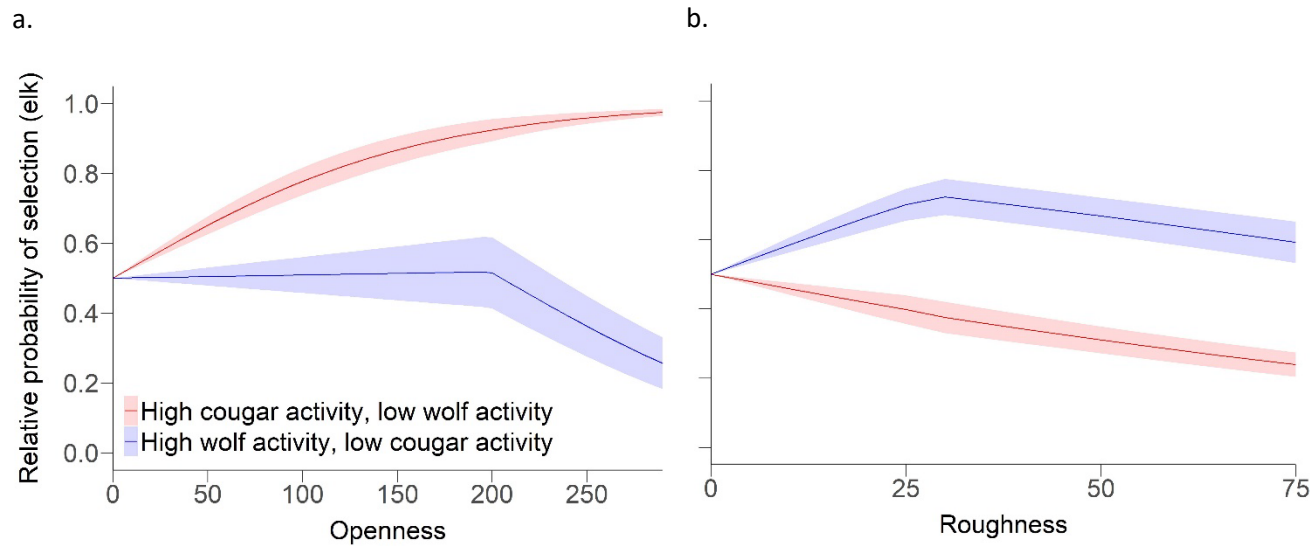


Figure 3-5. Effects of diel predator activity (estimated wolf or cougar movement rate [Figure 4b]) on elk habitat selection in northern Yellowstone. Elk selection for openness (a) and topographic roughness (b) differed significantly between periods when cougars were most active (1.59 km/6-hrs) and wolves were least active (1.42 km/5-hrs), and when cougars were least active (0.33 km/6-hrs) and wolves were most active (2.80 km/5-hrs). Lines are population-averaged fitted values with 95% confidence intervals from best fit space \times activity models (Appendix 8).

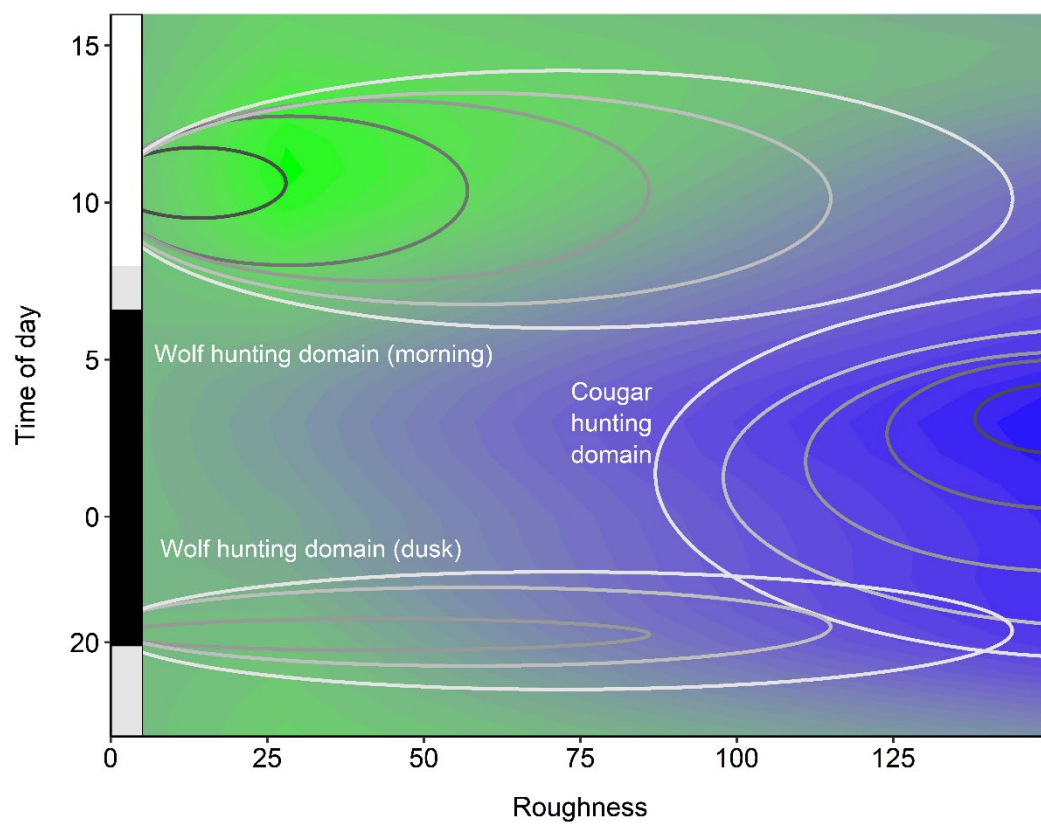
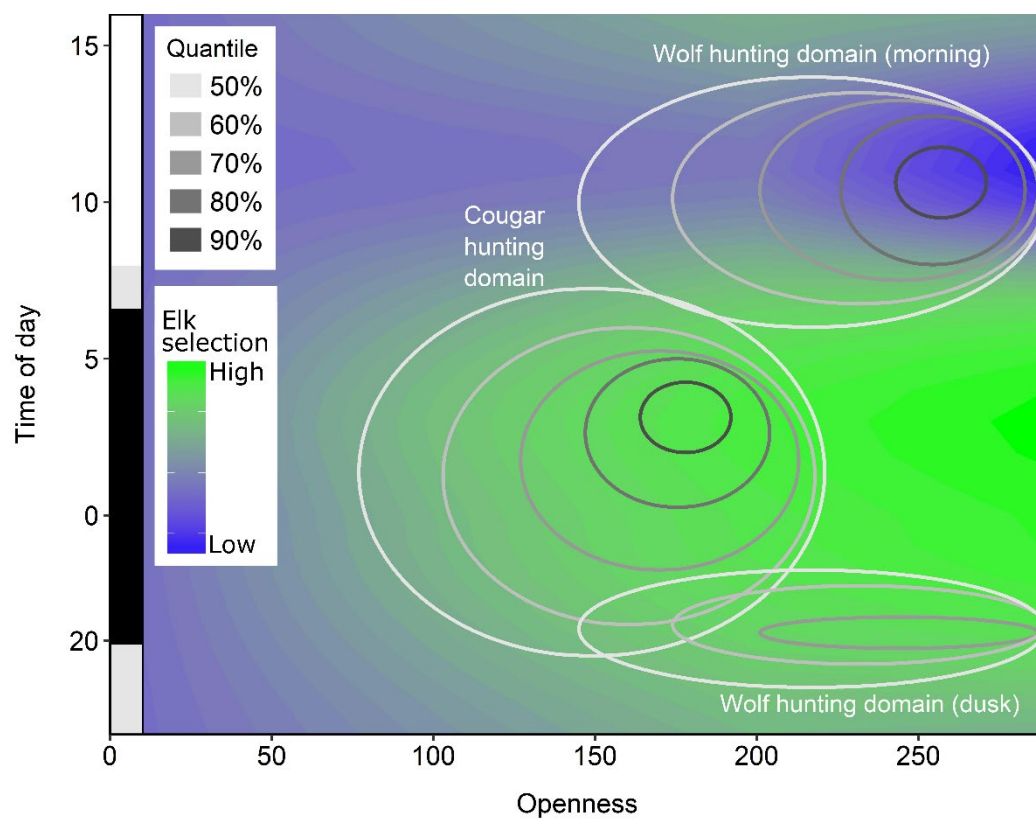


Figure 3-6. Visualization of elk habitat selection in relation to the hunting domains of wolves and cougars relative to openness (a) and topographic roughness (b) in northern Yellowstone National Park, 2001-2004. In accordance with the vacant hunting domain hypothesis, elk habitat selection was concentrated in the ‘nighttime-grassland’ and ‘nighttime-flat’ hunting domains. Use was more variable for the ‘daytime-forest/rough’ hunting domain, and yet, elk did demonstrate increased use of forest during daytime, thereby lending support to our prediction. The results are less clear for roughness. Elk selection is represented by graphing the fitted values from our best-fit openness model (Appendix 8). Hunting domains were visualized using the 10% quantiles extracted from models of kill probability (Fig. 3) and predator diel activity (Fig. 4b). Bars on y-axis represent day (white), night (black), and variation in dawn/dusk periods (grey) from 15 Nov – 15 April.

CHAPTER 4

DIRECT KILLING, NOT FEAR, EXPLAINS PREY RANGE SHIFTS
FOLLOWING PREDATOR REINTRODUCTION³

INTRODUCTION

Predators can shape the spatial distribution of prey species, and they may do so in one of two ways. The first is by eating more prey in some areas than in others. The level of predation in some areas may be so great that local prey abundance drops. Where there is little or no predation, prey abundance may increase or, if other factors limit population growth, remain stable. The net result of a spatial gradient in predation rate is that the distribution of the prey species is concentrated in the low predation area. This is a density-mediated effect insofar as direct killing is responsible for the shift in prey distribution.

The second way that predators can affect prey distribution is by scaring prey away from them. Fear of predation (perceived predation risk) can repulse prey from areas of high-perceived risk and attract them to areas of low-perceived risk. Such a spatial gradient in fear is expected to concentrate the distribution of prey in areas they perceive as low risk. This is a trait-mediated effect because a prey trait (i.e., movement behavior) causes the shift in prey distribution.

The hypothesis that fear of predation is an ecological force that rivals or exceeds that of direct killing (Brown et al. 1999, Priesser et al. 2005, Laundré et al. 2010) predicts

³ Kohl, M. T., P. J. Mahoney, L. M. Smith, S. R. Hoy, A. Nelson, T Wyman, P. J. White, D. R. Stahler, D. D. Smith, D. R. MacNulty. *In Review*. Does fear of wolves explain shifts in elk distribution? University of Chicago Press.

that the trait-mediated effect of fear is the primary way that predators shape prey distributions. Although changes in prey distribution can affect prey physiology (Zanette et al. 2014), demography (Preisser et al. 2007), and disease transmission (Hess 1996), as well as plant growth (Ford et al. 2014) and nutrient cycling (Hawlena et al. 2012), little is known about the relative influence of trait- and density-mediated effects on prey distribution, particularly in large-scale, free-living systems. We addressed this gap using long-term data from elk that inhabit the winter range of northern Yellowstone National Park.

This 1520-km² area is defined by the low-elevation (1500–2600 m) grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries along the northern border of Yellowstone National Park and adjacent areas in Montana (Lemke et al. 1998). Approximately 65% (995 km²) of the winter range is located within the park, and the remaining 35% (525 km²) extends north of the park boundary, where the State of Montana uses hunting to manage elk numbers (Lemke et al. 1998). Areas inside the park generally occur at higher elevations and have deeper snowpacks than areas outside the park. Northern Yellowstone elk migrate seasonally, moving from higher-elevation summer ranges to lower-elevation areas throughout the winter range. The elk population is spatially structured, with one segment occupying the ‘lower sector’ of the winter range (Fig. 4-1: 1500-1700-m, 736-km²), another segment occupying the ‘upper sector’ (Fig. 4-1; 1800-2100 m, 790-km²), and some elk floating between these areas in response to weather conditions (White et al. 2010).

Following wolf reintroduction, sightability-corrected numbers of elk in the upper sector decreased from 12,528 in 1996 to 715 in 2017 (Fig. 4-2). The number of elk in the

lower sector ranged from 3,722 and 5,147 (mean \pm SE = 5673 ± 223 elk) and exhibited no overall trend. There has been an upward trend in the lower sector since 2011, and this has contributed to a shift in winter distribution, with most elk (58-91%) located in the lower sector during 2007-2017. Thus, the overall decline in elk abundance across the entire winter range ($N_{1996} = 19,904$ elk; $N_{2017} = 7,616$ elk) mainly reflects decreased elk abundance within the park winter range.

Two hypotheses attribute the shift in elk winter distribution to wolves. Both are premised on the observation that wolf abundance is generally greater in the upper sector than in the lower sector (Fig. 4-3). The trait-mediated hypothesis proposes that elk relocated themselves downriver toward the lower sector, which elk are presumed to perceive as lower-risk given the relatively low numbers of elk in the lower sector, especially during 1995-2008 (Painter et al. 2015, Beschta and Ripple 2016). The density-mediated hypothesis proposes that the shift in elk distribution is due to attrition of elk from the upper sector due to higher rates of wolf-caused mortality and lower rates of elk calf recruitment (White et al. 2012). Because cervids, including northern Yellowstone elk, have high year-to-year fidelity to specific wintering areas (Irwin and Peek 1983, Linnell and Andersen 1995, Schaefer et al. 2000, White et al. 2010), we expected greater support for the density-mediated hypothesis.

ELK WINTER-RANGE FIDELITY

We first tested the trait-mediated hypothesis by evaluating the extent that VHF- and GPS-radio-collared adult female elk relocated their winter ranges downriver toward the lower sector. Elk location data were available for females only during each of three

periods that reflected different levels of wolf abundance: no-wolf (1985-1989), high-wolf (2000-2006), and low-wolf (2011-2016). To estimate winter site-fidelity, we measured annual variation in the position of individual winter ranges. We defined winter as 1 January – 31 March. All elk locations were randomly subsampled to record 1 location / week in order to provide direct comparisons between VHF and GPS locations (range = 5 – 14 telemetry locations / individual / winter), and we only included individuals that had ≥ 5 locations in each of two consecutive winters. This resulted in the following sample of individuals for each period: no-wolf = 31 elk, high-wolf = 57 elk, and low-wolf = 71 elk.

If the shift in elk distribution was due to a trait-mediated effect of wolves, we expected elk to shift their winter range down-river toward the lower sector where wolf abundance was least (Fig. 4-3). We assessed annual change in winter range location relative to the Yellowstone River Corridor (YRC) which we estimated using the National Hydrology Dataset. Our estimated YRC provided a means to measure the movement of elk down (or up) river. Next, we estimated MCP home range and extracted centroid estimates for individual elk for each winter (Gower et al. 2009). We then calculated the perpendicular intersection between the home range centroid and the YRC. From this intersection with the YRC, we were able to produce a standardized metric for all individuals that measures their annual movement up or downstream. See Appendix 5 for detailed methodology.

Elk on the Northern Range demonstrated high site-fidelity across winters and study periods suggesting that wolf reintroduction has had no behavioral effect on the large-scale spatial distribution of elk on the Northern Range (Fig. 4-4). During our baseline no-wolf study period, the median difference between winter-ranges was a 0.46

km (mean = 3.21 km) shift downriver toward the lower sector. However, this period was biased by the large downriver shifts that occurred following the catastrophic wild fires during the summer of 1988; 5 individuals moved ≥ 12 km downriver from 1988 to 1989. If we censor those individuals influenced by the 1988-89 fires, our pre-wolf data ($n = 15$) suggests that the general tendency was for high site-fidelity that may include small shifts upriver away from the lower sector (median = -0.46, mean = -1.6 km).

During the peak-wolf period, site-fidelity remained high (median = 0.27, mean = 0.01 km shift downriver); however, for individuals that demonstrated significant home range shifts (≥ 8 km), 83% moved upriver toward the upper sector. During the low-wolf period, site-fidelity again remained high (median = 0.08, mean = 2.27 km movement downriver); however, there were some individuals that exhibited substantial downriver shifts. In total, 5 individuals moved ≥ 15 km downriver from one winter to the next. Of these, three individuals moved from the upper sector to the lower sector, one individual moved within the lower sector to a portion outside of the park boundary, and the last individual moved further away from the park boundary within the lower sector.

ELK SURVIVAL AND WOLF-CAUSED MORTALITY RATES

If the shift in elk distribution was due to a density-mediated effect of wolves, we expected age-specific rates of adult female survival and wolf-caused mortality to be greater in the upper sector than in the lower sector. To assess survival and wolf-caused mortality by sector, we fit a fully-parametric, competing-risks model with a Weibull distribution and two mortality absorbing states, mortality due to wolves ($n = 54$) and mortality due to other causes ($n = 35$; R package *Flexsurv*; Jackson 2016). For mortalities

with an unknown cause of death, we assigned a wolf-caused mortality if field notes indicated wolves were active in the area ($n=3$) or if the spatial location of the mortality overlapped with a known wolf territory ($n=11$). The remaining 17 unknown mortalities were assigned as “other-caused mortality”. We censored all human-caused mortalities at their mortality date to focus on the influence of non-human caused mortalities. We used elk age in years as the model time scale to estimate mortality probability by age. Our data were left-staggered to account for elk radio-collared in different years and right censored in cases where elk were no longer monitored (e.g., missing and collar failure). See Appendix 5 for detailed methodology.

We obtained 89 mortalities across the study area, including 54 wolf-caused mortalities (11 lower sector, 43 upper sector). Age of our dead elk ranged from 11.25 to 21.15 years in the lower sector and from 9.33 to 23.96 years in the upper sector. Analyses of both sectors included 158 censored (alive during last location) elk. Elk had a higher probability of wolf-caused mortality in the upper sector compared to the lower sector (Fig. 4-5a). And although elk survival was similar between the two regions (Fig. 4-5b), suggesting that other sources of mortality in the lower sector (e.g., malnutrition) compensated for wolf mortality over the duration of the study, mean survival in the lower sector was still higher than the upper sector. Specifically, elk between 1-8 years of age had a $< 1\%$ probability of being killed by wolves in both sectors. At age 9, the probability of wolf-mortality increased for elk in the upper sector, reaching 45% at age 15 and 76% at age 20. The probability of wolf-mortality remained at $< 11\%$ for elk in the lower sector through age 15, increasing to 35% by age 20. By contrast, the probability of other-caused mortality was 30% at age 20 in the lower sector compared to 13% at age 20 in the upper

sector. Higher rates of wolf-caused mortality among older elk in the upper sector together with a relatively older female age structure in this sector (Fig. 4-6) suggests that wolves killed substantially more adult female elk in the upper sector than in the lower sector.

