5-2017

The Behavior and Ecology of Cursorial Predators and Dangerous Prey: Integrating Behavioral Mechanisms with Population-level Patterns in Large Mammal Systems

Aimee Tallian
Utah State University

Recommended Citation

Tallian, Aimee, "The Behavior and Ecology of Cursorial Predators and Dangerous Prey: Integrating Behavioral Mechanisms with Population-level Patterns in Large Mammal Systems" (2017). *All Graduate Theses and Dissertations*. 5629.
https://digitalcommons.usu.edu/etd/5629

THE BEHAVIOR AND ECOLOGY OF CURSORIAL PREDATORS AND DANGEROUS PREY: INTEGRATING BEHAVIORAL MECHANISMS WITH POPULATION-LEVEL PATTERNS IN LARGE MAMMAL SYSTEMS

by

Aimee Tallian

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

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

Daniel R. MacNulty Major Professor	Eric M. Gese Committee Member
Kari E. Veblen Committee Member	R. Douglas Ramsey Committee Member
Trisha B. Atwood Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2017

ABSTRACT

The Behavior and Ecology of Cursorial Predators and Dangerous Prey: Integrating Behavioral Mechanisms with Population-level Patterns in Large Mammal Systems

by

Aimee Tallian, Doctor of Philosophy

Utah State University, 2017

Major Professor: Dr. Daniel MacNulty
Department: Wildland Resources

The study of predator-prey behavior is of primary importance to the field of ecology. However, few studies measure interactions between predators and their most dangerous prey. The *objective* of this project was to improve understanding of the behavioral and ecological interactions between cursorial predators and dangerous prey in free-living systems. Specifically, I used data from Yellowstone National Park to evaluate 1) the role of cooperative hunting in the ability of predators to hunt dangerous prey, 2) how predator preference for differentially dangerous prey species changes in relation to their relative abundance, 3) the ability of cursorial predators to drive large-scale, landscape level shifts in prey habitat use, and 4) how the kill rate of a top predator was affected by the presence of another. In chapter 2, I found that wolves (*Canis lupus*) were more cooperative when hunting bison (*Bison bison*), their most dangerous prey, than when hunting elk (*Cervus elaphus*). The results from chapter 3 suggest that wolves in northern Yellowstone attacked and killed disproportionately more of the rarer, but safer prey species; wolves maintained a strong preference against bison, even when this species was more than twice as abundant as elk. Analyses of wolf-bison behavioral interactions indicate that wolf preference against bison likely reflected an inability to consistently overcome bison antipredator defenses. Chapter 4 presents several lines of evidence suggesting wolves are a plausible mechanism behind recent decreased bison preference for Yellowstone's high elevation winter range. For example, bison preference for the high elevation Pelican Valley region decreased after wolf reintroduction. This preference was strongly influenced by snow-cover, a proxy for predation risk. In Chapter 5, I collaborated with Scandinavian ecologists to determine how wolf kill rate was affected by a sympatric apex predator, the brown bear (*Ursus arctos*). My results suggest brown bear presence resulted in wolves killing less frequently in both Scandinavia and Yellowstone. My research contributes to the current body of work addressing the effects of wolf reintroduction in Yellowstone, and sheds light on the behavioral relationships at play in a special type of predator-prey interaction: predators that hunt dangerous prey.

(247 pages)

PUBLIC ABSTRACT

The Behavior and Ecology of Cursorial Predators and Dangerous Prey: Integrating Behavioral Mechanisms with Population-level Patterns in Large Mammal Systems

Aimee Tallian

Driving into Yellowstone National Park for the first time is a moving experience. Gazing over the sweeping landscapes, seeing a geyser erupt 80 feet into the air, and having your first ‘wildlife encounter’, whether that be a 2 ton bull bison aggressively wallowing on his dirt mound, snorting and kicking up dust, or watching a pack of 6 wolves move through a valley off in the distance, pausing to howl in search of their companions. Yellowstone staff wishes to manage our park in a way that preserves these remarkable experiences. In order to effectively manage this dynamic ecosystem, it is critical to thoroughly understand how different animal and plant species interact with each other and their environment.

Wolves were reintroduced to Yellowstone in 1995-1997 and park researchers and managers are still trying to understand how their presence impacts the ecosystem. In Yellowstone, wolves primarily prey on elk; however, predation on bison has started to increase in recent years. We still know little about how wolves hunt bison and what impacts wolves have had on how bison use their environment. The *objective* of this study was to better understand the behavioral and ecological interactions of wolves and bison, the most dangerous prey for wolves in North America. Since

reintroduction, researchers have collected data on how wolves hunt both elk and bison. I used these data to understand 1) the conditions that allow wolves to capture their most dangerous prey, bison, 2) whether wolves have started preying on bison more often as the bison population increased, and 3) whether wolf reintroduction has limited bison use of Yellowstone's most extreme high-elevation winter range. Finally, I collaborated with ecologists in Scandinavia to determine how wolf predation was affected by a competitor, the brown bear.

My study adds to the current body of work addressing the effects of wolf reintroduction in Yellowstone. This research is unique because it focuses on wolf-bison interactions, about which little is known in this system. This research also sheds light on the behavioral relationships at play in a special type of predator-prey interaction: predators that hunt dangerous prey.

ACKNOWLEDGMENTS

I first met Dr. Dan MacNulty on a hilltop in Pelican Valley in March, 2010. Travis Wyman asked me to ski into the valley with him on a resupply trip for the ongoing project that would ultimately become the focus of my dissertation. The morning after our long ski into the field site, and my first of many nights sleeping on the snow in a cold tent, the Mollies pack moved into the valley and targeted a bull bison. The hunt lasted most of the day; we watched as the wolves took turns attacking and harassing the old bull, until it finally succumbed late that evening. It was an incredible experience to witness such an interaction, especially on my first day in the valley, and I wanted to see more. With Travis's encouragement, I phoned Dan several months later to ask about the project. His enthusiasm for wolves, bison, and the Pelican Valley system was more than contagious, which has been the theme of our collaboration ever since. Dan's help, guidance, support, and belief in me is the foundation of this work, thank you. Dan and Travis seamlessly incorporated me into their crew and showed me the wily ways of Pelican, for which I cannot thank you both enough.

Many thanks go to my committee members, Drs. Trisha Atwood, Eric Gese, Douglas Ramsey and Kari Veblen for their help and support. Countless employees and students at Utah State University have helped me along the way. I would like to thank the Animal Ecology Lab, especially Dr. Lise Aubry, Dr. Johan Du Toit, Ryan Kindermann, Daniel Kinka, Michel Kohl, Peter Mahoney, Jarod Raithel, Dustin Ranglack, Joel Ruprecht, and Dr. Julie Young for all of the discussions, statistical guidance, manuscript revisions, and general help. I would not have gotten through it without you guys. To my other friends in Logan who provided so much support, Antra Boca, Julie Kelso, and Kerry Shea, thank you. I would like to thank Susan Durham, whose statistical help got me over countless hurdles, for her help and patience. Thanks also to the two women who keep our department running, Marsha Baily and Lana Barr.

I would especially like to thank my collaborators in Yellowstone National Park, Matthew C. Metz, and Drs. Douglas W. Smith, Daniel R. Stahler, P.J. White, Rick Wallen and Chris Geremia. We have known each other for many years, and it has truly been a pleasure to work with them in this new capacity. I also give special thanks to my collaborators in Scandinavia: Cyril Milleret and Drs. Jonas Kindberg, Andrés Ordiz, Håkan Sand, Jon E. Swenson, Petter Wabakken, and Camilla Wikenros. Their help and guidance resulted in a collaboration that was truly a highlight of my graduate school experience.

I would like to thank the numerous people that have participated in wolf capture and monitoring with the Yellowstone and Scandinavian wolf projects over the last two decades. I gratefully acknowledge field assistance from numerous Yellowstone Wolf Project technicians and volunteers, especially Erin Stahler, Nathan Varley, Jamie Walton, and Travis Wyman. I also acknowledge and thank the support of numerous volunteers, technicians and staff from Utah State University, the Yellowstone Center for Resources, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Hedmark University of Applied Sciences, and Scandinavian Brown Bear Research Project. I also thank staff from the Yellowstone

Center for Resources and Yellowstone Ranger Division for logistical support, and R. Stradley and personnel from Hawkins and Powers, Inc., and Central Copters, Inc., for safe piloting. My dissertation was supported by the National Science Foundation (NSF) Graduate Research Fellowship Program (DGE-1147384) and a Graduate Research Opportunities Worldwide grant provided by NSF and the Swedish Research Council. Further funding was provided by two NSF LTREB grants (DEB-0613730, DEB-1245373), the Yellowstone Center for Resources, and Utah State University's Ecology Center, School of Graduate Studies, Quinney College of Natural Resources, and Wildland Resources Department.

I give special thanks to my mother, who always seems to steer me in the right direction. Your belief in my ability to accomplish anything I put my mind to has been instrumental in pretty much everything I do. In loving memory of my father, who we lost two weeks before I started this project, I know you would have been there for me too. Thanks also to the rest of my family and friends for their encouragement, moral support, and patience. How you all put up with me, I will never know.

Aimee Tallian

CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The recent history of the gray wolf (*Canis lupus*) and bison (*Bison bison*) in North America is a tumultuous one. Starting with the wholesale slaughter of both species near the turn of the 19th century (Hornaday 1887; Isenberg 2000), and culminating with their successful conservation by the end of the 21st (Boyd 2003; Mech & Boitani 2010), their history reflects the progression of wildlife protection and conservation in the United States, and the learning curve that western culture has experienced over the last century about the importance of understanding and conserving the ecosystems we rely on. The return of wolves to Yellowstone National Park represents a unique opportunity to study how wolves and bison interact, advance our understanding of predator-prey interactions, evaluate the effects of large carnivore restoration on ecosystem and community dynamics, and gain insight into the mega-faunal predator-prey interactions that once dominated North America.

Bison formerly numbered in the millions (Seton 1929; McHugh 1972; Lott 2002) and ranged over almost all of North America (Gates & Ellison 2010). Wolves were also present throughout most of this region in numbers far greater than today (Boitani 2003). Early accounts suggest that wolves preyed on bison throughout the Great Plains. However, the European colonization of North America wreaked havoc on this system. Bison, whose vast numbers fostered the belief that their population would never be depleted, were slaughtered by the thousands, and essentially disappeared from the landscape by the late 1800's (Hornaday 1887; Seton 1929).

Wolves were viewed as a pest, a threat to settler's personal and economic safety, and were hunted to near extinction by around the same time (Boitani 2003).

Despite large scale extirpation, a very small population of wild bison persisted in an obscure corner of Yellowstone. Pelican Valley is a large drainage complex in Yellowstone's interior, just north of Yellowstone Lake. This region was the isolated refuge for the last two dozen remaining wild bison in the United States (Meagher 1973). This valley, and its inhabitants, played an important role in the recent history of North American bison, and the initiation of wildlife protection and conservation in the United States. In 1884, a bison poaching incident in Pelican Valley spurred the eventual passage of the Lacy Act. Importantly, this was the first piece of federal wildlife protection legislation passed in the United States, and it made poaching a prosecutable offense. Wildlife protection was now legally enforceable by the United States government, and one of the first tasks was to restore the Yellowstone bison population that was teetering on the brink of extinction. Over the next century, bison numbers rebounded. The bison population in North America is currently estimated near 500,000 animals, although only about 4% persist in wild herds (Boyd 2003). Yellowstone's recovered bison population is currently the largest wild herd in North America (Boyd 2003). Their recovery represents a milestone in bison conservation.

Wolves, on the other hand, took much longer to be considered for conservation by the American people. During the 19th century, wolves persisted in low numbers in only a few isolated areas in northern Minnesota and Michigan (Mech 1966; Van Ballenberghe 1974; Hendrickson, Robinson & Mech 1975). The protection of the gray wolf was finally initiated in 1974, when they were classified as ‘endangered’ under the newly passed Endangered Species Act. Conservation efforts followed in other areas of the United States, and wolves were reintroduced to Yellowstone National Park in 1995-1997 (Bangs & Fritts 1996).

The reintroduction of wolves to Yellowstone led to the first recovery of a wolf-bison system in the lower 48 states since their combined extirpation near the turn of the 19th century. This restored system provides a unique opportunity to gain insight into a special type of predator-prey interaction: predators that hunt dangerous prey. Predator-prey theory is often guided by experimental studies on small taxa, where predators are larger than their prey, and prey are helpless once attacked (e.g., Akre & Johnson 1979; Hugie & Dill 1994; Schmitz, Beckerman & O'Brien 1997; Werner & Peacor 2003). Yet, many free-living systems include dangerous prey species that can harm or kill their predators. Understanding how predators modify their foraging behavior to cope with dangerous prey species is important for understanding the dynamics of natural systems (Mukherjee & Heithaus 2013).

Research suggests that predators may adopt a variety of tactics for utilizing dangerous prey (Mukherjee & Heithaus 2013). For example, predators may be more cooperative when hunting prey that are difficult to kill. Theory predicts that the success of predators hunting difficult prey increases with predator group size (Packer & Ruttan 1988). This pattern is attributed to the very small chance that a solitary hunter will capture such prey by itself. In addition, predators may also shift foraging strategies from hunting to scavenging when subsidized by carrion from large, dangerous prey (Pereira, Owen-Smith & Moleón 2014).

Shifting foraging strategies may alter expectations about how prey preferences vary with respect to changes in the relative abundance of prey. A classic hypothesis in ecology is that generalist predators stabilize prey populations by ‘switching’ between prey as the prey species’ relative abundances change (Murdoch 1969; Murdoch & Oaten 1975). Switching occurs when preference for a prey species becomes stronger or weaker as that species forms a larger or smaller proportion of available prey (Murdoch 1969; Murdoch & Oaten 1975). This means the predator switches a disproportionate number of its attacks to the more abundant species, correspondingly sparing the rare species. However, accumulating evidence suggests that predators often select prey that minimize the risk of injury, rather than maximize energy gain (Rutten *et al.* 2006; Smallegange, Van Der Meer & Kurvers 2006; Berger-Tal *et al.* 2009; Mukherjee & Heithaus 2013). The potentially high fitness costs associated with attacking dangerous prey species may cause preference for them to lag behind increases in their relative abundance. This is important because an inability to switch to alternative prey could have destabilizing consequences on predator-prey dynamics (Murdoch 1969; Murdoch & Oaten 1975).

Interestingly, even though dangerous prey are generally invulnerable to predation, they may still behaviorally respond to predation risk (e.g., Prins & Iason 1989; Tambling *et al.* 2012). This is because certain landscape characteristics can neutralize prey antipredator defenses, making them less dangerous and more vulnerable to predation. The extent to which both prey defenses and predator hunting success are governed by landscape characteristics directly affects the strength of a prey species response to predation risk (Preisser, Orrock & Schmitz 2007). Prey are expected to be largely insensitive to cursorial predators, which generate weak and inconsistent landscape-specific risk cues, because they are spatially unpredictable (Schmitz 2005). However, coursing predators might produce strong and consistent risk cues if their hunting success is tightly coupled with landscape characteristics.

Interactions between competing predators can also be affected by dangerous prey in ways that are not always intuitive. For example, carnivores often compete over access to carcasses and interference competition between species can force a subordinate predator to prematurely abandon its kill (Krofel, Kos & Jerina 2012; Elbroch *et al.* 2014). These interactions can result in increased predation on the prey population. However, hunting often necessitates a significant energy investment for carnivores, and predators can face a high risk of injury, or even death, when hunting large prey that can fight back (MacNulty 2002; Mech, Smith & MacNulty 2015). Thus, it is also possible that predators might realize greater fitness benefits from lingering at a stolen carcass, striving for occasional access, rather than prematurely abandoning it to make a new kill. Interestingly, this behavior would increase predator handling time, lengthening time between kills, and potentially reducing predation on the prey population.

Although rarely studied, investigating this special type of predator-prey interaction (i.e., predators that hunt dangerous prey) represents an important step forward in our understanding of predator-prey behavior. This study uniquely links individual-level behavioral mechanisms with population-level patterns to understand the ecology of cursorial predators and dangerous prey in free-living large mammal systems. Specifically, I evaluated 1) the role of cooperative hunting in the ability of predators to hunt dangerous prey, 2) how predator preference for differentially dangerous prey species changes in relation to prey relative abundance, 3) the ability of cursorial predators to drive large-scale, landscape level shifts in prey habitat use, and 4) how a top predators kill rate is affected by the presence of another predator. The restored Yellowstone National Park system provides an ideal case study to evaluate these relationships for several reasons.

First, bison are the most dangerous prey for wolves in North America (Carbyn, Oosenbrug & Anions 1993; Mech & Peterson 2003). Bison are extremely large, regularly confront their predators (Carbyn, Oosenbrug & Anions 1993), require multiple attack and capture attempts, and often injure or kill wolves that attack them (MacNulty 2002). As a result, bison require relatively more time to subdue (MacNulty 2002), which is a classic characteristic of dangerous prey (Mukherjee & Heithaus 2013). Since their reintroduction to Yellowstone, wolves have primarily preyed upon elk (*Cervus elaphus*) (Metz *et al.* 2012). This is likely because the main available secondary prey are difficult to kill (i.e., bison) (Carbyn, Oosenbrug & Anions 1993; Mech & Peterson 2003). Although wolves rarely hunt bison, the open Yellowstone landscape provides an unparalleled ability to directly view wildlife interactions. This, in combination with long-term research efforts by park staff, resulted in an unprecedented observational data-set on the behavior of wolves hunting both elk and bison.

Second, a dramatic switch in the relative abundance of a dangerous (bison) versus safe (elk) prey in northern Yellowstone presents a rare opportunity to evaluate the ability of predators (wolves) to switch to dangerous prey in a free-living system.

In northern Yellowstone, multi-year drought, culling outside the park, wolf reintroduction, and natural recovery of brown bears (*Ursus arctos*) and cougars (*Felis concolor*) have decreased the abundance of elk (MacNulty *et al.* 2016). Concurrently, intensive management, shifts in migratory movements, and low culling and predation rates have increased the abundance of bison (Geremia, Wallen & White 2015; White, Wallen & Hallac 2015).

Third, the return of wolves to the Yellowstone ecosystem provides a unique case study to evaluate the ability of a cursorial predator to induce land-scape level shifts in prey habitat use. Bison occupy two main regions in Yellowstone during winter: the northern range (i.e., Lamar Valley) and central range (i.e., Madison/Firehole, Hayden and Pelican Valleys) (Meagher 1973). The high elevation central range experiences long, severe winters. This area is characterized by deep snowpack, interspersed with small patches of geothermal and windswept snow-free ground (Newman & Watson 2009). In contrast, the lower elevation northern range is characterized by mild winter conditions. Here, winters are shorter, snowpack is less severe, and patches of snow-free ground are larger and more numerous (Houston 1982). When wolves were reintroduced to Yellowstone, researchers predicted that central range bison would to be more vulnerable to wolf predation than bison wintering on the northern range (Singer 1992). Specifically, the anti-predator defenses of bison would be more likely to break down in areas with severe winter conditions, such as the interior Pelican and Hayden Valleys. The snow-covered landscape of these regions would limit the space available for defensive maneuvering (Singer 1992). Historically, the majority of Yellowstone’s bison population wintered in the central range (Meagher 1973), a pattern that switched in about 2005. Most of the population now winters in the northern range (Geremia *et al.* 2011). Cursorial predators are expected to induce a weak spatial response by prey (Schmitz 2005); however, if the hunting success of a cursorial predator is directly coupled with landscape characteristics, prey spatial response may be strong. Due to severe winter conditions in the central range, and the importance of snowpack in bison defensive capabilities and wolf hunting success, it is possible that the reintroduction of wolves has contributed to this landscape-scale shift in bison habitat use.

Finally, brown bears and wolves are both top predators that can affect prey demography and abundance (Gasaway *et al.* 1992; Griffin *et al.* 2011). Brown bears are efficient, and typically dominant, scavengers of wolf-killed prey. This has motivated the common, but untested, assumption that wolf kill rate is higher where wolves are sympatric with brown bears, because the loss of food biomass from kleptoparasitism forces additional hunting to meet energetic demands (Boertje *et al.* 1988; Ballard, Carbyn & Smith 2003). In Yellowstone, wolves and brown bears are sympatric throughout their range. In south-central Scandinavia, however, wolves are both sympatric and allopatric with the brown bear population. This dichotomy provided a novel opportunity to test for the effect of one apex predator (brown bear) on the kill rate of another (wolf) across two continents.

My first objective in this study, and the focus of chapter 2, was to understand how hunting group size influenced the success of wolves hunting bison. Enhanced ability to capture prey is a commonly cited benefit of group living in social predators, and a classic hypothesis for the evolution of sociality (Alexander 1974; Kruuk 1975;

Pulliam & Caraco 1984; Clark & Mangel 1986). Yet, previous research has shown that the benefit of improved hunting success is generally only realized in small groups (Eaton 1970; Kruuk 1972; Schaller 1972; Van Orsdol 1984; Mills 1985; Stander 1992; Fanshawe & Fitzgibbon 1993; Holekamp *et al.* 1997; Funston, Mills & Biggs 2001; MacNulty *et al.* 2012). However, empirical research has yet to establish how group size-specific hunting success varies across prey species that are differentially vulnerable to predation.

I tested the hypothesis that predators are more cooperative when hunting dangerous prey by measuring the influence of hunting group size on the probability that wolves attacked and captured bison, and then evaluated how it differed relative to comparable results for wolves hunting elk (MacNulty *et al.* 2012). I predicted that, because bison are more difficult to kill than elk (MacNulty 2002), wolves would be more cooperative when hunting bison; i.e., the success of wolves hunting bison would increase across large predator group sizes, and level off at a group size greater than that of wolves hunting elk.

In chapter 3, I examined the potential for prey switching behavior in systems where the alternative prey are dangerous. Prey switching occurs when a generalist predator kills disproportionately more of an abundant prey species and correspondingly spares a rare species (Murdoch 1969; Murdoch & Oaten 1975). This behavior is a classic stabilizing mechanism in food web models (e.g., Valdovinos *et al.* 2010; Morozov & Petrovskii 2013; van Leeuwen *et al.* 2013). However, little is known about its operation in free-living systems which often include dangerous prey species that resist predation.

I used long-term behavioral and population data (1995-2015) from northern Yellowstone to understand how prey preference of a free-ranging, generalist predator (wolves) responds to a dramatic change in the evenness of its prey community. This change involved increased abundance of a dangerous species (bison) and decreased abundance of a safer species (elk). I evaluated switching behavior by analyzing how the 1) relative frequency of attacks on bison and 2) relative frequency of bison kills changed with relative bison abundance. Prey switching is generally conceptualized in terms of relative abundance, but life history and behavioral traits also influence the ability of predators to utilize prey. Therefore, I determined how bison traits (group size, group composition, and flight response) affected the ability of wolves to attack and capture them.

The goal for chapter 4 was to understand the potential for cursorial predators to affect the large-scale habitat use of prey in a free-living system. I linked fine-scale spatial response to predation risk with long-term trends in bison preference for the Pelican Valley winter range. In free-living systems, prey spatially respond to predation risk at fine scales (e.g., Heithaus & Dill 2002; Fortin *et al.* 2009; Tambling *et al.* 2012; Kohl *et al.* in review). Yet, less is known about the ability of predators to induce large-scale, landscape-level shifts in prey habitat use.

Cursorial predators are expected to induce a weak spatial response by prey (Schmitz 2005); however, if the hunting success of a cursorial predator is directly coupled with landscape characteristics, prey spatial response may be strong. In temperate systems, deep snow increases the ability of cursorial predators to hunt ungulates (Mech & Peterson 2003). Thus, winter snow conditions are likely a key axis of spatial variation in predation risk. In Yellowstone, the high elevation Pelican Valley region is the most environmentally-extreme winter habitat for bison; winters are long and snow cover is severe.

I used direct observations of wolf-bison interactions in Pelican Valley (2001-2012) to understand the influence of the landscape on the hunting success of a cursorial predator by quantifying the effect of snow conditions on the ability of wolves to attack and capture bison. I predicted that wolves would be more likely to attack and successfully capture bison a) standing in deeper snow and b) bison located in habitats with less snow-free ground (i.e., habitats with more snow-free ground would be safer for bison). Next, I used data on bison locations and wolf presence/absence in Pelican Valley (2005-2008) to evaluate whether bison spatially responded to predation risk. Here, I expected that bison would be more likely to use safer habitats (i.e., habitats with more snow-free ground) as predation risk increased (i.e., as wolves stayed longer in the valley). Finally, I used historic data on regional bison abundance (1971-2014) to evaluate the effect of wolf reintroduction on bison preference for the high risk Pelican Valley winter range.

In chapter 5, I collaborated with ecologists in Scandinavia to evaluate how wolf kill rate was affected by a sympatric apex predator, the brown bear. Brown bears are efficient, and typically dominant, scavengers of wolf-killed prey. This has motivated the common assumption that wolf kill rates are higher where wolves are sympatric with brown bears (Boertje *et al.* 1988; Ballard, Carbyn & Smith 2003), because they are forced to hunt more often to compensate for the loss of food.

In a first transcontinental comparison, I used data from both systems to evaluate the assumption that brown bears cause wolves to kill more often. I used kill interval (i.e., the number of days between consecutive ungulate kills) as a measure of kill rate. I made three predictions: First, the kill interval of Scandinavian wolf packs sympatric with brown bears would decrease across the spring bear den emergence period (March-May) as bears progressively emerged from winter dens; wolf packs allopatric with brown bears should exhibit no such decline. Second, during summer, wolf kill interval would be lower for wolf packs that were sympatric, compared to allopatric, with bears in Scandinavia. Finally, I predicted that the presence of bears at wolf-killed ungulates would decrease wolf kill interval in Yellowstone, where the species are sympatric.