ELK CALF RECRUITMENT RATE

Because wolves are major predators of elk calves (Metz et al. 2012), we expected rates of elk calf recruitment (calves per 100 cows) to be lower in the upper sector than in the lower sector if the shift in elk distribution was due to a density-mediated effect. We estimated calf/cow ratios by obtaining sex-specific elk counts from helicopter surveys conducted in late winter (Feb. – Mar.) from 1998-2009. To reduce costs, helicopter surveys were replaced with ground observations (Jan. – Mar.) from 2010-2016. While transitioning from helicopter to ground surveys, intermittent helicopter surveys occurred in a subset of the Northern Range in 2011, 2012, and 2014, which allowed us evaluate differences in sampling technique. Analysis of variance tests demonstrated no significant difference between mean calf/cow ratios estimated from ground or aerial counts in any of the three test years ($p > 0.05$). Thus, we combined our ground count estimates from 2010-2016 with our helicopter surveys from 1998-2009 to provide a continuous measure of calf recruitment. See Appendix 5 for detailed methodology.

Calf/cow ratios were significantly lower in the upper sector than in the lower sector for much of the study (Fig. 4-7) consistent with a density-mediated effect. In the upper sector, calf/cow ratios declined from 17.4 calves / 100 cows ($CI \pm 4.6$) to 13.6 calves / 100 cows ($CI \pm 4.1$) over the 18-year study. The lower sector had more variation

in calf/cow ratios with a significant drop during the period when wolf abundance peaked in both sectors.

DISCUSSION

Our results support the hypothesis that the shift in elk spatial distribution following wolf reintroduction in northern Yellowstone is due to a density-mediated effect. The upper herd segment was older, had less recruitment, and was more susceptible to predation. More importantly, these factors, in combination, may have caused a positive feedback loop that contributed to the rapid shift in the spatial distribution of the elk population. Prior to wolf reintroduction, elk density was highest in the upper sector suggesting that herd sector may have reached carrying capacity (Houston 1982). This likely explains why the upper sector was historically composed of older elk prior to wolf reintroduction (Houston 1982), and as such, likely predisposed the herd segment to a rapid decline. This is because the upper herd segment would have experienced lower pregnancy rates (MacNulty et al. 2016), and ultimately reduced recruitment because of their age, regardless of wolf predation in the upper sector. However, because wolves are a significant predator of elk calves on the winter range (Metz et al. 2012), and because the upper sector supported a larger density of wolves (Fig. 4-3), it is likely that increased predation risk further diminished recruitment of this herd segment due to predation of elk calves. Together, these demographic processes would have accelerated the aging of the upper sector population. The older elk population would then be expected to experience higher wolf-caused mortality due to

age-specific survival (Fig. 4-5). The net result was a rapidly decreasing elk population in the upper herd segment.

We found little evidence for a trait-mediate effect. Elk winter ranges did not shift downriver toward the lower sector where wolf densities were least. On the contrary, some elk shifted their winter range upriver toward areas of higher wolf abundance. More specifically, these results do not support the hypothesis that the shift in elk distribution YNP is due to a movement response to wolf predation inside YNP (Painter et al. 2015, Beschta and Ripple 2016). The only support for this hypothesis is based on a narrow interpretation of an analysis by White et al. (2010) that documented a 39% change in their winter range home range fidelity. This analysis differed slightly from ours as they estimated changes in winter range fidelity via the Euclidean distance estimated from consecutive home range centroids (personal communication, P.J. White, National Park Service). Although Painter et al. (2015) assumed that this change involved movement toward the outside of the park, White et al.'s (2010) study did not analyze or specify directional shifts in their results. Our analysis of site-fidelity which includes most of the individuals analyzed by (White et al. 2010) found that 47% of the largest (≥ 5 km) home range shifts ($n = 15$) were toward the upper sector (highest wolf abundance) during the years of high-wolf abundance. During the low-wolf period, 77% of home range shifts ≥ 5 km ($n = 13$) were toward the lower sector.

Results from other studies corroborate our findings. Gower et al. (2009) showed that elk remained highly fidel to winter ranges despite increasing predation risk from wolves. This lead to the near extirpation of the local elk population from the two winter ranges in the western portion of Yellowstone National Park as a result of direct killing

(White et al. 2009). Similarly, the Environmental Impact Statement concerning the reintroduction of wolves to Isle Royal National Park highlight direct predation as the primary mechanism responsible for spatial changes in browsing intensity by moose (*Alces alces*; De Jager et al. 2017, National Park Service 2018). Our results are also in accordance with a more recent analysis which showed that elk do not spatially avoid wolves at the scale of northern Yellowstone (Cusack et al. In Press). This is likely because elk are able to manage predation risk at a fine-scale using a variety of anti-predator behaviors. For example, recent work has suggested that the crepuscular hunting behavior of wolves is highly predictable, and thus, allows elk to access otherwise risky areas during safe periods of the day (Kohl et al. 2018) which negates the need for large-scale spatial avoidance.

Other forces besides wolves certainly affected elk demographic rates and space use. For example, given that wolf densities were approximately equal between the upper and lower sectors during the low-wolf period, it is possible that the large percentage (77%) of large-scale shifts (≥ 5 km) toward the lower sector was driven by the cessation of a late-season cow elk hunt in 2010. This hunt has been characterized as “super additive” (Vucetich et al. 2005), and its cessation may have removed an important source of predation from the landscape that previously encouraged elk to maintain winter ranges in the upper sector. This is significant because human hunters preferentially harvest prime-age elk (Wright et al. 2006), and as a result, this suggests that the removal of that harvest would have removed a major source of mortality from an otherwise invulnerable elk population in the lower herd segment. Human harvest has been shown to

dramatically influence prey spatial distributions across taxa including edible plants (Moreno 2001), marine fisheries (Jackson et al. 2001), and large ungulates (Brown 2011).

However, harvest alone is unlikely to dictate prey spatial distributions. Since wolf reintroduction, significant land ownership changes, and associated management outside of the park has resulted in an increase in high-quality forage (e.g., alfalfa) as well as a refugia for elk from human harvest during the general fall hunt (Haggerty and Travis 2006). Furthermore, the State of Montana initiated an annual wolf harvest beginning in 2009, which may have reduced predation risk from wolves on properties that permitted wolf harvest. It is unclear from our data how black bear harvest may have influenced elk demography; however, elk that winter in the upper sectors of northern Yellowstone are known to summer in areas characterized by higher bear abundance which would, in turn, contribute to reduced recruitment (White et al. 2010). Thus, it is likely that variation in land use and predation risk played joint roles in the variable demographic rates we observed between elk in the upper and lower sectors.

Our results are broadly important because they suggest that trait-mediated effects such as home-range shifts may be less relevant to conservation and management than density-mediated effects. Many taxa exhibit high fidelity to home ranges, suggesting predation risk may seldom outweigh the enhanced risk of mortality associated with abandoning a familiar range (Forrester et al. 2015). If so, the effects of predators on prey distribution across large-spatial scales in free-living systems may be rarely the result of a trait-mediated effect of fear.

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FIGURES

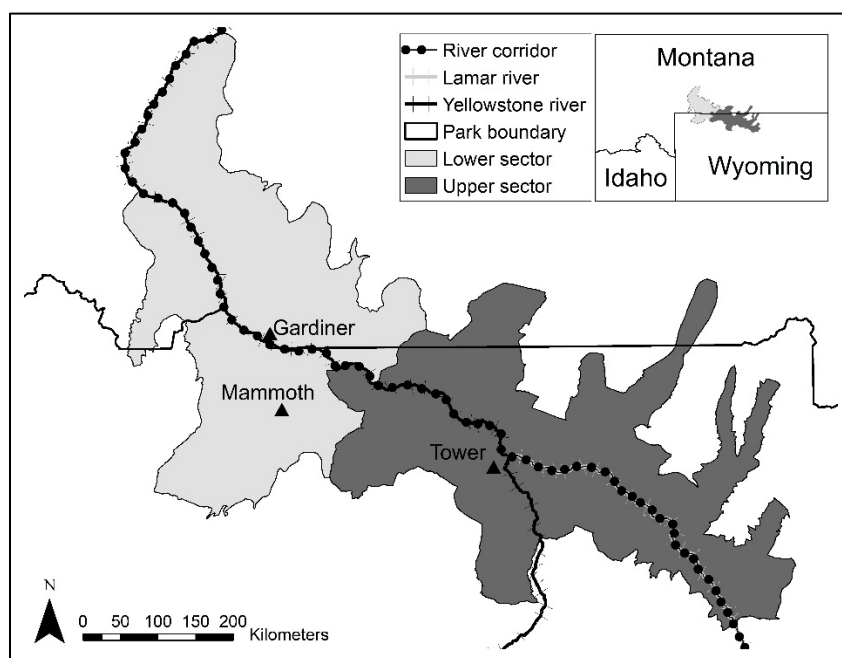


FIG. 4-1. Map of upper and lower sectors of northern elk winter range of Yellowstone.

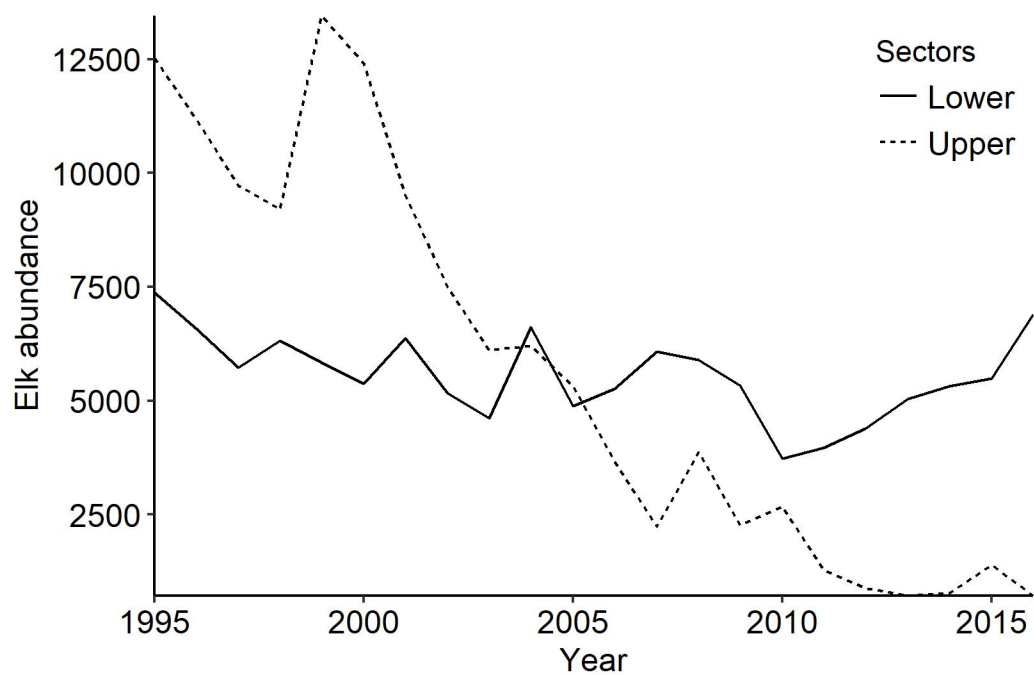


FIG. 4-2. Minimum estimated elk counts for upper and lower sectors of the Northern Range in northern Yellowstone, 1985 – 2016. Elk counts were interpolated from a state-space model for years when counts were not performed.



FIG. 4-3. Minimum wolf counts for upper and lower sectors of northern Yellowstone, 1995-2016. Counts are the sum of all December 31 wolf pack counts for packs that primarily occur in either sector. For packs that resided in both sectors, the minimum pack count was halved and then applied equally to both sectors.

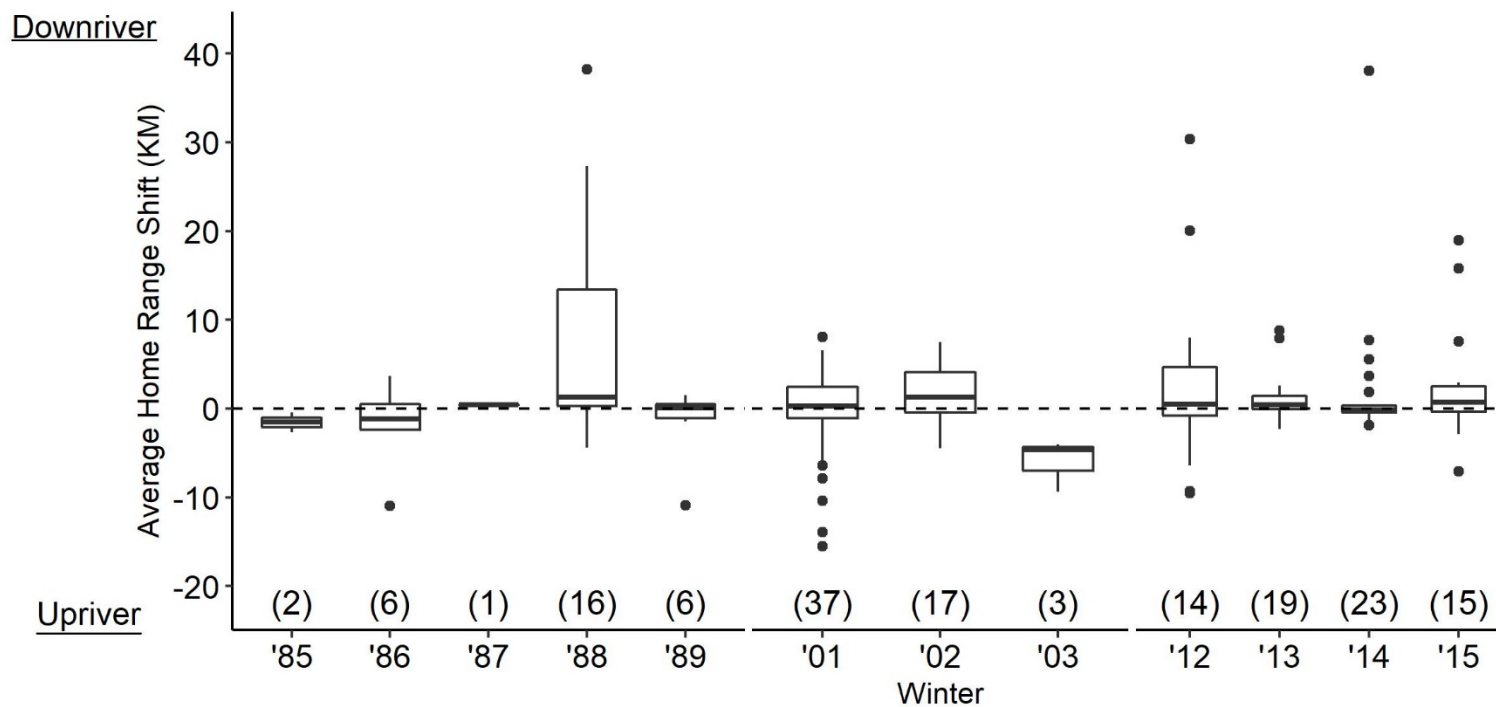


FIG. 4-4. Annual home range shifts by adult female elk in northern Yellowstone, 1984 – 2016. Winter represents the difference between T-1 and T. Sample sizes are identified in parentheses. For example, 1985 represents the home range shift for 2 elk during winter (Jan. – Mar.) 1985 and winter 1986.

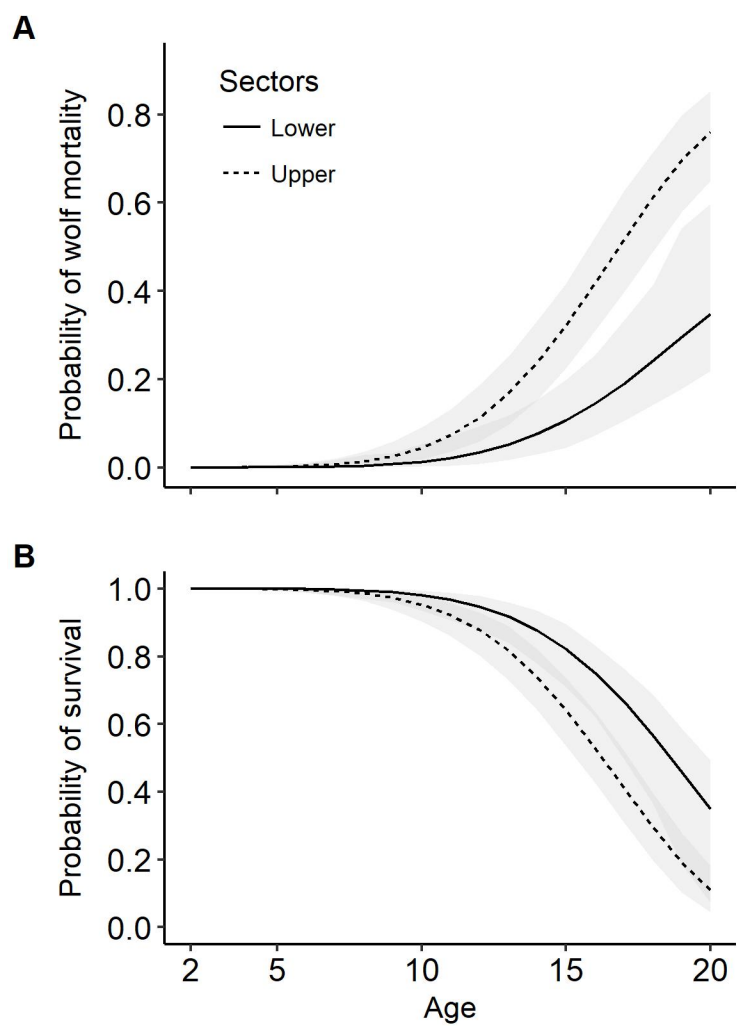


FIG. 4-5. Sector-specific probability of adult female elk mortality by wolves (a) and survival (b) as a function of age in northern Yellowstone, 2001 – 2016.

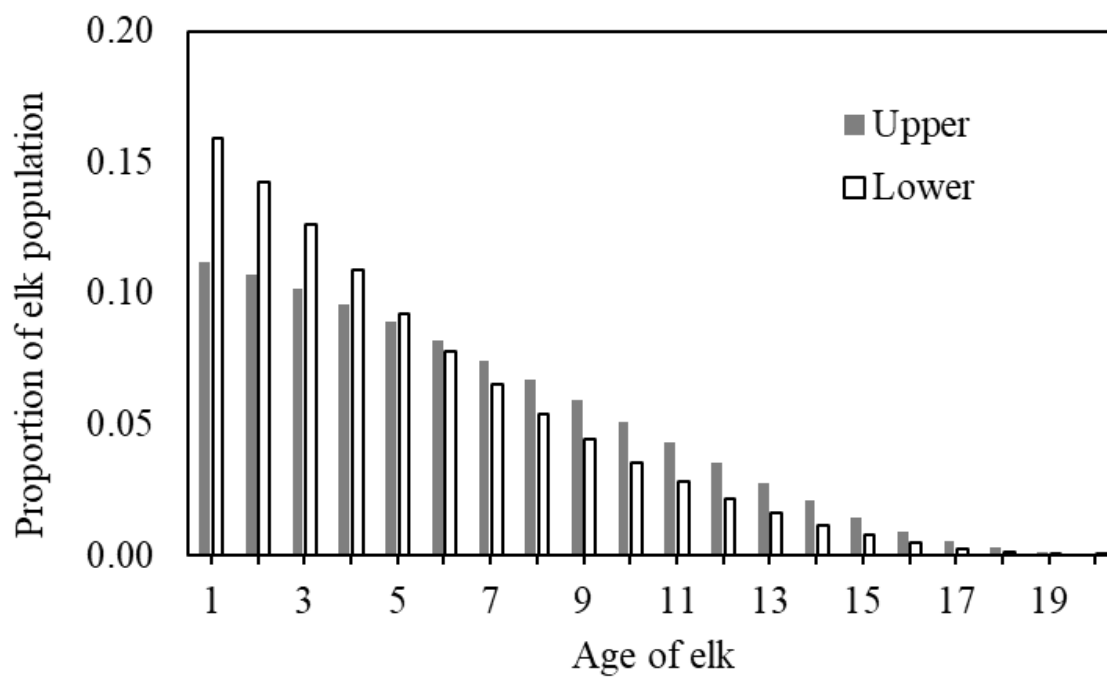


FIG. 4-6. Proportion of population by age for the upper and lower sectors of northern Yellowstone, 1995 – 2016.

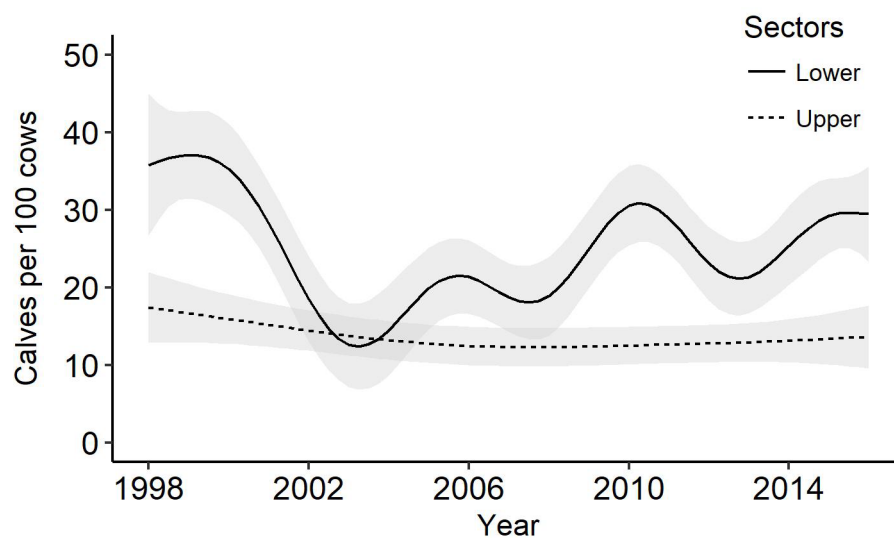


FIG. 4-7. Cow – calf ratios for the upper and lower sectors of northern Yellowstone, 1998 – 2016. Ratios are estimated from a generalized additive model fit to annual winter classification flights with 95% confidence intervals.

CHAPTER 5

DISCUSSION

The re-establishment of a landscape of fear and subsequent trophic cascades are widely cited to argue for predator restoration in the United States and around the world. However, we know little about the mechanisms driving the effects of predators on prey space use in large-scale, free-living systems. The preceding chapters attempt to address this at multiple spatial and temporal scales. In chapter 2, I addressed how elk (*Cervus elaphus*) can use risky places during safe times, effectively dampening the landscape of fear in northern Yellowstone. In chapter 3, I continued my examination of predator diel activity to demonstrate how contrasting diel activity schedules of wolves (*Canis lupis*) and cougars (*Puma concolor*) established a temporally predictable spatial refugia that may minimize predation risk in an otherwise, spatially-saturated predator environment. Finally, in chapter 4, I used numerous analytical approaches to quantify the relative role of density-mediated and behaviorally-mediated effects on driving the spatial distribution of elk across northern Yellowstone.

In chapter 2, I make two key advances regarding the landscape of fear in northern Yellowstone. First, I demonstrate that wolf diel activity is a critical driver of the LOF. This deviates significantly from previous studies in which predation risk is held constant across time. This is important because I show that if I had also ignored variation in temporal predation risk (i.e., constant predation risk), I would have incorrectly concluded that elk had little fear of risky places. Rather, my consideration of diel predator activity revealed a LOF with peaks and valleys that oscillated across the diel cycle according to

the predator's activity rhythm. This dynamic landscape of fear allowed elk to use risky places during safe times.

My second key advance was the first approximation of the landscape of fear that prevailed in northern Yellowstone in the decade after the reintroduction of wolves. This is an important contribution to the field of ecology because the Yellowstone case study serves as an empirical cornerstone of the landscape of fear concept. As previously mentioned, I show that this landscape of fear ebbs and flows with the daily activity patterns of wolves. As a result, elk were able to continue using risky places despite the presence of wolves, a finding contrary to a number of previous studies which had assumed that the mere presence of wolves in northern Yellowstone excluded elk from areas of high wolf density (Ripple and Beschta 2004, Fortin et al. 2005, Beyer et al. 2007, Ripple and Beschta 2012, Beschta and Ripple 2013, Beschta and Ripple 2016).

In combination, these results clarify the potential for a behaviorally-mediated trophic cascade (BMTC) in northern Yellowstone. Elk behavioral abandonment of risky places is the key mechanism in the BMTC hypothesis. Specifically, the BMTC asserts that fear of wolves increases productivity of palatable woody deciduous plants in risky places via reductions in elk browsing (Ripple and Beschta 2004, Beyer et al. 2007, Kauffman et al. 2010, Winnie 2012, Peterson et al. 2014). However, the results within chapter 2 demonstrate that 1) elk used these risky sites during periods when wolves were inactive, and 2) that much of the browse species were not found in risky sites. These findings suggest that any recovery of riparian browse is likely to be due to changes in elk abundance rather than changes in elk behavior. As such, these results shed light on the controversy within northern Yellowstone regarding the effects wolves have on lower

trophic levels. More broadly, these results suggest that the activity schedule of predators may be an underappreciated aspect of animal behavior can help explain why strong antipredator responses (e.g., movement, vigilance) may have weak ecological effects. It also provides a basis for understanding why a landscape of fear may have less relevance to conservation and management than direct killing.

In chapter 3, I extended my analysis to consider the effects of a second predator, cougars, on my evaluation of predator diel activity to understand how prey species may operate within a landscape that is spatially saturated with predators. This differs from previous analyses which assumed wolves were the only predator affecting elk habitat selection; an unrealistic assumption given cougars are a major elk predator that peaked in abundance during the early 2000's (Ruth et al. In press). Thus, elk must simultaneously manage predation risk from both cougars and wolves in northern Yellowstone. Specifically, whereas cougar-killed elk were concentrated in areas that were moderately forested and rugged, wolf-killed elk were concentrated in areas that were in open grasslands and flat. This spatial saturation of where predators kill prey often lead to predictions of predator facilitation in which a prey species prioritizes its response to one predator (e.g., wolves) at the expense of increasing its risk to another (e.g., cougars; Charnov 1976, Kotler et al. 1992), and ultimately, facilitating an overall rate of prey mortality that exceeds the sum of each predator-specific mortality rate (Sih et al. 1998). However, I show that the diel activity schedules of predators serve as a key niche axis that provided a temporally predictable spatial refugia for elk across northern Yellowstone. Whereas wolves were crepuscular, male cougars were nocturnal. This created two predator niche vacancies: flat, open areas at night (nighttime grassland

niche), and rugged, forest areas during daylight (daytime forest niche) that elk could select for.

As I predicted, elk selected for these predator niche vacancies: daytime forests and nighttime grasslands. As a result, elk were able to simultaneously manage predation risk from both predators. Moreover, this anti-predator mechanism that may be prevalent across biological systems. Resource partitioning is a common mechanism that promotes coexistence among predators (Schoener 1974, Kronfeld-Schor and Dayan 2003) with predators using different resources, or the same resources at different places or times (Bruno and Cardinale 2008). Thus, it would not be surprising if the use of predator niche vacancies is common across systems. Given that, the use of predator niche vacancies may represent an important, though underappreciated, influence on biological systems that, when ignored, could overestimate of the effects predators will on prey space use and demography.

In chapter 5, I evaluated the relative role of density-mediated and behaviorally-mediated interactions in determining the spatial distribution of elk in northern Yellowstone. This is important because predation is a key mechanism that directs prey spatial distributions. This happens in one of two ways: predator either reduce the local prey population through direct consumption, or predators induce a change in habitat use (Preisser et al. 2005). This distinction is important because both pathways can influence prey spatial distributions, and in turn, facilitate positive effects on plant communities (i.e., trophic cascades). Despite this, this work represents the first evaluation of the relative role of these two pathways in determining prey spatial distributions at a large spatial scale.

In this chapter, I also evaluated seasonal shifts in elk winter-range, elk calf recruitment, elk adult survival, and elk age structure. Together, these analyses demonstrate that the shifting spatial distribution of elk on the northern range of Yellowstone is the function of a density-mediated effect. These results contradict previous work that suggested that the current elk distribution in YNP is the function of a behavioral response to wolf predation inside YNP (Painter et al. 2015, Beschta and Ripple 2016). However, they align with previous work within the greater Yellowstone Ecosystem (Gower et al. 2009) and elsewhere (De Jager et al. 2017) that demonstrate prey spatial distributions are often the consequence of density-mediated interactions.

It is clear from other systems that density-mediated (Terborgh and Estes 2010, Estes et al. 2011) and behaviorally-mediated interactions (Schmitz et al. 1997, Suraci et al. 2016) can have positive effects on lower trophic levels. However, my results suggest that ecologists should not expect home range shifts to serve as a mechanism for ecological recovery following predator repatriation because many taxa exhibit high fidelity to home ranges. This is because predation seldom outweighs the reduced forage quality and the increased probability of mortality prey may experience when leaving their core range (Forrester et al. 2015). As a result, conservation planners should include an adequate number of predators in their restoration actions if ecological recovery of a system through trophic regulation is a goal because my results suggest it is unlikely to happen through behaviorally-mediated interactions.

The overall goal of this dissertation was to better understand the spatial ecology of predator-prey interactions within northern Yellowstone. Yellowstone provides the ideal study system to address these questions due to high-quality, long-term monitoring

on multiple predator and prey species. Using this information, I was able to examine the role that wolves and cougars play in driving elk habitat selection at fine- and large-spatial scales. Within this context, I was able to identify a primary predator trait, diel predator activity, which serves as an important avenue which elk can utilize to manage predation risk during winter.

More generally, I demonstrate that predator activity schedules are an important but previously overlooked anti-predator mechanism that may minimize the importance of fear effects in ecological systems. In particular, understanding the effect of predators on prey behavior and its subsequent effects on lower trophic levels is of high interest to both the scientific community and general public. Thus, by identifying how prey species may use diel predator activity to minimize predation risk, I have identified an anti-predator mechanism that is likely commonplace across biological systems. This is a significant contribution to the scientific literature because it helps explain why fear effects may not elicit the same ecological consequences in free-living systems as those seen in small-scale experimental systems (Middleton et al. 2013).

Moreover, by evaluating the role of fear effects in northern Yellowstone, this research is well suited to address long-standing debates regarding the ecological consequences of wolf reintroduction. Despite Yellowstone serving as the foundation for the landscape of fear concept, the landscape of fear was never quantified in this system. Rather, the landscape of fear was inferred from broad-scale, population-level data on elk vigilance (Laundré et al. 2001), fecal pellets (Hernández and Laundré 2005), and herbivory (Ripple and Beschta 2004). Thus, researchers never quantified whether or not elk actually avoided risky habitat, and as such, it was unclear whether any observed

patterns in vegetation response were due to wolves or other factors (Peterson et al. 2014). This dissertation serves as the first attempt to reconcile competing views regarding the ecological significance of fear in this system, and as a result, highlight the importance of clarifying the elk landscape of fear in Yellowstone. More broadly, these results matter because the elk landscape of fear in Yellowstone is a seminal example in the broader debates about the ecological consequences of fear (Ripple and Beschta 2004, Zaretzky et al. 2011) and the importance of apex predators to the structure and function of ecosystems (Terborgh and Estes 2010, Estes et al. 2011).

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APPENDICES

Appendix 1-Chapter 2 Supplemental Information

Table S1. Sample size of movement steps used to calculate diel activity pattern for 21 GPS-collared wolves in northern Yellowstone National Park during winter, 2004-2013. Values represent the steps calculated from consecutive 1-hour (outside parentheses) and 5-hour (inside parentheses) locations recorded during two 30-day periods in early (mid-November to mid-December) and late (March) winter.

Wolf ID	Sex	Winter									
		2004-05	2005-06	2006-07	2007-08	2008-09	2009-10	2010-11	2011-12	2012-13	2013-14
227	M	580 (120)									
470	F	629 (120)									
525	F		670 (135)	1387 (272)							
527	F		629 (127)								
593	F			438 (81)							
625	F				718 (144)	714 (140)					
627	M				714 (144)						
642	F						714 (142)	709 (144)			
685	M					714 (144)	1413 (282)				
692	F					620 (120)					
693	F					692 (140)	708 (144)				
752	F							704 (142)			
775	M							704 (140)	700 (138)		
777	M							708 (139)	1416 (282)		
829	F								712 (144)		
832	F								715 (144)	506 (100)	
889	F									533 (108)	652 (128)
890	M										714 (144)
907	F										694 (138)
910	M										694 (138)
SW763	M									698 (144)	1417 (275)
Total 1-Hr Steps		1209	1299	1825	1432	2740	2835	2825	3543	1737	4171
Total 5-Hr Steps		240	262	353	288	544	568	565	708	352	823

Table S2. Model selection results for matched case-control logistic regression models describing the relationship between elk habitat selection and four indices of spatial risk (predicted kill occurrence [a], kill density [b], openness [c], and wolf density [d]) in northern Yellowstone National Park, 2001-2004. Variables risk1 and risk2 contain a linear spline for spatial risk at the indicated threshold. The simple linear model (risk) includes no threshold. Number of parameters (K), QIC, and differences in QIC compared to the best model (Δ QIC) are given for each model. The best model for each spatial risk index is in bold face.

Model set	Threshold	K	QIC	Δ QIC
(a) Predicted kill occurrence				
risk	n/a	1	27560.52	347.13
risk1 + risk2	2.50	2	27214.47	0.83
risk1 + risk2	2.60	2	27213.61	0.00
risk1 + risk2	2.70	2	27214.12	0.48
(b) Kill density				
risk	n/a	1	28052.84	78.72
risk1 + risk2	0.11	2	27974.83	0.71
risk1 + risk2	0.12	2	27974.12	0.00
risk1 + risk2	0.13	2	27976.56	2.44
(c) Openness				
risk	n/a	1	27392.60	16.35
risk1 + risk2	1.00	2	27376.26	0.01
risk1 + risk2	2.00	2	27376.25	0.00
risk1 + risk2	3.00	2	27377.97	1.72
(d) Wolf density				
risk	n/a	1	28109.00	9.98
risk1 + risk2	0.40	2	28099.19	0.17
risk1 + risk2	0.41	2	28099.02	0.00
risk1 + risk2	0.42	2	28099.13	0.11

Table S3. Best-fit matched case-control logistic regression models for the effects of four indices of spatial risk (predicted kill occurrence [a], kill density [b], openness [c], and wolf density [d]) on elk habitat selection in northern Yellowstone National Park, 2001-2004. Variables risk1 and risk2 are the slopes before and after each index-specific threshold. Model selection results are presented in Appendix S4. Confidence intervals were computed using robust standard errors.

Parameter	Threshold	β	SE	P	[95% confidence interval]	
(a) Predicted kill occurrence						
risk1	2.60	0.479	0.030	<0.001	0.421	0.536
risk2		-0.001	0.003	0.755	-0.006	0.004
(b) Kill density						
risk1	0.12	6.82	0.62	<0.01	-13.25	13.49
risk2		0.67	0.13	<0.01	-1.321	1.321
(c) Openness						
risk1	2.00	0.1630	0.0400	<0.001	0.0760	0.2500
risk2		0.0025	0.0002	<0.001	0.0021	0.0029
(d) Wolf density						
risk1	0.41	0.84	0.18	<0.01	0.49	1.19
risk2		-2.06	0.84	0.02	-3.71	-0.40

Table S4. Model selection results for matched case-control logistic regression models describing the interactive effect of spatial risk (predicted kill occurrence [a], kill density [b], openness [c], and wolf density [d]) and diel wolf activity (WA; km travelled/5-hr) on elk habitat selection in Yellowstone National Park, 2001-2004. Variables risk1 and risk2 contain a linear spline for spatial risk at the indicated threshold. Space-only models (risk1 + risk2) are the best-fit models from Appendix S5. Space x activity models are the top models from a grid search of thresholds for each hourly lag (≤ 5) in diel wolf activity. Number of parameters (K), QIC, and differences in QIC compared to the best model (Δ QIC) are given for each model. Average Spearman-rank correlation between observed and predicted values calculated from K-fold cross validation (r_s) is given for the best-fit model (identified in bold).