The reintroduction of wolves to Yellowstone National Park is an important ecological case study of the consequences of large carnivore restoration. A large amount of research in Yellowstone has sought to understand the effects of wolf recovery on their preferred prey, elk (e.g., Mech *et al.* 2001; Smith *et al.* 2004; Creel & Winnie 2005; Creel *et al.* 2005; Mao *et al.* 2005; Vucetich, Smith & Stahler 2005; White & Garrott 2005; Creel *et al.* 2008), and their cascading effects on other park inhabitants such as scavenger (e.g., Gunther & Smith 2004; Wilmers & Getz 2005; Atwood & Gese 2008; Merkle, Stahler & Smith 2009) and plant populations (e.g., Ripple *et al.* 2001; Beschta 2003; Ripple & Beschta 2004; Fortin *et al.* 2005; Beyer *et al.* 2007; Creel & Christianson 2009; Kauffman, Brodie & Jules 2010; Painter *et al.* 2014). There has also been a wealth of research exploring the ecology of wolves (e.g., Stahler, Smith & Guernsey 2006; MacNulty *et al.* 2009a; MacNulty *et al.*

2009b; Metz *et al.* 2011; Cubaynes *et al.* 2014) and bison (e.g., Plumb *et al.* 2009; Geremia *et al.* 2011; Geremia *et al.* 2014), independent of one another. However, less research in Yellowstone has been dedicated towards understanding interactions between wolves and bison (but see Laundré, Hernández & Altendorf 2001; MacNulty & Smith 2004), and the effects of wolf recovery on the bison population (but see Hernández & Laundré 2005). My study adds to the current body of work addressing the effects of wolf-reintroduction in Yellowstone. This research is unique because it focuses on wolf-bison interactions, about which little is known in this system.

The full effects of wolf recovery will likely take decades to unfold (Smith, Peterson & Houston 2003). In the central range, the abundance of alternative prey during winter has declined dramatically, leaving bison as the only viable ungulate prey for resident wolf packs. Elk do not over-winter in either Hayden or Pelican Valley. In the Madison/Firehole, the resident elk herd underwent sharp declines after wolf reintroduction (Hamlin *et al.* 2009) and the elk population that once over-wintered in the Madison/Firehole region is now essentially extirpated (Robert Garrott; *personal communication*). Furthermore, since 2008, the wolf population in the interior of the park has been consistently larger than the wolf population on the northern range (Smith *et al.* 2016). These shifts suggest that the central range of Yellowstone has transitioned from a wolf-elk system to a wolf-bison system during winter. Thus, understanding wolf-bison interactions in Yellowstone will become especially important in the future as the long-term effects of wolf restoration are realized.

The almost complete continent-wide loss of wolf and bison populations before any research efforts took place resulted in limited knowledge about how these animals interacted on the landscape before European settlement. Therefore, we have little understanding of how these systems might function once restored. This is important because efforts are currently underway in northern temperate systems to restore wolves and bison to parts of their former range (e.g., The American Prairie Reserve; Banff National Park). Understanding the traits that make wolves successful at hunting bison, the ability of wolves to incorporate bison into their diet, the behavioral response of bison to wolf predation, and how competition between apex predators affects predation provides insight into how wolf-bison systems function. This information can help guide restoration and recovery efforts of these once iconic and wide-spread species.

Finally, this research also contributes to a growing body of theory on interactions between predators and dangerous prey. Understanding how predators modify their foraging behavior to cope with dangerous prey species is important for understanding the dynamics of natural systems (Mukherjee & Heithaus 2013). This study sheds light on whether predators alter their behavior when hunting difficult prey, the ability of predators to switch to dangerous prey species in free-living systems, and how competition between apex predators affects the predation patterns of predators that hunt dangerous prey.

References

Akre, B. & Johnson, D. (1979) Switching and sigmoid functional-response curves in damselfly naiads with alternative prey available. *J Anim Ecol,* **48,** 703-720.

Alexander, R.D. (1974) The evolution of social behavior. *Annual Review of Ecology and Systematics,* **5,** 325-383.

Atwood, T.C. & Gese, E.M. (2008) Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses. *Animal Behaviour,* **75,** 753-762.

Ballard, W.B., Carbyn, L.N. & Smith, D.W. (2003) Wolf interactions with non-prey. *Wolves: Behavior, Ecology, and Conservation* (eds L.D. Mech & L. Boitani), pp. 259-271. The University of Chicago Press, Chicago and London.

Bangs, E.E. & Fritts, S. (1996) Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin,* **24,** 402-413.

Berger-Tal, O., Mukherjee, S., Kotler, B. & Brown, J. (2009) Look before you leap: Is risk of injury a foraging cost? *Behavioral Ecology and Sociobiology,* **63,** 1821-1827.

Beschta, R.L. (2003) Cottonwoods , elk , and wolves in the Lamar Valley of Yellowstone National Park. *Ecological Applications,* **13,** 1295-1309.

Beyer, H.L., Merrill, E., Varley, N. & Boyce, M.S. (2007) Willow on Yellowstone's northern range evidence for a trophic cascade. *Ecological Applications,* **17,** 1563-1571.

Boertje, R.D., Gasaway, W.C., Grangaard, D.V. & Kelleyhouse, D.G. (1988) Predation on moose and caribou by radio-collared grizzly bears in east central

Alaska. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **66,** 2492-2499.

Boitani, L. (2003) Wolf Conservation and Recovery. *Wolves: Behavior, Ecology and Conservation* (eds D. Mech & L. Boitani), pp. 317-340. University of Chicago Press, Chicago, Illinois, USA.

Boyd, D. (2003) Conservation of North American bison: status and recommendations. Master of Science, University of Calgary.

Carbyn, L.N., Oosenbrug, S. & Anions, D. (1993) *Wolves, Bison and the Dynamics Related to the Peace-Athabaska Delta in Canada's Wood Buffalo National Park.* Circumpolar Research Series Number 4; Canadian Circumpolar Institute, Edmonton, Alberta.

Clark, C.W. & Mangel, M. (1986) The evolutionary advantages of group foraging. *Theoretical Population Biology,* **30,** 45-75.

Creel, S. & Christianson, D. (2009) Wolf presence and increased willow consumption by Yellowstone elk implications for trophic cascades. *Ecology,* **90,** 2454-2466.

Creel, S. & Winnie, J.A. (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour,* **69,** 1181-1189.

Creel, S., Winnie, J.A., Christianson, D. & Liley, S. (2008) Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour,* **76,** 1139-1146.

Creel, S., Winnie, J.A., Jr., Maxwell, B., Hamlin, K.L. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology,* **86,** 3387-3397.

Cubaynes, S., MacNulty, D.R., Stahler, D.R., Quimby, K.A., Smith, D.W. & Coulson, T. (2014) Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology,* **83,** 1344-1356.

Eaton, R. (1970) Hunting behavior of the cheetah. *Journal of Wildlife Management,* **34,** 56-67.

Elbroch, L., Lendrum, P., Allen, M. & Wittmer, H. (2014) Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology,* **00,** 1-8.

Fanshawe, J.H. & Fitzgibbon, C.D. (1993) Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour,* **45,** 479-490.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology,* **86,** 1320-1330.

Fortin, D., Fortin, M., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009) Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology,* **90,** 2480-2490.

Funston, P.J., Mills, M.G.L. & Biggs, H.C. (2001) Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology,* **253,** 419-431.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O. & Larsen, D.G. (1992) The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs,* **120,** 3-59.

Gates, C.C. & Ellison, K. (2010) Numerical and geographic status. *American Bison: Status, survey and conservation guidelines 2010* (eds C.C. Gates, C. Freese, P. Gogan & M. Kotzman), pp. 55-62. International Union for Conservation of Nature, Gland, Switzerland.

Geremia, C., Wallen, R.L. & White, P.J. (2015) Population dynamics and adaptive management of Yellowstone bison. National Park Service, Yellowstone National Park, Mammoth, WY.

Geremia, C., White, P.J., Hoeting, J., Wallen, R.L., Watson, F.G., Blanton, D. & Hobbs, N.T. (2014) Integrating population- and individual-level information in a movement model of Yellowstone bison. *Ecological Applications,* **24,** 346-362.

Geremia, C., White, P.J., Wallen, R.L., Watson, F.G., Treanor, J.J., Borkowski, J., Potter, C.S. & Crabtree, R.L. (2011) Predicting bison migration out of Yellowstone National Park using bayesian models. *PLoS One,* **6,** e16848.

Griffin, K., Hebblewhite, M., Robinson, H., Zager, P., Barber-Meyer, S., Christianson, D., Creel, S., Harris, N., Hurley, M., Jackson, D., Johnson, B., Myers, W., Raithel, J., Schlegel, M., Smith, B., White, C. & White, P. (2011) Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology,* **80,** 1246-1257.

Gunther, K.A. & Smith, D.W. (2004) Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park. *Ursus,* **15,** 232-238.

Hamlin, K.L., Garrott, R.A., White, P.J. & Cunningham, J.A. (2009) Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. *The Ecology of*

Large Mammals in Central Yellowstone (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 541-577. Elsevier, San Diego, CA.

Heithaus, M.R. & Dill, L.M. (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology,* **83,** 480-491.

Hendrickson, J., Robinson, W. & Mech, D. (1975) The status of the wolf in Michigan. *American Midland Naturalist,* **94,** 226-232.

Hernández, L. & Laundré, J.W. (2005) Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology,* **11,** 215-220.

Holekamp, K.E., Smale, L., Berg, R. & Cooper, S.M. (1997) Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology,* **242,** 1-15.

Hornaday, W. (1887) The extermination of the American bison with a sketch of its discovery and life history.

Houston, D. (1982) *The Northern Yellowstone Elk: Ecology and Management*. MacMillan, New York, NY.

Hugie, D. & Dill, L.M. (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey*. *J Fish Biol,* **45,** 151-169.

Isenberg, A. (2000) *The destruction of the bison: an environmental history 1750-1920*. Cambridge University Press, Cambridge, UK.

Kauffman, M.J., Brodie, J.F. & Jules, E.S. (2010) Are wolves saving Yellowstone's aspen A landscape-level test of a behaviorally mediated trophic cascade. *Ecology,* **91,** 2742-2755.

Krofel, M., Kos, I. & Jerina, K. (2012) The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology,* **66,** 1297-1304.

Kruuk, H. (1972) *The Spotted Hyena*. The University of Chicago Press, Chicago, IL.

Kruuk, H. (1975) Functional aspects of social hunting in carnivores. *Function and Evolution in Behavior* (eds R. Sibley & R. Smith), pp. 521-526. Blackwell Scientific Publications, Oxford.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology,* **79,** 1401-1409.

Lott, D.F. (2002) *American Bison: A Natutal History*. University of California Press, Ltd., London, England.

MacNulty, D.R. (2002) The predatory sequence and the influence of injury risk on hunting behavior in the wolf. Master of Science, The University of Minnesota.

MacNulty, D.R. & Smith, D.W. (2004) Bison foraging response to the risk of wolf predation in a spatially heterogeneous winter environment: a preliminary assessment. (ed. H.J. Harlow). National Park Service Research Center, University of Wyoming.

MacNulty, D.R., Smith, D.W., Mech, L.D. & Eberly, L.E. (2009a) Body size and predatory performance in wolves: Is bigger better? *J Anim Ecol,* **78,** 532-539.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2012) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology,* **23,** 75-82.

MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R. & Packer, C. (2009b) Predatory senescence in ageing wolves. *Ecol Lett,* **12,** 1347-1356.

MacNulty, D.R., Stahler, D.R., Wyman, C.T., Ruprecht, J. & Smith, D.W. (2016) The challenge of understanding northern Yellowstone elk dynamics after wolf reintroduction. *Yellowstone Science*, pp. 25-33. Yellowstone National Park, Mammoth, WY.

Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M., Merrill, E.H. & Hudson (2005) Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management,* **69,** 1691-1707.

McHugh, T. (1972) *The time of the buffalo*. University of Nebraska Press, Lincoln, Nebraska, USA.

Meagher, M.M. (1973) *The Bison of Yellowstone National Park*. National Park Service, Washington D.C.

Mech, D. & Boitani, L. (2010) *Canis Lupus*. IUCN SSC Wolf Specialist Group, www.iucnredlist.org.

Mech, L.D. (1966) Hunting Behavior of Timber Wolves in Minnesota. *Journal of Mammalogy,* **47,** 347-348.

Mech, L.D. & Peterson, R.O. (2003) Wolf-Prey Relations. *Wolves: Behavior, Ecology and Conservation* (eds L.D. Mech & L. Boitani), pp. 131-160. The University of Chicago Press, Chicago, IL.

Mech, L.D., Smith, D.W. & MacNulty, D.R. (2015) *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press, USA.

Mech, L.D., Smith, D.W., Murphy, K.M. & MacNulty, D.R. (2001) Winter severity and wolf predation on a formerly wolf-free elk herd. *The Journal of Wildlife Management,* **65,** 998-1003.

Merkle, J.A., Stahler, D.R. & Smith, D.W. (2009) Interference competition between gray wolves and coyotes in Yellowstone National Park. *Canadian Journal of Zoology,* **87,** 56-63.

Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology,* **81,** 553-563.

Metz, M.C., Vucetich, J.A., Smith, D.W., Stahler, D.R. & Peterson, R.O. (2011) Effect of sociality and season on gray wolf (Canis lupus) foraging behavior: implications for estimating summer kill rate. *PLoS One,* **6,** e17332.

Mills, M.G.L. (1985) Related spotted hyaenas forage together but do not cooperate in rearing young. *Nature,* **316,** 61-62.

Morozov, A. & Petrovskii, S. (2013) Feeding on multiple sources: Towards a universal parameterization of the functional response of a generalist predator allowing for switching. *PlosOne,* **8,** 1-8.

Mukherjee, S. & Heithaus, M.R. (2013) Dangerous prey and daring predators: A review. *Biological Reviews,* **88,** 550-563.

Murdoch, W. (1969) Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs,* **39,** 335-354.

Murdoch, W. & Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research,* **9,** 1-131.

Newman, W. & Watson, F.G.R. (2009) The central Yellowstone landscape: terrain, geology, climate, vegetation. *The Ecolog of Large Mammals in Central Yellowstone* (eds R. Garrott, P.J. White & F.G.R. Watson), pp. 17-36. Elsevier, San Diego, CA.

Packer, C. & Ruttan, L. (1988) The evolution of cooperative hunting. *American Naturalist,* **132,** 159-198.

Painter, L., Beschta, R.L., Larsen, E.J. & Ripple, W.J. (2014) After long-term decline, are aspen recovering in northern Yellowstone? . *Forest Ecology and Management,* **329,** 108-117.

Pereira, L., Owen-Smith, N. & Moleón, M. (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review,* **44,** 44-55.

Plumb, G.E., White, P.J., Coughenour, M.B. & Wallen, R.L. (2009) Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation,* **142,** 2377-2387.

Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology,* **88,** 2744-2751.

Prins, H.H.T. & Iason, G.R. (1989) Dangerous Lions and Nonchalant Buffalo. *?*

Pulliam, H. & Caraco, T. (1984) Living in groups: is there an optimal group size? *Behavioral Ecology: An Evolutionary Approach* (eds J. Krebs & N. Davies), pp. 122-127. Sinauer, Sunderland, MA.

Ripple, W.J. & Beschta, R.L. (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience,* **54,** 755.

Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation,* **203,** 227-234.

Rutten, A., Oosterbeek, K., Ens, B. & Verhulst, S. (2006) Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers. *Behavioral Ecology,* **17,** 297-302.

Schaller, G. (1972) *The Serengeti Lion*. The University of Chicago Press, Chicago, IL.

Schmitz, O.J. (2005) Behavior of predators and prey and links with population level processes. *Ecology of Predator Prey Interactions* (eds P. Barbosa & I. Castellanos), pp. 256-278. Oxford University Press, New York, NY.

Schmitz, O.J., Beckerman, A. & O'Brien, K. (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology,* **78,** 1388-1399.

Seton, E. (1929) *Lives of game animals*. Doubleday, Doran and Co., Garden City, New York, USA.

Singer, F.J. (1992) Some predictions concerning a wolf recovery in to Yellowstone National Park: How wolf recovery may affect park visitors, ungulates, and other predators. *Wolves for Yellowstone? A Report to the United States Congress* (eds J. Varley & W. Brewster).

Smallegange, I., Van Der Meer, J. & Kurvers, R. (2006) Disentangling interference competition from exploitative competition in a crab-bivalve system using a novel experimental approach. *Oikos,* **113,** 157-167.

Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management,* **68,** 153-166.

Smith, D.W., Peterson, R.O. & Houston, D.B. (2003) Yellowstone after wolves. *BioScience,* **53,** 330-340.

Smith, D.W., Stahler, D.R., Metz, M.C., Cassidy, K., Stahler, E., Almberg, E. & McIntyre, R. (2016) Wolf restoration in Yellowstone: Reintroduction to recovery. *Yellowstone Science*, pp. 5-12. Yellowstone National Park, Mammoth, WY.

Stahler, D.R., Smith, D.W. & Guernsey, D.S. (2006) Foraging and Feeding Ecology of the Gray Wolf (*Canis lupus*) Lessons from Yellowstone National Park, Wyoming, USA. *Journal of Nutrition***,** 1923-1926.

Stander, P.E. (1992) Forgaing dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **70,** 8-21.

Tambling, C.J., Druce, D.J., Hayward, M.W., Castley, J.G., Adendorff, J. & Kerley, G.I.H. (2012) Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology,* **96,** 1297-1304.

Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narva´ ez, L., Urbani, P. & Dunne, J.A. (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol Lett,* **13,** 1546-1559.

Van Ballenberghe, V. (1974) Wolf managament in Minnesota: An endangered species case history. *Transactions of the North American Wildlife and Natural Resources Conference*, pp. 313-322.

van Leeuwen, E., Brännströmb, Å., Jansen, V.A.A., Dieckmann, U. & Rossberg, A.G. (2013) A generalized functional response for predators that switch between multiple prey species. *Journal of Theoretcial Biology,* **328,** 89-98.

Van Orsdol, K.G. (1984) Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology,* **22,** 79-99.

Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *Oikos,* **111,** 259-270.

Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology,* **84,** 1083-1100.

White, P.J. & Garrott, R.A. (2005) Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin,* **33,** 942-955.

White, P.J., Wallen, R.L. & Hallac, D. (2015) *Yellowstone bison - conserving an American icon in modern society*. Yellowstone Association, Yellowstone National Park, WY.

Wilmers, C.C. & Getz, W.M. (2005) Gray wolves as climate change buffers in Yellowstone. *PLoS Biol,* **3,** e92.

CHAPTER 2

INFLUENCE OF GROUP SIZE ON THE SUCCESS OF WOLVES HUNTING BISON[1]

Abstract

An intriguing aspect of social foraging behaviour is that large groups are often no better at capturing prey than are small groups, a pattern that has been attributed to diminished cooperation (i.e., free riding) in large groups. Although this suggests the formation of large groups is unrelated to prey capture, little is known about cooperation in large groups that hunt hard-to-catch prey. Here, we used direct observations of Yellowstone wolves (*Canis lupus*) hunting their most formidable prey, bison (*Bison bison*), to test the hypothesis that large groups are more cooperative when hunting difficult prey. We quantified the relationship between capture success and wolf group size, and compared it to previously reported results for Yellowstone wolves hunting elk (*Cervus elaphus*), a prey that was, on average, 3 times easier to capture than bison. Whereas improvement in elk capture success levelled off at 2-6 wolves, bison capture success levelled off at 9-13 wolves with evidence that it continued to increase beyond 13 wolves. These results are consistent with the hypothesis that hunters in large groups are more cooperative when hunting more formidable prey. Improved ability to capture formidable prey could therefore promote the formation and maintenance of large predator groups, particularly among predators that specialize on such prey.

---

[1] MacNulty, Daniel R., Aimee G. Tallian, Daniel R. Stahler, Douglas W. Smith (2014). Influence of group size on the success of wolves hunting bison. *PlosOne* 9(11):1-8.

Introduction

Enhanced ability to capture prey is a commonly cited benefit of group living in social predators and a classic hypothesis for the evolution of sociality [1-4]. Yet, previous research has shown that the benefit of improved hunting success (defined as the likelihood of capturing prey) is generally only realized in small groups. In many group-hunting taxa, ranging from insects to primates, hunting success fails to increase over larger group sizes despite apparent cooperation among hunters [5-10]. This nonlinear pattern is well documented in large social carnivores, which have been model organisms in the study of group hunting behavior. Numerous studies show that carnivore hunting success peaks at 2-5 hunters then levels off, or even declines, across larger group sizes [10-19]. Although this suggests the formation and maintenance of large groups is unrelated to prey capture, predators that hunt hard-to-catch prey may follow a different pattern.

Theory predicts that the success of predators hunting formidable prey increases across large group sizes [5]. This pattern is attributed to greater cooperation (i.e., increased individual effort) in large groups due to the small chance a solitary hunter will capture such prey by itself. Low solo hunting success promotes cooperation because an additional hunter can improve group hunting success sufficiently to overcome its own costs of hunting (e.g., risk of injury and energetic loss). Conversely, high solo hunting success suppresses cooperation because an additional hunter can do little to improve the outcome and this fails to offset hunting costs. As a result, hunters pursuing relatively easy prey are expected to hold back in large groups, thereby capping further increases in hunting success with group size. A study of wolves (*Canis lupus*) hunting elk (*Cervus elaphus*) supports this prediction: group hunting success leveled off at 4 wolves, which was also the group size beyond which individual effort decreased [10].

Empirical research has yet to establish how group size-specific hunting success (H_n) of large groups varies across prey species that are differentially vulnerable to predation. Behavioral studies of large carnivores, for example, rarely include data on large groups (e.g., >6 hunters) [14, 16, 17, 19-21] and few have measured how H_n varies across prey species. Among those that have, the results were ambiguous [14, 16, 17, 22]. For example, Scheel and Packer [22] found that African lions (*Panthera leo*) were apparently more cooperative when hunting larger, more dangerous prey (e.g., zebra, *Equus burchelli*; buffalo, *Syncerus caffer*), but they observed too few hunts to relate this to changes in H_n. Positive correlation between prey size and group size across the Carnivora [23, 24] is consistent with the prediction that larger groups are more successful hunters of formidable prey. But it is unclear whether this reflects the need to capture large prey to satisfy increased group demands or because larger groups can capture large prey more easily [16, 24].

Here, we use a unique dataset of observations of wolves hunting bison (*Bison bison*) in Yellowstone National Park (YNP) to test the hypothesis that predators in large groups are more cooperative when hunting formidable prey. Bison are the most difficult prey for wolves to kill in North America [25, 26] and in YNP they are 3 times more difficult to kill than elk [27], which are the main year-round prey for Yellowstone wolves [28, 29]. Bison are more difficult to kill than elk because they are larger, more aggressive, and more likely to injure or kill wolves that attack them

[30]. As a result, bison require relatively more time to subdue [30], which is characteristic of dangerous prey [31]. Groups of wolves are more likely to attack bison than are solitary wolves [32], but the effect of group size on the ability of wolves to capture bison is unknown. We measured the influence of group size on the probability that wolves attacked and captured bison, and evaluated how it differed relative to comparable results for Yellowstone wolves hunting elk [10]. If large groups are more cooperative when hunting formidable prey, we predicted the success of wolves hunting bison to increase across large group sizes and level off at a group size greater than that of wolves hunting elk.

Methods

Ethics statement

We captured and handled wolves following protocols in accord with applicable guidelines from the American Society of Mammalogists [33] and approved by the National Park Service Institutional Animal Care and Use Committee. Yellowstone National Park issued the permit authorizing this study (Study#: YELL-01818; Permit#: YELL-2014-SCI-1818).

Study area

Yellowstone National Park extends across 891,000 ha of a primarily forested plateau in northwestern Wyoming, USA that ranges from 1500 to 3300 m. Large montane grasslands provide excellent views of wildlife. We observed wolf-bison interactions in the northern portion of YNP, also referred to as the Northern Range

(NR; 995 km²), and in the central portion of the park (Pelican Valley; 100 km²). Low elevations (1500-2000 m) in the NR create the warmest and driest conditions in YNP during winter, providing critical winter range for migratory ungulates including bison and elk [34]. A maintained road runs the length of the NR and provides year-round vehicle access. Pelican Valley is a roadless area at 2500 m elevation. Elk are seasonally present in the valley (May-November) whereas bison persist year-round because they overwinter in geothermal sites [35]. Deep snow around these sites hinders bison movement which generates a higher risk of wolf predation in Pelican Valley than in the NR [27, 36].

Study population

A total of 41 radio-marked wolves were reintroduced to Yellowstone National Park in 1995-1997 [37]. Wolves observed in this study were either members or descendants of the reintroduced population. In each year following the reintroduction, about 30-50% of the pups born were captured and radio-marked [28]. This study focused mainly on 5 wolf packs: Druid Peak, Geode Creek, Leopold, Mollie's, and Rose Creek. Only the Mollie's pack inhabited Pelican Valley whereas the others occurred in the NR. To facilitate monitoring and research, the Yellowstone Wolf Project maintained radio-collars on at least 2 individuals in each pack [38].

Behavior Sampling

The methods we used to sample the behavior of wolves hunting bison were the same as those we used previously to sample the behavior of wolves hunting elk [10, 39]. We observed hunting behavior during biannual 30-day follows of 3-5 wolf packs from the ground and fixed-wing aircraft in early (mid-November to mid-December) and late (March) winter and during opportunistic ground and aerial surveys throughout the remainder of the year [28]. Many observations in this study were recorded from the ground in Pelican Valley during a 2-3 week period in March, 1999-2013. Comparable observations were recorded in the NR, 1996-2003. Over half of our observations (60% of 239 wolf-bison encounters) were recorded in Pelican Valley.