Model set	Threshold	Lag	K	QIC	Δ QIC	r_s
(a) Predicted kill occurrence						
risk1 + risk2	2.60	NA	2	27213.61	126.73	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	3.40	0	4	27167.92	81.04	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.40	1	4	27126.15	39.27	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.50	2	4	27092.01	5.13	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.50	3	4	27086.88	0.00	0.99
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.20	4	4	27117.72	30.84	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	3.40	5	4	27171.30	84.42	
(b) Kill density						
risk1 + risk2	0.12	NA	2	27974.12	95.28	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	0	4	27906.66	27.82	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	1	4	27885.45	6.61	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	2	4	27878.84	0.00	0.97
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	3	4	27884.87	6.03	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	4	4	27909.96	31.12	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	5	4	27948.24	69.40	
(c) Openness						
risk1 + risk2	2.0	NA	2	27376.25	200.98	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	145.0	0	4	27257.81	82.54	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	147.0	1	4	27208.14	32.87	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	159.0	2	4	27175.27	0.00	0.99
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	165.0	3	4	27185.38	10.11	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	2.0	4	4	27242.36	67.09	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	2.0	5	4	27319.06	143.79	
(d) Wolf density						
risk1 + risk2	0.41	NA	2	28099.02	35.28	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.01	0	4	28077.67	13.93	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.02	1	4	28069.14	5.40	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.02	2	4	28063.74	0.00	0.67
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.03	3	4	28064.41	0.67	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.03	4	4	28071.01	7.27	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.03	5	4	28086.39	22.65	

Table S5. Best-fit matched case-control logistic regression models for the interactive effects of spatial risk (predicted kill occurrence [a], kill density [b], and openness [c]) and diel wolf activity (WA; km travelled/5-hr) on elk habitat selection in northern Yellowstone National Park, 2001-2004. Variables risk1 and risk2 are the slopes before and after each index-specific threshold. Model selection results are presented in Appendix S6. Confidence intervals were computed using robust standard errors.

Parameter	Threshold	Lag	β	SE	<i>P</i>	[95% confidence interval]	
(a) Predicted kill occurrence							
risk1	4.50	3	1.103	0.072	<0.001	0.96	1.24
risk2			-0.009	0.028	0.744	-0.07	0.05
risk1 x WA			-0.456	0.036	<0.001	-0.53	-0.39
risk2 x WA			0.002	0.015	0.873	-0.03	0.03
(b) Kill density							
risk1	0.12	2	8.65	3.28	0.008	2.22	15.08
risk2			7.44	0.86	<0.001	5.75	9.13
risk1 x WA			-0.95	1.65	0.564	-4.18	2.28
risk2 x WA			-3.51	0.44	<0.001	-4.38	-2.64
(c) Openness							
risk1	159.00	2	0.011	0.002	<0.001	0.006	0.015
risk2			0.020	0.002	<0.001	0.016	0.024
risk1 x WA			-0.003	0.001	0.001	-0.005	-0.001
risk2 x WA			-0.009	0.001	<0.001	-0.011	-0.007

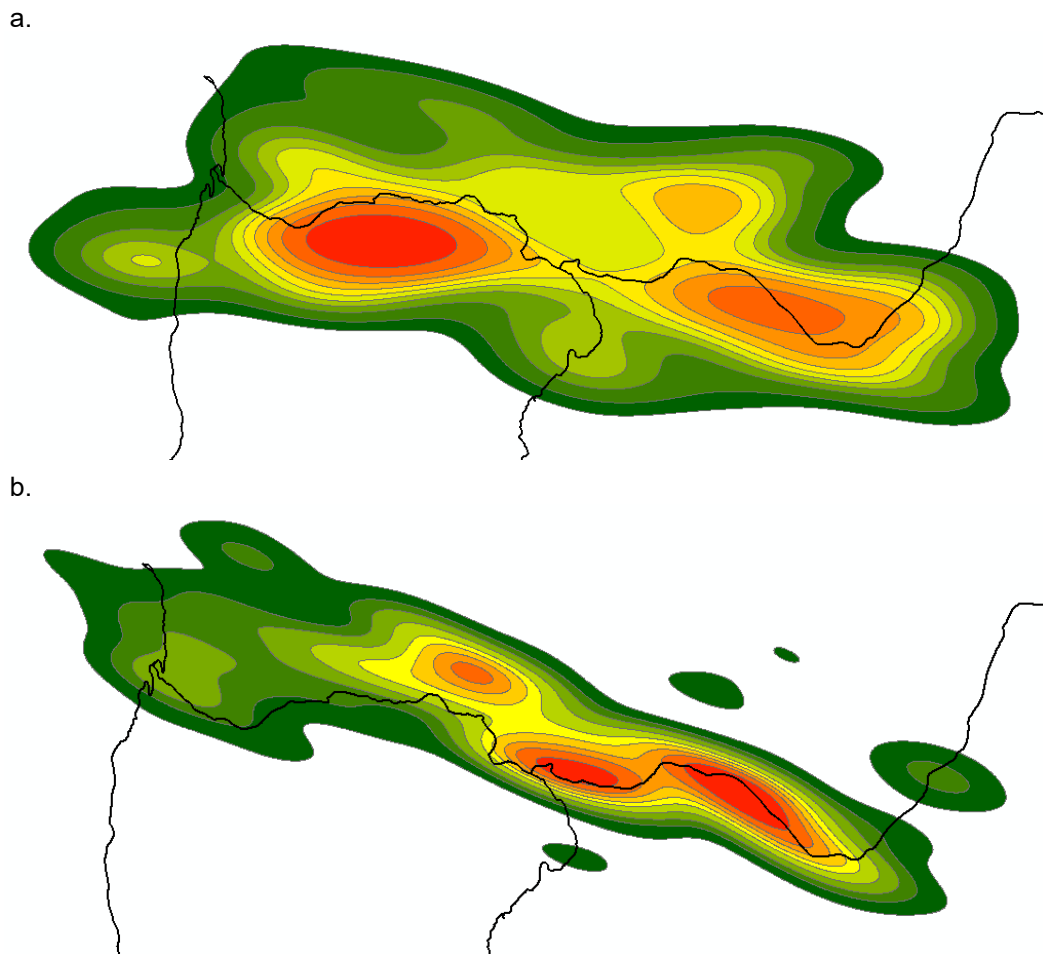


Fig. S1. Distribution of wolf-killed (a) adult male elk, and (b) adult female and calf elk during winter in northern Yellowstone National Park, 2001-2004. Contours are 10% kernel isopleths from a kernel density estimator applied to kill locations pooled across years. Red represents the highest density of kills and black lines denote roads.

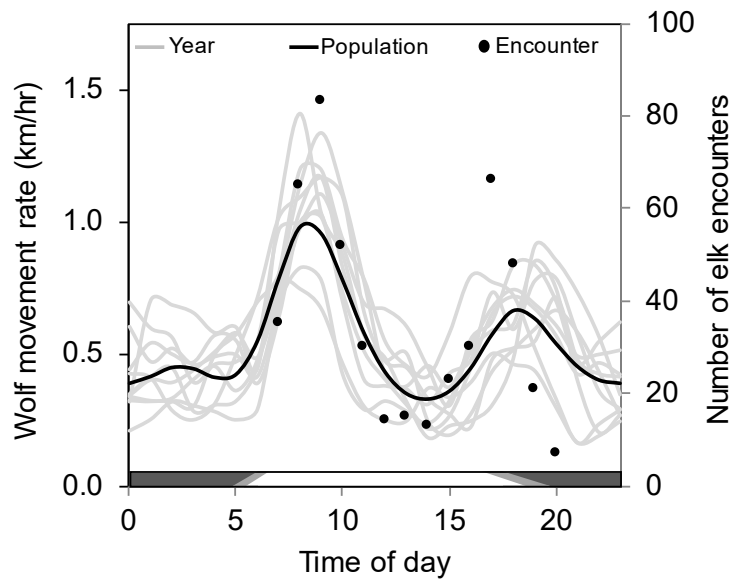


Fig. S2. Annual diel activity patterns of wolves during winter in northern Yellowstone National Park, 2004-2013. Mean hourly movement rate for each of 10 years (2-5 GPS-collared wolves per year; Appendix 1 – Table S1) and predicted population mean from a general additive mixed model (left ordinate), and hourly number of directly-observed daylight encounters between wolves and elk (right ordinate). Bars represent day (white), night (black), and variation in dawn/dusk periods (grey) from 15 Oct. – 31 May.

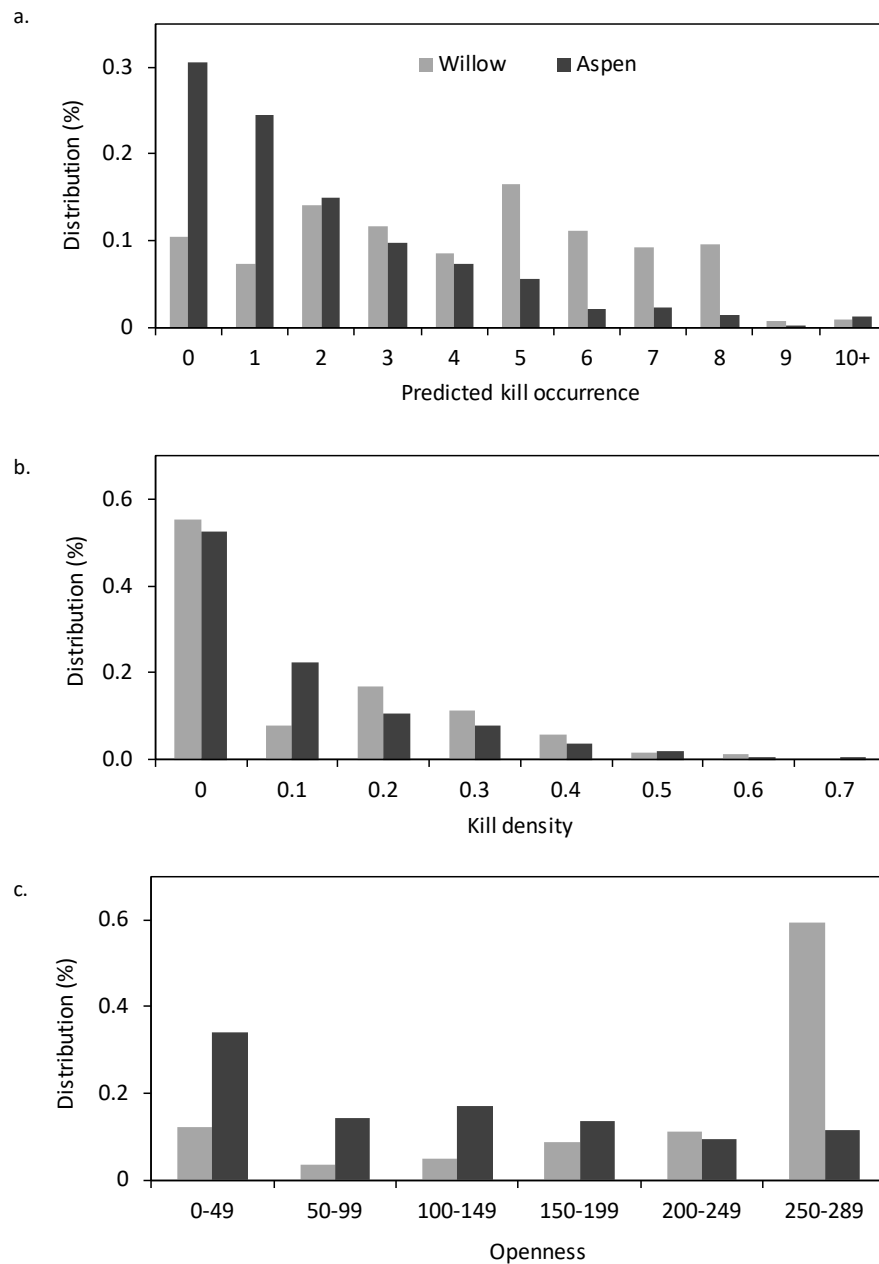


Fig. S3. Aspen and willow distribution in northern Yellowstone National Park in relation to spatial variation in wolf predation risk (predicted kill occurrence [a], kill density [b], and openness [c]). Predation risk values in [a] and [b] are the average predicted kill occurrence and kill density at willow and aspen locations from 2000-2004. Aspen location data are from the 1999 Northern Range Vegetation Layer of Yellowstone National Park (Spatial Analysis Center at Yellowstone National Park). Willow location data are from a comprehensive field mapping and inventory that concluded in 2010 (M. Tercek; <http://www.yellowstoneecology.com/>). Openness data are from a 1991 vegetation layer that accounted for vegetative changes follow the 1988 fires (Mattson et al. 1998).

Video S4. Animated visualization of how diel wolf activity shaped the landscape of fear for adult female elk in northern Yellowstone National Park, 2001-2004. We examined kill density in one part of our study area, (a), and used the corresponding best-fit space \times activity habitat selection model, (b), to calculate elk avoidance across this area throughout the diel cycle. Risky places where kills were densely concentrated are represented in red. Peaks identify risky places elk avoided; valleys represent safe places they utilized. Black lines denote roads. Video, compiled by Michel T. Kohl, can be seen at:

<https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fecm.1313&file=ecm1313-sup-0002-VideoS1.mp4>

Appendix 2-Chapter 3 Data Visualizations

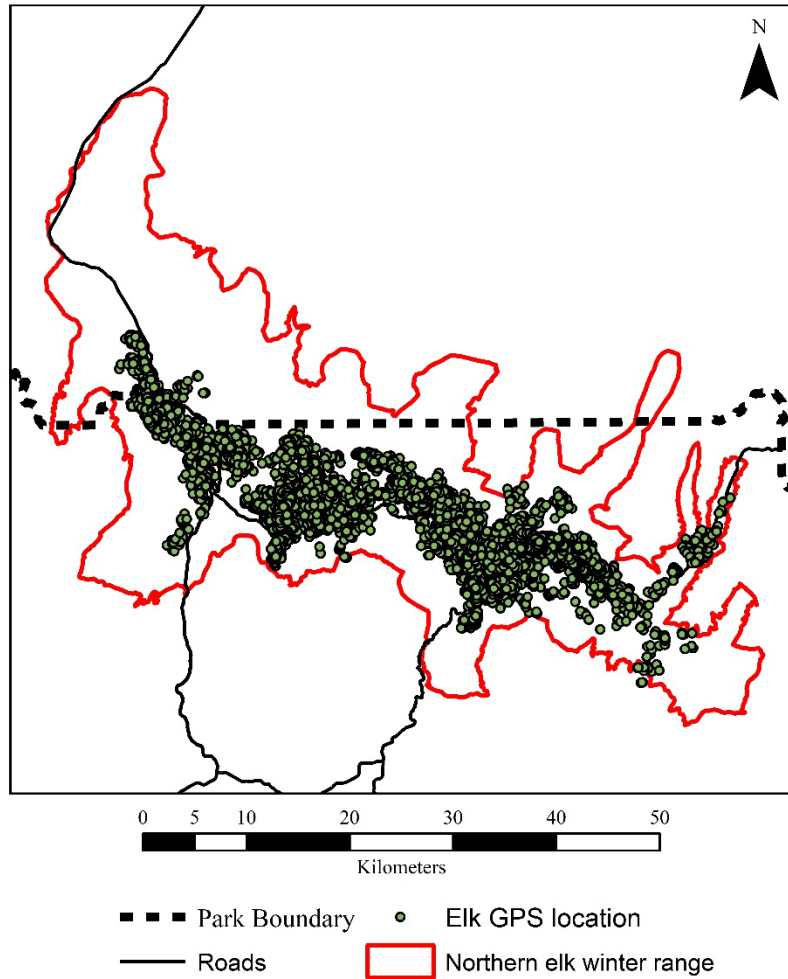


Figure S1. Winter (01 November – 30 April) locations of GPS-collared northern Yellowstone adult female elk ($n = 27$) from 09 February 2001 to 31 March 2004. We used these data to analyze elk habitat selection.

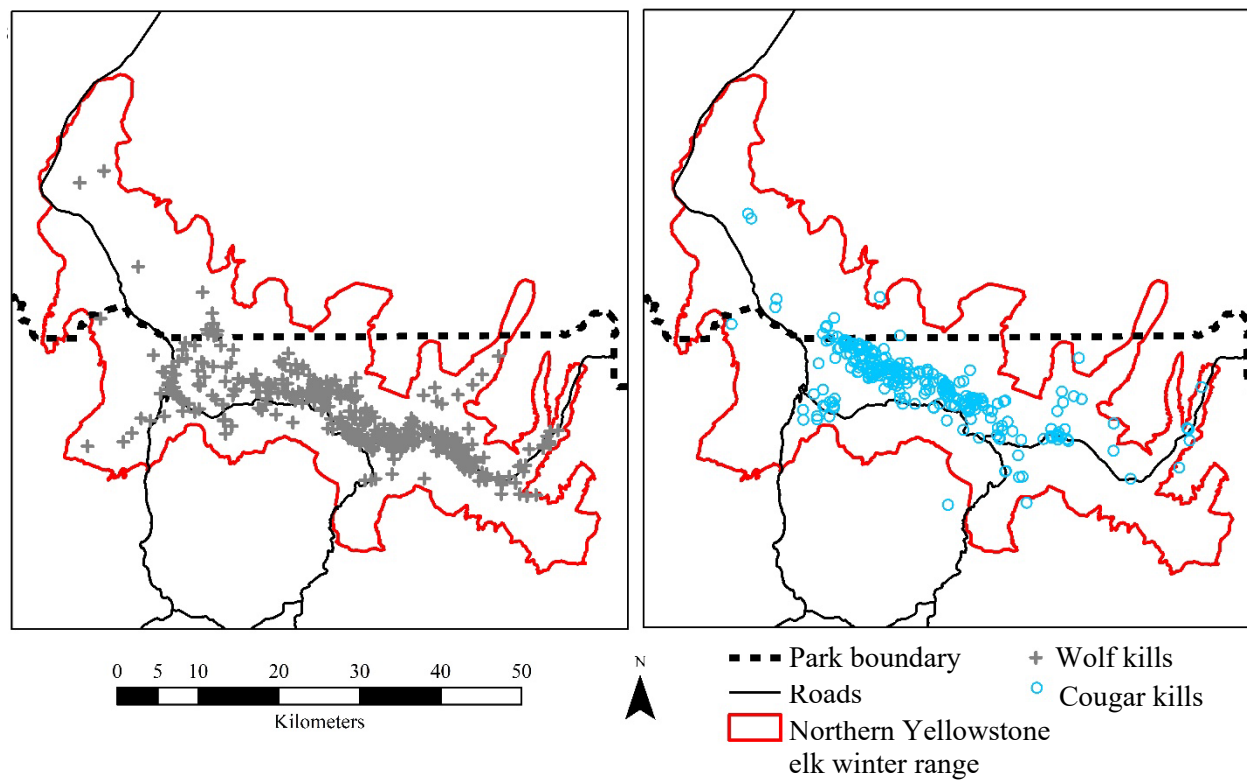


Figure S2. Winter (01 November – 31 May) locations of northern Yellowstone adult female elk and calves killed by wolves during 2000-2004, $n = 400$ (a), and cougars during 1998-2006, $n = 257$ (b). We used these data to assess if vegetation openness and topographic roughness were valid indices of spatial variation in elk predation risk from wolves and cougars.