When wolves encountered bison – defined as at least 1 wolf orienting and moving (walking, trotting or running) toward bison – we followed the progress of the encounter by noting the foraging state (approach, watch, attack-group, attack-individual, capture) of the individual(s) closest to making a kill. We therefore recorded the sequential occurrence of the most escalated state and the number of wolves participating in that state. A wolf was scored as participating in a foraging state if it exhibited the behavioral acts characterizing that particular state (Table 2-1; Fig. 2-1). We considered non-participation in a given state as when a wolf was in view but engaged in another foraging state or a non-predatory behavior (e.g., resting). We refer to the number of wolves participating in a foraging state as the "hunting group". Hunting group size differs from pack size because it pertains to the subset of pack members participating in a hunt. We use "group size" throughout this article to refer to the size of hunting groups. We also recorded the number and age/sex class of bison present at the end of each foraging state. We used body size and horn morphology to identify three age/sex classes: bull, cow, calf [40].

We scored group hunting success according to whether wolves completed each of 2 predatory tasks that corresponded to the following 2 behavioral transitions: approach (or watch) → attack-group (or attack-individual) = “attacking”; attack-group (or attack-individual) → capture = “capturing” (Fig. 2-1). Note that capturing was not necessarily killing because bison that were bit and physically restrained by wolves often escaped [39]. A hunting group completed a task, and was therefore “successful”, if the task was performed by at least 1 group member. If not, we considered the group to have “failed” in that task. This scheme generated a binary score for a hunting group in each sequential foraging state.

Data Analysis

To understand how H_n differs between wolves hunting bison and elk, we followed the same analytical approach that we used previously to estimate H_n of wolves hunting elk [10]. We analyzed how hunting group size influenced the probability that wolves attacked and captured bison based on the binary scores described above. We limited our analyses of capturing to adult bison to control for the effects of prey size on group hunting behavior [5, 10]. Analyses were conducted using generalized linear mixed models (GLMMs) with a binomial error distribution. Such models account for correlation between the multiple observations taken on each pack. Pack identity was fitted as a random intercept to account for the influence of unmeasured pack-related factors on hunting success, including age and size of individuals within packs [41, 42] and differences in prey density between pack territories.

Observations of repeated attempts to perform the same task during the same encounter were also correlated, but these were used in only models of capturing, which fitted encounter identity as a random intercept within pack. Models of attacking included only the first attempt because we were mainly interested in how group size affected the probability of attacking on first encountering bison. All models included a compound symmetric correlation structure, which assumed that all observations within packs and encounters were, on average, equally correlated [43]. Models were estimated with adaptive Gaussian quadrature with parameters estimated from maximum likelihood, and significance of effects determined by an approximate *z*-test.

We used piecewise linear splines to test for nonlinear effects of group size on the probability that wolves attacked and captured bison. Specifically, we tested for a threshold group size beyond which the probability of group hunting success abruptly changed. To determine the presence and position of group-size specific thresholds in attacking and capturing, we evaluated a set of competing GLMMs for each task. Each model set included models with a single knot placed at 2-13 hunters, a model with no knot representing the hypothesis of no threshold in group hunting success, and an intercept-only model representing the null hypothesis that group size had no effect on hunting success. A knot was the join point between two linear splines. We selected knots *a priori* based on the prediction that the success of wolves hunting bison should level off at large group sizes. Our placement of knots is consistent with guidelines for the efficient use of knots [44-46]. By definition, knots selected *a priori* are fixed (i.e., not random variables) and are therefore not estimated as parameters in models. We created variables containing a linear spline for group size with the MKSPLINE command in STATA 13.1. The variables were constructed so that the estimated coefficients measure the slopes of the segments before and after a given knot.

To determine if bison herd size and composition affected the relationship between hunting success and group size, we analyzed a subset of observations (N = 92-187 wolf-bison encounters) in which this information was known. First, we evaluated a set of competing GLMMs as above, except that each model also included main effects for bison herd size and composition. The latter was a dummy variable indicating whether a herd was comprised of bulls only or some mixture of bulls, cows, and calves. Second, we tested whether interactions of herd size and composition with wolf group size improved the fit of the top model.

We conducted all analyses in STATA 13.1 and compared GLMMs using information-theoretic statistics [47]. Our scope of inference concerned the population, so we performed model selection using marginal likelihoods. The most parsimonious model was the one with the lowest Akaike Information Criterion (adjusted for small sample, AIC_c) and smallest ΔAIC_c. ΔAIC_c equals the AIC_c for the model of interest minus the smallest AIC_c for the set of models being considered. The best model has a ΔAIC_c of zero, and models with $\Delta AIC_c < 2$ are plausibly the best. To assess uncertainty about the best model, we identified models with $\Delta AIC_c < 2$ as the confidence set of models (analogous to a confidence interval for a mean estimate [47]). We calculated population-averaged fitted values from best-fit GLMMs by deriving marginal expectations of the responses averaged over the random effects but conditional on the observed covariates. We also used likelihood-ratio statistics to test specific hypotheses among nested models, and results were considered significant at

$P < 0.05$. Means are reported with standard errors unless indicated otherwise.

To determine how H_n differs between wolves hunting bison and elk, we compared our best-fit GLMMs of wolves attacking and capturing bison with our previously reported best-fit GLMMs of wolves attacking and killing elk (Fig. 1a and 1c in [10]). Wolves rarely killed captured bison, but nearly always killed captured elk [39]. Thus, the comparison of capturing with killing is a conservative test given that capturing a bison probably requires fewer wolves than killing it. The transition between attack-group and attack-individual ("selecting") was rare in wolf-bison encounters [39] and this precluded comparison of the effects of group size on selecting between hunts of bison and elk.

Results

Group-size specific success of wolves hunting bison

The influence of group size on the success of wolves attacking and capturing bison was not linear (Fig. 2-2). The top models of attacking and capturing included a linear spline for group size (Table 2-2), indicating a threshold at which the effect of group size on hunting success suddenly changed. Evidence against a model describing a simple linear relationship between group size and success was reasonably strong for attacking ($\Delta AIC_c = 5.79$; Table 2-2a) but weak for capturing ($\Delta AIC_c = 0.46$; Table 2-2b). The latter suggests that capture success may have increased across the largest observed group sizes (11-16 wolves). Yet, the collective fit (summed AIC_c weights) of the confidence set of spline models ($\Delta AIC_c < 2$) was nearly 5 times (AIC_c weights = 0.58/0.12) greater than the linear model, indicating that the effect of group size on capture success was more likely nonlinear than linear. The intercept models fit the data poorly ($\Delta AIC_c = 13.99-32.58$), implying that the overall influence of group size on attacking and capturing was strong.

The threshold group size was smaller for attacking than for capturing. The confidence set of spline models for each predatory task (Table 2-2) indicates the threshold group size was 3-6 wolves for attacking and 9-13 wolves for capturing. The most parsimonious models in the set included thresholds at 4 and 11 wolves for attacking and capturing, respectively (Fig. 2-2a-b). Beyond each threshold, groups size had no significant effect on success ($P = 0.10-0.50$; Fig. 2-2). But below these thresholds, each additional wolf improved group success by 67% (odds ratio [OR] = 1.67 ± 0.25, $P < 0.001$) and 40% (OR = 1.40 ± 0.13, $P < 0.001$) in attacking and capturing, respectively. Results were the same for a subset of observations that included data on bison herd size and composition. Moreover, interactions of herd size and composition with wolf group size did not improve fit of top models (attacking: $\chi^2_1 = 0.00-0.63$, $P = 0.23-0.99$; capturing: $\chi^2_1 = 0.03-0.96$, $P = 0.33-0.87$). Thus, the influence of group size on the success of large groups hunting bison was independent of bison herd size and composition.

Comparative effects of group size on the success of wolves hunting bison and elk

Comparing fitted values from our best-fit GLMMs of wolves attacking and capturing bison (Fig. 2-2a-b) and elk (Fig. 2-1a, 1c in [10]) revealed a similar influence of group size on the success of wolves hunting these prey insofar as success initially increased with group size then leveled off (Fig. 2-3). Trends were statistically significant below each threshold group size ($P < 0.001$-0.05) but not above ($P \geq 0.10$-0.50) such that attack and capture success were effectively constant beyond each threshold. Below these thresholds, each additional wolf had a slightly larger effect on the odds of attacking bison (OR = 1.67) versus elk (OR = 1.45; Fig. 2-3a) but a similar effect on the odds of capturing each species (bison: OR = 1.40; elk: OR = 1.44; Fig. 2-3b).

Whereas the threshold group size of wolves attacking bison and elk was the same (4 wolves; Fig. 2-3a), the threshold group size of wolves capturing bison (11 wolves) was nearly 3 times larger than that of wolves capturing elk (4 wolves; Fig. 2-3b). This pattern was evident even after accounting for uncertainty about the location of the thresholds (i.e., width of shaded areas in Fig. 2-3) identified in the confidence set of spline models for each analysis (ΔAICc < 2; Table 2-1a-b in this study; Table S1a and S1c in [10]). Specifically, the range of plausible threshold group sizes was similar when attacking bison (3-6 wolves) and elk (4-7 wolves; Fig. 2-3a) but higher when capturing bison (9-13 wolves) versus elk (2-6 wolves; Fig. 2-3b).

Taken together, these results indicate that bison capture success increased across group sizes over which elk capture success was constant (4-11 wolves) and leveled off at a group size larger than that of wolves hunting elk. Given that solo bison capture success (0.01) was 93% less than solo elk capture success (0.14; Fig. 2-3b), this pattern is consistent with the prediction that large groups are more cooperative when the success of a single hunter is very low.

Discussion

Our finding that the success of wolves capturing bison increased over large group sizes is unusual. Data from many group-hunting taxa indicate that the benefit of improved hunting success only applies to small groups [5-9]. In most carnivore studies, for example, hunting success levels off beyond 2-5 hunters [10-19]. Yet, these studies included little or no data on large groups (> 6 hunters) hunting difficult-to-catch prey. A notable exception is Creel and Creel [21] who show that the success of wild dogs (*Lycaon pictus*) hunting wildebeest (*Connochaetes taurinus*), a prey they classified as "hard" to capture, increased across large group sizes and leveled off at 12-14 wild dogs, which was comparable to the group size at which the success of wolves hunting bison leveled off (9-13 wolves). Additional studies of large groups hunting formidable prey may therefore reveal that the benefit of improved hunting success is not as limited to small groups as existing studies suggest.

We attribute the increase in bison capture success across large group sizes to enhanced cooperation motivated by the very low capture rate of a single hunter (1%; Fig. 2-2b). Low solo capture success is expected to foster cooperation because it leaves ample scope for an additional hunter to improve the outcome enough to outweigh its costs of active participation [5]. In support of this prediction, studies of wild dog and African lion have shown that individuals are more likely to participate in a group hunt when the success rate of a single hunter is low [16, 22]. Low solo success was related to larger, more dangerous prey, consistent with our results. And in our previous study of wolves hunting elk, which are >10 times easier than bison for a single wolf to capture (Fig. 2-3b), we found that wolves in groups with >4 hunters withheld effort, which kept elk capture success constant across large group sizes [10]. Wolves held back at this group size because it was apparently where the costs of hunting exceeded the diminishing improvements in group hunting success with each additional hunter.

In contrast to capture success, the rate at which wolves attacked bison leveled off at small group sizes (3-6 wolves) comparable to that of wolves attacking elk (Fig. 2-3a). That this reflects reduced cooperation in large groups is consistent with a relatively high rate of solo attack success (15%; Fig. 2-2a). On the other hand, a positive, albeit statistically weak ($P = 0.10$) trend in attack probability with group size beyond 4 wolves suggests that large groups approaching bison were more cooperative than those approaching elk. Additional data are necessary to resolve this ambiguity.

Another way that formidable prey may increase cooperative hunting behavior in large groups is by affecting group spatial configuration. Simulations from a particle model of group-hunting in wolves suggests that as prey become more dangerous, as measured by a minimum safe distance to prey, the spatial configuration of a group around the prey switches from an unstable, multi-orbit configuration to a stable, single-orbit one [48]. Wolves in the outer orbit of a large group may have less incentive to cooperate than individuals within the inner orbit because they are further from the prey, whereas wolves in a single orbit may more easily contribute to the outcome. Thus, the joint effects of formidable prey on group-spatial dynamics and solo capture success may boost cooperation in large groups. However, our observations of wolves hunting bison suggest that multi-orbit configurations are not exclusive of dangerous prey (Fig. 2-1b).

Our evidence that bigger groups were better hunters of larger, more dangerous prey provides rare empirical support for the hypothesis that an advantage of grouping in carnivores is that it increases the diversity and size of prey they can capture [4]. It is well-established that larger groups consume larger prey in Carnivora [21, 23, 24]. But because data on large groups hunting multiple prey species are scarce, it has been difficult to determine whether the correlation between prey size and group size results from greater food requirements of large groups or because large groups can indeed capture large prey more easily [16, 24]. Although our results do not address the relative importance of these two mechanisms, they at least suggest that improved hunting ability is a plausible explanation, despite the tendency of individuals to withhold hunting effort as group size increases [10, 22].

The ability to exploit a wide range of prey is likely a particular advantage in migratory ungulate systems, where the availability of different species is irregular [16]. For example, in Yellowstone's Pelican Valley, where we recorded many wolf-bison interactions, migratory elk were absent in winter (December-April), leaving non-migratory bison as the main prey resource for the resident wolf pack [27, 36]. Correspondence between the mean (± SE) annual size of this pack (10.6 ± 1.1 wolves, 95% CI = 8.3, 12.9) during the study (1999-2013) and the group size that apparently maximized bison capture success (11 wolves, range = 9-13; Fig. 2-2b) implies that this pack is well-adapted to hunting bison. However, this pack also periodically left Pelican Valley in winter to hunt elk in northern Yellowstone, where the size of resident, mainly elk-hunting packs was similar (10.0 ± 0.7 wolves, 95% CI = 8.7, 11.3). In northern Yellowstone, bison were more often scavenged than killed [29].

Thus, the optimal group size for capturing bison may exceed 11 wolves; a possibility that is supported by our results showing a linear model of the effect of group size on bison capture success fit the data nearly as well as a nonlinear model with a threshold at 11 wolves.

This could explain why wolves in northern and western Yellowstone continue to hunt mainly elk [27, 29, 49] despite decreasing elk availability relative to bison [50-52]. On the other hand, wolves in Wood Buffalo National Park, Canada, hunt mainly bison yet live in packs somewhat smaller than those in Yellowstone (8.6 ± 0.7 wolves, 95% CI = 7.2, 9.9; see Table 27 in [25]). So it seems unlikely that insufficient pack size constrains the ability of Yellowstone wolves to hunt bison. We suspect large wolf packs avoid hunting bison when and where less dangerous prey exist because the profitability (energetic gain/handling time) of bison, discounted for the fitness consequences of injury and probability of injury [31], is relatively low despite improved group hunting success. This highlights how generally invulnerable bison are to wolf predation as well as how the benefit of group hunting for increasing carnivore diet breadth can be contingent on other predator and prey traits that determine the outcome of predator-prey interactions.

Although improved ability to capture formidable prey is not an obvious driver of grouping patterns in Yellowstone wolves, our results demonstrate the potential for such an effect. This is a significant finding because most empirical studies of group-size specific hunting success imply that the formation and maintenance of large predator groups is unrelated to prey capture. Our study clarifies that the benefit of improved hunting success could favor large groups in populations and species that hunt large, dangerous prey.

References

1. Alexander RD. The evolution of social behavior. Annual Review of Ecology and Systematics. 1974;5:325-83.
2. Pulliam H, Caraco T. Living in groups: is there an optimal group size? In: Krebs J, Davies N, editors. Behavioral Ecology: An Evolutionary Approach. 2nd ed. Sunderland, MA: Sinauer; 1984. p. 122-7.
3. Clark CW, Mangel M. The evolutionary advantages of group foraging. Theoretical Population Biology. 1986;30(1):45-75. doi: 10.1016/0040-5809(86)90024-9. PubMed PMID: WOS:A1986D376900004.
4. Kruuk H. Functional aspects of social hunting in carnivores. In: Sibley R, Smith R, editors. Function and Evolution in Behavior. Oxford: Blackwell Scientific Publications; 1975. p. 521-6.
5. Packer C, Ruttan L. The evolution of cooperative hunting. American Naturalist. 1988;132(2):159-98. doi: 10.1086/284844. PubMed PMID: WOS:A1988Q161800001.
6. Boesch C. Cooperative hunting in wild chimpanzees. Animal Behaviour. 1994;48(3):653-67. doi: 10.1006/anbe.1994.1285. PubMed PMID: WOS:A1994PG43600015.
7. Boesch C, Boesch H. Hunting behavior of wild chimpanzees in the Tai-National Park. American Journal of Physical Anthropology. 1989;78(4):547-73. doi: 10.1002/ajpa.1330780410. PubMed PMID: WOS:A1989T585300009.

8. Rose LM. Vertebrate predation and food-sharing in Cebus and Pan. International Journal of Primatology. 1997;18(5):727-65. doi: 10.1023/a:1026343812980. PubMed PMID: WOS:A1997YF53300004.
9. Kim K, Krafft B, Choe J. Cooperative prey capture by young subsocial spiders I. Fuctional value. Behavioral Ecology and Sociobiology. 2005;59(1):92-100. doi: 10.1007/s00265-005-0013-z. PubMed PMID: WOS:000233242600013.
10. MacNulty DR, Smith DW, Mech LD, Vucetich JA, Packer C. Nonlinear effects of group size on the success of wolves hunting elk. Behavioral Ecology. 2012;23(1):75-82.
11. Eaton R. Hunting behavior of the cheetah. Journal of Wildlife Management. 1970;34(1):56-67.
12. Kruuk H. The Spotted Hyena. Chicago, IL: The University of Chicago Press; 1972.
13. Schaller G. The Serengeti Lion. Chicago, IL: The University of Chicago Press; 1972.
14. Mills MGL. Related spotted hyaenas forage together but do not cooperate in rearing young. Nature. 1985;316(6023):61-2. doi: 10.1038/316061a0. PubMed PMID: WOS:A1985ALT8600057.
15. Stander PE. Forgaing dynamics of lions in a semi-arid environment. Canadian Journal of Zoology-Revue Canadienne De Zoologie. 1992;70(1):8-21. doi: 10.1139/z92-002. PubMed PMID: WOS:A1992HK93500002.

16. Fanshawe JH, Fitzgibbon CD. Factors influencing the hunting success of an African wild dog pack. Animal Behaviour. 1993;45(3):479-90. doi: 10.1006/anbe.1993.1059. PubMed PMID: WOS:A1993KW24700006.

17. Holekamp KE, Smale L, Berg R, Cooper SM. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). Journal of Zoology. 1997;242:1-15. PubMed PMID: WOS:A1997XJ25900001.

18. Funston PJ, Mills MGL, Biggs HC. Factors affecting the hunting success of male and female lions in the Kruger National Park. Journal of Zoology. 2001;253:419-31. doi: 10.1017/s0952836901000395. PubMed PMID: WOS:000168615500001.

19. Van Orsdol KG. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. African Journal of Ecology. 1984;22:79-99.

20. Creel S, Creel NM. Communal hunting and pack size in African wild dogs, *(Lycaon-pictus)*. Animal Behaviour. 1995;50:1325-39. doi: 10.1016/0003-3472(95)80048-4. PubMed PMID: WOS:A1995TE32500019.

21. Creel S, Creel N. The African Wild Dog. Princeton, NJ: Princeton University Press; 2002.

22. Scheel D, Packer C. Group hunting behavior of lions - a search for cooperation. Animal Behaviour. 1991;41:697-709. doi: 10.1016/s0003-3472(05)80907-8. PubMed PMID: WOS:A1991FK33100013.

23. Gittleman J. Carnivore group living; comparative trends. In: Gittleman J, editor. Carnivore Behavior, Ecology and Evolution. New York, NY: Cornell University Press; 1989. p. 183-207.

24. Caro T. Cheetahs of the Serengeti Plains. Chicago, IL: The University of Chicago Press; 1994.
25. Carbyn L, Oosenbrug S, Anions D. Wolves, Bison and the Dynamics Related to the Peace-Athabaska Delta in Canada's Wood Buffalo National Park. Edmonton, Alberta: Canadian Circumpolar Institute; 1993.
26. Mech L, Peterson R. Wolf-prey relations. In: Mech L, Boitani L, editors. Wolves: Behavior, Ecology and Conservation. 11. Chicago, IL: The University of Chicago Press; 2003. p. 131-60.
27. Smith DW, Mech LD, Meagher M, Clark WE, Jaffe R, Phillips MK, et al. Wolf-bison interactions in Yellowstone National Park. Journal of Mammalogy. 2000;81(4):1128-35. doi: 10.1644/1545-1542(2000)081<1128:wbiiyn>2.0.co;2. PubMed PMID: WOS:000165637900021.
28. Smith DW, Drummer TD, Murphy KM, Guernsey DS, Evans SB. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management. 2004;68(1):153-66. doi: 10.2193/0022-541x(2004)068[0153:wpsaeo]2.0.co;2. PubMed PMID: WOS:000188243400015.
29. Metz MC, Smith DW, Vucetich JA, Stahler DR, Peterson RO. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. Journal of Animal Ecology. 2012;81(3):553-63. doi: 10.1111/j.1365-2656.2011.01945.x. PubMed PMID: 22260633.
30. MacNulty D. The predatory sequence and the influence of injury risk on hunting behavior in the wolf. Saint Paul, MN: The University of Minnesota; 2002.

31. Mukherjee S, Heithaus MR. Dangerous prey and daring predators: a review. Biol Rev. 2013;88(3):550-63. doi: 10.1111/brv.12014. PubMed PMID: WOS:000328952600003.
32. Carbyn LN, Trottier T. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. Canadian Journal of Zoology-Revue Canadienne De Zoologie. 1987;65(8):2072-8. doi: 10.1139/z87-317. PubMed PMID: WOS:A1987K178500031.
33. Sikes RS, Gannon WL, Amer Soc M. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy. 2011;92(1):235-53. doi: 10.1644/10-mamm-f-355.1. PubMed PMID: WOS:000287898700025.
34. Houston D. The Northern Yellowstone Elk: Ecology and Management. New York, NY: MacMillan; 1982.
35. MacNulty DR, Plumb GE, Smith DW. Validation of a new video and telemetry system for remotely monitoring wildlife. Journal of Wildlife Management. 2008;72(8):1834-44. doi: 10.2193/2008-069.
36. MacNulty DR, Varley N, Smith DW. Grizzly bear, *Ursus arctos,* usurps bison calf, *Bison bison*, captured by wolves, Canis lupus, in Yellowstone National Park, Wyoming. Canadian Field-Naturalist. 2001;115(3):495-8. PubMed PMID: WOS:000175520500017.
37. Bangs EE, Fritts SH. Reintroducing the gray wolf to central Idaho and Yellowstone National Park (vol 24, pg 402, 1996). Wildlife Society Bulletin. 1996;24(4):780-. PubMed PMID: WOS:A1996WD87900033.

38. Stahler DR, MacNulty DR, Wayne RK, vonHoldt B, Smith DW. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. Journal of Animal Ecology. 2013;82(1):222-34. doi: 10.1111/j.1365-2656.2012.02039.x. PubMed PMID: WOS:000313752300023.
39. MacNulty DR, Mech LD, Smith DW. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. Journal of Mammalogy. 2007;88(3):595-605. doi: 10.1644/06-mamm-a-119r1.1.
40. Fuller W. The horns and teeth as indicators of age in bison. Journal of Wildlife Management. 1959;23:342-4.
41. MacNulty DR, Smith DW, Mech LD, Eberly LE. Body size and predatory performance in wolves: is bigger better? Journal of Animal Ecology. 2009;78(3):532-9. doi: 10.1111/j.1365-2656.2008.01517.x. PubMed PMID: WOS:000264784900006.
42. MacNulty DR, Smith DW, Vucetich JA, Mech LD, Stahler DR, Packer C. Predatory senescence in ageing wolves. Ecology Letters. 2009;12(12):1347-56. doi: 10.1111/j.1461-0248.2009.01385.x. PubMed PMID: WOS:000271631500010.
43. Weiss R. Modeling longitudinal data. New York, NY: Springer; 2005.
44. Wold S. Spline Functions in Data Analysis. Technometrics. 1974;16:1-11.
45. Eubanks R. Approximate regression models and splines. Communications in Statistics - Theory and Methods. 1984;13(4):433-84.
46. Seber G, Wild C. Nonlinear Regression. New York, NY: John Wiley and Sons; 2003.

47. Burnham KP, Anderson DR. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach. 2nd ed. New York, New York: Springer; 2002.
48. Escobedo R, Muro C, Spector L, Coppinger R. Group size, individual role differentiation and effectiveness of cooperation in a homogeneous group of hunters. Journal of the Royal Society Interface. 2014;11(95):20140204.
49. Becker M, Garrott R, White P, Gower C, Bergman E, Jaffe R. Wolf prey selection in an elk-bison system: choice or circumstance? In: Garrott R, White P, Watson F, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Terrestrial Ecology Series. New York, NY: Elsevier; 2008. p. 305-37.
50. Garrott R, White P, Rotella J. The Madison headwaters elk herd: stability in an inherently variable environement. In: Garrott R, White P, Watson F, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Terrestrial Ecology Series. New York, NY: Elsevier; 2009. p. 191-216.
51. White PJ, Wallen RL, Geremia C, Treanor JJ, Blanton DW. Management of Yellowstone bison and brucellosis transmission risk - Implications for conservation and restoration. Biological Conservation. 2011;144(5):1322-34. doi: 10.1016/j.biocon.2011.01.003. PubMed PMID: WOS:000292668200013.
52. Cubaynes S, MacNulty D, Stahler D, Quimby K, Smith D, Coulson T. Density dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). Journal of Animal Ecology. 2014.

Tables and Figures

Table 2-1. Ethogram of wolf predatory behavior

Foraging State	Definition
Approach	Fixating on and traveling toward prey.
Attack-group	Running after a fleeing prey group or lunging at a standing group while glancing about at different group members (i.e., scanning).
Attack-individual	Running after or lunging at a solitary prey or a single member of a prey group while ignoring all other group members.
Capture	Biting and restraining prey.

See [40] for additional details.

Table 2-2. Model-selection results for GLMM models describing the effects of group size (grp) on the probability that a wolf hunting group attacked (a) and captured (b) bison in Yellowstone National Park, 1996-2013. Variables grp1 and grp2 contain a linear spline for group size at the indicated knot (Kn). The intercept and simple-linear models included no knot. Log-likelihood (LL), number of parameters (*K*), AIC_c, differences in AIC_c compared to the best scoring model (ΔAIC_c), and AIC_c weights (*W*) are given for each model. The best model for each predatory task is in boldface.

Model	Kn	LL	*K*	AIC_c	ΔAIC_c	*W*
(a) Attacking						
intercept	n/a	-144.84	2	293.74	29.36	0.00
grp	n/a	-130.40	3	266.91	2.53	0.07
grp1, grp2	2	-130.12	4	268.43	4.05	0.03
grp1, grp2	3	-128.84	4	265.86	1.48	0.11
grp1, grp2	**4**	**-128.10**	**4**	**264.38**	**0.00**	**0.24**
grp1, grp2	5	-128.72	4	265.63	1.25	0.13
grp1, grp2	6	-128.71	4	265.62	1.24	0.13
grp1, grp2	7	-129.29	4	266.77	2.39	0.07
grp1, grp2	8	-129.84	4	267.87	3.49	0.04
grp1, grp2	9	-129.89	4	267.97	3.59	0.04
grp1, grp2	10	-130.26	4	268.71	4.33	0.03
grp1, grp2	11	-130.10	4	268.39	4.01	0.03
grp1, grp2	12	-129.89	4	267.96	3.58	0.04
grp1, grp2	13	-129.68	4	267.55	3.17	0.05

Table 2-2 cont.

(b) Capturing

intercept	n/a	-63.92	3	133.95	14.32	0.00
grp	n/a	-56.02	4	120.22	0.58	0.11
grp1, grp2	2	-56.02	5	122.29	2.65	0.04
grp1, grp2	3	-56.02	**5**	122.30	2.67	0.04
grp1, grp2	4	-55.98	5	122.22	2.58	0.04
grp1, grp2	5	-55.91	5	122.08	2.45	0.04
grp1, grp2	6	-55.94	5	122.13	2.50	0.04
grp1, grp2	7	-55.78	5	121.82	2.18	0.05
grp1, grp2	8	-55.71	5	121.67	2.03	0.05
grp1, grp2	9	-55.46	5	121.18	1.55	0.07
grp1, grp2	10	-55.08	5	120.41	0.78	0.10
grp1, grp2	**11**	**-54.69**	**5**	119.64	**0.00**	**0.15**
grp1, grp2	12	-54.76	5	119.77	0.14	0.14
grp1, grp2	13	-54.86	5	119.98	0.35	0.12

Figure 2-1. Behavior of wolves hunting bison: (a) approach, (b) attack-individual, (c, d) capture (see Table 2-1 for definitions). "Attacking" is the transition from (a) to (b), and "capturing" is the transition from (b) to (c, d). (Photo credit: Daniel Stahler, Douglas Smith)

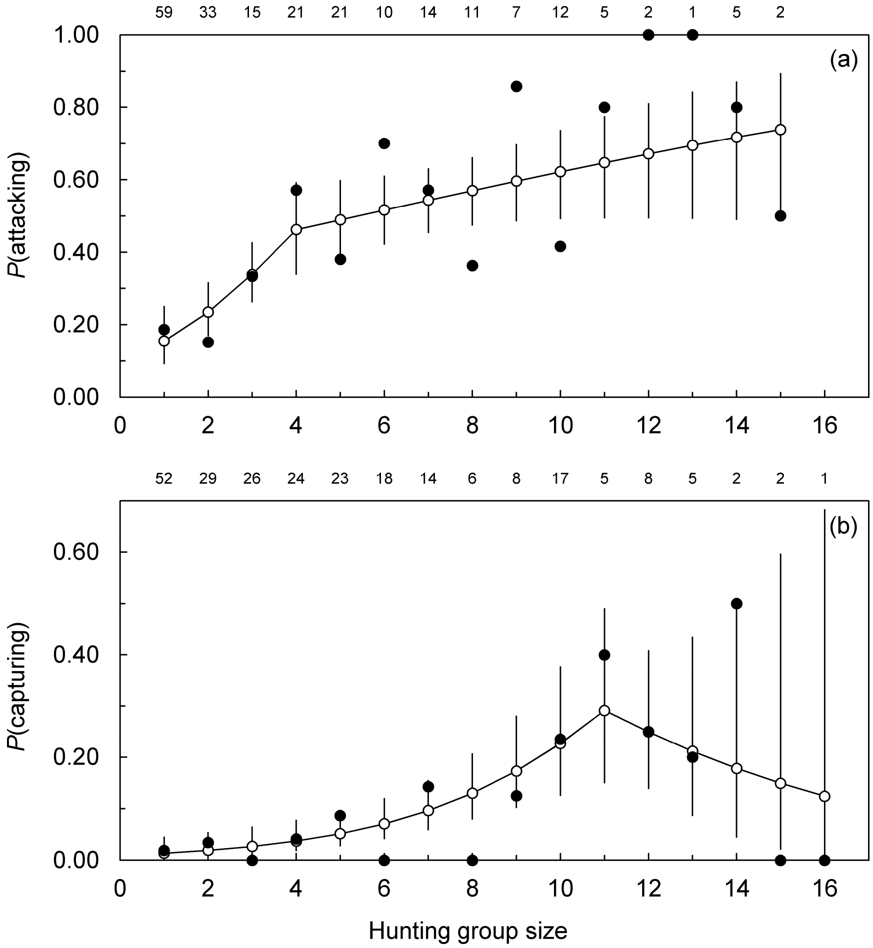


Figure 2-2. Effects of hunting group size on the probability that wolves attack (a) and capture (b), bison. Open circles are population-averaged fitted values with 95% confidence intervals from the best-fit GLMM models of hunting success (Table 2-2). The estimated coefficients before and after each breakpoint are: 0.52 ± 0.15 ($P < 0.001$) and 0.11 ± 0.07 ($P = 0.10$) (a); 0.34 ± 0.09 ($P < 0.001$) and -0.21 ± 0.32 ($P = 0.50$) (b). The number of wolf-bison encounters included in each analysis is: 218 (a) and 106 (b). Filled circles are observed frequencies with sample size indicated above each point. Analyses were performed on the raw binary data and not the illustrated data points, which are provided as a visual aid.

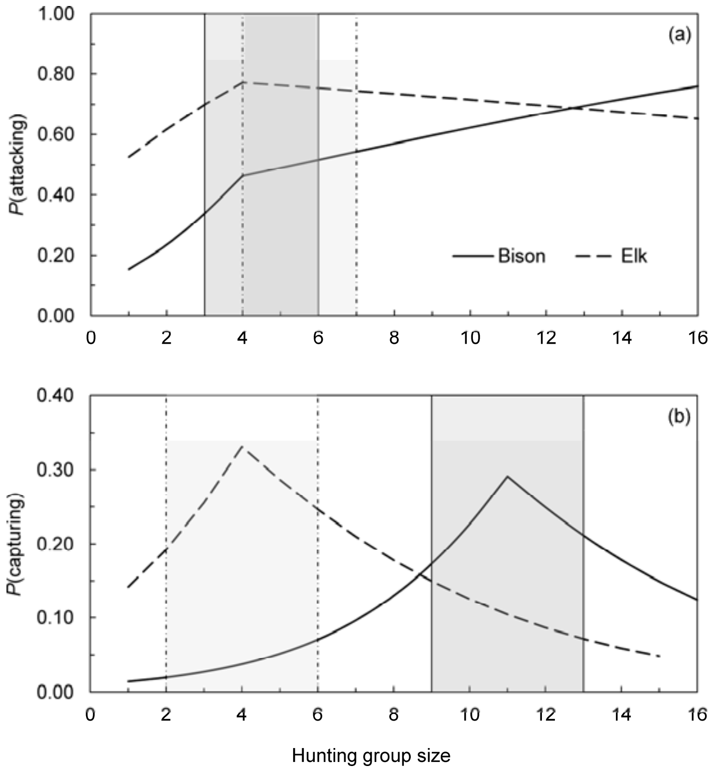


Figure 2-3. Comparative effects of group size on the success of wolves attacking (a) and capturing (b) bison and elk. Lines are population-averaged fitted values from the best-fit GLMMs of wolves hunting bison (Fig. 2-2a-b in this study; N = 106-218 wolf-bison encounters) and elk (Fig 1a, 1c in [12]; N = 235-355 wolf-elk encounters). Slopes were statistically different from zero before each breakpoint (β = 0.34-0.52, SE = 0.09-0.19, *P* < 0.001-0.05) but not after (β = -0.21-0.11, SE = 0.05-0.32, *P* > 0.10-0.50), indicating that success was effectively constant beyond each breakpoint. Shaded areas (dark = bison; light = elk) highlight uncertainty about the location of each breakpoint as identified in the confidence set of spline models (ΔAICc < 2) for each analysis (Table 2-2a-b in this study; Table S1a and S1c in [12]). Identical methods were used to collect and analyze data for each species.

CHAPTER 3

PREDATOR FORAGING RESPONSE TO A RESURGENT DANGEROUS PREY[2]

Summary

1. Prey switching occurs when a generalist predator kills disproportionately more of an abundant prey species and correspondingly spares a rarer species. Although this behavior is a classic stabilizing mechanism in food web models, little is known about its operation in free-living systems which often include dangerous prey species that resist predation.

2. We used long-term (1995-2015) data from a large mammal system in northern Yellowstone National Park, USA, to understand how prey preference of a wild, generalist predator (*Canis lupus*) responds to a shift in prey species evenness involving rising numbers of dangerous prey (*Bison bison*) and dropping numbers of relatively safer prey (*Cervus elaphus*).

3. Contrary to the prey switching hypothesis, wolves attacked and killed disproportionately more of the rarer, but safer, species. Wolves maintained a strong preference against bison even when this species was more than twice as abundant as elk. There was also evidence that wolves were increasingly averse to hunting bison as relative bison abundance increased.

---

[2] Tallian, Aimee, Douglas W. Smith, Daniel R. Stahler, Matthew C. Metz, Rick Wallen, Chris Geremia, C. Travis Wyman, Joel Ruprecht, Daniel R. MacNulty (*in review*). Predator foraging response to a resurgent dangerous prey. *Functional Ecology*.

4. Wolves seldom hunted bison because capture success was limited to a narrow set of conditions: larger packs (>11 wolves) chasing smaller herds (10-20 bison) with calves. Wolves scavenged bison carrion instead and did so more frequently as bison abundance increased.

5. Our study demonstrates the overarching importance of prey vulnerability to understanding the prey preferences of generalist predators in ecological communities with dangerous prey. The formidable defenses of such prey diminish the potential for switching and its stabilizing influence on population dynamics. In these communities, shifts from hunting to scavenging are perhaps more likely than shifts in prey preference. The assumption of switching may, therefore, overestimate the stability of multi-prey systems that include dangerous prey species.

Introduction

A classic hypothesis in ecology is that generalist predators stabilize prey populations by 'switching' between prey as the prey species' relative abundances change (Murdoch 1969; Murdoch & Oaten 1975). Switching occurs when preference for a prey species (defined as the relative frequency of finding, attacking, and capturing prey) becomes stronger or weaker as that species forms a larger or smaller proportion of available prey (Murdoch 1969; Murdoch & Oaten 1975). This means the predator directs a disproportionate number of its attacks to the more abundant species and correspondingly spares the rarer species. Although switching is often invoked to stabilize population dynamics in food web models (e.g., Valdovinos *et al.* 2010; Morozov & Petrovskii 2013; van Leeuwen *et al.* 2013), empirical evidence of switching is not well-developed. Much of it is based on experimental studies of small taxa that are helpless when attacked by a predator (reviewed by Garrott *et al.* 2007). This is problematic because many free-living systems include dangerous prey species that can harm or kill their predators (Mukherjee & Heithaus 2013) and interspecific differences in prey vulnerability may have an overriding influence on predator preference that prevents switching (Becker *et al.* 2009).

Many prey species are dangerous, and accumulating evidence suggests that predators often select prey that minimize the risk of injury, rather than maximize intake rate (Rutten *et al.* 2006; Mukherjee & Heithaus 2013). The potentially high fitness costs associated with attacking dangerous prey, including the extra time necessary to safely handle them, may cause preference for them to lag behind increases in their relative abundance. As a result, predators may concentrate a disproportionate number of attacks on the rarer but safer prey. The extent that preference decouples from relative abundance ultimately depends on the ability of predators to overcome prey antipredator defenses. If these defenses are robust, predator preference may increase slowly, or even decrease, if predators shift from hunting dangerous prey to scavenging them as carrion (Pereira, Owen-Smith & Moleón 2014). This is a broadly-important issue in ecology and conservation because climate change, variable culling rates, species invasions, (re)introductions, and recoveries can all modify the species composition and evenness of prey communities in ways that allow dangerous prey to predominate (e.g., Crossland 2000; Ripple *et al.* 2010; Albins & Hixon 2013).

In northern Yellowstone National Park, for example, multi-year drought, culling outside the park, wolf (*Canis lupus*) reintroduction, and natural recovery of grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*) have decreased the abundance of elk (*Cervus elaphus*) (MacNulty *et al.* 2016), while immigration/ redistribution, high survival and recruitment, and low predation rates have increased the abundance of bison (*Bison bison*) (Geremia, Wallen & White 2015; White, Wallen & Hallac 2015). Predictions about the impact of wolf reintroduction on elk abundance in northern Yellowstone hinge on the untested assumption that wolves switch between elk and bison (Garton *et al.* 1990; Boyce 1993; Boyce 1995; Messier 1995; Varley & Boyce 2006). However, bison are the largest, most dangerous native ungulate species in North America (Mech, Smith & MacNulty 2015). A high and constant proportion (96% during winter) of elk among prey killed by wolves in northern Yellowstone from 1995 to 2009, together with a tendency for wolves to scavenge bison carrion (Metz *et al.* 2012), suggests this assumption is unfounded. On the other hand, bison abundance did not rival elk abundance until after 2009 (Geremia, Wallen & White 2015; Northern Yellowstone Cooperative Wildlife Working Group 2016).

Here, we used long-term data (1995-2015) on wolf hunting behavior, wolf-killed prey, and elk and bison abundances to test for prey switching behavior in a dangerous prey system. We measured how wolf preference responded to increasing numbers of bison in northern Yellowstone by relating the relative abundance of bison and elk to the ratios of the two species attacked and killed by wolves. We calculated attack ratios from observations of wolf hunting behavior and kill ratios from carcasses attributed to wolf predation. To understand underlying controls on wolf preference for bison, we also examined how 1) the behavioral and life history traits of bison (flight response, herd size, age, and sex) and wolves (pack size) shaped the ability of wolves to attack and capture them, and 2) bison abundance affected wolf scavenging behavior.

Materials and Methods

STUDY AREA

Our study focused on the wolves, elk, and bison that inhabit the winter range of northern Yellowstone. This 1,520 km^2 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 and adjacent areas in Montana (Lemke, Mack & Houston 1998). Approximately 65% (995 km^2) of the winter range is located within the park, whereas the remaining 35% (525 km^2) extends north of the park boundary. For the purposes of this study, we refer to the entire northern Yellowstone elk winter range as the 'total winter range' and the park portion of this area as the 'park winter range' (Fig. 3-1).

Northern Yellowstone elk migrate seasonally, moving from higher-elevation summer ranges to lower-elevation areas throughout the total winter range (White *et al.* 2010). Northern Yellowstone bison similarly seek lower-elevation areas in winter except their distribution is mainly restricted to the park winter range by management intervention in response to concerns of brucellosis transmission to cattle outside the park (White, Wallen & Hallac 2015). Wolves were reintroduced to Yellowstone in

1995-1997 (Bangs & Fritts 1996) and their distribution is also concentrated in the park winter range (Stahler, Smith & Stahler 2016), mainly because this is where elk abundance was highest (White, Proffitt & Lemke 2012). Wolf abundance in northern Yellowstone ranged between 19 and 98 individuals (Smith *et al.* 2016). Besides elk and bison, wolves occasionally killed deer (*Odocoileus* spp.), bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), and pronghorn (*Antilocapra americana*) (Metz *et al.* 2012). All wolf predation data in our prey switching analysis were collected in the park winter range. Elk abundance data were collected across the total winter range and the location of elk sightings was used to determine elk abundance in the park winter range (see below).

Because wolves were rarely observed hunting bison in northern Yellowstone (Smith *et al.* 2000), our analysis of wolf-bison behavioral interactions includes data collected in Pelican Valley. This 100 km² area is located in the central portion of the park at 2500 m, north of Yellowstone Lake (Fig. 3-1). We often observed wolves hunting bison in Pelican Valley during winter because alternate prey were scarce (MacNulty *et al.* 2014).

DATA COLLECTION

Prey abundance

Bison were counted during annual aerial winter surveys, conducted by 1-2 fixed-wing aircraft, between 19 January and 10 March, 1995-2015 (Geremia et al. 2014). Uncorrected count data provided an unbiased measure of bison abundance because bison formed large groups that congregated in visible, open areas (Hess

2002). If any bison were culled at the northern park boundary during winter prior to a flight, we added the number culled to the aerial count (Geremia, Wallen & White 2015).

Elk were counted during annual aerial winter surveys, conducted by 3-4 aircraft, each simultaneously flying non-overlapping areas between 3 December and 7 March, 1995-2015 (see Northern Yellowstone Cooperative Wildlife Working Group 2016). We used a state-space model to interpolate elk counts for years when no survey occurred (1996, 1997, 2006, 2014), then applied a modified version of the Singer and Garton (1994) northern Yellowstone elk sightability model to adjust every count for imperfect detection (see Supporting Information). 'Total' and 'park' elk abundances refer to the estimated number of elk within the total and park winter ranges, respectively. We separately measured the relative abundance of bison and elk (N_{bison} / N_{elk}) in the total and park winter ranges to account for variation in numbers of elk migrating outside the park. This approximated the minimum and maximum ratios of their abundances in the park winter range where we measured wolf prey preference.

Prey preference

We measured annual variation in the ratios of elk and bison attacked and killed by wolves in the park winter range between 1995-2015 with data collected 1) during biannual 30-day follows of 3-5 wolf packs from the ground and fixed-wing aircraft in early (mid-November to mid-December) and late (March) winter and 2) during opportunistic ground and aerial surveys on all wolf packs throughout the entire winter (Smith et al. 2004). We defined winter as 1 November - 30 April. Field crews used radio telemetry to monitor packs. At least one wolf in each pack was fitted with a VHF radio-collar. Wolves were captured and handled following animal handling guidelines of the American Society of Mammalogists (Sikes, Gannon & Amer Soc M 2011) and approved by the National Park Service Institutional Animal Care and Use Committee (Permit: IMR_Yell_Smith_Wolf _2012). Over the 20-year study, 30 different packs inhabited northern Yellowstone; 18 were intensively monitored.

Field crews identified elk and bison carcasses and recorded cause of death, date of death, species, sex, and age. Cause of death was 'wolf-killed' when wolves were observed making the kill, or evidence at the carcass site supported wolves as the cause of death. This included chase tracks, blood trails, disturbed vegetation, and extensive disarticulation of the carcass. Cougar kills were generally discernable by evidence that cougars had cached a carcass. Grizzly bears and black bears also occasionally kill ungulates, but usually not in winter when bears are denning. We excluded scavenged carcasses from analyses of prey switching because switching concerns changes in predatory behavior. Field crews documented 2687 carcasses of elk and 52 carcasses of bison killed by wolves. We used these data to calculate the annual ratio of bison and elk killed by wolves (g_{bison} / g_{elk}; 'relative kill frequency').

Carcasses of non-wolf killed ungulates with obvious amounts of consumable biomass were identified as 'wolf-scavenged' if they were visited by wolves. Carcass biomass was determined by visual observation, duration of wolf visit, and the presence and abundance of other scavenger species (e.g., *Corvus corax*, *Canis* *latrans*). Between 1995 and 2015, field crews documented 137 bison carcasses scavenged by wolves.

When field crews observed wolves encountering elk (or bison), defined as at least 1 wolf orienting and moving (walking, trotting or running) toward prey, they followed the progress of the encounter by noting the foraging state (approach, watch, attack-group, attack-individual, or capture) of the individual(s) closest to making a kill (see MacNulty, Mech & Smith 2007). We scored an encounter as escalating to an attack if ≥ 1 wolf transitioned from approach (or watch) to attack-group (or attack-individual) at any time during the encounter. This yielded 964 attacks of elk and 178 attacks of bison. We used these data to calculate the annual ratio of bison and elk attacks (a_{bison} / a_{elk}; 'relative attack frequency'). Within the park winter range, wolf encounter rate with elk covaries with elk abundance (Martin 2016).

Wolf-bison behavioral interactions – A subset of wolf-bison encounters included detailed information about the sequential occurrence of each foraging state during each encounter, and the traits of wolves (group size) and bison (group size, age, sex, and behavioral response) involved in those states. We used these data to understand how these traits governed the ability of wolves to attack and capture bison. In this case, the unit of analysis was the foraging state, and we examined how traits influenced the probability of a state transition that corresponded to 'attacking' (approach [or watch] → attack-group [or attack-individual]) or 'capturing' (attack-group [or attack-individual] → capture). Capturing was not necessarily killing because bison that were grabbed by wolves often escaped (see MacNulty, Mech & Smith 2007).

A wolf was scored as participating in a foraging state if it exhibited the behavioral acts characterizing that particular state as described by MacNulty *et al.* (2014: Table 1; Fig.1). We considered non-participation in a given state as when a wolf was in view but engaged in another foraging state or a non-predatory behavior (e.g., resting). We defined 'wolf group size' as the number of wolves participating in a foraging state. This differs from pack size because it pertains to the subset of pack members participating in a hunt.

We defined 'bison group size' as the number of bison within 100 m of one another (Fortin *et al.* 2003) that were present at the end of each foraging state. We used body size and horn morphology to identify three age/sex classes: bull, cow, and calf. In winter, bulls aggregate in small bull-only groups separate from larger mixed age-sex groups of cows, immature bulls, and calves (Meagher 1973). Accordingly, we defined the age-sex composition of each bison group in each foraging state as 'bull' or 'mixed'.

We recorded two types of bison behavioral responses during each foraging state. The 'charge response' considered whether or not ≥1adult member of a bison group charged (ran) at wolves. The 'flight response' considered whether a group fled or stood and confronted wolves. We scored a group as fleeing if >50% of the group ran or walked away from wolves.

Our detailed wolf-bison encounter data are based on observations of 5 different wolf packs (Druid Peak, Geode Creek, Leopold, Mollie's, and Rose Creek) hunting in northern Yellowstone (1996-2003) and Pelican Valley (1999-2013). Most of these observations (75% of 187 wolf-bison encounters) involved the Mollie's pack in Pelican Valley. Annual turnover in pack membership due to births, deaths, and dispersal minimized the influence of pack identity on the outcome of wolf-bison encounters.

DATA ANALYSIS

Prey switching

We conducted two separate tests for prey switching behavior, which is defined by an increase in a predator's preference for a prey species that is disproportionate to the increase in the relative abundance of that prey species (Murdoch 1969; Murdoch & Oaten 1975). Our first test examined the relationship between relative attack frequency (a_{bison} / a_{elk}) and relative bison abundance (N_{bison} / N_{elk}). If switching occurred, relative attack frequency should increase as a curvilinear function of relative bison abundance. We tested this prediction by comparing a simple linear model of this relationship to a linear model with log-transformed relative bison abundance using Akaike's Information Criterion, AIC_c (Burnham & Anderson 2002).

Our second test examined the relationship between relative kill frequency (g_{bison} / g_{elk}) and relative bison abundance using Murdoch's (1969) classic diet equation as modified by Greenwood and Elton (1979) and Elliott (2004):

$$\frac{g_{bison}}{g_{elk}} = \left(c\,\frac{N_{bison}}{N_{elk}}\right)^{b}$$

where g_{bison} / g_{elk} is the ratio of bison and elk killed by wolves, and N_{bison} / N_{elk} is the ratio of bison and elk in the environment. The variable c measures the bias in wolf kills towards one species: $c > 1$ indicates preference for bison, whereas $c < 1$ indicates preference for elk. The variable b measures the extent of switching such that $b > 1$ indicates a switch to bison as relative bison abundance increases. This is visualized as a curvilinear, concave-up relationship between relative kill frequency and relative bison abundance. We fit the diet equation to our data and estimated parameter coefficients using nonlinear least squares regression.

We performed each test separately for the relative abundance of bison across the total and park winter ranges. Data were annual estimates of relative attack and kill frequencies, and relative bison abundance (N = 20 years).

Wolf-bison behavioral interactions

We analyzed the effects of wolf and bison traits on the probability that wolves attacked and captured bison using generalized linear mixed models (GLMMs) with a binomial error distribution. We constructed these models to account for the influence of unmeasured pack- and encounter-related factors on hunting success (e.g., age and size of individuals within packs; (MacNulty *et al.* 2009a; MacNulty *et al.* 2009b)) and differences in prey densities between pack territories. All models fitted pack and encounter identity as nested random intercepts (encounter within pack) and included a compound symmetric correlation structure which assumed that all observations within encounters were, on average, equally correlated (Weiss 2005). Capture models included only a random intercept for encounter identity because our sample was too small to support a multivariate GLMM with more than one random effect. We estimated models with adaptive Gaussian quadrature with parameters estimated from maximum likelihood, and significance of effects determined by an approximate *z*-test.