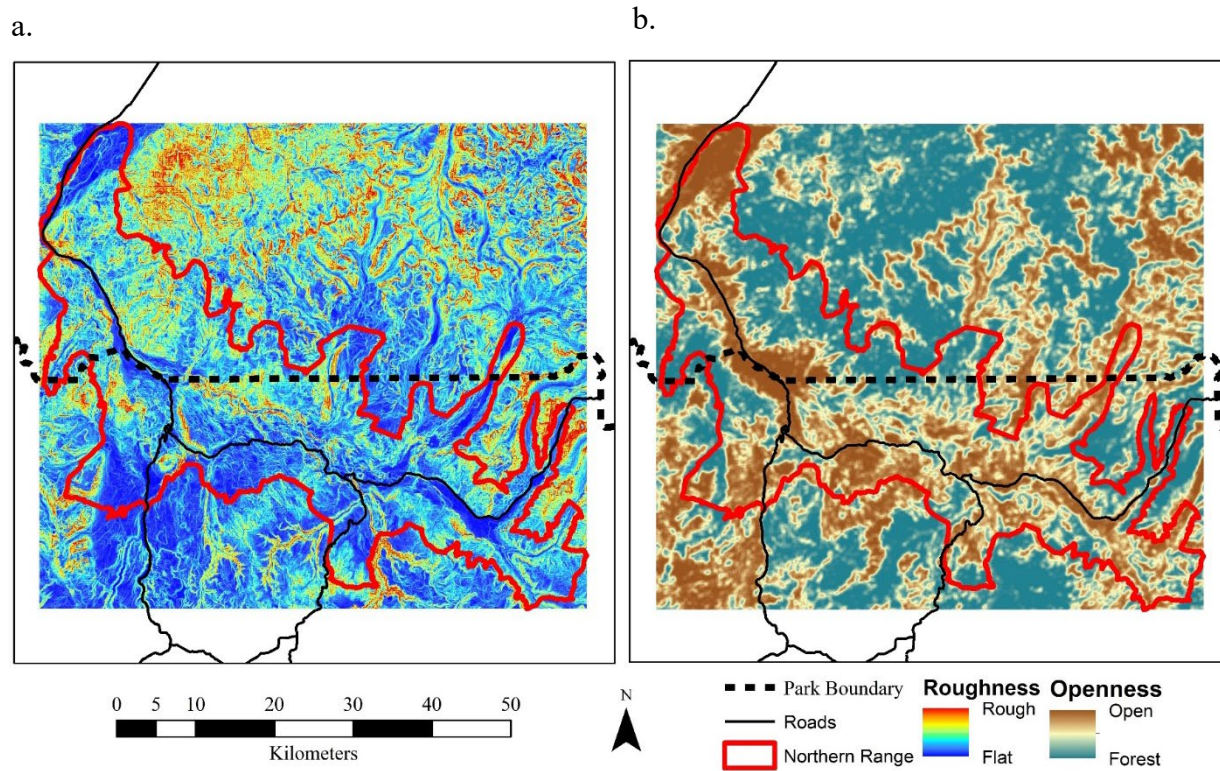


Figure S3. Spatial distribution of topographic roughness (a) and vegetation openness (b) in northern Yellowstone, 2000-2004. Topographic roughness and vegetation openness were not highly correlated (Pearson's correlation coefficient, $r = -0.18$). We used these data to index spatial variation in elk predation risk from wolves and cougars.

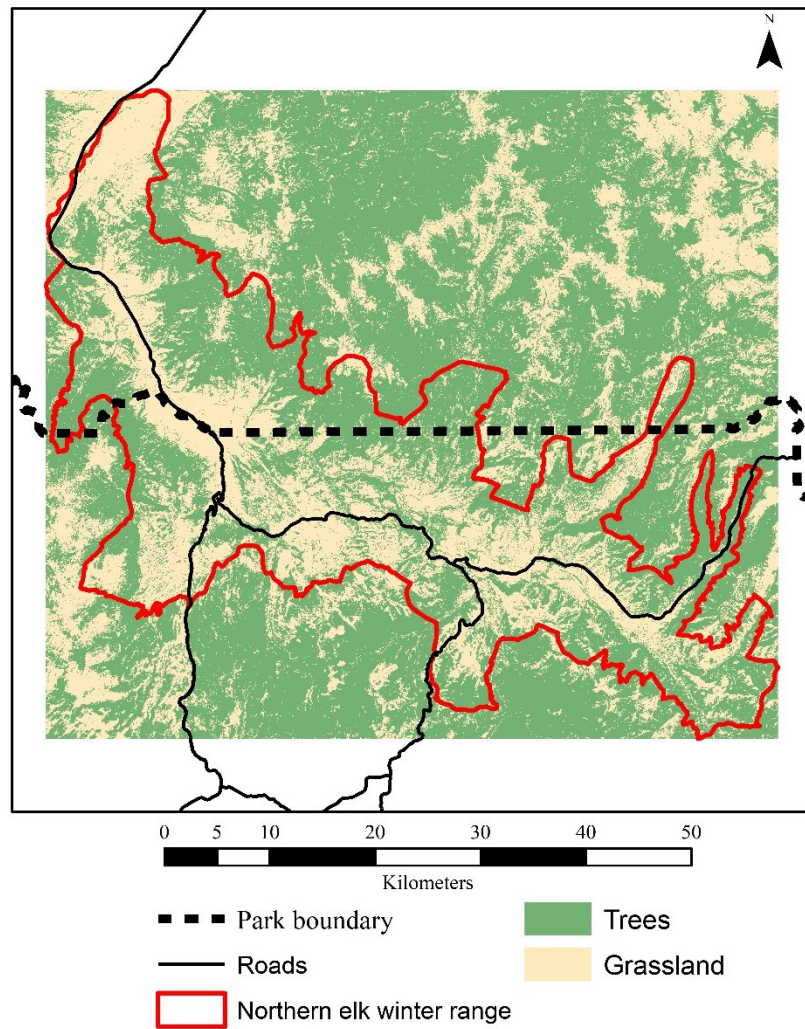


Figure S4. Spatial distribution of forest canopy cover in northern Yellowstone during 2001. Data are from the LANDFIRE program and were used to estimate vegetation openness (see Appendix S1. Fig 3b).

Dataset	Winter								
	1998-99	1999-00	2000-01	2001-02	2002-03	2003-04	2004-05	2005-06	2006-13
Elk gps data			x	x	x	x			
Cougar kill data	x	x	x	x	x	x	x		
Cougar gps data			x	x	x	x	x	x	
Wolf kill data			x	x	x	x			
Wolf gps data							x	x	x

Animal handling

We captured and handled elk, wolves, and cougars following protocols in accord with applicable guidelines from the American Society of Mammalogists (Sikes & Gannon 2011) and approved by the Hornocker Wildlife Institute/Wildlife Conservation Society or National Park Service Institutional Animal Care and Use Committees. Elk were captured in February (2001-2003) via helicopter net-gunning (Hawkins and Powers, Greybull, Wyoming, USA; Leading Edge Aviation, Lewiston, Idaho, USA) and fitted with Telonics (Telonics, Mesa, Arizona, USA) or Advanced Telemetry Systems Inc. (Isanti, Minnesota, USA). Wolves were fitted with VHF (Telonics Inc., Mesa, AZ, USA) or GPS (Televilt, Lindesberg, Sweden; Lotek, Newmarket, ON, Canada) radio-collars. Cougars were fit with VHF (Telonics Inc., Mesa, AZ, USA) or GPS (Telonics, Inc. and Televilt, Inc., Lindesberg, Sweden) radio-collars.

Predation sampling

Wolf sampling:

During the early and late 30-day winter periods of intense monitoring, ground crews operated daily, whereas aircraft were limited by weather conditions. Kills outside of these periods were located opportunistically by either ground or air crews. The location of wolf kills were tallied independently by ground and air crews. If ground or air crews did not acquire GPS locations while necropsying or flying directly over kills, locations were estimated from topographic maps. If more than one spatial location was available for a given kill, our criteria for inclusion in the analysis followed: necropsy > air sampling > locations estimated from ground observations using topographic maps. We used only wolf kill identified as definite or probable (Mech *et al.* 2001) during winters, 2000-2004 (n = 400 kills).

Cougar sampling:

Cougar kills were identified opportunistically on predetermined sampling routes (55%) or during a predation sampling sequence on a randomly selected radiocollared cougar (45%). All sampling sequences were searched for cougar-killed ungulates until at least 2 ungulate prey (elk, deer, or bighorn sheep) were identified. A VHF predation sampling sequence entailed triangulation on the radio-collared individual 1-3 times per day. A GPS predation sampling sequence involved analysis of GPS location clusters using ArcGIS 8.0 to identify potential kills. Location clusters consisting of at least 2 locations and located less than 200 m apart were selected as candidates for investigation (Ruth *et al.* 2010). We used only probable and definite kills as determined by previously developed criteria (Kunkel *et al.* 1999) in our analyses. See Ruth *et al.* (2010) for further details on cougar predation sampling. All cougar-killed elk that occurred during winter and matched the above criteria during the 7-year period (n = 257) were included in the analyses to maximize sample size.

Sampling protocol used to assign availability for spatial predation risk

We analyzed wolf and cougar kill resource selection functions (RSF) using a generalized additive model (GAM) with a binomial distribution (used vs. available) and a logit-link function implemented in the *mgcv* package of R. We employed the default settings such that cross-validation determined the optimal amount of smoothing (Wood 2006). To account for the spatial characteristics of the landscape, we first randomly sampled potential kill locations ($n = 10,000$) within northern Yellowstone and calculated the corresponding openness and roughness for those ‘available’ locations. Because cougar and wolf kill RSFs separately estimate the relative probability of a kill for each predator, their predicted kill distributions cannot be directly compared partly because of sample size differences (400 wolf kills vs. 257 cougar kills). To account for the proportional difference in the number of cougar and wolf kills (64.25%), we rescaled the cougar kill RSF by comparing cougar kill locations to 6,425 locations randomly selected from the 10,000 available locations. This adjusted the magnitude of the predicted cougar kill distribution to approximate that of the predicted wolf kill distribution. Sample mean, standard deviation, and median were similar between the full and reduced cougar kill datasets, which indicates that our proportional sampling did not bias model coefficients.

Modeling details for diel predator activity

We fitted the Generalized Additive Mixed Model (GAMM) using the negative binomial family and a cyclic cubic regression spline so that the first and last hour of the day matched in accordance with the diel cycle (Kohl *et al.* 2018). We included a random intercept for individual identity to account for repeated measures within the study period. Each wolf was considered an independent measure of movement rate because it was solitary, the only GPS radio-collared wolf in a pack, or rarely associated with other GPS-collar pack members (Kohl *et al.* 2018). Moreover, our estimated wolf diel pattern was most likely representative of the wolf diel pattern prior to 2004 because it was (1) correlated with the time of day that we directly observed wolves encountering ($r = 0.79$) and killing ($r = 0.87$) elk prior to 2004; (2) consistent across the years in which it was measured; and (3) similar to diel patterns described for other wolf populations (Kohl *et al.* 2018). Each cougar was also considered an independent measure of movement because of the solitary nature of cougars (Ruth *et al.* In press).

Modeling elk habitat selection

We used a step-selection function (SSF; where each observed step was compared to a sample of available steps that originated from the same starting location) to estimate the parameters of a resource selection function, $\exp(\mathbf{Z}'\boldsymbol{\beta})$, where \mathbf{Z} is a vector of environmental covariates, and $\boldsymbol{\beta}$ is a vector of selection coefficients (Forester *et al.* 2009; Merkle *et al.* 2017). The SSF describes the relative probability of a movement step, p , which is the straight-line segment between successive locations at 5-hour intervals. Movement steps with a higher score (p) relative to the set of possible steps have higher odds of being chosen by an animal (Fortin *et al.* 2005; Kohl *et al.* 2018). We could not estimate the main effect of wolf or cougar movement rate because neither varied within a

stratum owing to how used and available locations within a stratum share the same point in time. We did not include a distance function in our SSF model because the combination of an empirical distribution with linear splines contributes to an appreciable reduction in parameter estimate bias that can occur in other SSF designs (Forester et al. 2009). Furthermore, empirical sampling produces relatively unbiased estimates when parameter estimates were low ($\beta \leq 1.0$; Forester et al. 2009) which is applicable to our study here (see Appendix S6).

When evaluating threshold locations, we constrained thresholds to occur within 1 – 99% of all used data points for each spatial risk index in an effort to minimize the influence of outliers. The precision (i.e., decimal units) and scale (i.e., difference in minimum/maximum values) of the spatial risk index determined the number of candidate spline models (roughness = 99 models; openness = 269 models). We did not evaluate the potential for behavioral lags or leads (e.g., Kohl *et al.* 2018) in this analyses because the inclusion of multiple predator schedules, combined with variation in knot location (i.e., grid search), already led to a high number of candidate models. The inclusion of behavior lags or leads would have further increased the number of candidate models, leading to potentially spurious results as a result of model over-fitting. To evaluate candidate models, we used the quasi-likelihood under independence criteria (QIC; Pan 2001) because it considers independent clusters of observations while also accounting for non-independence between subsequent observations (Craiu *et al.* 2008). However, because we have previously shown that results from our elk habitat selection model do not differ between models fitted to all clusters and models fitted to every other independent cluster ($n = 2$ independent data sets; Kohl *et al.* 2018), we presented results from the analysis of all clusters to maximize sample size.

We assessed multicollinearity using variance inflation factors using the R package “HH”. We examined the VIF scores of covariate data that we included in our linear models examining the relationship between elk selection and the interaction between spatial risk (openness or roughness) and predator activity (male cougars, female cougars, or wolves). Female cougar and wolf activity VIF scores exceeded 10 for roughness, requiring that we exclude models with these combinations (Table S2). We did not assess VIF scores between covariates that included linear piecewise spline models and interactions with predator activity because the variation in knot locations led to incomparable VIF scores, and thus, difficulties assessing correlations in the non-linear models. To maintain consistency between the openness and roughness metric we similarly excluded combinations of female cougar activity and wolf activity for openness.

Table S2. Variation Inflation Factor scores for all potential covariates that could be included in linear combinations of roughness (a) and openness (b) and the associated interaction with predator activity schedules for male cougars (M), female cougars (F), and wolves (W). Roughness (R) and openness (O) were highly correlated with all other variables because they were included within space \times activity combinations. However, they (R, O) were maintained in all analyses because they represent the main effect of spatial risk.

a.			
R	R x M	R x F	R x W
24.1	4.3	10.4	13.9

b.			
O	O x M	O x F	O x W
6.3	2.2	3.3	4.1

Visualizing elk selection for vacant hunting domains

We used a three-step process to visualize elk selection of vacant hunting domains. We first combined our predator activity and kill distribution models to describe the foraging domain of wolves and cougars with respect to our spatial metrics (openness or roughness). To quantify hunting domains, we calculated every 10th quantile from 50% to 90% of the fitted values estimated from the kill distribution (Fig. 3) and predator activity models (Fig. 4) for both predator species. For example, the 90th percentile for cougars provided us with the range of openness (e.g., 164 – 192) and time (e.g., 0200 - 0415 hours) that the probability of a cougar kill and activity was highest. We used this information to calculate ellipses for each predator-specific quantile. This produced a visualization of the hunting domain for each predator. We next built an illustration of elk habitat selection with respect to our spatial metrics and time of day. To do this, we multiplied each spatial metric (i.e., openness, roughness) and time of day by the corresponding SSF selection coefficient from the best-fitting model (Singer *et al.* 2017). This approach is sufficient for producing SSF-based maps when GPS sampling rates are low and/or spatial metrics are not overly complex (Singer *et al.* 2017). This produced an estimate of elk habitat selection at each integer value of openness (or roughness) and each hour of day (i.e., 1 to 24). We then smoothed these elk habitat selection values across the full range of values for the spatial metric and time of day using the default parameters of the *stat_contour* function in the *ggplot2* package of R version 3.3.3. Lastly, we overlaid the predator-specific hunting domains (i.e., ellipses) on the elk habitat selection illustration.