Models of attacking and capturing included fixed effects for three bison traits (group size and composition, flight response) and one wolf trait (group size). To account for the possibility that carnivore hunting success peaks at intermediate ungulate group sizes (Creel & Creel 2002; Hebblewhite & Pletscher 2002), we used restricted cubic splines ($N_{\text{knots}} = 3$) to test for a nonlinear effect of bison group size on the probability of attack and capture. We tested the strength of these effects with likelihood ratio statistics.

We modeled bison group composition (bull versus mixed) and flight response (flee versus confront) as dummy variables. We expected the probability of attack and capture to be greatest for mixed groups and for bison that fled because mixed groups include vulnerable calves (Carbyn & Trottier 1987; Becker *et al.* 2009) and wolves are often intimidated by ungulates that stand and fight (Mech, Smith & MacNulty 2015). We modelled the effect of wolf group size as a piecewise linear spline with knots at 4 and 11 for attacking and capturing following MacNulty *et al.* (2014).

To evaluate the relative influence of wolf and bison traits in our models of attack and capture, we performed a sensitivity analysis that allowed comparison of effects across a common scale. First, we calculated the predicted probability of attack (or capture) with wolf and bison group sizes set to observed means and categorical variables, bison group composition and flight response, set to ‘mixed’ and ‘flee’. Next, we separately perturbed each model parameter by 10%, recalculated the prediction, and computed the difference between the initial and perturbed prediction. A large difference indicates a high sensitivity, and parameters with the highest sensitivity had the greatest effect on the ability of wolves to attack (or capture). We report absolute sensitivity values and sum those for spline parameters to show the overall influence of a nonlinear effect and to allow comparison between linear and nonlinear effects (Stahler *et al.* 2013).

We also used GLMMs to evaluate potential differences in the behavioral responses of bull and mixed groups when attacked by wolves. Anecdotal evidence suggests that bulls are generally more aggressive toward wolves than cows (Carbyn, Oosenbrug & Anions 1993). We expected bull groups to charge more and flee less in response to wolf attack relative to mixed groups. Models included covariates for bison and wolf group sizes to control for their potential effects on bison response.

Wolf-bison scavenging

To determine the effects of scavenging on prey switching behavior we examined how annual bison attack and kill frequencies varied with the number of wolf-scavenged bison. We compared linear and nonlinear (log-transformed scavenged bison) models of this relationship using AIC_c.

Results

TEMPORAL TRENDS

Prey abundance

Numbers of bison in the northern Yellowstone park winter range increased from 681 in 1995-1996 to 2,164 in 2014-2015 (Fig. 3-2a). During this same period, sightability-corrected elk numbers decreased from 15,913 to 1,853 in the park winter range. Numbers of elk wintering outside the park varied between 2,449 and 5,147 (mean ± SE = 3,539 ±163 elk) and exhibited no trend. Thus, the overall decline in elk abundance across the total winter range ($N_{1995\text{-}1996}$ = 19,904 elk; $N_{2014\text{-}2015}$ = 6,090 elk) mainly reflects decreased elk abundance within the park winter range (Fig. 3-2a). This explains why the increase in relative bison abundance was greater in the park winter range than in the total winter range (Fig. 3-2b). Relative bison abundance in the park winter range increased from 0.04 bison per elk in winter 1995-1996 to 1.17 bison per elk in winter 2014-2015. By contrast, relative bison abundance in the total winter range increased from 0.03 bison per elk in winter 1995-1996 to 0.36 bison per elk in winter 2014-2015.

Attack frequency

Direct observations of wolf-prey encounters in the park winter range indicated that the overall frequency of wolves attacking bison (41% of 436 bison encounters) was less than that of wolves attacking elk (67% of 1434 elk encounters). Nevertheless, the relative frequency that wolves attacked bison versus elk tended to increase over the study ($r^2 = 0.11$; range = 0.03-0.69; Fig. 3-2c). Relative attack frequency was notably high in 1995-1996 (0.54) and 2012-2013 (0.69). Excluding these outliers strengthened the upward trend in relative attack frequency ($r^2 = 0.45$). Annual number of attacks ranged between 1-37 (8.2 ±1.8 attacks/year) for bison, and 13-107 (48.2 ±6.5 attacks/year) for elk.

Kill frequency

Although bison comprised only 2% of 2739 carcasses of elk and bison killed by wolves, the relative frequency of bison kills tended to increase from 1995-1996 to 2014-2015 ($r^2 = 0.37$; range = 0.00-0.11; Fig. 3-2d). Annual number of kills ranged from 0-10 (2.6±0.59 kills/year) for bison, and 76-236 (134.4 ±9.8 kills/year) for elk. The 52 bison kills included 7 calves, 28 cows, 7 bulls, and 10 adults of unknown sex. Mean (±SE) age of known individuals for each age/sex class was 7.95 ±1.00 for cows (N = 20), 8.83 ±2.30 for bulls (N = 6), and 5.00 ±0.58 for unknown adults (N = 3).

PREY SWITCHING

Despite the suggestive temporal trends in relative attack and kill frequencies (Fig 3-2c-d), we found no quantitative evidence of prey switching. The most parsimonious models of relative attack frequency in the total and park winter ranges included a linear effect of relative bison abundance, indicating that the relative frequency that wolves attacked bison increased proportionately to relative bison abundance (Fig. 3-3a-b). Evidence against a model describing a nonlinear relationship between relative attack frequency and relative bison abundance was reasonably strong in the total ($\Delta AIC_c = 3.23$) and park ($\Delta AIC_c = 4.29$) winter ranges. Excluding the outlying data points from 1995-1996 and 2012-2013 improved the fit of these nonlinear models (total winter range: $\Delta AIC_c = 1.70$; park winter range: $\Delta AIC_c = 0.65$). However, the shape of the relationship described by these models was concave-down, indicating that the relative frequency of bison attacks *decreased* with relative bison abundance. This negatively frequency-dependent pattern is opposite of that predicted by the switching hypothesis.

Fitting a nonlinear model of Murdoch's (1969) modified equation to the data similarly revealed no evidence of prey switching. This model suggested that wolves maintained a strong aversion to killing bison in the total winter range ($c = 0.04$ [95% CI = -0.10, 0.17]) and park winter range ($c = 0.001$ [-0.01, 0.01]) that seemed to strengthen as relative bison abundance increased: $b = 0.74$ [0.12, 1.35] (total winter range), $b = 0.47$ [0.10, 0.84] (park winter range). The curvilinear, concave-down relationship described by these models (Fig. 3-3c-d) also indicates negatively frequency-dependent predation. This pattern is particularly strong in the park winter range where the 95% CI for the switching variable b excludes 1.

WOLF-BISON BEHAVIORAL INTERACTIONS

We obtained detailed behavioral data for 187 wolf-bison encounters; 74 (40%) included ≥ 1 attack (mean [± SE] = 0.93 ± 0.20 attacks/encounter; range = 0-26), and 11 (6%) included ≥ 1 capture (mean [± SE] = 0.13 ± 0.12 captures/encounter; range = 0-5). These encounters included a total of 173 attacks, 24 captures, and 8 kills.

Mixed groups were less aggressive than bull groups when wolves attacked: they were less likely to charge (odds ratio, OR [95% CI] = 0.33 [0.16, 0.69], $P =$

0.003) and more likely to flee (OR = 3.89 [1.19, 12.68], *P* = 0.02). Bison were also more likely to flee as the number of wolves attacking increased (OR = 1.24 [1.10, 1.41], *P* < 0.001).

Attack probability decreased linearly with bison group size (OR = 0.94 [0.90, 0.99], *P* = 0.02; Fig. 3-4a); a nonlinear effect of bison group size did not improve model fit (χ_1^2 = 0.20, *P* = 0.65). Wolves were more likely to attack mixed groups than bull groups (OR = 6.24 [1.33, 29.33], *P* = 0.02) and bison that fled versus those that stood their ground (OR = 10.38 [2.70, 39.97], *P* = 0.001).

The effect of bison group size on capturing was nonlinear; a cubic transformation of bison group size outperformed the simple linear effect (χ_1^2 = 7.23, *P* = 0.007). Capture probability increased with group size up to about 15 bison (β_1 = 0.51 [0.05, 0.96], *P* = 0.03) after which it declined (β_2 = -4.81 [-9.00, -0.63], *P* = 0.02). Wolves were most likely to capture bison when they attacked groups numbering between about 10-20 animals (Fig. 3-4b). Wolves were also more likely to capture bison in groups that fled versus those that confronted them (OR = 7.83 [1.73, 35.49], *P* = 0.008). Bison group composition (bulls versus mixed group) had no apparent effect on capture probability (OR = 0.97 [0.14, 6.53], *P* = 0.97). However, once wolves targeted an individual bison, they were more likely to capture a calf than a bull (OR = 17.79 [3.83, 82.56], *P* < 0.001) or a cow (OR = 11.15 [2.01, 62.00], *P* = 0.006); capture probability did not differ between cows and bulls (OR = 1.60 [0.37, 6.96], *P* = 0.53).

Sensitivity scores suggest that attack probability was most influenced by wolf group size (0.008), followed by bison flight response (0.005), bison group composition (0.004), and bison group size (0.001) (Fig. 3-4c). Capture probability was most influenced by bison group size (0.15), flight response (0.05), wolf group size (0.03), and bison group composition (0.001) (Fig. 3-4d).

BISON SCAVENGING

Wolf use of bison carrion increased during 1995-2015 ($r^2 = 0.64$; range = 0-20; Fig. 3-5a), and was well-correlated with bison abundance ($r^2 = 0.71$; Fig. 3-5b). There was evidence that high-levels of bison scavenging depressed bison attack and kill frequencies. A nonlinear effect of bison scavenging fitted these data as well as or better than a linear effect (attacking: $\Delta AIC_c = 0.23$; killing: $\Delta AIC_c = 0.00$; Fig. 3-5c-d).

Discussion

Identifying the biological mechanisms that promote the stability of multi-prey systems is a long-standing goal in ecology (May 1972; Valdovinos *et al.* 2010). Prey switching behavior is one of the most venerable of these mechanisms (Murdoch 1969); one that has found wide use in models of predator-prey interactions (e.g., Varley & Boyce 2006; Valdovinos *et al.* 2010; Morozov & Petrovskii 2013; van Leeuwen *et al.* 2013). It is frequently invoked to justify a stabilizing Type III functional response (Holling 1959). However, empirical studies of switching behavior in free-living multi-prey systems are rare and seldom clarify the underlying mechanisms that drive patterns in prey preference. Our study provides one of the first comprehensive tests of the switching hypothesis in a large-scale, free-living predator-prey system. An important feature of this natural system, like many others, is that prey species were not uniformly vulnerable to predation; some species were more dangerous than others.

In the northern Yellowstone wolf-elk-bison system we studied, the predator (wolves) maintained a strong preference for the safer prey species (elk). Contrary to the switching hypothesis, this preference did not weaken as the relative abundance of the safer prey species decreased. Likewise, preference for the more dangerous prey species (bison) did not strengthen as the relative abundance of this species increased. We obtained the same results regardless of whether we defined the study system as the entire northern Yellowstone elk winter range, or only that portion of the winter range inside Yellowstone where elk abundance was lowest. Results were also consistent across two separate measures of predator preference. The first involved direct behavioral observations of wolves encountering and attacking each prey species, and the second involved identification of remains from wolf-killed prey.

Overall, our results indicate that wolves maintained a strong and constant aversion to attacking and killing bison across a range of relative abundance ratios that varied from 1 bison per 35 elk to >2 bison per 1 elk. These findings are consistent with similar analyses of wolves, elk, and bison in the Madison headwaters region of central Yellowstone (Becker *et al.* 2009). Wolves in the Mackenzie Bison Sanctuary, Canada, similarly avoided bison in favor of safer prey (moose), even though bison were more numerous (Larter, Sinclair & Gates 1994). In northern Yellowstone, there was some evidence that wolf aversion to bison actually strengthened as the relative abundance of bison increased. This was most apparent in the analysis of kill ratios inside the park (Fig. 3-3d). In this case, *b* < 1 (b = 0.47, 95% CI = 0.10-0.84) implies a decreasing preference for bison and an increasing preference for elk as the ratio of bison to elk increased. We detected a similar but weaker pattern when this analysis included the area outside Yellowstone (b=0.74, 95% CI = 0.12-1.35; Fig. 3-3c).

Results from the attack ratio analysis provide additional support for this pattern. At low relative bison abundance, most of the observed attack ratios were >1, whereas at high relative bison abundance, most of the observed attack ratios were <1. This pattern was the same when calculated across both the total and park winter range. This implies that wolves preferred attacking bison when they were relatively rare, but avoided attacking them when they were relatively abundant. A nonlinear relationship between attack ratio and relative abundance described the data nearly as well as a linear relationship (ΔAIC $\leq$ 1.70) when two outliers were excluded from the analysis, providing additional support for this pattern. Taken together, our results suggest that wolf predation on bison in northern Yellowstone was potentially negatively frequency-dependent, contrary to the positively frequency-dependent predation predicted by the switching hypothesis.

Strong preference against attacking and killing bison was a fundamental consequence of the inability of wolves to consistently overcome bison antipredator defenses. Less than 5% of 187 directly observed wolf-bison interactions resulted in a kill. This is consistent with previous research indicating that bison are the most difficult ungulate prey for wolves to kill in North America (Carbyn, Oosenbrug & Anions 1993; Mech & Peterson 2003; Mech, Smith & MacNulty 2015). Our behavioral analysis indicates this is because the ability of wolves to kill bison was limited to a narrow range of conditions, characterized by small mixed groups of bison (10-20 animals; Fig. 3-4b) fleeing from large groups of wolves (>11 wolves; MacNulty *et al.* 2014). These results are broadly consistent with observations of wolves hunting bison in Wood Buffalo National Park, Canada, which is the only other wolf-bison system where comparable behavioral data are available (Carbyn & Trottier 1987; Carbyn & Trottier 1988; Carbyn, Oosenbrug & Anions 1993).

A unique aspect of our study is that we quantified the influence of predator and prey traits on the success of wolves hunting bison. We found that herds with >20 bison were effective at repelling wolves, which accords with a general understanding of the antipredator benefits of grouping (Krause & Ruxton 2002; Caro 2005). On the other hand, we also found that wolves were *less* likely to capture a bison as herd size dropped below about 10 animals (Fig. 3-4b). Similar nonlinear effects of ungulate group size on predator success have been documented in other wolf populations (Hebblewhite & Pletscher 2002) and carnivore species (Creel & Creel 2002). Predators that hunt dangerous prey depend on individuals that are either young, old, or in poor body condition (Temple 1987; Carbyn, Oosenbrug & Anions 1993; Wright *et al.* 2001), which are typically rare in any given prey population (Hamilton 1971). The ability of wolves to capture bison calves, together with the tendency of bison calves to aggregate in large mixed age-sex groups, suggests the ascending limb of the of the curve in Fig. 3-4b reflects an increased likelihood of finding a calf as herd size increases.

Our sensitivity analysis revealed that bison group size had the strongest influence on wolf capture success compared to wolf group size, bison flight response, and bison group composition (Fig. 3-4d). By contrast, wolf group size was the best predictor of the probability of attack, followed by bison flight response, group composition and group size (Fig. 3-4c). Previous work shows that the probability of attacking and capturing bison increases with wolf group size (MacNulty *et al.* 2014). Our results suggest that larger packs may be more likely to attack bison because they are better able to provoke a flight response. Similarly, wolves probably attacked mixed groups more often than bull groups, in part, because the former fled more often than the latter. Flight response was the second best predictor of attacking and capturing, which aligns with findings from other studies that demonstrate the importance of ungulate flight response to carnivore hunting success (Lingle & Pellis 2002; Caro 2005).

The difficulty of hunting bison, together with the availability of bison carrion, encouraged wolves to scavenge dead bison rather than attack live ones. The ability of wolves to shift from hunting to scavenging as bison abundance increased (Fig. 3-5) is one reason why wolf predation on bison could be negatively frequency-dependent. Increased availability of bison carrion with bison population size (Reagan 2016) may have reduced the incentive to attack bison when they were relatively abundant. By 2014, wolves acquired nearly as much biomass from scavenged bison as they did from hunted elk (Metz *et al.* 2016). Thus, one potential outcome of an increasing population of dangerous prey is that predators shift foraging strategies (e.g., hunting to scavenging) rather than shift prey preference.

The consequences of shifting foraging strategies for the dynamics of the preferred, safer prey species (e.g., elk) depends on the predator's numerical response

(Moléon *et al.* 2014). For example, if the carrion of dangerous prey boosts predator numbers, it could increase predation pressure on the safer prey if the proportional increase in predator numbers exceeds the proportional decrease in per capita intake of safer prey. Alternatively, increased carrion availability could decrease predation pressure on the safer prey, provided that predator numerical responses to carrion availability do not compensate for lower individual predation rate (Moléon *et al.* 2014). Wolf numbers in northern Yellowstone have decreased as bison numbers increased (Stahler, Smith & Stahler 2016), implying a lack of numerical response. Thus, wolf scavenging on bison may divert predation away from elk, helping to stabilize wolf-elk interactions.

In conclusion, our results suggest that prey switching is an unlikely stabilizing mechanism in predator-prey systems where the alternative prey is dangerous. This is because the potentially severe fitness costs of attacking dangerous prey (e.g., injury or death) causes predator preference for different prey species to vary in relation to relative prey vulnerability, which is ultimately a function of the predator and prey traits that determine the outcome of interactions. Moreover, predators may respond to the rise of a dangerous prey species by shifting foraging strategies not prey preferences. This is a departure from classic theory which maintains that prey preference is primarily a function of relative prey abundance (Murdoch 1969; Murdoch & Oaten 1975). This is important for understanding the dynamics of dangerous prey systems because incorrectly assuming prey switching overestimates the stability of ecological communities (van Leeuwen *et al.* 2013). We encourage future studies of dangerous prey systems to explore alternative stabilizing mechanisms, including facultative shifts between hunting and scavenging.

References

Albins, M. & Hixon, M. (2013) Worst case scenario: Potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes,* **96,** 1151-1157.

Bangs, E.E. & Fritts, S. (1996) Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin,* **24,** 402-413.

Becker, M.S., Garrott, R.A., White, P.J., Gower, C.N., Bergman, E.J. & Jaffe, R. (2009) Wolf prey selection in an elk-bison system: Choice or circumstance? *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 305-337. Elsevier, San Diego, CA.

Boyce, M.S. (1993) Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. *Ecological issues on reintroducing wolves into Yellowstone National Park* (ed. R. Cook), pp. 234-269. Scientific Monograph NPS/NRYELL/NRSM-93/22, USDI National Park Service, Denver, Colorado, USA.

Boyce, M.S. (1995) Anticipating consequences of wolves in Yellowstone: Model validation. *Ecology and Conservation of Wolves in a Changing World* (eds L.N. Carbyn, S.H. Fritts & D.R. Seip), pp. 199-210. Canadian Circumpolar Institute, Edmonton, Alberta.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodal inference, a practical information theoretic approach,* 2nd edn. Springer-Verlag, New York.

Carbyn, L.N., Oosenbrug, S. & Anions, D. (1993) *Wolves, Bison and the Dynamics Related to the Peace-Athabaska Delta in Canada's Wood Buffalo National Park.* Circumpolar Research Series Number 4; Canadian Circumpolar Institute, Edmonton, Alberta.

Carbyn, L.N. & Trottier, T. (1987) Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Canadian Journal of Zoology,* **65,** 2072-2078.

Carbyn, L.N. & Trottier, T. (1988) Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. *Arctic,* **41,** 297-302.

Caro, T. (2005) *Antipredator Defenses in Birds and Mammals*. The University of Chicago Press, Chicago, IL and London.

Creel, S. & Creel, N.M. (2002) *The African Wild Dog*. Princeton University Press, Princeton, NJ.

Crossland, M. (2000) Direct and indirect effects of the introduced toad *Bufo marinus* (Anura: Bufonidae) on populations of native anuran larvae in Australia. *Ecography,* **23,** 283-290.

Elliott, J. (2004) Prey switching in four species of carnivorous stoneflies. *Freshwater Biology,* **49,** 709-720.

Fortin, D., Fryxell, J.M., O'Brodovich, L. & Frandsen, D. (2003) Foraging ecology of bison at the landscape and plant community levels the applicability of energy maximization principles. *Oecologia,* **134,** 219-227.

Garrott, R.A., Bruggeman, J.E., Becker, M.S., Kalinowski, S. & White, P.J. (2007) Evaluating prey switching in wolf-ungulate systems. *Ecological Applications,* **17,** 1588-1597.

Garton, E.O., Crabtree, R.L., Ackerman, B.B. & Wright, G. (1990) The potential impact of a reintroduced wolf population on the northernYellowstone elk herd. *A report to the United States Congress, vol. 2*, pp. 359-391. Yellowstone National Park, U.S., Fish, Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, the University of Minnesota Cooperative Parks Study Unit, Wolves forYellowstone, Research, Analysis, National Park Service, Yellowstone National Park, Mammoth, WY.

Geremia, C., Wallen, R.L. & White, P.J. (2015) Population dynamics and adaptive management of Yellowstone bison. National Park Service, Yellowstone National Park, Mammoth, WY.

Geremia, C., White, P.J., Hoeting, J., Wallen, R.L., Watson, F.G.R., Blanton, D. & Hobbs, N.T. (2014) Integrating population- and individual-level information in a movement model of Yellowstone bison. *Ecological Applications,* **24,** 346-362.

Greenwood, J. & Elton, R. (1979) Analysing experiments on frequency-dependent selection by predators. *Journal of Animal Ecology,* **48,** 721-737.

Hamilton, W.D. (1971) Geometry of the selfish herd. *J Theor Biol,* **31,** 295-311.

Hebblewhite, M. & Pletscher, D.H. (2002) Effects of elk group size on predation by wolves. *Canadian Journal of Zoology,* **80,** 800-809.

Hess, S. (2002) Aerial survey methodology for bison population estimation in Yellowstone National Park. Dissertation., Montana State University.

Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist,* **91,** 293-320.

Krause, J. & Ruxton, G.D. (2002) *Living in Groups*. Oxford University Press, Oxford.

Larter, N.C., Sinclair, A.R.E. & Gates, C.C. (1994) The response of predators to an erupting bison, *Bison bison athabascae*, population. *The Canadian Field-Naturalist,* **108,** 318-327.

Lemke, T.O., Mack, J.A. & Houston, D.B. (1998) Winter range expansion by the northern Yellowstone elk herd. *Intermountain Journal of Sciences,* **4,** 1-9.

Lingle, S. & Pellis, S. (2002) Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. *Oecologia,* **131,** 154-164.

MacNulty, D.R., Mech, L.D. & Smith, D.W. (2007) A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy,* **88,** 595-605.

MacNulty, D.R., Smith, D.W., Mech, L.D. & Eberly, L.E. (2009a) Body size and predatory performance in wolves: Is bigger better? *J Anim Ecol,* **78,** 532-539.

MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R. & Packer, C. (2009b) Predatory senescence in ageing wolves. *Ecol Lett,* **12,** 1347-1356.

MacNulty, D.R., Stahler, D.R., Wyman, C.T., Ruprecht, J. & Smith, D.W. (2016) The challenge of understanding northern Yellowstone elk dynamics after wolf reintroduction. *Yellowstone Science*, pp. 25-33. Yellowstone National Park, Mammoth, WY.

MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W. (2014) Influence of group size on the success of wolves hunting bison. *PLoS One*, **9,** e112884.

Martin, H. (2016) Factors affecting elk (*Cervus elaphus*) encounter rate by gray wolves (*Canis lupus*) in Yellowstone National Park. Thesis, University of Minnesota.

May, R. (1972) Will a large complex system be stable? *Nature,* **238,** 413-414.

Meagher, M.M. (1973) *The Bison of Yellowstone National Park*. National Park Service, Washington D.C.

Mech, L.D. & Peterson, R.O. (2003) Wolf-Prey Relations. *Wolves: Behavior, Ecology and Conservation* (eds L.D. Mech & L. Boitani), pp. 131-160. The University of Chicago Press, Chicago, IL.

Mech, L.D., Smith, D.W. & MacNulty, D.R. (2015) *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press, USA.

Messier, F. (1995) On the functional and numerical responses of wolves to changing prey density. *Ecology and Conservation of Wolves in a Changing World* (eds L.N. Carbyn, S. Fritts & D.R. Seip). Canadian Circumpolar Institute, Edmonton, Alberta.

Metz, M.C., Smith, D.W., Stahler, D.R., Vucetich, J.A. & Peterson, R.O. (2016) Temporal variation in wolf predation dynamics in Yellowstone National Park: Lessons learned from two decades of research. *Yellowstone Science*, pp. 55-60. National Park Service, Mammoth, WY.

Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology,* **81,** 553-563.

Moléon, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A. & Owen-Smith, N. (2014) Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews,* **89,** 1042-1054.

Morozov, A. & Petrovskii, S. (2013) Feeding on multiple sources: Towards a universal parameterization of the functional response of a generalist predator allowing for switching. *PlosOne,* **8,** 1-8.

Mukherjee, S. & Heithaus, M.R. (2013) Dangerous prey and daring predators: A review. *Biological Reviews,* **88,** 550-563.

Murdoch, W. (1969) Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs,* **39,** 335-354.

Murdoch, W. & Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research,* **9,** 1-131.

Northern Yellowstone Cooperative Wildlife Working Group (2016) 2016 Annual Winter Trend Count of Northern Yellowstone Elk pp. 1-6. Montana Department of Fish, Wildlife & Parks, the National Park Service

Pereira, L., Owen-Smith, N. & Moleón, M. (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review,* **44,** 44-55.

Reagan, B. (2016) Carcass monitoring and grizzly bear scavenging across two management jurisdictions of the northern Yellowsyone winter range (1997-2012). Masters, Montana State University.

Ripple, W.J., Painter, L., Beschta, R.L. & Gates, C.C. (2010) Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. *The Open Ecology Journal,* **3,** 31-37.

Rutten, A., Oosterbeek, K., Ens, B. & Verhulst, S. (2006) Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers. *Behavioral Ecology,* **17,** 297-302.

Sikes, R., Gannon, W. & Amer Soc M (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy,* **92,** 235-253.

Singer, F.J. & Garton, E.O. (1994) Elk sightability model for the Super Cub. *Aerial survey; user's manual with practical tips for designing and conducting aerial big game surveys*. Idaho Department of Fish and Game, Boise, ID.

Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management,* **68,** 153-166.

Smith, D.W., Mech, L.D., Meagher, M., Clark, W., Jaffe, R., Phillips, M.K. & Mack, J.A. (2000) Wolf-bison interactions in Yellowstone National Park. *Journal of Mammalogy,* **81,** 1128-1135.

Smith, D.W., Stahler, D.R., Metz, M.C., Cassidy, K., Stahler, E., Almberg, E. & McIntyre, R. (2016) Wolf restoration in Yellowstone: Reintroduction to recovery. *Yellowstone Science*, pp. 5-12. Yellowstone National Park, Mammoth, WY.

Stahler, D.R., MacNulty, D.R., Wayne, R.K., vonholdt, B. & Smith, D.W. (2013) The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *Journal of Animal Ecology,* **82,** 222-234.

Stahler, E., Smith, D.W. & Stahler, D.R. (2016) Wolf turf: a glimpse at 20 years of spatial ecology in Yellowstone. *Yellowstone Science*, pp. 50-54. National Park Service, Mammoth, WY.

Temple, S.A. (1987) Do predators always capture substandard individuals disproportionately from prey populations? *Ecology,* **68,** 669-674.

Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narva´ ez, L., Urbani, P. & Dunne, J.A. (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol Lett,* **13,** 1546-1559.

van Leeuwen, E., Brännströmb, Å., Jansen, V.A.A., Dieckmann, U. & Rossberg, A.G. (2013) A generalized functional response for predators that switch between multiple prey species. *Journal of Theoretcial Biology,* **328,** 89-98.

Varley, N. & Boyce, M.S. (2006) Adaptive management for reintroductions: Updating a wolf recovery model for Yellowstone National Park. *Ecological Modelling,* **193,** 315-339.

Weiss, R. (2005) *Modeling longitudinal data*. Springer, New York, NY.

White, P., Proffitt, K.M., Mech, D., Evans, S., Cunningham, J. & Hamlin, K.L. (2010) Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy,* **91,** 827-837.

White, P.J., Proffitt, K.M. & Lemke, T.O. (2012) Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist,* **167,** 174-187.

White, P.J., Wallen, R.L. & Hallac, D. (2015) *Yellowstone bison - conserving an American icon in modern society*. Yellowstone Association, Yellowstone National Park, WY.

Wright, G.J., Peterson, R.O., Smith, D.W. & Lemke, T.O. (2001) Selection of Northern Yellowstone elk by gray wolves and hunters. *The Journal of Wildlife Management,* **70,** 1070-1078.

Figures

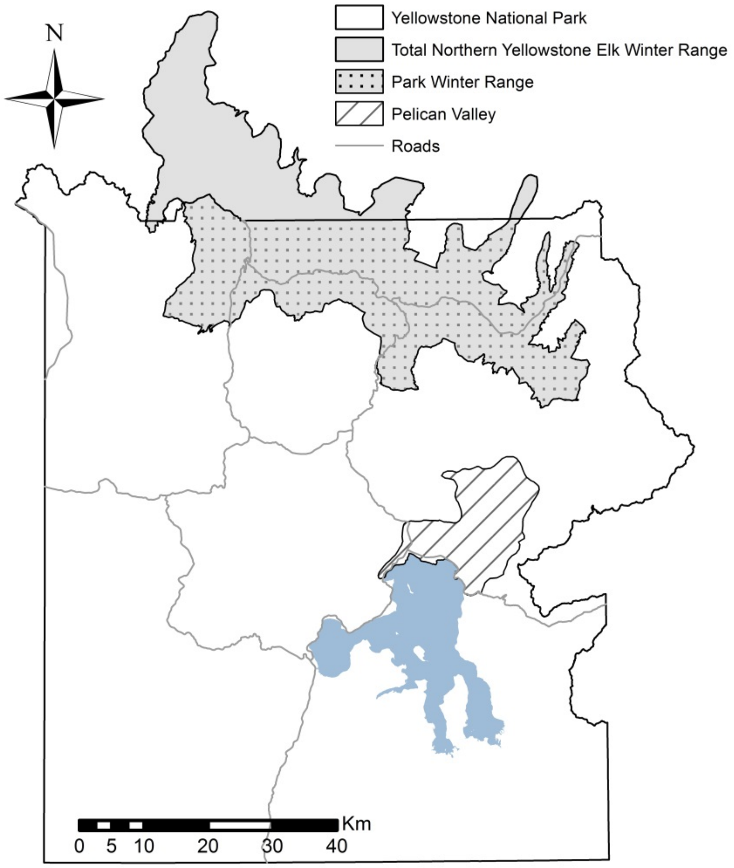


Fig. 3-1. Yellowstone National Park including the northern Yellowstone elk winter range and Pelican Valley areas that were the focus of this study.

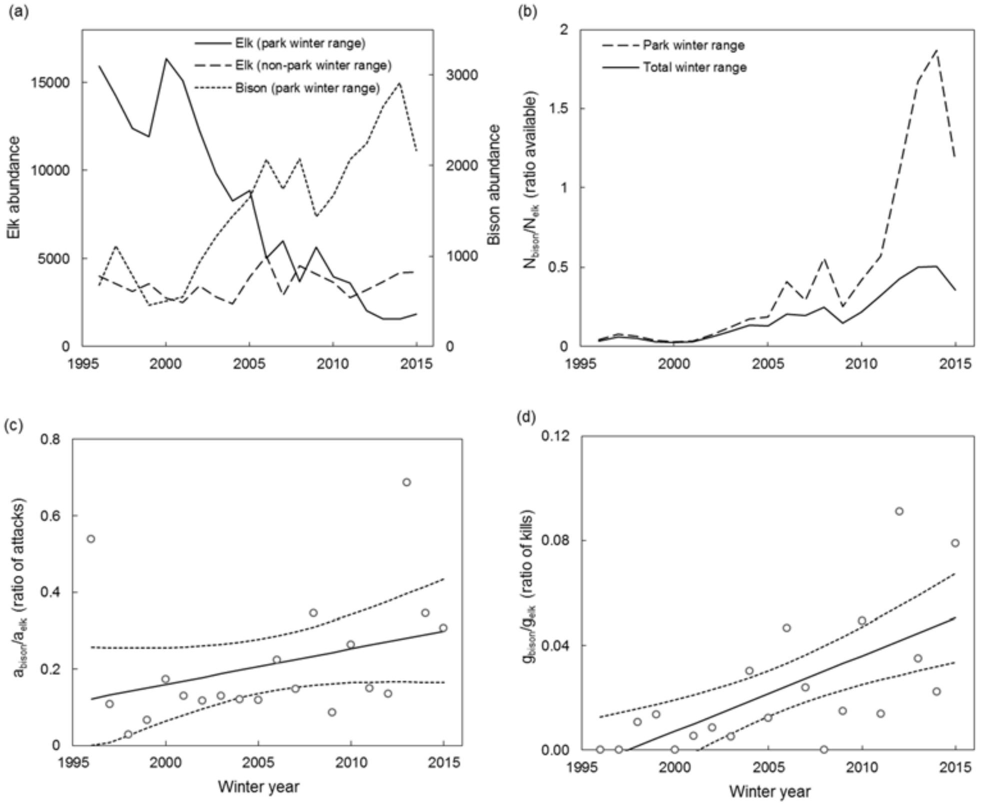


Fig. 3-2. Trends in bison and elk abundance in the park and non-park portions of the northern Yellowstone elk winter range (a), relative bison and elk abundance in the total and park winter ranges (b), relative frequency of wolf attacks on bison and elk in the park winter range (c), and relative frequency of bison and elk killed by wolves in the park winter range (d) during winter (1 November - 30 April), 1995-2015. 'Winter year' starts 1 January (e.g., 1996 represents the 1 November - 30 April, 1995-1996 winter year). In (c) and (d), open circles are observed values, solid lines are fitted values, dotted lines indicate 95% confidence intervals.

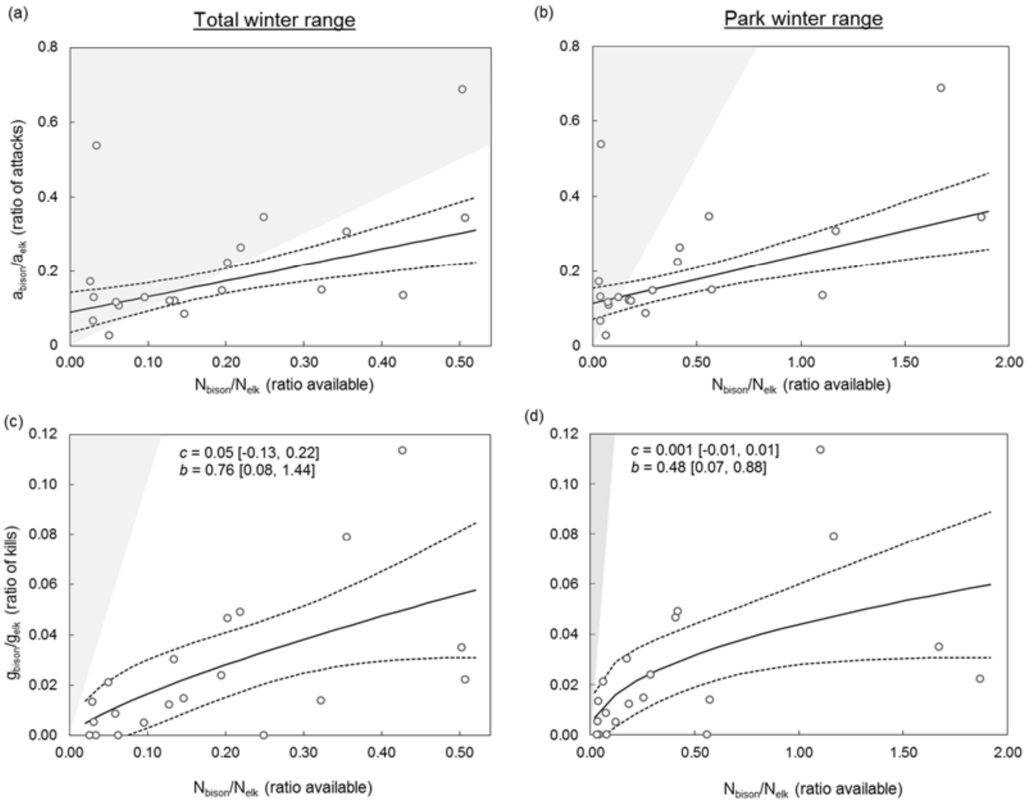


Fig. 3-3. Effects of relative bison abundance on the relative frequency that wolves attacked (a,b) and killed (c,d) bison in the total (a,c) and park (b,d) winter ranges. Solid lines are fitted values with dotted lines indicating 95% confidence intervals. Open circles are observed annual ratios. Shaded areas are the parameter spaces indicative of preference for bison. The dividing lines between shaded and non-shaded areas indicate values where the relative frequency of attacks and kills is exactly proportional to relative bison abundance.

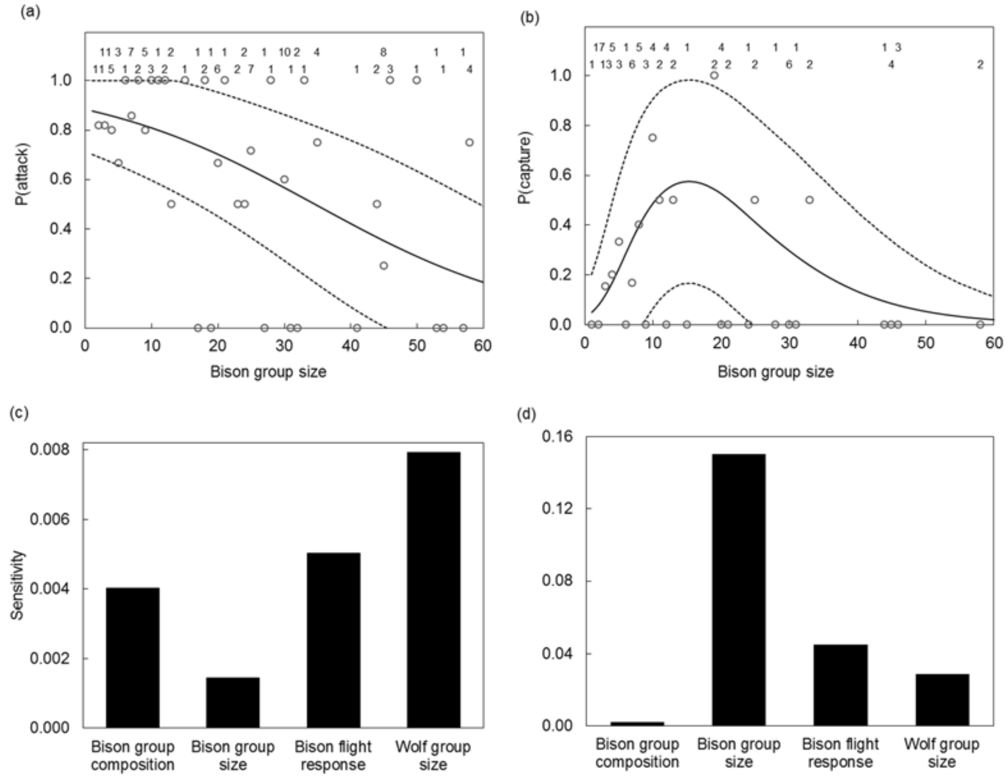


Fig. 3-4. Effects of bison group size on attacking (a) and capturing (b) and the relative influence of bison group composition and size, flight response, and wolf group size on attacking (c) and capturing (d). In (a) and (b), lines are population-averaged fitted values with associated 95% confidence intervals, and open circles are observed frequencies with sample sizes denoted above each point; analyses were performed on the raw binary data and not the illustrated data points. The number of encounters included in each analysis is 171 (a,c) and 91 (b,d). Each bar in (c) and (d) represents a sensitivity value generated by taking the difference between initial and perturbed (10%) predicted values for each parameter. The greater the sensitivity value, the more influential that parameter is on attack and capture probability.

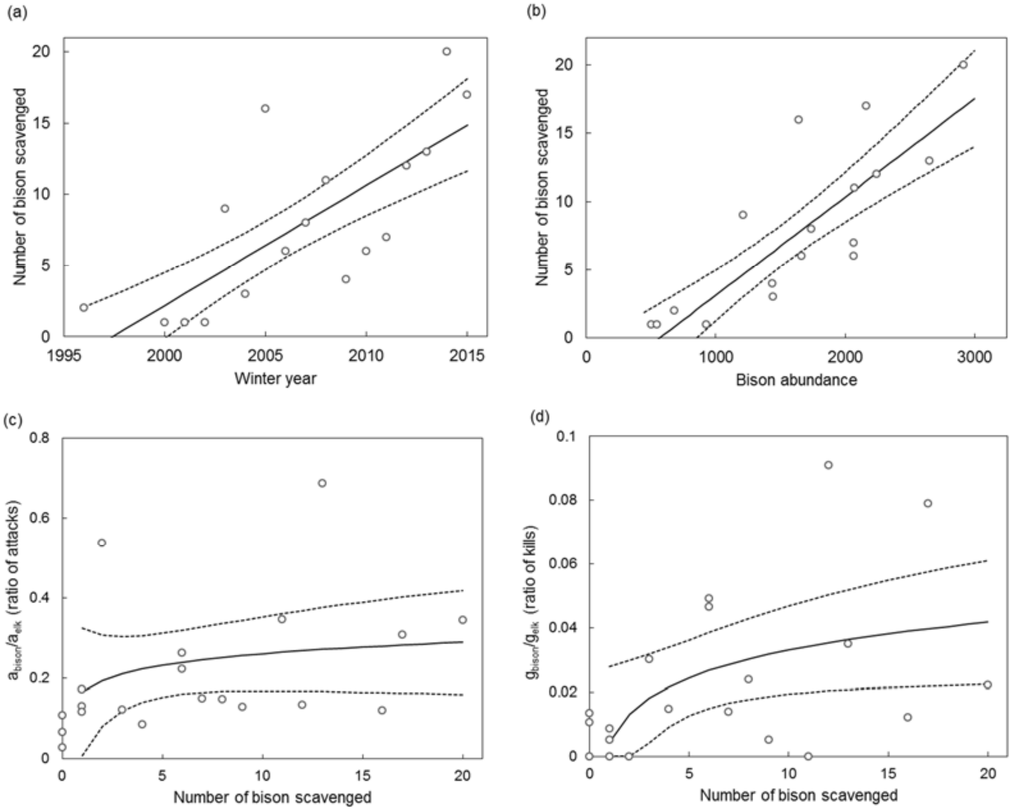


Fig. 3-5. Number of wolf-scavenged bison in the northern Yellowstone National Park winter range, 1996-2015 (a) in relation to bison abundance (b), and the relative frequency that wolves attacked (c) and killed (d) bison. Open circles are observed values, solid lines are fitted values, dotted lines indicate 95% confidence intervals.

CHAPTER 4

BISON SPATIAL RESPONSE TO WOLF PREDATION RISK IN AN EXTREME WINTER ENVIRONMENT

Summary

1. Determining the effects of predators on prey behavior is crucial for understanding the potential for top-down forcing in ecosystems. In free-living systems, prey spatially respond to predation risk at fine scales, however, less is known about the ability of predators to induce large-scale, landscape-level shifts in prey habitat use. In general, prey are expected to be largely insensitive to cursorial predators that are spatially unpredictable. On the other hand, especially dangerous landscapes may generate strong prey spatial responses irrespective of predator hunting mode. In temperate systems, deep snow increases the ability of cursorial predators to hunt ungulates; thus, snow conditions are likely a key axis of spatial variation in predation risk.

2. In Yellowstone National Park, the high-elevation Pelican Valley (2500 m) is the most environmentally-extreme winter habitat for bison; winters are long and snow cover is severe. I used the Pelican Valley system as a case study to understand the potential for a cursorial predator (wolves; *Canis lupus*) to induce large-scale shifts in prey (bison; *Bison bison*) habitat use.

3. First, I used direct observations of wolf-bison interactions (2001-2012) to evaluate the influence of snow conditions on wolf hunting success. Next, I used data on bison locations and wolf presence/absence in Pelican Valley (2005-2008) to determine

whether bison limited their use of risky habitat patches in response to predation risk. Finally, I used historic bison abundance data in Yellowstone (1971-2014) to evaluate the potential effect of wolf reintroduction on bison use of the Pelican Valley winter range.

4. Several lines of evidence are consistent with the hypothesis that diminished numbers of bison wintering in Pelican Valley could, in part, reflect a spatial response to wolf predation risk. First, snow cover dictated bison vulnerability to wolf predation. Second, when wolves were present, bison moved to rare snow-free habitats, decreasing the likelihood of predation. Third, the influence of snow cover on bison use of the Pelican Valley winter range was 30 times stronger after wolf reintroduction than before. Finally, a model that predicted how bison wintering numbers might have been realized after wolf reintroduction, had wolves never been reintroduced, predicted a fairly stable wintering bison population instead of the declining one that was observed.

5. These results highlight the potential role of wolves in modifying the habitat use, movement, and distribution of bison in Yellowstone's interior high-elevation winter ranges. This study uniquely links individual-level behavioral mechanisms (i.e., fine-scale spatial response to predation risk) with population level patterns (i.e., long-term trends in the use of high risk winter range) to explore the hypothesis that cursorial predators can contribute to large-scale shifts in prey habitat use. Although cursorial predators are often expected to incite weak prey responses, this study suggests that these predators can produce consistent risk cues when their hunting success is coupled with landscape characteristics that shape prey vulnerability.

Introduction

Predators structure ecosystems via consumptive effects on prey demography (Estes & Duggins 1995; Terborgh *et al.* 2001; Kauffman, Brodie & Jules 2010), and nonconsumptive effects on prey behavior (Schmitz, Beckerman & O'Brien 1997; Werner & Peacor 2003; Preisser, Bolnick & Benard 2005; Ford *et al.* 2014). Determining how prey species behaviorally respond to predators is, therefore, an important step toward understanding the strength of top-down predator effects. In free-living systems, prey spatially and temporally respond to predation risk at fine scales, e.g., within prey home ranges (e.g., Heithaus & Dill 2002; Fortin *et al.* 2009; Tambling *et al.* 2012; Kohl *et al.* in review). However, less is known about the ability of predators to induce large-scale, landscape-level shifts in prey habitat use. Understanding the extent that individual-level spatial responses foster landscape-level shifts in prey habitat use is important for understanding the ecology of predator-prey interactions, as well as the consequences of world-wide efforts to restore wild predator populations (Bruskotter & Shelby 2010; Chapron *et al.* 2014).

The extent that predator hunting success is governed by landscape characteristics directly affects the strength of a prey species response to predation risk (Preisser, Orrock & Schmitz 2007). Ambush predators are expected to incite strong spatial responses from their prey because their hunting success is often tied to landscape features, thus, their landscape-specific risk cues are generally strong and consistent through time (Schmitz 2005). Conversely, prey are expected to be largely insensitive to cursorial predators, which generate weak and inconsistent landscape-specific risk cues because they are spatially unpredictable (Schmitz 2005). However, coursing predators might produce strong and consistent risk cues if their hunting success is tightly coupled with landscape characteristics.

In northern temperate systems, snow conditions are an important abiotic component of the landscape that affects the hunting success of coursing predators, including wolves (*Canis lupus*). During winter, wolves are more successful hunting ungulates in deep snow (Mech & Peterson 2003) that saps ungulate vigor (Gaillard *et al.* 2000) and inhibits escape ability (Singer 1992; MacNulty & Smith 2004). It is well-established that heavy snow-fall increases wolf predation on deer (*Odocoileus sp.*) (Nelson & Mech 1986), elk (*Cervus elaphus*) (Carbyn 1983; Huggard 1993; Becker *et al.* 2009), and moose (*Alces alces*) (Post *et al.* 1999). Bison (*Bison bison*) are similarly vulnerable to wolf predation during winter (Smith *et al.* 2000), especially in habitats with severe snowpack that can handicap their anti-predator response.

During winter, wolves affect bison behavior (Fortin & Fortin 2009), movements (Harvey & Fortin 2013) and space use (Carbyn & Trottier 1987; Fortin *et al.* 2009) in systems where the two species coincide. For example, wolf predation risk is an important driver of bison winter habitat selection (Fortin *et al.* 2009) and movement (Harvey & Fortin 2013) in Prince Albert National Park, Canada. Evidence from Wood Buffalo National Park, Canada, also suggests that bison herds will relocate after a wolf attack, sometimes moving great distances (up to 47 km) from the attack site (Carbyn & Trottier 1987; Carbyn, Oosenbrug & Anions 1993). Studies of bison space use and movement in Yellowstone National Park have yet to consider the potential effects of wolves (e.g., Bjornlie & Garrott 2001; Bruggeman *et al.* 2009a;

Fuller, Garrott & White 2009; Geremia *et al.* 2011; Geremia, Wallen & White 2015; but see Hernández & Laundré 2005), in part because bison are relatively invulnerable to wolf predation (Mech & Peterson 2003; MacNulty *et al.* 2014; Mech, Smith & MacNulty 2015).

In Yellowstone, bison generally occupy two main regions during winter: the northern (including Lamar Valley and Blacktail Deer Plateau) and central range (including Madison/Firehole, Hayden and Pelican Valleys) (Meagher 1973) (Fig. 4-1). The high-elevation central range is subject to long, severe winters; the landscape is characterized by deep snowpack interspersed with small patches of geothermal and windswept snow-free ground (Newman & Watson 2009). In contrast, the lower-elevation northern range has comparatively mild winter conditions; winters are shorter, snowpack is less severe, and patches of snow-free ground are larger and more numerous (Houston 1982). Wolves were reintroduced to Yellowstone in 1995 and 1996 (Bangs & Fritts 1996), and researchers predicted that bison wintering in the central range would to be more vulnerable to wolf predation than northern range bison (Singer 1992). Specifically, the low availability of snow-free ground would inhibit ungulate anti-predator defenses in high elevation regions such as Pelican and Hayden Valleys (Singer 1992). Historically, the majority of Yellowstone's bison population wintered in the central range (Meagher 1973), a pattern that switched in about 2005. Most of the population now winters in the northern range (Geremia *et al.* 2011). Previous studies indicate that bison started emigrating from the central range to the northern range in response to density-dependent resource limitation before wolves were reintroduced in 1995/1996 (Bruggeman *et al.* 2009b; Fuller, Garrott &

White 2009). Wolves have not been considered a factor in this range shift despite severe winter conditions in the central range that favor wolf predation on bison.

The reintroduction of wolves to Yellowstone National Park provides a novel case study to understand the potential for cursorial predators to contribute to large-scale shifts in prey habitat use. The Pelican Valley region is the most extreme winter habitat for Yellowstone bison (Meagher 1973; Singer 1992; Meagher, Taper & Jerde 2001). Bison wintering in Pelican Valley endure a higher risk of predation than elsewhere in the park, because of the severe winter conditions and lack of alternative prey (Smith *et al.* 2000). I used direct observations of wolf-bison interactions in Pelican Valley (2001-2012) to understand how the snowscape affected the hunting success of a cursorial predator. I predicted that wolves would be more likely to attack and capture bison standing in deeper snow, and bison located in habitats with more snow-covered ground. Next, I used data on bison locations and wolf presence/absence in Pelican Valley (2005-2008) to evaluate whether bison spatially-responded to predation risk. I expected bison use of safer habitats (i.e., habitats with more snow-free ground) to increase as predation risk increased (i.e., as wolves stayed longer in the valley). Finally, I used historic data on regional bison abundance in Yellowstone (1971-2014) to evaluate the potential effect of wolf reintroduction on bison use of the Pelican Valley winter range. This study uniquely links individual level behavioral mechanisms (i.e., fine-scale spatial response to predation risk) with population level patterns (i.e., long-term trends in the use of high risk winter habitat) to understand the potential for a cursorial predator to affect the large-scale habitat use of a free-living prey species.