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Appendix 4-Chapter 3 Supplemental Figures and Tables

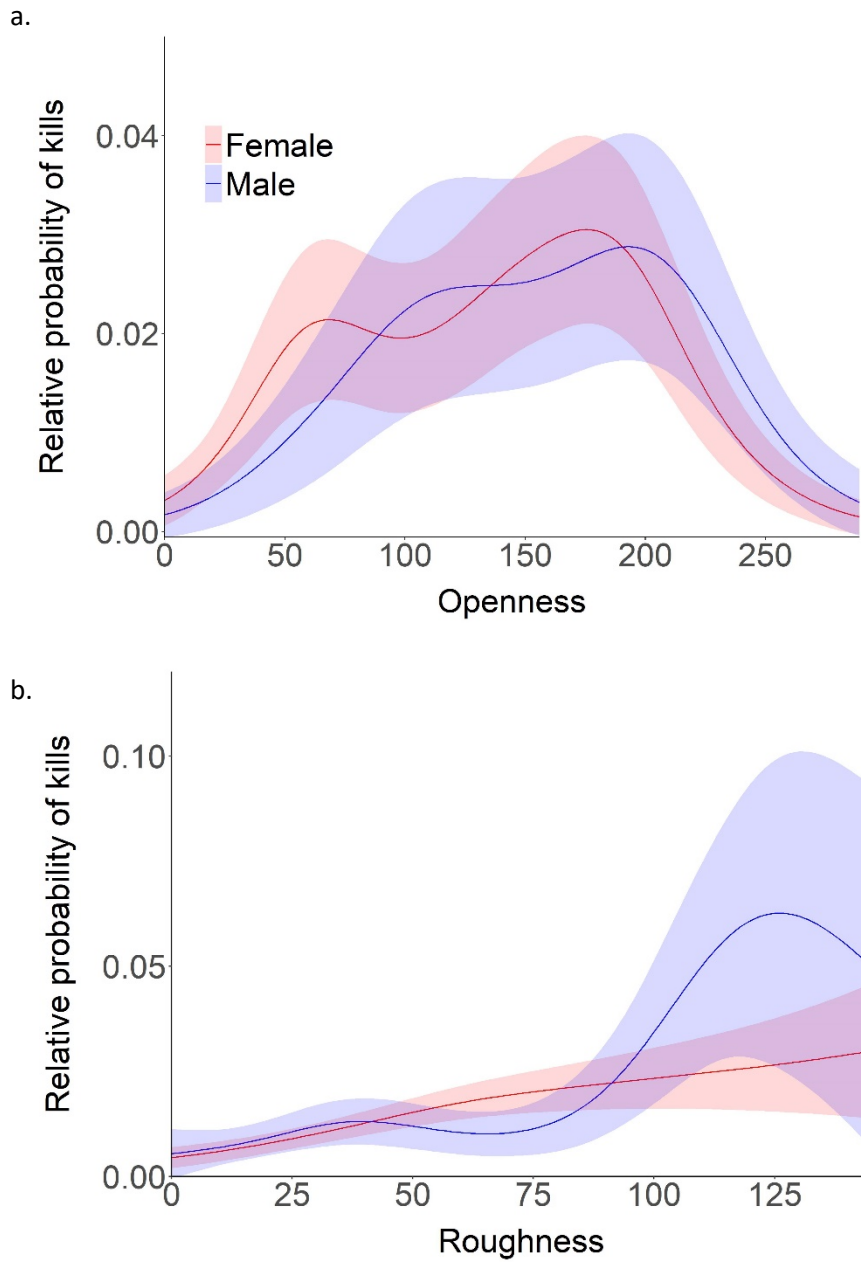


Figure S1. Predicted relative probability of a kill by male and female cougars (1998-2006) relative to openness (a) and topographic roughness (b) in northern Yellowstone during winter.

Table S1. Model selection results for a step-selection function describing the interactive effect of openness and predator activity for male cougars (M; km travelled/6-hr), female cougars (F; km travelled/6 hr), and/or wolves (W; km travelled/5-hr) on elk habitat selection in Yellowstone National Park, 2001-2004. Variable ‘Open’ represents a linear measure of spatial risk (openness). Variables O1 and O2 contain a linear spline for spatial risk (openness) at the indicated threshold. Each model listed describes the best-fit model from all possible functional forms of that model. For example, model set O1 + O2 + (O1 x W) + (O2 x W) with a threshold at 288 was the best-fit model from 269 possible functional forms (openness values 20-288). Number of parameters (K), QIC, and differences in QIC compared to the best scoring model (Δ QIC) are given for each model. The best-fit model across all model combinations is identified in bold.

Model set	Threshold	K	QIC	Δ QIC
Space-only models				
Open	NA	1	27971.4	436.6
O1 + O2	20	2	27934.1	399.3
Single-predator space x activity models				
Open + (Open x W)	NA	2	27819.0	284.2
Open + (Open x M)	NA	2	27635.3	100.5
Open + (Open x F)	NA	2	27962.5	427.7
O1 + O2 + (O1 x W) + (O2 x W)	288	4	27591.8	57.0
O1 + O2 + (O1 x M) + (O2 x M)	199	4	27573.5	38.7
O1 + O2 + (O1 x F) + (O2 x F)	201	4	27931.5	396.7
Multi-predator space x activity models				
Open + (Open x W) + (Open x M)	NA	3	27596.4	61.6
Open + (Open x M) + (Open x F)	NA	3	27613.6	78.8
O1 + O2 + (O1 x W) + (O1 x M) + (O2 x W) + (O2 x M)	199	6	27534.8	0.0
O1 + O2 + (O1 x M) + (O1 x F) + (O2 x M) + (O2 x F)	199	6	27548.4	13.5

Table S2. Model selection results for a step-selection function describing the interactive effect of roughness and predator activity for male cougars (M; km travelled/6-hr), female cougars (F; km travelled/6 hr), and/or wolves (W; km travelled/5-hr) on elk habitat selection in Yellowstone National Park, 2001-2004. Variable ‘Rough’ represents a linear measure of spatial risk (roughness). Variables R1 and R2 contain a linear spline for spatial risk (roughness) at the indicated threshold. Each model listed describes the best-fit model from all possible functional forms of that model. For example, model set R1 + R2 + (R1 x W) + (R2 x W) with a threshold at 29 was the best-fit model from 99 possible functional forms (roughness values 1-99). Number of parameters (K), QIC, and differences in QIC compared to the best scoring model (Δ QIC) are given for each model. The best-fit model across all model combinations is identified in bold.

Model set	Threshold	K	QIC	Δ QIC
Space-only models				
Rough	NA	1	28030.1	211.4
R1 + R2	29	2	27961.1	122.2
Single-predator space x activity models				
Rough + (Rough x W)	NA	2	28023.4	184.6
Rough + (Rough x M)	NA	2	27946.6	107.7
Rough + (Rough x F)	NA	2	28029.4	190.5
R1 + R2 + (R1 x W) + (R2 x W)	29	4	27926.5	87.7
R1 + R2 + (R1 x M) + (R2 x M)	26	4	27849.7	10.9
R1 + R2 + (R1 x F) + (R2 x F)	29	4	27961.8	122.9
Multi-predator space x activity models				
Rough + (Rough x W) + (Rough x M)	NA	3	27947.1	108.2
Rough + (Rough x M) + (Rough x F)	NA	3	27941.6	102.7
R1 + R2 + (R1 x W) + (R1 x M) + (R2 x W) + (R2 x M)	28	6	27838.9	0.0
R1 + R2 + (R1 x M) + (R1 x F) + (R2 x M) + (R2 x F)	29	6	27840.8	1.9

Table S3. Coefficient estimates for best-fit step-selection function models describing the additive effect of spatial risk (openness [a] and topographic roughness [b]) and male cougar (C; km/6-hrs) and wolf (W; km/5-hrs) activity on elk habitat selection in northern Yellowstone, 2001-2004. Variables O1 and O2 and R1 and R2 are the slopes before and after, respectively, each index-specific threshold. Model selection results are presented in Appendix S4 and Appendix S5. Confidence intervals were computed using robust standard errors.

Parameter	Threshold	β	SE	P	[95% confidence interval]	
(a) Openness						
O1	199	0.005	0.003	0.040	0.000	0.011
O2		0.002	0.004	0.657	-0.005	0.009
O1 x W		-0.003	0.001	0.017	-0.005	-0.000
O2 x W		-0.007	0.001	<0.01	-0.009	-0.004
O1 x M		0.007	0.001	<0.01	0.005	0.009
O2 x M		0.013	0.001	<0.01	0.010	0.016
Parameter	Threshold	β	SE	P	[95% confidence interval]	
(b) Roughness						
R1	28	0.001	0.011	0.949	-0.022	0.023
R2		0.010	0.004	0.022	0.001	0.018
R1 x W		0.015	0.005	<0.01	0.005	0.024
R2 x W		-0.007	0.002	<0.01	-0.011	-0.003
R1 x M		-0.024	0.004	<0.01	-0.033	-0.015
R2 x M		-0.009	0.002	<0.01	-0.012	-0.005

Appendix 5-Chapter 4 Supplemental Information

Supplementary information pertaining to study methodology and data collection for Chapter 4.

METHODS

Study Area

Our study occurred in a 1525-km² area that defines the northern elk winter range of Yellowstone (hereafter “Northern Range”; 44° 56' N, 110° 24' W). Approximately 65% of the winter range is located inside YNP, and the remaining 35% extends outside YNP into Montana (Tallian et al. 2017). Approximately 14,000 – 18,000 elk occupied the Northern Range from 1985-1989. The elk population peaked at 22000 elk in 1994, the year prior to wolf reintroduction, subsequently declined to 5,000-6,000, and started increasing after about 2012 (Tallian et al. 2017). Following reintroduction, wolves quickly in abundance and distribution. Wolf abundance peaked in the Northern Range in 2003 ($n = 106$), after which it declined and has since stabilized at 45-50 wolves since 2010. As the wolf population increased, wolves expanded their range throughout the park and into neighboring states including Montana. Additional sources of elk mortality include cougars (*Puma concolor*; Ruth et al. *In press*) and bears (*Ursus americanus*, *U. arctos*), which focus on calves (Barber-Meyer et al. 2008). Human harvest also occurred outside YNP and was a major source of mortality for adult female elk prior to the termination of the late-season cow harvest in 2010 (Vucetich et al. 2005, MacNulty et al. 2016).

Prior authors have delineated the Northern Range into four elevational sectors (lower inside, lower outside, middle, upper; Coughenour and Singer 1996); the lower inside and lower outside are approximately delineated according to the YNP boundary. Because elk in the Northern Range assemble themselves among two herd segments corresponding to elevation and winter conditions (White et al. 2010), we merged the lower inside and lower outside sectors (1500-1700 m), hereafter ‘lower sector’ (736-km²), and the upper and middle sectors (1800-2100 m), hereafter ‘upper sector’ (790-km²; Fig. 4-1). The upper sector of the Northern Range is bisected by the Lamar River until the confluence with the Yellowstone River at Tower Junction (Fig. 4-1). The lower sector is bisected by the Yellowstone River as it flows downriver into Montana. Together, these serve as critical winter range for ungulates, including elk, because they provide the warmest and driest conditions in YNP during winter. Vegetation inside of YNP includes montane forest (44%; e.g., lodgepole pine [*Pinus contorta*] and Douglas fir [*Pseudotsuga menziesii*]), open sagebrush-grassland (37%; e.g., Idaho fescue [*Festuca idahoensis*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], big sagebrush [*Artemisia tridentata*]), upland grasslands, wet meadows, and non-vegetated areas (19%) (DeSpain 1990). Outside of YNP, native vegetation communities are similar, however, increasing amounts of areas have been converted to irrigated pasture land (Haggerty and Travis 2006).

Data Analysis

Elk and wolf abundance - We conducted aerial winter surveys of elk annually using 3-4 fixed wing aircraft, each simultaneously flying non-overlapping areas between 3 December and 7 March, 1995-2016 (see Northern Yellowstone Cooperative Wildlife Working Group 2016). We apportioned the survey counts to the upper and lower sectors. These sector-specific counts also facilitated an estimation of the proportional shift in elk abundance from upper to lower sections across time. In years in which no survey occurred (1996, 1997, 2006, 2014), we used a state-space model to interpolate elk counts for those years following Tallian et al. (2017). From these minimum counts, we applied a sightability model developed for elk in northern Yellowstone to provided corrected total counts. These counts were then separated according to the spatial location of elk on the Northern Range to provide an estimated minimum corrected count of elk in the upper and lower sectors of the Northern Range.

We estimated end-of-year (Dec. 31) wolf packs sizes following intensive field observations of radio-collared wolves within YNP. Approximately 35-40% of the YNP wolf population was radio-collared ($n = 20-30$ annually; Smith et al. 2004) with either very-high-frequency (VHF; (Telonics Inc., Mesa, AZ, USA) or Global-Positioning System (GPS; Televilt, Lindesberg, Sweden; Lotek, Newmarket, ON, Canada) radio-collars. Radio-collared wolves were located daily from the ground and fixed-wing aircraft during two 30-day periods in early (mid-November to mid-December) and late (March) winter, and approximately weekly during the rest of the year.

We obtained estimated end-of-year pack sizes for wolf packs outside YNP from U.S. Fish and Wildlife Service (USFWS) and Montana Fish, Wildlife, and Parks (FWP) annual wolf reports. Outside YNP, wolf pack monitoring techniques shifted over time. During the early years of wolf recovery, FWP attempted to radio-collar at least one wolf per pack, which allowed for the identification and monitoring of established and new packs, as well as most individuals within packs. As the population expanded, FWP began using a combination of monitoring techniques including radio-telemetry collars, direct observation counts, howling and track surveys, trail cameras, and public wolf sighting reports (Coltrane et al. 2015). These techniques provided an estimate of minimum wolf counts, packs sizes, and distribution outside of the park. Wolves were captured and handled following protocols in accordance with applicable guidelines from the American Society of Mammalogists (Sikes and Gannon 2011) and approved by the National Park Service Institutional Animal Care and Use Committees.

We aggregated minimum end-of-year wolf pack counts for packs inside and outside of YNP with their associated home-range estimations to calculate end-of-year wolf abundance for the upper and lower sectors of the Northern Range. Home range estimates were based on minimum convex polygon (MCP) estimates derived from winter-specific VHF and GPS telemetry locations for each pack. For wolf packs that overlapped both upper and lower sectors of the Northern Range, we assigned half of the pack size to each unit. Any wolf pack territories that did not significantly overlap ($> 25\%$) with the Northern Range were excluded from abundance estimates.

Elk winter-range fidelity - We captured elk in the Northern Range during three periods that reflected different levels of wolf abundance: no-wolf (1985-1989), high-wolf (2000-2006), and low-wolf (2011-2016). Adult female elk were radiocollared with either VHF or GPS collars. In total, we collared 28 individuals during the no-wolf period, 162 individuals during the high-wolf period, and 105 individuals during the low-wolf period. Specific details on animal capture, handling, and data collection for each study period are provided in the supplemental information. Elk were captured and handled following protocols in accordance with applicable guidelines from the American Society of Mammalogists (Sikes and Gannon 2011) and approved by the National Park Service Institutional Animal Care and Use Committees.

To estimate elk site-fidelity, we measured annual variation in the position of individual winter ranges which we define here as 1 January – 31 March. This period mostly excluded fall migrations or early spring migrations (*unpublished data*, Utah State University). Elk with fewer than five locations per winter were excluded from the analysis. All elk locations were randomly subsampled to record 1 location / week in order to provide direct comparisons between VHF and GPS locations (range = 5 – 14 telemetry locations / individual / winter). To estimate winter site-fidelity, we only included individuals that we acquired ≥ 5 locations in each of two consecutive winters. This constraint reduced the sample of individuals for all study periods (no-wolf = 31, high-wolf = 57, low-wolf = 71). Because individuals may have been sampled multiple times (e.g., an individual captured in 2012 may have provided information for 3 consecutive winters resulting in 2 site-fidelity samples), these sample sizes represent site-fidelity samples, rather than absolute number of individuals monitored.

If the observed shift in elk distribution reflects elk behavioral responses to wolves, we expected elk to shift their winter range down-river toward the lower sector where wolf numbers were relatively lower. We assessed annual change in winter range location relative to the Yellowstone River Corridor (YRC) which we estimated using the National Hydrology Dataset. To calculate shifts in site fidelity, we first produced a generalization of the primary Northern Range rivers (Lamar, Yellowstone) as defined in the National Hydrography Dataset. This generalization, which effectively straightened the river by eliminating twists and turn, was necessary for intersecting the YRC with home range centroids which are explained below. This generalization of the YRC served as our measuring tape of Euclidean movement by elk across the Northern Range while ignoring the intricacies of the river itself. We produced the YCR by employing a 10 km smoothing tolerance (PAEK algorithm) within the Smooth Line tool in ArcGIS 10.3 on the aforementioned rivers. Next, we estimated MCP home range and extracted centroid estimates for individual elk for each winter (Gower et al. 2009). We then calculated the perpendicular intersection between the home range centroid and the Yellowstone River Corridor (YRC). From this intersection with the YRC, we were able to produce a standardized metric for all individuals that calculates their annual movement up or downstream. We expected elk to move downstream if changes in elk distribution were due to a large-scale behavioral shift away from wolves.

Elk recruitment - If the observed shift in the elk distribution across the Northern Range was due to direct killing, we expected to see variation between the upper and lower sector

for at least one demographic rate that we measured including elk recruitment, adult elk survival, and age structure. We first estimated if differences occurred in elk recruitment. To do this, we estimated calf/cow ratios by obtaining sex-specific elk counts from helicopter surveys conducted from in late winter (Feb. – Mar.) from 1998-2009. To reduce costs, helicopter surveys were replaced with ground observations (Jan. – Mar.) from 2010-2016. While transitioning from helicopter to ground surveys, intermittent helicopter surveys occurred in a subset of the Northern Range in 2011, 2012, and 2014 which allowed us evaluate differences in sampling technique. Analysis of variance tests demonstrated no significant difference between mean calf/cow ratios estimated from ground or aerial counts in any of the three test years ($p > 0.05$). Thus, we combined our ground count estimates from 2010-2016 with our helicopter surveys from 1998-2009 to provide a continuous measure of calf recruitment.

This provided us with sex-specific information for all elk groups within one of 68 possible count units distributed across the Northern Range. We then summed all year-specific groups within a given count unit (e.g., 14 different groups in count unit 7). This diminished the effects of small groups that were not reproductively active (e.g., 0 calves, 6 cows) on our estimates. The produced an annual dataset that included up to 68 samples (if elk were recorded in all units in a given year) which were then categorized according to placement within the upper or lower sector. We then modeled these upper and lower sector of calf/cow ratios by applying a generalized additive model (GAM) using the *mgcv* package (version 1.8.0) in R 3.2.3. The result is an estimate of calf/cow ratios by sector by year from 1998 – 2016.

Elk survival - To assess wolf-caused mortality by NR sector, we fit a fully-parametric, competing-risks model with a Weibull distribution and two mortality absorbing states, mortality due to wolves ($n = 54$) and mortality due to other causes ($n = 35$; R package *Flexsurv*; Jackson 2016). For mortalities with an unknown cause of death, we assigned a wolf-caused mortality if field notes indicated wolves were active in the area ($n=3$) or if the spatial location of the mortality overlapped with a known wolf territory and there were no notes indicating a lack of predation ($n=11$). The remaining 17 unknown mortalities were assigned as other-caused mortality. We censored all human-caused mortalities at their mortality date to focus on the influence of non-human caused mortalities.

Transitions are only possible from the initial state to one absorbing state and absorbing states are mutually exclusive. Mortality probability is the compliment of survival probability, and in a competing-risks model, mortality probability per unit time is the sum of the mortality probabilities for each cause-specific mortality. We used elk age in years as the model time scale to estimate mortality probability by age. Our data was left-staggered to account for elk radio-collared in different years and right censored in cases where elk were no longer monitored (e.g., missing and collar failure). We assigned elk mortalities to upper and lower sectors conducted a sector-specific mortality analysis. We modelled annual survival based on an elk year, from 1 June to 31 May. We included elk that lived through a gap in monitoring between Peak-wolf and Current-wolf study period but excluded the years corresponding to that gap in our analysis. We

censored elk that died during the monitoring gap the beginning of the gap interval (i.e. they were excluded as mortalities).

Elk age structure - The age structure of the female portion of the elk population in the upper and lower sectors was estimated for a 15-year period (1995-2009) using reconstruction analysis of dead-recovery data (Fryxell et al. 1988, Fryxell et al. 1999). This approach involved: 1) creating a database of year-of-death and age-at-death for females in the upper and lower elk sectors and then using this database to calculate the minimum number of females alive in each age-class, every year for each of the two sectors. The age-at death database for the lower sector was compiled from examination of the carcasses of female elk killed by hunters outside the park between 1996-2009 and from the carcasses of elk that died from natural causes or that were detected during ground and aerial surveys inside the park from 1995-2016. No elk were harvested inside the park, therefore, the database for the upper sector only included individuals that died from natural causes from 1995-2016. The individuals' age-at-death was estimated by counting tooth cementum lines (Haagenrud 1978, Rolandsen et al. 2008). Year-of-birth was estimated by subtracting age-at-death from the individuals known year-of-death. Although we had dead-recovery data up until 2016, our estimates of elk age structure were not reliable (biased towards younger individuals) after 2010 because a high proportion of individuals in the population were still alive, hence their ages unknown (median life span = 17 years-old). It is for this reason that our measurement of age structure ends in 2009.

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Appendix 6-Permission Letters

7/31/2018

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Title: Diel predator activity drives a dynamic landscape of fear

Author: Michel T. Kohl, Daniel R. Stahler, Matthew C. Metz, et al

Publication: Ecological Monographs

Publisher: John Wiley and Sons

Date: Jun 22, 2018

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Utah State University

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31 July 2018

Michel Kohl
Wildland Resources Department
Utah State University
Logan, UT 84321

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406-480-0775
Michel.kohl@usu.edu

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Name:

Matthew C. Metz

Signature:

Date:

7-31-2018

31 July 2018

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Logan, UT 84321

Dear Coauthors:

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Name: P. J. White

Signature:

Date: July 31, 2018

31 July 2018

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Name: Nathan Varley

Signature:

Date: July 31, 2018

31 July 2018

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Name:

Signature: _____

Date: 7/31/18

31 July 2018

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Name: Matthew Kauffman

Signature: _____

Date: 12/18/2018

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Name: James D. Forester

Signature: _____

Date: 23 September 2018

31 July 2018

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8/13/18

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EDUCATION

- 2018 **Ph.D., Ecology** (Specialization Wildlife Ecology) – Defended 2 May 2018
 Department of Wildland Resources, Utah State University, Logan, UT.
 S.J. and Jesse E. Quinney Fellow, Ford Foundation Doctoral Fellow.
 Advisor: Daniel R. MacNulty.
 Project title: *The spatial ecology of predator-prey interactions: A case study of Yellowstone elk, wolves, and cougars.*
- 2012 **M.S., Wildlife and Fisheries Biology**
 Wildlife Biology Program, University of Montana, Missoula, MT.
 Alfred P. Sloan Scholar, Boone and Crockett Fellow.
 Advisor: Paul R. Krausman.
 Project title: *Bison conservation in the Northern Great Plains.*
- 2008 **B.S., Wildlife and Fisheries Biology**
 Wildlife Biology Program, University of Montana, Missoula, MT.
 Advisor: Mark Hebblewhite
 Project title: *Relationships between elk and spotted knapweed in the wildlife urban interface of western Montana.*
- 2006 **A.S. with Honors**
 Dawson Community College, Glendive, MT.

WEBPAGES/URLS

Personal Website: <https://mtkohlwildlife.wordpress.com/>
 GoogleScholar: <https://scholar.google.com/citations?user=UhHWoh0AAAAJ&hl=en>
 ResearchGate: https://www.researchgate.net/profile/Michel_Kohl

PROFESSIONAL EXPERIENCE

- 2017 – Pres. **Jack H. Berryman Postdoctoral Fellow**, Utah State University
Extension
- Supervisors: Terry A. Messmer, Dave K. Dahlgren
Duties: Coordinate the Habitat Assessment Framework program for Utah. The HAF is a state-wide initiative composed of public land management partners (USFS, BLM, UTDWR), private landowners, and other constituent groups that is designed to implement a landscape-scale monitoring approach that better manages an at-risk species – the greater sage-grouse. Specific duties include the management of state-wide database, the deployment and field and remote monitoring of global positioning system radio-transmitters, coordination of progress meetings with partners, and the development and distribution of science-based, wildlife management information related to seasonal sage-grouse use. Science dissemination includes professional conferences, peer-reviewed journals, local working groups, and extension products.
- 2010 – Pres. **North Hills Elk Herbivory Study, Project PI**, University of Montana
Co-PIs: Mark Hebblewhite, Ray Callaway
Duties: Oversee long-term vegetation program addressing the impacts of large-scale invasive weed treatment on domestic and native wildlife grazing. As project coordinator, I oversaw project development, and currently coordinate field logistics, monitoring, data entry, and data analysis. This program occurs entirely on private property that requires consistent communication with private landowners.

PUBLICATIONS

Peer reviewed

- 2018 **Kohl, M. T.**, D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88:638-652, doi:10.1002/ecm.1313
- 2017 Puritty, C., L. R. Strickland, E. Alia, B. Blonder, E. Klein, **M. T. Kohl**, E. McGee, M. Quintana, R. E. Ridley, B. Tellman, and L. R. Gerber. For diversity initiatives, current best efforts may not be enough. *Science* 6356:1101-1102, doi: 10.1126/science.aai9054
- 2017 **Kohl, M. T.** Bison versus beef: today's western range war? *The Wildlife Professional* 11:27-30.

- 2017 Sandford, P. C., **M. T. Kohl**, T. A. Messmer, D. K. Dahlgren, A. Cook, and B. R. Wing. Greater sage-grouse resource selection drives reproductive fitness in conifer removal system. *Journal of Rangeland Ecology and Management* 70:59-67, doi: 10.1016/j.rama.2016.09.002
- 2016 Smith, D. W., R. O. Peterson, D. R. MacNulty, and **M. T. Kohl**. The big scientific debate – trophic cascades. *Yellowstone Science* 24:70-71
- 2013 **Kohl, M. T.**, P. R. Krausman, K. Kunkel, and D. M. Williams. Bison versus cattle: are they ecologically synonymous? *Journal of Rangeland Ecology and Management* 66:721-731, doi: 10.2111/REM-D-12-00113.1
- 2012 **Kohl, M. T.**, M. Hebblewhite, S. M. Cleveland, and R. M. Callaway. [2012]. Forage value of invasive species to the diet of rocky mountain elk. *Rangelands* 34:24-28, doi: 10.2111/RANGELANDS-D-11-00055.1

Extension publications

- 2018 Dahlgren, D. K., **M. T. Kohl**, T. A. Messmer. Telemetry bias: data limitations for radio-marked wildlife. Utah State University Extension, Logan, UT. Paper 1862. https://digitalcommons.usu.edu/extension_curall/1862

Book contributions

- In press Stricker, H., P. M. Schmidt, J. Gilbert, J. Dau, D. L. Doan-Crider, S. J. Hoagland, **M. T. Kohl**, C. A. Perez, L. J. Van Daele, M. B. Van Daele, and D. Dupont. Managing wildlife resources with North American indigenous peoples. In *The Wildlife Techniques Manual* 8th Edition. Eds. N. Silvy. *John Hopkins University Press*.
- 2017 **Kohl, M. T.**, S. J. Hoagland, A. R. Gramza, and J. A. Homyack. Professional diversity: the key to conserving wildlife diversity. In *On becoming a wildlife professional*. Eds. S. E. Henke and P. R. Krausman. *John Hopkins University Press*.

Non-peer reviewed publications

- 2013 Gramza, A., **M. Kohl**, and M. Bucci. Three tales from South Africa. *The Wildlife Professional* 7:44-46.
- 2013 **Kohl, M. T.**, J. A. Merkle, P. R. Krausman, K. Kunkel, K. Aune, C. C. Gates, and S. D. Fuhlendorf. What is the future of bison conservation? IVth International Wildlife Management Congress – Proceedings, Durban, South Africa.

- 2010 **Kohl, M. T.**, K. Kunkel, and P. R. Krausman. Bison restoration on the American Prairie Reserve. Unpublished report to the M.J. Murdock Charitable Trust, Vancouver, WA.

Manuscripts submitted, in review, or revision

- Kohl, M. T.**, T. A. Messmer, B. A. Crabb, M. R. Guttery, D. K. Dahlgren, R. T. Larsen, S. N. Frey, S. Liguori, and R. J. Baxter. The effects of electric power lines on the breeding ecology of greater sage-grouse. *Plos One*.

- Dahlgren, D. K., T. A. Messmer, B. A. Crabb, **M. T. Kohl**, S. N. Frey, E. Thacker, R. T. Larsen, and R. J. Baxter. An empirical approach to refining greater sage-grouse (*Centrocercus urophasianus*) habitat guidelines. *Wildlife Society Bulletin*

- Kohl, M. T.**, M. S. Chelak, T. A. Messmer. Greater sage-grouse translocation in Utah: the science behind our conservation policy. Utah State University Extension, Logan, UT.

- Kohl, M. T.**, P. J. Mahoney, L. M. Smith, S. R. Hoy, A. Nelson, P. J. White, D. R. Stahler, D. D. Smith, D. R. MacNulty. Does fear of wolves explain shifts in elk distribution? In *Yellowstone wolves: reintroduction, ecology, behavior, and conservation*. Eds. D. W. Smith, D. R. Stahler, and D. R. MacNulty. *University of Chicago Press*.

- Kohl, M. T.**, T. K. Ruth, D. R. Stahler, M. C. Metz, D. W. Smith, and D. R. MacNulty. Selection for predator niche vacancies minimizes a multi-predator threat. *Ecology Letters*

- Cusack, J, **M. T. Kohl**, M. C. Metz, T. Coulson, D. R. Stahler, D. W. Smith, and D. R. MacNulty. Weak spatiotemporal response of prey to predation risk in a freely interacting system. *Journal of Animal Ecology*. Preprint: doi: 10.1101/215475

Manuscripts to be submitted within 6 months (drafts available upon request)

- Raithel, J. D., M. J. Reynolds-Hogland, P. C. Carr, C. A. Falvo, **M. T. Kohl**, A. N. Tri, and L. M. Aubry. The doughnut effect: black bear behavioral responses to fear in a wildland-urban interface in the Mid-Atlantic United States. Target: *Conservation Biology*

- Crabb, B. A., T. A. Messmer, D. K. Dahlgren, **M. T. Kohl**. Ecological minimums for greater sage-grouse revisited: using updated information from Utah. Target: *Ecology and Evolution*

- Stoner, D. C., D. K. Dahlgren, J. O. Sexton, **M. T. Kohl**, S. N. Frey, R. T. Larson, and T. A. Messmer. Using satellite-derived estimates of plant phenology to predict sage-grouse nest initiation dates. Target: *Oikos*.

Flack, B. M., **M. T. Kohl**, T. A. Messmer. Habitat selection of greater sage-grouse inhabiting the southern portion of the Rich-Morgan-Summit Sage-Grouse Management Area. Target: *Wildlife Society Bulletin*

MacNulty, D. R., R. J. Kindermann, **M. T. Kohl**, D. R. Stahler, D. W. Smith, P. J. White, J. O. Sexton, J. Nagol, M. J. Kauffman, D. E. McWhiter, and A. D. Middleton. Simpson's paradox reverses an apparent non-consumptive effect of a large carnivore. Target: *Journal of Animal Ecology*

Wilmers, C., M. Metz, **M. T. Kohl**, D. Stahler, and D. Smith. Influence of climate on prey composition in a wolf-elk system. Target: *Journal of Animal Ecology*

GRANTS AND RESEARCH SUPPORT (Total: \$398,010, Extramural: \$264,650)

- 2018 Bureau of Land Management – Utah State Office. Building a state-wide tool for identifying and prioritizing conifer removal projects in sage-grouse habitat. Co-PI with T.A. Messmer, D.K. Dahlgren (\$122,000)
- 2016 Ford Foundation, Doctoral Fellowship. (\$25,000)
- 2016 Utah State University Office of Research and Graduate Studies, Doctoral Dissertation Enhancement Award. Population declines and trophic cascades in a wolf-elk system: does calf recruitment explain the controversy? Project PI (\$9,995)
- 2016 Utah State University Ecology Center, Dissertation Research Award. Population declines and trophic cascades in a wolf-elk system: does calf recruitment explain the controversy? Project Co-PI with DR MacNulty (\$4,000)
- 2014 Utah State University Ecology Center, Dissertation Research Award. Population declines and trophic cascades in a wolf-elk system: does calf recruitment explain the controversy? Project Co-PI with DR MacNulty (\$6,000)
- 2012 S.J. and Jesse E. Quinney Foundation, Doctoral Fellowship. (\$108,165)
- 2012 Ford Foundation, Predoctoral Fellowship. Declined (\$66,000)
- 2012 Montana Institute on Ecosystems, Graduate Fellowship. (\$4,700)
- 2011 Wildlife Conservation Society. Habitat use and the importance of water for bison and cattle. Co-PI with PR Krausman and K Kunkel (\$12,000)
- 2009 Alfred P. Sloan Foundation, Indigenous Graduate Student Fellowship. (\$32,100)
- 2008 University of Montana Native American Mentoring Program. Do high elk densities promote spotted knapweed reinvasion? Project PI (\$1,200)
- 2008 Missoula County Weed District. Do high elk densities promote spotted knapweed reinvasion? Project PI (\$2,200)
- 2007 Montana Integrative Learning for Students. Do high elk densities promote spotted knapweed reinvasion? Project PI (\$1,500)
- 2007 Circle H Ranch. Do high elk densities promote spotted knapweed reinvasion? Project PI (\$650)

- 2007 University of Montana College of Forestry and Conservation, Iren Ever's Undergraduate Research Award. Do high elk densities promote spotted knapweed reinvasion? Project PI (\$2,500)

OUTREACH AND EXTENSION ACTIVITIES

- 2019 **Coordinator**, Utah Sage-grouse Summit - Science Session
Recruited and coordinated speakers for a public forum designed to transfer recent science information regarding sage-grouse and sagebrush management to management agencies, scientists, private landowners, industry personnel, local wildlife working groups, and other interested parties.
- 2018 – Pres. **Utah Representative**, Multi-state Greater Sage-grouse Research Collaboration
Working group comprising members from Idaho, Montana, and Utah that are collaborating across shared research priorities on sage-grouse (e.g., cattle grazing, habitat guidelines).
- 2017 – Pres. **Developer**, Utah Greater Sage-grouse Habitat Field Requests
A request process that allows local biologists to submit data requests for identifying quality sage-grouse habitat in and around potential habitat improvement projects.
- 2017 – Pres. **Participant**, Utah Local Wildlife Working Group Meetings
Participated and presented to meetings of local working groups in three of Utah's counties since beginning the Utah Statewide Sage-grouse Research.

CURRENT PROJECTS/COLLABORATIONS

Utah Statewide Sage-grouse Research

Evaluating sage-grouse population level movements and habitat use to inform conservation through a shared database of over 250,000 sage-grouse locations and vegetation information.

Partners:

Utah State University, Brigham Young University, Utah Public Lands Policy and Coordination Office, Utah Division of Wildlife Resources, Bureau of Land Management, U.S. Forest Service, Many Private Landowners,

Anticipated Manuscripts:

Kohl, M. T., T. A. Messmer, D. K. Dahlgren, N. Frey, B. Maxfield, R. Larsen.

Building a better map: how GPS data can fill the gaps to better manage multiple sage-grouse populations across Utah. Utah State University.

Kohl, M. T., T. A. Messmer, D. K. Dahlgren, N. Frey, B. Maxfield, R. Larsen.

Surfing the green wave: how cattle provide habitat for grouse in a working landscape.

Dahlgren, D. K., M. T. Kohl, C. P. Sandford, T. A. Messmer, Paul R. Rodgers, and M. R. Guttery. Trees are not all bad: aspen as critical mesic habitat in an otherwise dry landscape.

Small, J., M. Chelak, M. T. Kohl, T. A. Messmer, D. K. Dahlgren. Our GPS units really better: the impact of transmitter type on sage-grouse survival.

Sage-grouse and Livestock Grazing Research, Rich County, Utah.

Evaluating sage-grouse movement behavior in response to different grazing systems

Partners:

Utah State University, USDA Sage-grouse Initiative, Pheasants Forever, Deseret Land and Livestock, BLM

Manuscripts in advanced preparation:

Smith, W., M. T. Kohl, T. A. Messmer, D.K Dahlgren. Using cattle to improve sage-grouse brooding habitat. To be submitted to *Rangeland Ecology and Management*

Anticipated Manuscripts:

Wayment, H., M. T. Kohl, W. Smith, T. A. Messmer, D.K Dahlgren. Sage-brush treatments to improve habitat for cattle and sage-grouse. Utah State University.

Prioritizing sage-grouse translocation release sites, North Dakota / Utah.

Evaluating protocols and release sites for the effective translocation of sage-grouse.

Partners:

Utah Division of Wildlife Resources, North Dakota Fish and Game, Wyoming Fish and Game, U.S. Geological Survey, Utah State University, Utah Public Lands Policy Coordination Office.

Anticipated Manuscripts:

Chelak, M., M. T. Kohl, T. A. Messmer, D. K Dahlgren, P. Coates. Evaluating release site to minimize large-scale post-translocation movement by translocated sage-grouse.

Lazenby, K., M. Chelak, M. T. Kohl, T. A. Messmer, D. K. Dahlgren, P. Coates. A critical multi-state evaluation of sage-grouse translocations release sites.

Sage-grouse response to conifer removal, Utah.

Evaluating sage-grouse habitat use, movements, and vital rates in the presence of landscape-scale conifer removal.

Partners:

Utah State University, Utah Watershed Restoration Initiative, Utah Division of Wildlife Resources, Utah Public Lands Policy Coordination Office, NRCS, Multiple Private Landowners, U.S. Fish and Wildlife Service Partner Program.