Materials and Methods

STUDY AREA

Yellowstone National Park is a 891,000 ha reserve (elevation 1500-3300 m) in northwestern Wyoming, USA that supports 8 different ungulate species, including bison (Houston 1982). My study focused on wolf-bison interactions and bison habitat use in the high elevation Pelican Valley region (hereafter, Pelican Valley; 2500 m; ~100 km^2), northeast of Yellowstone Lake (Fig. 4-1a) which experiences long winters characterized by severe snow conditions (Meagher 1973; Newman & Watson 2009). As the only ungulate species to persist there year-round, bison survive by foraging across a network of geothermal and wind-swept patches of snow-free ground (Meagher, Taper & Jerde 2001; MacNulty, Plumb & Smith 2008). These patches were similar in location, shape, and size each winter (MacNulty & Smith 2004). All observations of wolf-bison interactions were recorded from a centrally located overlook that afforded relatively uninterrupted views of Pelican Valley and its surrounding drainages (Fig. 4-1b). Observers, who had participated in the study for between 6 and 15 years, were very familiar with the network of patches and their locations. Although GPS collars have been fitted to Yellowstone bison since 2004 to evaluate bison movement and habitat use within the park (e.g., Geremia *et al.* 2014), few of these animals over-wintered in Pelican Valley.

Wolves were reintroduced to Yellowstone in 1995 and 1996 (Bangs & Fritts 1996) and, in 1996, the Mollies pack moved into Pelican Valley. Since then, the Mollies territory has encompassed both Pelican and Hayden Valleys, occasionally extending into northern Yellowstone (Stahler, Smith & Stahler 2016). During winter, the Mollies continuously moved throughout their territory in search of prey; cumulatively, about half their time was spent in Pelican Valley (MacNulty, Plumb & Smith 2008). Their itinerant presence created temporally heterogeneous predation risk for bison wintering in Pelican Valley. At least one wolf in this pack was captured annually and fitted with a VHF radio collar following animal handling guidelines of the American Society of Mammalogists (Sikes, Gannon & Amer Soc M 2011) and approved by the National Park Service Institutional Animal Care and Use Committee (Permit: IMR_Yell_Smith_Wolf _2012).

DATA COLLECTION

Influence of snowscape on wolf hunting success

Wolf hunting success – I followed previously established protocols to measure the behavior of wolves hunting bison (MacNulty, Mech & Smith 2007; MacNulty *et al.* 2012; MacNulty *et al.* 2014). Most encounters in this study were recorded from the ground during an annual 2 week study period in March, 1999-2012 and some were aerially recorded from fixed-wing aircraft. When wolves encountered bison – defined as at least 1 wolf orienting and moving (walking, trotting or running) toward bison – I followed the progress of the encounter by noting the foraging state (approach, watch, attack-group, attack-individual, capture) of the individual(s) closest to making a kill. I therefore recorded the sequential occurrence of the most escalated state. I scored escalation in the predatory sequence according to whether wolves completed each of

2 predatory tasks that corresponded to the following 2 behavioral transitions: approach (or watch) → attack-group (or attack-individual) = 'attacking'; attack-group (or attack-individual) → capture = 'capturing'. Note that capturing was not necessarily killing because bison that were bit and physically restrained by wolves often escaped (MacNulty, Mech & Smith 2007). A hunting group completed a task, and was therefore 'successful', if the task was performed by at least 1 group member. If not, I considered the group to have 'failed' in that task. This scheme generated a binary score for each sequential foraging state. 'Hunting group size' was defined as the number of wolves participating in the most escalated foraging state (MacNulty *et al.* 2014). I also recorded the bison 'group size', 'group type', and 'flight response' associated with each foraging state (see Chapter 3).

I plotted the location of each attempted attack and capture on a Digital Orthophoto Quadrangle (DOQ) (i.e., digitized aerial photograph) of Pelican Valley on a handheld computer in the field (i.e., while directly observing the interaction), or on a desktop computer in the lab (i.e., from video-recorded interactions). Observers also recorded snow depth, relative to the bison group, at the location of each attempted attack and capture (i.e., no snow, packed snow, or hoof, ankle, knee, or stomach deep). I then categorized snow depth as either 'shallow' (e.g., no snow, packed snow, and hoof deep) or 'deep' (ankle, knee, and stomach deep).

Quantifying the snowscape – I used satellite imagery to quantify the Pelican Valley snowscape. I analyzed all satellite imagery in ArcMap version 10.1 (Environmental Systems Research Institute, Redlands, CA) and Geospatial Modeling Environment

(GME) version 0.7.2.1 (Beyer 2012). High resolution (2.5 m^2) images were acquired from the Ikonos (14 March, 2003), Ortho (20 March and 2 April, 2006), and GeoEye1 (12 April, 2009) satellites (Space Imaging, Inc. and Digital Globe). Data were projected in NAD83_UTM_Zone_12 and rectified in ERDAS Imagine 13.0 (Leica Geosystems, Atlanta, GA). The snow conditions in these images ($SWE_{3/14/2003}$ = 182.88 mm; $SWE_{3/20/2006}$ = 213.36 mm; $SWE_{4/2/2006}$ = 213.36; $SWE_{4/12/009}$ = 266.70) are representative of average snow conditions during the study period (mean (±SD) SWE on median study date, 24 March, 1999-2012 = 205.2 mm ±66.8 mm).

I classified snow-free areas in Pelican Valley by tracing a ‘polygon’ around the perimeter of each patch of snow-free ground, in each satellite image; patches of snow-free ground were easily distinguished from snow cover, forest cover and streams (see Fig. 4-1b-c). To create one data layer that characterized the size and location of snow-free ‘patches’ throughout the study period, I used the ArcMap tool ‘aggregate’ to combine the polygons from all four images. Then, I calculated the area of each patch (m^2), using the ArcMap tool ‘summary statistics’. To determine how the snowscape affected wolf hunting success, I calculated the total amount of ‘snow-free area’ (m^2) surrounding each attempted attack and capture location. To capture variation in the scale at which the snowscape might affect wolf hunting success, I generated a series of increasingly large ‘buffers’ around the UTM location of each attempted attack and capture using the GME tool ‘buffer’. These were constructed at 10 m incrementally increasing radii (i.e., at radii of 10, 20, 30, 40, 50, 60, 70, 80, and 90 m); radii were < 100 m to restrict the influence of winter landscape characteristics on wolf hunting success to more immediate surroundings (Fig. 4-1c). Using the GME tool ‘isectpolypoly’, I intersected all buffers with overlapping patches to generate the total area of snow-free ground (m^2) surrounding each location, or ‘snow-free area’ (m^2), within the 9 different buffer zones.

Bison spatial response to wolf predation risk

This portion of the study was conducted in Pelican Valley during two-week periods ~17 March – 30 March, 2005-2008. Each day, two field observers performed ‘scans’ every 3 hours (generally at 0730, 1030, 1330, and 1630) by using binoculars and spotting scopes to systematically scan the valley and its surrounding drainages from a central observation point (Fig. 4-1b). Observers used a handheld computer to record the scan date and time, a unique scan identity number, visibility conditions, wolf presence, and bison location, group type and size. Locations were mapped on a DOQ of Pelican Valley. Bison groups were counted, and classified as ‘mixed’ (i.e., any combination of males, females and young-of-the-year) or ‘bull’ (i.e., males only). ‘Bison group size’ refers to the number of bison individuals < 100 m apart (Fortin *et al.* 2003). A visibility score (0-100%) described the proportion of the viewshed visible during each scan.

Predation risk – Observers used radio telemetry during each scan to record the presence of wolves in Pelican Valley. Wolf packs were also located daily via fixed-wing aircraft previous to, and during, the two week study period, weather permitting. I categorized scans as occurring during either high (0700-1100 and 1600-1800) or low (1101-1559) ‘wolf activity periods’(Kohl *et al.* in review). Wolves were scored as ‘present’ for the day if they were detected during at least 1 scan that day. Wolves are more successful at hunting bison the longer they remain near a herd (Carbyn, Oosenbrug & Anions 1993; MacNulty 2002). Therefore, bison may be more likely to respond to cumulative, rather than instantaneous, wolf presence. To capture variation in the duration of wolf presence, I calculated the total number of days wolves were present within 1, 2, 3, 4, 5, 6, and 7 days prior to each scan. For example, wolf presence measured 1-day prior to the scan captured variation in wolf presence the previous day, while wolf presence measured within 7-days prior to the scan captured variation in wolf presence over the previous week.

Spatial response – To determine whether bison spatially responded to predation risk, I evaluated the use of safe versus risky habitats by bison with respect to wolf presence. Habitats with less snow-free ground were more risky for bison, while areas with more snow-free ground were safer (see Results - Spatial predation risk). To quantify bison habitat use, I generated a 'buffer' around each bison group's geographic position using a 50 m radius. I chose a 50 m radius because it best represented the effect of snow-free area on the probability that wolves attacked bison (see Results - Spatial predation risk). I then calculated the area (m^2) of snow-free ground around each bison group, using the methods described above.

Use of Pelican Valley winter range

Bison abundance – The number of bison wintering in Pelican Valley was counted during annual winter surveys conducted between 19 January and 11 March, 1970-2014 (N=45). Most counts occurred in February (N=37), and some occurred in late

January (N=3) or early March (N=5). The Pelican Valley winter count covered the region south and east of Le Hardy rapids, including Astringent Creek, Raven Creek, Upper Pelican Creek, Mary Bay and the northern shore of Yellowstone Lake (Fig. 4-1a). The park-wide bison population was counted during annual aerial summer surveys conducted by observers in 1 or 2 fixed-wing aircraft between 26 May and 29 July, 1970-2014; during the survey, bison abundance was also counted for each region (Fig. 4-1a). Uncorrected counts were a reliable enumeration of the park's bison population, as bison often formed large groups that congregated in visible, open areas (Hess 2002). One hypothesis for declining numbers of bison wintering in Pelican Valley is that management culls at the park boundaries erased the bison population's collective memory for this traditional winter range. I therefore measured 'bison cull' as the total number of bison removed from the Yellowstone population each year (Geremia, Wallen & White 2015).

Predation risk in Yellowstone – To gauge differences in regional predation risk across Yellowstone, I used long-term data collected on wolf-killed bison and regional bison abundances (1995-2014). Between 1995 and 2014, field crews intensively monitored the wolf population over 30 day intervals in the early (15 November – 14 December) and late (1 March – 30 March) winter. For further details on data collection methods see Smith *et al.* (2004). Briefly, ground-based observation crews attempted to monitor wolf packs continuously during daylight hours throughout each study period. Field crews also opportunistically monitored Yellowstone wolves throughout the rest of the winter (1 November – 30 April, 1995-2014). During both study periods, ground and air crews searched for ungulate prey utilized by wolves and recorded location, cause of death (i.e., wolf killed or not; see Appendix 2), date of death, species, estimated age, and sex. I calculated the mean annual proportion of bison killed by wolves ($N_{\text{bison killed}}$ / $N_{\text{bison abundance}}$) in Pelican Valley, elsewhere in the central range (i.e., Madison/Firehole and Hayden Valley), and in the northern range (Fig. 4-1a). To gauge the overall level of predation risk for bison in each region, I then calculated the mean annual proportion of bison killed in each area from 1995 to 2014.

Weather data – Weather data were collected at the Lake Yellowstone weather station (operated by the National Weather Service) located within the Pelican Valley region, about 10 km southwest of Pelican Valley (44°33'04"N, 110°28'50"W; elevation 2370 m). I used winter precipitation and temperature to estimate winter severity in Pelican Valley. Winter precipitation was measured as the total winter precipitation (mm) and maximum SWE (mm) between 1 November and 31 April. SWE was estimated using snow depth, precipitation and temperature measurements (see Farnes 2012). I also compiled data on the average minimum, maximum, and average daily temperatures (°C) between 1 November and 31 April. The number of days in the growing season, total growing degree days for grasses, and total summer precipitation (mm) between 1 May and 31 October were used as indices for summer grass growing condition, or forage availability, in Pelican Valley.

DATA ANALYSIS

I conducted all analyses in R version 3.0.1 (R Core Team 2014), unless otherwise stated. I dropped variables when correlation coefficients were > 0.6; bison group type was collinear with bison group size, and was excluded from subsequent analyses. I compared models using Akaike Information Criterion model selection, which was adjusted for small sample size (AIC_c) (Burnham & Anderson 2002), using the 'AICcmodavg' package, version 2.0 (Mazerolle 2014). The best-fit model had the lowest AIC_c score and models with a $\Delta AIC_c < 2$ were considered plausible. Population-averaged fitted values were calculated from the most parsimonious models, unless otherwise stated, and Wald 95% confidence intervals (95% CI) are reported. To determine the relative importance of my variables of interest, I examined whether they were retained in top models (models with a ΔAICc < 2; Burnham & Anderson 2002), and evaluated whether 95% CIs overlapped zero.

Influence of snowscape on wolf hunting success

To quantify spatial variation in wolf predation risk, I examined the influence of the snowscape on wolf hunting success. I did this using generalized linear mixed models (GLMMs) with a binomial error distribution using the 'glmer' function in the 'lme4' package version 1.1-7 (Bates & Maechler 2014). Such models account for correlation between repeated attempts to perform the same predatory task during the same encounter. I fitted encounter identity was as a random intercept in all mixed effect models. Models included all attempts to perform the same task within an encounter, as interaction locations were dynamic and I was interested in the affect location changes had on hunting success. I limited the capture analysis to adult bison to control for the effects of prey size on hunting behavior (Packer & Ruttan 1988; MacNulty *et al.* 2012). Models were estimated using adaptive Gaussian quadrature with 25 integration points, and included a compound symmetric correlation structure, which assumed that all observations within encounters were, on average, equally correlated (Weiss 2005).

I analyzed the effects of the snowscape on wolf hunting success in two ways. First, I built simple, univariate models testing the categorical effect of snow depth (i.e., shallow versus deep) on the probability of attacking and capturing. Second, to determine the effect of snow-free area on attacking and capturing, I built a set of competing GLMMs for each task. Here, each model set included models with snow-free area measured at 10, 20, 30, 40, 50, 60, 70, 80, and 90 meter radii around each attempted attack and capture location, and an intercept-only model, which represented the null hypothesis that snow-free area had no effect on hunting success. Snow-free area was rescaled by dividing it by 100 to enhance model performance (β coefficients and 95% CI are reported with respect to the rescaled variable). To assess uncertainty, I identified models with $\Delta AIC_c < 2$ as the confidence set of models (analogous to a confidence interval for a mean estimate; Burnham & Anderson 2002). To determine if wolf hunting group size and bison group size and flight response affected the relationship between hunting success and snow-free area, I analyzed a subset of observations in which this information was known. Here, I evaluated a set of competing GLMMs as above, except that each model also included main effects for wolf hunting group size, and bison group size and flight response. The attack models included a piecewise linear spline for wolf hunting group size, with a knot specified at 4 (MacNulty *et al.* 2014). The capture data were not robust enough to include a linear spline for wolf hunting group size, so it was included as a linear term.

Bison spatial response to wolf predation risk

I used cumulative link mixed models (CLMMs) in Stata 13.1 to determine whether bison moved from high and low risk areas in response to wolf presence. A relatively high proportion of bison in Pelican Valley used areas with no snow-free ground, which caused the data to be zero-inflated. Grouping a response variable into ordered categories and performing ordinal logistic regression is a convenient method for dealing with zero-inflated data (Min & Agresti 2002). I used k-fold cluster analysis to group the response variable, snow-free area within a 50 m radius, into 3 different categories: low = 0-1212 m^2, medium = 1220-3870 m^2, or high = 3870-7780 m^2 amount of snow-free ground. To control for visibility, I limited the analysis to scans in which ≥ 75% of the viewshed was visible. I constructed separate model sets which predicted the probability that bison groups were located in 1 of the 3 categories of snow-free area based on the number of days wolves were present in the valley (i.e., measured 1, 2, 3, 4, 5, 6, or 7 days prior to each scan; henceforth referred to as 1-7-day model sets). Due to the lack of knowledge about wolf presence before each study period, the data sets became progressively smaller as the number of days in which prior wolf presence was measured increased. For example, for a 14 day study period, prior wolf presence within 1-day (i.e., the previous day) could be determined for 13 total scan days; however, prior wolf presence within 7-days (i.e., within the previous week) could only be determined for 7 total scan days. Because this prohibited the comparison of models with different wolf presence metrics, I built separate model sets to test for a wolf effect, and compare and discuss the results of all model sets. All model sets included main effects of bison group size and wolf activity period; an intercept-only model was also included. Scan identity and year were included as nested random intercepts in all models; scan identity was nested within year.

Use of Pelican Valley winter range

To assess the potential effect of wolves on winter bison abundance in Pelican Valley, I conducted three separate tests. First, I tested for a categorical effect of wolf reintroduction on the number of bison wintering in Pelican Valley by performing stepwise regression, using the 'step' function in the 'MASS' package (Venables & Ripley 2002), using data from the entire study period (1971-2014). The full model included a binary variable representing years before and after wolf reintroduction (i.e., all years $< 1996 = 0$ and all years $\geq 1996 = 1$), and metrics for park-wide bison abundance, number of bison culled, winter temperature, winter precipitation, and summer growing conditions. I reported results from the final model, and use the retained variables to parameterize models in the next two analyses.

Second, I developed a model of Pelican Valley bison abundance based on data prior to reintroduction (1971-1995) and used it to predict how bison abundance might have been realized after wolf reintroduction (1996-2014), had wolves never been reintroduced. Third, I built a 'post-wolf' model using data collected post reintroduction (1996-2014) and compared its standardized regression coefficients to those from the pre-wolf model. The purpose of this analysis was to gauge the influence of each variable in predicting bison abundance in Pelican Valley before and after wolf reintroduction (see Vucetich, Smith & Stahler 2005). I expected snowpack to have a stronger effect on bison abundance after wolf reintroduction given the influential effect of snowpack on bison vulnerability to wolf predation (Smith *et al.* 2000).

I conducted these analyses using generalized linear models (GLMs) with a negative binomial distribution; all variables were centered and scaled. To select climate variables for analysis, I built a set of competing models for each climate metric (i.e., winter temperature, winter precipitation, and summer growing conditions), using data from the entire study period (1971-2014). Each model set included univariate models predicting bison abundance in Pelican Valley using one of a set of collinear climate variables (e.g., minimum, maximum, and average winter temperature). The weather variables included in the highest ranked model ($\Delta AIC_c = 0$) from each model set were used for analyses. I used the previous summer's park-wide bison count as the measure of 'park-wide bison abundance' for each winter. To meet model assumptions, I also tested for a nonlinear relationship between Pelican Valley and park-wide bison abundance using a quadratic term for park-wide abundance. To facilitate comparison, I included park-wide bison abundance as a linear term in both the pre- and post-wolf models when calculating standardized regression coefficients. To account for potential memory loss of the Pelican Valley winter range from culling operations, I measured 'bison cull' as the total number of bison removed from the population the previous year. I assessed model performance using Cragg and Uhler's pseudo r-squared value (pR^2) (Long 1997) generated using package 'pscl' version 1.4.9 (Jackman 2015). I assessed the performance of the pre-wolf model in predicting post-wolf bison abundance by performing a two sample

Kolmogorov-Smirnov test; a p-value <0.05 indicates the observed and predicted values come from different distributions.

Results

INFLUENCE OF SNOWSCAPE ON WOLF HUNTING SUCCESS

The success of wolves hunting bison was directly tied to snow conditions. Wolves were more likely to attack (OR = 71.95 [1.41, 3668.57], P = 0.033) and capture (OR = 5.21 [0.98, 27.62], P = 0.053) bison in deep snow than in shallow snow, although the 95% CI for capturing overlapped 1 (Fig. 4-2a-b).

The amount of snow-free area surrounding wolf-bison encounter locations influenced the probability that wolves attacked and captured bison. The most parsimonious models of attacking and capturing included radii at 50 m and 20 m, respectively (Table 4-1a-b). Attack models with other radii also performed well (ΔAICc < 2.0), suggesting a broad scale over which snow-free area affected the probability that wolves attacked bison (Table 4-1a). No other capture model performed well, implying that the ability of wolves to capture bison was affected by snow conditions close to the attack site. The null model did not fit the data well for attacking ($\Delta AIC_c = 3.84$) or capturing ($\Delta AIC_c = 5.40$) (Table 4-1a-b), providing support for an overall influence of snow-free area on wolf hunting success. Results were similar for a subset of observations that included data on wolf and bison group sizes and bison flight response.

Attack probability decreased as the amount of snow-free area within 50 m of a bison group increased (OR = 0.93 [0.86, 0.99], P = 0.04) (Fig. 4-2c). Capture probability also decreased as the amount of snow-free area within 20 m of a bison group increased, but the 95% CI for this effect overlapped 1 (OR = 0.21 [0.04, 1.11], P = 0.07) (Fig. 4-2d), likely due to the relatively small sample size (43 wolf-bison encounters). To account for this possibility, I tested for a simple binary effect of snow-free area ($\leq 100\text{m}^2$ and $> 100\text{m}^2$) and found a similar effect. Wolves were 10% more likely to capture a bison in areas with $\leq 100\text{m}^2$ than in areas with $> 100\text{m}^2$ (OR = 0.10 [0.01, 0.82], P = 0.032). Overall, these results suggest that habitats with more snow-free ground were safer for bison, whereas habitats with less snow-free ground were riskier.

BISON SPATIAL RESPONSE TO WOLF PREDATION RISK

Wolf presence was retained in 1 of 3 top models in the 1- and 2-day model sets (Table 4-2a-b). For the 3- and 4-day model sets, wolf presence was retained in 2 of the 4 top models (Table 4-2c-d). For the 5-, 6-, and 7-day model sets, wolf presence was retained in the best model, and in 2 of the 3 top models (Table 4-2e-g). The positive effect of wolf presence in all models indicates that bison were more likely to use safer habitats (i.e., habitats with more snow-free ground) as the number of days that wolves were in the valley increased (Table 4-3a-g). Interestingly, the magnitude of the wolf effect increased as the measure of cumulative wolf presence increased (Fig. 4-3a), suggesting that bison responded to cumulative, rather than instantaneous, predation risk.

For illustrative purposes, I highlighted the effect of wolf presence within 7-days on bison habitat use. The estimate of this effect did not overlap 0, providing support for the wolf effect (Table 4-3g; Fig. 4-3a); all the other effects of wolf presence included a 95% CI that overlapped 0 (Table 4-3a-f; Fig. 4-3a). The likelihood that bison were located in habitats with a high, versus low or medium, amount of snow-free ground increased with every additional day wolves were present (OR = 1.19 [1.02, 1.38]; P = 0.027) (Fig. 4-3b). Because ordinal logistic regression coefficients are interpreted as cumulative probabilities, this means that the combined probability that bison were located in habitats with a high or medium, rather than a small, amount of snow-free ground increased by 19% with each additional day wolves were present (OR = 1.19 [1.02, 1.38]; P = 0.027) (Fig. 4-3b). In addition, the probability that bison used habitats with a medium or high amount of snow-free ground increased with increasing bison group size (OR = 1.10 [1.08, 1.13]; P < 0.001).

I classified 373 unique patches of snow-free ground in Pelican Valley. Most (85%) of these patches were small (0-1212 m^2). Only 15% were medium to large patches (> 1213 m^2 of) (Fig. 4-3c).

USE OF PELICAN VALLEY WINTER RANGE

The total Yellowstone bison population grew from about 500 to almost 5000 between 1970 and 2014 (Fig. 4-4a). The number of bison wintering in Pelican Valley grew steadily after 1970, and started to decline during the early 1990's (Fig. 4-4b). Even though evidence indicates that mixed groups of bison have used Pelican Valley as winter range since the establishment of Yellowstone (Meagher 1971; Meagher

1973), mixed groups were not observed wintering in Pelican Valley during the final 6 years of my study (2009-2014).

Predation risk in Yellowstone

Wolves killed 239 bison during winter in Yellowstone, 1995-2014. Seventy-five percent (N=179) of these kills were in the central range, whereas 25% (N=55) were in the northern range. Thirty-four percent (N = 60) of all central range kills occurred in Pelican Valley. To understand broad-scale variation in bison predation risk across Yellowstone, I calculated the mean of the yearly proportion of bison killed by wolves in each winter range between 1995 and 2014. The average [95% CI] proportion of the wintering bison population that was killed was 3 times greater in Pelican Valley (0.013 [0.007, 0.017]) than in the rest of the central range (0.004 [0.002, 0.005]), and 6 times greater than in the northern range (0.002 [0.001, 0.003]). Overall, these results indicate the risk of wolf predation was higher for bison wintering in Pelican Valley than elsewhere in the park, especially the northern range of Yellowstone.

Variable selection

The top climate predictors of winter bison abundance in Pelican Valley were maximum SWE (mm), average daily temperature (°C) (hereafter 'temperature'), and total summer precipitation (mm) (Table 4-4). I used these variables in all subsequent models; importantly, these three weather variables were not collinear. A quadratic term for park-wide bison abundance was included in the complete time series (χ^2_1=

11.91, $P < 0.001$) and pre-wolf models ($\chi^2_1 = 12.88$, $P < 0.001$), but not the post-wolf model ($\chi^2_1 = 1.16$, $P = 0.282$).