Anticipated Manuscripts:

Small, J., M. T. Kohl, T. A. Messmer, D. K. Dahlgren. Using GPS technology to track use of conifer removal projects at a landscape scale. Utah State University.

Forest Grouse (dusky and ruffed grouse) Research, Utah / Nevada.

Evaluation of forest grouse habitat use, livestock grazing interactions, management, and population monitoring

Partners:

Utah Division of Wildlife Resources, Nevada Division of Wildlife, Utah
Agricultural Experiment Station, U.S. Forest Service, Utah State University

Manuscripts in advanced preparation:

Farnsworth, S., M. T. Kohl, D. Dahlgren, and E. Thacker. Dusky grouse and
livestock
interactions and habitat use. Utah State University

Farnsworth, S., M. T. Kohl, D. Dahlgren, and E. Thacker. Developing trapping
protocols in time and space for efficient forest grouse monitoring. Utah State
University.

Predator-Prey Relationships in a Free-Living System, Yellowstone National Park.

Evaluating the spatial, behavioral, and demographic consequences of predator recovery
on elk populations.

Partners:

National Park Service, Montana Fish, Wildlife, and Parks, Yellowstone Foundation,
National Science Foundation, Utah State University, University of Oxford,
University of Montana, University of California – Santa Cruz.

Manuscripts in Development:

Cusack, J. J., M. T. Kohl, T. Coulson, C. Carbone, M. Rowcliffe, D. W. Smith, D.
R. Stahler, and D. R. MacNulty. Camera traps offer limited potential for
inferring on the spatio-temporal responses of prey to predators: a simulation
study based on wolf-elk behavior.

Anticipated Manuscripts:

McDonald, B., M. T. Kohl, D. W. Smith, D. R. Stahler, and D. R. MacNulty. A
reproductive trade-off: how elk manage predation risk and forage when
selecting elk calving sites.

Influence of native and domestic herbivory on exotic weed invasions, Montana.

Evaluating long-term impacts of native and domestic ungulate grazing on spotted
knapweed treatments on critical Rocky Mountain winter range.

Partners:

University of Montana, Missoula County Weed District, Circle H Ranch, National
Wildlife Federation, Montana Fish, Wildlife, and Parks, University of Montana.

Anticipated Manuscripts:

Kohl, M. T., R. Callaway, M. Hebblewhite, S. Cleveland. A long-term evaluation
of the impacts native and domestic grazing has on invasive species return
intervals. University of Montana.

Moose Demographics at their Southern Range Limit, Utah.

Evaluating relationship between moose space use, tick prevalence, and calf recruitment.

Partners:

Utah State University, Utah Division of Wildlife Resources, U.S. Forest Service,
Private landowners

Anticipated Manuscripts:

Robertson, S, M. T. Kohl, D. MacNulty. Winter ticks as a driving force in moose calf
recruitment. Utah State University.

Bison and Cattle Ecology in the Northern Great Plains, Montana, Saskatchewan.

Evaluating the space use, management implications, and grazing practices of cattle and bison.

Partners:

University of Montana, Clemson University, Smithsonian Institute, American
Prairie Reserve, Grasslands National Park, Bureau of Land Management, U.S. Fish
and Wildlife, Many Private Landowners.

Anticipated Manuscripts:

Titus, K, D. S. Jachowski, M. T. Kohl, K. Kunkel. How to achieve wildlife
conservation across spatial scales in a working landscape.

INSTRUCTION AND TRAINING EXPERIENCE*Instructor*

2018

Wildlife Habitat and Movement Modeling (WILD 6900-06)

Utah State University [Graduate Level, 2 credits, 10 students]

Course provided instruction and training on recent advances and approaches in the study of wildlife-habitat relationships with a particular emphasis on Resource Selection Functions. Within this context, students were exposed to relevant terminology and definitions, theory, and quantitative methods required for assessing wildlife-habitat relationships.

2018

Animal Resource Selection

International Grouse Symposium – Logan, UT [Graduate/Professional, 1 day workshop, 16 participants]

This workshop was designed for an international audience such that participants would have the knowledge and capabilities to proceed from a dataset containing raw animal locations thru the interpretation of a resource selection model.

2016

Animal Resource Selection

Utah State University [Graduate/Professional, 3 day workshop, 28 participants]

This workshop provided instruction and training such that at completion, participants would have the knowledge and capabilities

to proceed from a dataset containing raw animal locations thru the interpretation of a resource selection model.

- 2012, '13, '14 **Resource Selection by Wildlife**
 Utah State University [Graduate level, ½ day workshop, ~ 10 students]
 Half-day workshop that covered the fundamental principles and terminology relevant to resource selection analyses.

Teaching Assistant

- 2016, '17 **Wildland Resource Techniques (WILD 2400)**
 Utah State University [Undergraduate level, 3 credits, 50 students]
 Exposed underclassman to essential skills necessary to successfully apply for summer technician positions. Within this course, I handled logistics for all field trips while teaching one traditional format lecture and lab per year.
- 2011, '12 **Upshot: Applied Wildlife Management (WILD 480)**
 University of Montana [Undergraduate level, 3 credits, 10-20 students]
 Oversaw senior-level capstone course as they developed a wildlife management plan for a predesignated focal area that took into account diverse stakeholder views.

STUDENT MENTORSHIP

- 2017 – Pres. **Statistical advisor** of Wayne Smith's Master's thesis project entitled "Brooding ecology of greater sage-grouse under varying grazing strategies." Utah State University.
- 2017 – 2018. **Statistical advisor** of Skyler Farnsworth's Master's thesis project entitled "Breeding ecology of forest grouse of Utah." Utah State University.
- 2017 – 2018. **Supervisor** of Annalisa Crow's undergraduate thesis project entitled "Population declines and trophic cascades in a wolf-elk system: does calf recruitment explain the controversy?" Utah State University.
- 2016 – 2017 **Statistical advisor** of Brandon Flack's Master's thesis project entitled "Ecology of greater sage-grouse inhabiting the southern portion of the Rich-Morgan-Summit Sage-Grouse Management Area." Utah State University.

- 2015 – 2016 **Statistical advisor** of Charles Sandford’s Master’s thesis project entitled “Greater sage-grouse vital rates and habitat use response to landscape scale habitat manipulations and vegetation micro-sites in northwestern Utah.” Utah State University.
- 2014 – 2015 **Supervisor** of Olivia Schwanda’s undergraduate thesis project entitled “Elk herbivory and reinvasion of invasive plants in western Montana.” Utah State University.
- 2011 – 2012 **Supervisor** of Kenneth Plourde’s undergraduate thesis project entitled “Bison habitat use in the Northern Glaciated Plains.” University of Montana.

PROFESSIONAL ACTIVITIES AND SERVICE

Invited reviews

Behavioral Ecology
 Biological Conservation
 Bioscience
 Ecological Modeling
 Ecosphere
 Ecology
 Ecology Letters
 Human-Wildlife Interactions
 Journal of Animal Ecology
 Journal of Wildlife Management
 Movement Ecology
 Oecologia
 Oikos
 Plos One

Other reviews

The Environment and Natural Resources Trust Fund ($n = 1$),
 Alberta Conservation Associations Grants in Biodiversity ($n = 1$),
 U.S.F.S. Native American Professional Development Assistantship Projects ($n = 10$),
 U.S.F.S. Native American Professional Development Assistantships (2 years; total = 14),
 TWS Wildlife Publication Awards (2 years; total = 106),
 TWS Native American Professional Development Program (5 years; total a= 124),
 TWS Annual Conference Student Travel Grant ($n = 25$),
 5th International Wildlife Management Congress ($n = 15$),

Professional membership

The Wildlife Society – National (Since 2008), Montana Chapter (since 2008), Utah Chapter (since 2012), Central Mountain and Plains Section (since 2014)

Ecological Society of America – National (since 2014)

Society for Advancement of Chicanos and Native Americans in Science – National (since 2013), USU student chapter (since 2013)

American Association for the Advancement of Science – National (since 2018).

Leadership training

2014 The Wildlife Society Leadership Institute Class
 2011 The Institute on Teaching and Mentoring Conference

Professional development

2016 Bayesian integrated population modeling using BUGS and JAGS. Instructors: Drs. Marc Kery, Michael Schaub, David Koons. Utah State University, Logan, UT.
 2013 Analysis of Wildlife Spatial Behaviors and Habitat Use with the adehabitat* R Packages. Instructors: Clément Calenge and James Sheppard. The Wildlife Society, Milwaukee, WI.

Appointments

2016-2017 **Past-Chair**, Native People's Wildlife Management Working Group of TWS
 2014-2015 **Chair**, Native People's Wildlife Management Working Group of TWS
 2012-2013 **Chair-Elect**, Native People's Wildlife Management Working Group of TWS
 2013-2014 **Vice President**, USU student chapter of SACNAS
 2012-2013 **Treasurer**, Student Development Working Group of TWS
 2009-2011 **Treasurer**, Native People's Wildlife Management Working Group of TWS

Others

- 2014** **Co-organizer** of symposium entitled, “Human diversity and changing professional identities in wildlife professions.” The Wildlife Society. 21st Annual Meeting. Pittsburgh, PA.
- 2012** **Co-organizer** of symposium entitled, “Bison conservation in Montana.” Montana Chapter of The Wildlife Society. Great Falls, MT.
- 2011** **Co-organizer** of symposium entitled, “Past, present, future: implementing Hawaiian culture in conservation.” *The Wildlife Society*. 17th Annual Meeting. Waikoloa, HI.

Committees

- 2018 U.S. Fish and Wildlife Service & The Wildlife Society Diversity Initiative, Program titled: *Recruitment and retention of minorities and underrepresented groups in the conservation workforce*.
- 2012 Student/Professional Mixer - Montana Chapter/Northwest Section of The Wildlife Society.
- 2011 University of Montana College of Forestry and Conservation. Graduate student representative, Dean Search Committee.
- 2009 University of Montana Wildlife Biology Faculty. Graduate student representative.

AWARDS AND HONORS

- 2018 Murray F. Buell Award (best student oral presentation). 2017 Annual Meeting of the Ecological Society of America.
- 2018 Best Oral Presentation (professional category). Annual Meeting of the Utah Chapter of The Wildlife Society.
- 2016 Utah State University Student Association Graduate Enhancement Award (\$4,000)
- 2016 African Safari Club of Florida Graduate Scholarship (\$2,000)
- 2015 African Safari Club of Florida Graduate Scholarship (\$2,500)
- 2014 Travel scholarship for Predator-Prey Interactions, Gordon’s Research Conference, National Science Foundation DEB – 1357368 (\$200).
- 2014 Travel scholarship for Predator-Prey Interactions, Gordon’s Research Conference, Carl Storm Underrepresented Minority Foundation (\$600).
- 2014 American Indian Education Foundation Scholarship (\$2,000)
- 2013 Travel scholarship for 2013 TWS conference, TWS Wildlife and Habitat Restoration Working Group (\$340).
- 2013 African Safari Club of Florida Graduate Scholarship (\$1,667)
- 2012 American Indian Education Foundation Scholarship (\$2,000)
- 2012 Knute W. Bergan Native American Scholarship (\$1,200)
- 2011 American Indian Education Foundation Scholarship (\$2,000)
- 2011 Knute W. Bergan Native American Scholarship (\$1,200)

- 2010 Knute W. Bergan Native American Scholarship (\$1,200)
- 2008 Montana Weed Control Association Scholarship (\$1,000)
- 2008 Phil Tawney Memorial Hunter Scholarship (\$1,400)
- 2008 Native American Studies Scholarship (\$1,000)

INVITED PRESENTATIONS

- 2018 **Kohl, M. T.,** et al. Direct killing, not fear, explain prey range shifts in Yellowstone. The Wildlife Society 25th Annual Conference. The ecology of fear: linking theory to management practices symposium. Cleveland, OH.
- 2017 **Kohl, M. T.,** et al. Sage-grouse: the more you know, the more your grow! Society for Range Management Utah State Meeting. Midway, UT.
- 2017. **Kohl, M. T.,** et al. Greater sage-grouse resource selection drives reproductive fitness in a conifer removal system. The Wildlife Society 24th Annual Conference. Wildlife are individuals too: considering inter-individual variation to inform management symposium. Albuquerque, NM.
- 2016 **Kohl, M. T.** Human diversity: the bridge from science to conservation success. Native Voices native Issues Seminar Series. University of Montana, Missoula, MT.
- 2011 **Kohl, M. T.,** et al. Habitat use and the importance of water for bison and cattle. Boone and Crockett Club Annual Meeting. Charleston, SC.
- 2011 **Kohl, M. T.,** et al. Ecological monitoring of bison with telemetry data. Panel on Documenting Bison Ecological Interactions. 3rd American Bison Society Conference: Bison Ecological Restoration. Tulsa, OK.
- 2010 **Kohl, M. T.,** et al. Habitat use and the importance of water for bison and cattle. Grasslands National Park Summer Science Series, Val Marie, Saskatchewan, Canada.

PROFESSIONAL MEETINGS WITH PUBLISHED ABSTRACTS

* = advised student

- 2018 **Kohl, M. T.**, et al. The effects of electric powerlines on the breeding ecology of greater sage-grouse. *The Wildlife Society 25th Annual Conference*. Grouse Session. Cleveland, OH.
- 2018 **Kohl, M. T.**, et al. The effects of electric powerlines on the breeding ecology of greater sage-grouse. *International Grouse Symposium*. Logan, UT.
- 2018 **Kohl, M. T.**, et al. The effects of electric powerlines on the breeding ecology of greater sage-grouse. *The Wildlife Society Utah State Meeting*. Vernal, UT.
- 2018 **Kohl, M. T.**, et al. Sage-grouse: the more you know, the more you grow. *The Wildlife Society Utah State Meeting*. Vernal, UT.
- 2017 **Kohl, M. T.**, et al. Selection for predator niche vacancies minimizes a multi-predator threat. *The Wildlife Society 24th Annual Conference*. Conservation and Ecology of Mammals VI Session. Albuquerque, NM.
- 2017 **Kohl, M. T.**, et al. Selection for predator niche vacancies minimizes a multi-predator threat. *Ecological Society of America 102nd Annual Meeting*. Predation and Predator-Prey Interactions II. Portland, OR.
- 2015 **Kohl, M. T.**, et al. Diel activity pattern of wolves shapes elk response to spatial predation risk in northern Yellowstone. *Ecological Society of America 100th Annual Meeting*. Predation and Predator-Prey Interactions I Session. Baltimore, MD.
- 2013 **Kohl, M. T.**, et al. Influence of wolf predation risk on elk movement in Yellowstone National Park. *The Wildlife Society 20th Annual Conference*. Conservation of Recovered Wolves Session: Milwaukee, WI.
- 2013 **Kohl, M. T.**, et al. Influence of wolf predation risk on elk movement in Yellowstone National Park. 2013 *International Wolf Symposium*. Wolf Ecology, Behavior, Genetics Session: Duluth, MN.
- 2012 **Kohl, M. T.**, et al. The future of bison conservation and the role of large landscapes. *4th International Wildlife Management Congress*. Durban, South Africa.
- 2012 **Kohl, M. T.**, et al. Bison versus cattle: are they ecologically synonymous? *2nd Annual Grasslands Symposium*. Dodson, MT.
- 2012 **Kohl, M. T.**, et al. Icons of the prairie: conserving the international grassland highway. *Montana Chapter of The Wildlife Society*. Great Falls, MT.
- 2010 **Kohl, M. T.**, et al. Habitat use and the importance of water for bison and cattle. *University of Montana Graduate Student Research Conference*. Missoula, MT.
- 2009 **Kohl, M. T.**, et al. Do High Elk Densities Promote Spotted Knapweed Reinvasion? *Montana Chapter of The Wildlife Society*. Helena, MT.

Poster presentations

- 2015 Schwanda, O.*, **M. T. Kohl**, R. M. Callaway, S. Durham, and M. Hebblewhite. Influence of elk herbivory on spotted knapweed reinvasions in western

- Montana. *Student Research Symposium*. Utah State University, Logan, UT, USA.
- 2014 **Kohl, M. T.**, D. R. MacNulty, J. D. Forester, M. J. Kauffman, D. W. Smith, and D. R. Stahler. Influence of wolf predation risk on elk movement in Yellowstone National Park. *2014 Conference on Predator – Prey Interactions “From Genes to Ecosystems to Human Mental Health*. Gordon Research Conference, Ventura, CA, USA.
- 2012 **Kohl, M. T.**, P. R. Krausman, and K. Kunkel. Bison and cattle: are they ecologically synonymous? *The Wildlife Society*. 19th Annual Conference. Conservation of Mammals Session: Portland, OR, USA.
- 2012 **Kohl, M. T.**, P. R. Krausman, and K. Kunkel. Habitat use and the importance of water for bison and cattle. *3rd American Bison Society Meeting*. Bison Ecological Restoration Poster Session. Tulsa, OK, USA.
- 2010 **Kohl, M. T.**, P. R. Krausman, and K. Kunkel. Habitat use and the importance of water for bison and cattle. *The Wildlife Society*. 17th Annual Conference – Research in Progress Session: Snowbird, UT, USA.
- 2008 **Kohl, M. T.**, M. Hebblewhite, S. M. Cleveland. Do High Elk Densities Promote Spotted Knapweed Reinvasion? *The Wildlife Society*. 15th Annual Conference – Research in Progress Session: Miami, FL, USA.
- 2008 **Kohl, M. T.**, M. Hebblewhite, S. M. Cleveland. Do High Elk Densities Promote Spotted Knapweed Reinvasion? *University of Montana Conference on Undergraduate Research*. Missoula, MT, USA.

SCIENCE MEDIA COVERAGE

Print

- 2018 Billings Gazette, 24 June, *Yellowstone elk are skilled at working around wolf's schedule, study shows*.
- 2018 Herald Journal, 5 July, *USU researchers challenge Yellowstone elk's 'landscape of fear.'*
- 2018 The Wildlife Professional, September/October Issue, *Yellowstone elk adapt behavior to avoid wolves*.

Online

- 2018 Yellowstone Insider, 18 July, *Examining the “Landscape of Fear” in Yellowstone*.
- 2018 PHYS.org, 22 June, *Yellowstone's 'Landscape of Fear' not so scary after all*.
- 2017 Western Farmer-Stockman, 6 April, *Making habitat better for sage grouse nesting, brooding*.
- 2017 CacheValleyDaily, 7 March, *USU extension protects sage-grouse by clearing conifers*.