Stepwise regression and the complete time series model

The stepwise procedure generated a model with terms for wolf reintroduction, park-wide bison abundance, SWE, and temperature; terms for total summer precipitation and bison cull did not contribute to model fit and were dropped from the analysis. A model fitted to the complete time-series (1971-2014) performed well ($pR^2 = 0.55$), and indicates that the number of bison in Pelican Valley decreased after wolf reintroduction, ($\beta = -0.35$ [-0.60, -0.11]; $P = 0.007$) (Table 4-5a; Fig. 4-4c). Pelican Valley bison abundance also changed as a quadratic function of park-wide bison abundance ($\beta = 0.21$ [0.09, 0.32]; $P < 0.001$; $\beta^2 = -0.16$ [-0.24, -0.08]; $P < 0.001$), and decreased with increasing SWE ($\beta = -0.13$ [-0.23, -0.04]; $P = 0.006$) (Table 4-5a). Bison abundance also tended to increase with increasing winter temperature ($\beta = 0.08$ [-0.02, 0.18]; $P = 0.101$) (Table 4-5a). To rule out the influence of management culling on bison abundance in Pelican Valley, I compared the final complete time series model (Table 4-5a) to one that also included the bison cull variable. Bison culling had no apparent effect on winter bison abundance in Pelican Valley ($\beta = 0.03$ [-0.11, 0.18]; $P = 0.634$), and did not improve model fit ($\chi^2_1 = 0.22$, $P = 0.64$).

Pre-wolf reintroduction model projections

The pre-wolf model performed well ($pR^2 = 0.86$; Fig. 4-5a). The number of bison in Pelican Valley increased as the park-wide bison population increased ($\beta = 0.38$ [0.32, 0.44]; $P < 0.001$; $\beta^2 = -0.13$ [-0.19, -0.06]; $P < 0.001$) (Table 4-5b). Winter temperature (β = 0.02 [-0.04, 0.08]; P = 0.557) and maximum SWE (β = 0.01 [-0.05, 0.07]; P = 0.734; Table 4-5b) had no effect on bison abundance. However, the pre-wolf model performed poorly at predicting bison abundance in Pelican Valley post-wolf reintroduction (D(19) = 0.72; P < 0.001). In contrast to the observed decline in the number of bison wintering in Pelican Valley, the pre-wolf model predicted a fairly stable wintering bison population post-wolf reintroduction, had wolves never been reintroduced (Fig. 4-5b).

Pre- and post-wolf reintroduction model comparison

The post-wolf model also performed well ($pR^2 = 0.45$; Fig. 4-5c). After wolf reintroduction, the number of bison in Pelican Valley decreased with increasing maximum SWE (β = -0.30 [-0.49, -0.10]; P = 0.002) (Table 4-5c). Bison abundance also tended to increase with winter temperature (β = 0.02 [-0.19, 0.22]; P = 0.864) and decrease with park-wide bison abundance (β = -0.06 [-0.23, 0.12]; P =0.524) (Table 4-5c). Pre-wolf reintroduction, bison abundance was strongly influenced by park-wide bison abundance, and minimally influenced by winter temperature and SWE (Fig. 4-6). Post-wolf reintroduction, bison abundance was strongly influenced by SWE, and minimally influenced by park-wide bison abundance, and winter temperature (Fig. 4-6).

Relationship between park-wide and Pelican Valley bison abundances

Pre-wolf reintroduction, the number of bison wintering in Pelican Valley tracked park-wide bison abundance (Fig. 4-6 & 4-7a). However, after wolf reintroduction, that relationship deteriorated (Fig. 4-6 & 4-7b), and snow conditions became the primary driver of bison abundance in Pelican Valley (Fig. 4-6 & 4-7c-d). To assess whether this pattern was a methodological artifact, I compared a set of competing models using data from the entire study period (i.e., 1971-2014). Each model included an interaction between park-wide bison abundance and year (i.e., 1972 – 2013). Year was categorized as a binary variable (e.g., for 1980, all years < 1980 = 0 and all years ≥ 1980 = 1). Models also included main effects for SWE and winter temperature. The top model indicated a threshold at 1995 at which time Pelican Valley bison abundance was no longer strongly influenced by park-wide bison abundance (Table 4-6). There was also support for a breakpoint at 2002 ($\Delta AIC_c = 0.98$; Table 4-6).

Discussion

Results from this study are consistent with the hypothesis that wolf predation risk may have played a role in reducing the numbers of bison that spend winter in the most environmentally-challenging portion of Yellowstone's historic bison winter range. The potential for bison to respond to wolf predation risk is well-documented in studies of other wolf-bison systems. These responses range from fine-scale changes in winter habitat selection (Fortin *et al.* 2009) and movement (Harvey & Fortin 2013) to large-scale shifts in space use (≤ 47 km) following attacks (Carbyn, Oosenbrug & Anions 1993). Several lines of evidence highlight the potential for wolves to decrease the numbers of bison wintering in Yellowstone's Pelican Valley.

First, bison wintering in Pelican Valley (1995-2014) were more vulnerable to predation than bison using other park winter ranges. The Yellowstone winter landscape varies between deep snow cover and geothermal and windswept ‘patches’ of snow-free ground that ungulates use for both foraging and safety (MacNulty & Smith 2004). My results suggest that the ability of wolves to hunt bison was linked to extensive snow cover (Fig. 4-2b), thus, bison were more vulnerable to predation in habitats with severe snow conditions. In Pelican Valley, patches of snow-free ground are smaller and less numerous than in other regions of the park (Meagher 1971; Meagher 1973), making this landscape more risky for bison (Smith *et al.* 2000). Furthermore, although elk are the primary prey species for wolves in Yellowstone (Smith *et al.* 2004; Metz *et al.* 2012), bison are the only ungulate prey that remain in Pelican Valley throughout the winter. A lack of alternative prey probably also heightened wolf predation risk (Smith *et al.* 2000).

Second, bison were sensitive to variation in wolf predation risk in Pelican Valley. They spatially responded to this risk by adjusting their use of snow-free patches to decrease their vulnerability to wolves. Interestingly, bison responded to cumulative predation risk (Fig. 4-3a); bison moved to safer habitats (i.e., areas with more snow-free ground) when wolves stayed longer in the valley (Fig. 4-3b). Even though bison spatially responded to predation risk, Pelican Valley bison were always more likely to use risky, rather than safe, habitats (Fig. 4-3b). Preference for risky habitats was probably due to the low availability of safe habitats within the valley (Fig. 4-3c), and the need to access limited winter forage (Meagher 1973; Meagher, Taper & Jerde 2001). An inability of bison to balance predation risk with foraging requirements during winter could help explain decreased preference for this region after wolf-reintroduction.

Third, my results suggest that the number of bison wintering in Pelican Valley decreased after wolves were reintroduced to the system (Fig. 4-4c). Model predictions indicate that, in the absence of wolves, a greater number of bison would have continued to winter in Pelican Valley after 1996 (Fig. 4-5b). Interestingly, bison preference for the Pelican Valley winter range initially tracked park-wide bison abundance, but this relationship deteriorated around 1995, the initial year wolves were reintroduced (Fig. 4-6; Fig. 4-7a-b).

In mountainous areas, ungulate predation risk in winter increases as a function of elevation due to progressively greater snow depths that hinder the ability to escape from predators. The high elevation Pelican Valley region is the most environmentally-extreme winter range for bison in Yellowstone; bison there endure long winters characterized by deep snow conditions. After wolf reintroduction, bison preference for wintering in Pelican Valley grew more sensitive to snow conditions (Fig. 4-6; Fig. 4-7c-d), even though snowpack (SWE) did not change between pre- and post-wolf periods ($t(35.93) = 1.55$, $p = 0.13$). Because snow is an index of risk, this enhanced sensitivity is potentially a response to wolf predation risk.

Finally, the severe winter landscape of Pelican Valley restricted bison group formation (Meagher 1973; Meagher, Taper & Jerde 2001), increasing bison susceptibility to wolf predation. Wolves are more successful at hunting small mixed groups of bison, compared to bulls or larger mixed groups. My results suggest that bison required relatively large tracts of snow-free ground to form larger groups. However, most patches of snow-free ground in Pelican Valley were small (Fig. 4-3c), which likely constrained mixed group size during winter (2004-2008, mean ±SE =

11.88 ± 0.98). In addition, between 1996 and 2014, the mean annual size of the resident wolf pack (i.e., Mollies) was large enough to effectively hunt bison (mean (± SD) = 10.7 ± 4.7; median = 11.5; range: 2-19) (MacNulty *et al.* 2014).

The results of this case study contribute towards understanding the large-scale changes in bison distribution that have occurred over the last 20 years in Yellowstone. Historically, the majority of the bison population wintered in the central range (Meagher 1973), but this pattern switched around 2005; a greater proportion of the bison population now winters in northern Yellowstone (Geremia *et al.* 2011). Our results are consistent with the expectation that bison wintering in the central, rather than northern, range would be more susceptible to predation after wolf reintroduction (Singer 1992). In the high elevation central range, winters are more severe, patches of bare ground used for foraging and safety are less numerous, and there is a lower abundance of alternative prey. Because the ability of wolves to hunt bison is closely linked to snow conditions, it is possible that wolf predation risk contributed to the declining number of bison wintering in the central range of Yellowstone.

However, there are several alternative explanations for decreased bison use of Yellowstone's central range. First, changes in management resulted in the large scale culling of bison herds at the park boundaries (White *et al.* 2011) which could have facilitated collective memory loss of specific winter ranges, such as Pelican Valley. However, mixed groups of bison persisted in Pelican Valley during culling operations, implying that at least some portion of the bison population would have retained memory for this winter range. Furthermore, my results suggest that culling was unrelated to the decline in bison abundance in Pelican Valley; the effect of culling on bison abundance was marginal ($\beta = 0.03$ [-0.11, 0.18]; $P = 0.63$), and the term was dropped from the final model ($\chi^2_1 = 0.22$, $P = 0.64$). It has also been argued that the grooming of park roads for the use of over-the-snow vehicles triggered the movement of bison from the central to the northern range (Meagher 1993; Meagher, Taper & Jerde 2001). However, several studies make clear that road grooming did not alter the movement patterns of central range bison (Bjornlie & Garrott 2001; Bruggeman *et al.* 2009a). Ripple *et al.* (2010) suggested that wolf reintroduction triggered a secondary trophic cascade, causing bison migration to the northern range because of decreased competition with the diminished elk population. However, because there is minimal diet overlap between bison and elk, intraspecific, rather than interspecific, competition is a more plausible driver of bison habitat use (Singer & Norland 1994). The best evidence to date suggests that large scale changes to bison movement and distribution were primarily triggered by high densities of bison in the parks interior, causing increased intraspecific competition for limited food resources during winter (Bruggeman *et al.* 2009b; Fuller, Garrott & White 2009; Geremia *et al.* 2011). All of these studies, however, neglected to test for an effect of wolves. My case study suggests that wolf predation risk should be incorporated into the suite of factors that could affect bison habitat use and movement in Yellowstone.

It is particularly important to test for an effect of wolves on bison movement and distribution in Yellowstone in future research, as predation pressure on bison wintering in the central range will likely continue to increase. In the central range, the abundance of alternative prey (i.e., elk) during winter has declined dramatically, leaving bison as the only viable ungulate prey for resident wolf packs. Elk do not over-winter in either Hayden or Pelican Valley. In the Madison/Firehole, the resident elk herd underwent sharp declines after wolf reintroduction (Hamlin *et al.* 2009); the elk population that once over-wintered in the Madison/Firehole region are now almost extirpated (R. Garrott; *personal communication*). Furthermore, since 2008, the number of wolves counted in the interior of the park has been consistently larger than the number of wolves in the northern range (Smith *et al.* 2016). These shifts suggest that, during winter, the Madison/Firehole region in the central range of Yellowstone has transitioned from a wolf-elk system to a wolf-bison system. The full effects of wolf recovery may take decades to unfold (Smith, Peterson & Houston 2003), and the observed and projected trends in wolf, bison, and elk demography and habitat use throughout the park suggest that wolves may have stronger effects on bison distribution, movement and behavior in the future.

Understanding how the winter landscape affects predation risk and prey behavior is of primary importance in understanding the potential impacts of climate change on predator-prey interactions, and their cascading effects within ecosystems (Post *et al.* 1999). Predator-prey interactions may be vulnerable to climate induced transitions (Post *et al.* 1999), particularly in systems where predator hunting efficiency and prey vulnerability are tightly coupled with climate conditions. My results suggest that decreased bison abundance in Pelican Valley during winter may partly reflect a behavioral shift in response to spatial predation risk, characterized by snow conditions. Increasingly mild winters in Yellowstone (Chang & Hansen 2015) could relax predation risk, promoting an increase in the number of bison wintering in Pelican Valley, and other interior regions of the park. Interestingly, a 2016 survey discovered a small mixed group of bison wintering in the Pelican Valley region (C. T. Wyman; *personal communication*); to my knowledge, this is the first time mixed groups have wintered there since 2008.

This study uniquely links individual level behavioral mechanisms (i.e., fine-scale spatial response to predation risk) with population level patterns (i.e., long-term trends in the use of high risk winter range) to explore the hypothesis that a cursorial predator contributes to shifts in prey habitat use in response to predation risk. Ambush predators are expected to incite stronger spatial responses by prey than coursing predators, because their landscape-specific risk cues are more consistent through time (Schmitz 2005). However, my results suggest that even coursing predators can produce consistent risk cues when their hunting success is tightly coupled with landscape characteristics. In this case study, the hunting success of the cursorial predator (wolves) was directly tied to snow conditions. The direct link between prey (bison) vulnerability and snow conditions incited fine-scale changes in prey habitat use in response to extended predator presence. Thus, it is possible that predator reintroduction, contributed to decreased prey preference for winter range that was spatially risky (i.e., high elevation habitat with severe winter conditions) at the landscape level in a large scale free-living system. Importantly, the availability of an alternative, safe habitat (i.e., lower elevation habitat with milder winter conditions) likely regulated the ability of prey to respond to risk at the landscape level. This is important for understanding the consequences of predator restoration and recovery on prey populations. During extended predator absence, prey populations may expand into habitats that would have otherwise been high risk. The reintroduction and recovery of predators could, therefore, cause prey populations to abandon high risk habitats, resulting in range contractions or shifts.

References

Bangs, E.E. & Fritts, S. (1996) Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin,* **24,** 402-413.

Bates, D. & Maechler, M. (2014) Package 'lme4': Linear mixed-effects models using S4 classes.

Becker, M.S., Garrott, R.A., White, P.J., Gower, C.N., Bergman, E.J. & Jaffe, R. (2009) Wolf prey selection in an elk-bison system: Choice or circumstance? *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 305-337. Elsevier, San Diego, CA.

Beyer, H. (2012) Geospatial Modelling Environment

Bjornlie, D.D. & Garrott, R.A. (2001) Effects of winter road grooming on bison in Yellowstone National Park. *The Journal of Wildlife Management,* **65,** 560-572.

Bruggeman, J.E., Garrott, R.A., White, P.J., Bjornlie, D.D., Watson, F.G. & Borkowski, J. (2009a) Bison winter road travel: facilitated by road grooming or a manifestation of natural trends. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 604-621. Elesevier, San Diego, CA.

Bruggeman, J.E., White, P., Garrott, R. & Watson, F.G. (2009b) Partial migration in central Yellowstone bison. *The ecology of large mammals in central Yellowstone:*

Sixteen years of integrated field studies (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 217-235. Elsevier, San Diego, CA.

Bruskotter, J. & Shelby, L. (2010) Human dimensions of large carnivore conservation and management: introduction to the special issue. *Human Dimensions of Wildlife,* **15,** 311-314.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodal inference, a practical information theoretic approach,* 2nd edn. Springer-Verlag, New York.

Carbyn, L.N. (1983) Wolf predation on elk in Riding Mountain National Park, Manitoba. *The Journal of Wildlife Management,* **47,** 963-976.

Carbyn, L.N., Oosenbrug, S. & Anions, D. (1993) *Wolves, Bison and the Dynamics Related to the Peace-Athabaska Delta in Canada's Wood Buffalo National Park.* Circumpolar Research Series Number 4; Canadian Circumpolar Institute, Edmonton, Alberta.

Carbyn, L.N. & Trottier, T. (1987) Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Canadian Journal of Zoology,* **65,** 2072-2078.

Chang, T. & Hansen, A. (2015) Historic & projected climate change in the Greater Yellowstone Ecosystem. *Yellowstone Science*, pp. 14-19. Yellowstone National Park.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H., Lopez-Bao, J.V., Adamec, M., Alvares, F., Anders, O., Balciauskas, L., Balys, V., Bedo, P., Bego, F., Blanco, J.C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjager, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremic, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majic, A., Mannil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Myslajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunovic, M., Persson, J., Potocnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinsek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Vana, M., Veeroja, R., Wabakken, P., Wofl, M., Wolfl, S., Zimmermann, F., Zlatanova, D. & Boitani, L. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science,* **346,** 1517-1519.

Estes, J.A. & Duggins, D. (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs,* **65,** 75-100.

Farnes, P.C. (2012) Value added products. *Proceedings of 80th Annual Western Snow Conference*, pp. 33-44. Anchorage, AK.

Ford, A., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M., Ward, D., Woodroffe, R. & Pringle, R.M. (2014) Large carnivores make savanna tree communities less thorny. *Science,* **346,** 346-349.

Fortin, D. & Fortin, M.-E. (2009) Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. *Animal Behaviour,* **78,** 887-892.

Fortin, D., Fortin, M., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009) Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology,* **90,** 2480-2490.

Fortin, D., Fryxell, J.M., O'Brodovich, L. & Frandsen, D. (2003) Foraging ecology of bison at the landscape and plant community levels the applicability of energy maximization principles. *Oecologia,* **134,** 219-227.

Fuller, J.A., Garrott, R.A. & White, P.J. (2009) Emigration and density dependence in Yellowstone bison. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 237-254. Elsevier Inc., San Diego, CA.

Gaillard, J., Festa-Bianchet, M., Yoccoz, N., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics,* **31,** 367-393.

Geremia, C., Wallen, R.L. & White, P.J. (2015) Population dynamics and adaptive management of Yellowstone bison. National Park Service, Yellowstone National Park, Mammoth, WY.

Geremia, C., White, P.J., Hoeting, J., Wallen, R.L., Watson, F.G., Blanton, D. & Hobbs, N.T. (2014) Integrating population- and individual-level information in a movement model of Yellowstone bison. *Ecological Applications,* **24,** 346-362.

Geremia, C., White, P.J., Wallen, R.L., Watson, F.G., Treanor, J.J., Borkowski, J., Potter, C.S. & Crabtree, R.L. (2011) Predicting bison migration out of Yellowstone National Park using bayesian models. *PLoS One,* **6,** e16848.

Hamlin, K.L., Garrott, R.A., White, P.J. & Cunningham, J.A. (2009) Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 541-577. Elsevier, San Diego, CA.

Harvey, L. & Fortin, D. (2013) Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in wolf country. *PLoS One,* **8,** e73324.

Heithaus, M.R. & Dill, L.M. (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology,* **83,** 480-491.

Hernández, L. & Laundré, J.W. (2005) Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology,* **11,** 215-220.

Hess, S. (2002) Aerial survey methodology for bison population estimation in Yellowstone National Park. Dissertation., Montana State University.

Houston, D. (1982) *The Northern Yellowstone Elk: Ecology and Management*. MacMillan, New York, NY.

Huggard, D.J. (1993) Effect of Snow Depth on Predation and Scavenging by Gray Wolves. *The Journal of Wildlife Management,* **57,** 382-388.

Jackman, S. (2015) Package 'pscl': Classes and methods for R developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University, Stanford, California.

Kauffman, M.J., Brodie, J.F. & Jules, E.S. (2010) Are wolves saving Yellowstone's aspen A landscape-level test of a behaviorally mediated trophic cascade. *Ecology,* **91,** 2742-2755.

Long, J. (1997) *Regression Models for Categorical and Limited Dependent Variables*. Thousand Oaks: Sage Publications.

MacNulty, D.R. (2002) The predatory sequence and the influence of injury risk on hunting behavior in the wolf. Master of Science, The University of Minnesota.

MacNulty, D.R., Mech, L.D. & Smith, D.W. (2007) A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy,* **88,** 595-605.

MacNulty, D.R., Plumb, G.E. & Smith, D.W. (2008) Validation of a new video and telemetry system for remotely monitoring wildlife. *Journal of Wildlife Management,* **72,** 1834-1844.

MacNulty, D.R. & Smith, D.W. (2004) Bison foraging response to the risk of wolf predation in a spatially heterogeneous winter environment: a preliminary assessment. (ed. H.J. Harlow). National Park Service Research Center, University of Wyoming.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2012) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology,* **23,** 75-82.

MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W. (2014) Influence of group size on the success of wolves hunting bison. *PLoS One,* **9,** e112884.

Mazerolle, M.J. (2014) Package 'AICcmodavg': Model selection and multimodel inference based on (Q)AIC(c).

Meagher, M. (1971) Snow as a Factor Influencing Bison Distribution and Numbers in Pelican Valley, Yellowstone National Park. 63-67.

Meagher, M. (1993) Winter recreation-induced changes in bison numbers and distribution in Yellowstone National Park. Unpublished National Park Service report, Yellowstone National Park, Wymoing, USA.

Meagher, M., Taper, M.L. & Jerde, C.L. (2001) Recent changes in population distribution the Pelican bison and the domino effect. *6th Biennial Scientific Conference*, pp. 135-147.

Meagher, M.M. (1973) *The Bison of Yellowstone National Park*. National Park Service, Washington D.C.

Mech, L.D. & Peterson, R.O. (2003) Wolf-Prey Relations. *Wolves: Behavior, Ecology and Conservation* (eds L.D. Mech & L. Boitani), pp. 131-160. The University of Chicago Press, Chicago, IL.

Mech, L.D., Smith, D.W. & MacNulty, D.R. (2015) *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press, USA.

Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology,* **81,** 553-563.

Min, Y. & Agresti, A. (2002) Modeling nonnegative data with clumping at zero: A survey. *Journal of the Iranian Statistical Society,* **1,** 7-33.

Nelson, M.E. & Mech, L.D. (1986) Relationship between Snow Depth and Gray Wolf Predation on White-tailed Deer. *The Journal of Wildlife Management,* **50,** 471-474.

Newman, W. & Watson, F.G.R. (2009) The central Yellowstone landscape: terrain, geology, climate, vegetation. *The Ecolog of Large Mammals in Central Yellowstone* (eds R. Garrott, P.J. White & F.G.R. Watson), pp. 17-36. Elsevier, San Diego, CA.

Packer, C. & Ruttan, L. (1988) The evolution of cooperative hunting. *Am Nat,* **132,** 159-198.

Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature,* **401,** 905-907.

Preisser, E.L., Bolnick, D.I. & Benard, M. (2005) Resource competition modifies the strength of trait-mediated predator-prey interactions. *Ecology,* **86,** 501-509.

Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology,* **88,** 2744-2751.

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ripple, W.J., Painter, L., Beschta, R.L. & Gates, C.C. (2010) Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. *The Open Ecology Journal,* **3,** 31-37.

Schmitz, O.J. (2005) Behavior of predators and prey and links with population level processes. *Ecology of Predator Prey Interactions* (eds P. Barbosa & I. Castellanos), pp. 256-278. Oxford University Press, New York, NY.

Schmitz, O.J., Beckerman, A. & O'Brien, K. (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology,* **78,** 1388-1399.

Sikes, R., Gannon, W. & Amer Soc M (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy,* **92,** 235-253.

Singer, F.J. (1992) Some predictions concerning a wolf recovery in to Yellowstone National Park: How wolf recovery may affect park visitors, ungulates, and other predators. *Wolves for Yellowstone? A Report to the United States Congress* (eds J. Varley & W. Brewster).

Singer, F.J. & Norland, J. (1994) Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. *Canadian Journal of Zoology,* **72,** 1393-1394.

Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management,* **68,** 153-166.

Smith, D.W., Mech, L.D., Meagher, M., Clark, W., Jaffe, R., Phillips, M.K. & Mack, J.A. (2000) Wolf-bison interactions in Yellowstone National Park. *Journal of Mammalogy,* **81,** 1128-1135.

Smith, D.W., Peterson, R.O. & Houston, D.B. (2003) Yellowstone after wolves. *BioScience,* **53,** 330-340.

Smith, D.W., Stahler, D.R., Metz, M.C., Cassidy, K., Stahler, E., Almberg, E. & McIntyre, R. (2016) Wolf restoration in Yellowstone: Reintroduction to recovery. *Yellowstone Science*, pp. 5-12. Yellowstone National Park, Mammoth, WY.

Stahler, E., Smith, D.W. & Stahler, D.R. (2016) Wolf turf: a glimpse at 20 years of spatial ecology in Yellowstone. *Yellowstone Science*, pp. 50-54. National Park Service, Mammoth, WY.

Tambling, C.J., Druce, D.J., Hayward, M.W., Castley, J.G., Adendorff, J. & Kerley, G.I.H. (2012) Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology,* **96,** 1297-1304.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science,* **294,** 1923-1926.

Venables, W.N. & Ripley, B.D. (2002) Modern Applied Statistics with S. Springer, New York.

Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *Oikos,* **111,** 259-270.

Weiss, R. (2005) *Modeling longitudinal data*. Springer, New York, NY.

Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology,* **84,** 1083-1100.

White, P.J., Wallen, R.L., Geremia, C., Treanor, J.J. & Blanton, D. (2011) Management of Yellowstone bison and brucellosis transmission risk -

Implications for conservation and restoration. *Biological Conservation,* **144,** 1322-1334.

Tables and Figures

Table 4-1. Model-selection results for GLMMs describing the effects of snow-free area (m^2), measured at increasing 10 m radii (i.e., 10 m-90 m) on the probability that wolves attacked (a) and captured (b) bison in Pelican Valley, Yellowstone National Park. Null models contain the intercept and a random intercept for encounter identity. Log-likelihood (LL), number of parameters (*K*), AIC_c, differences in AIC_c compared to the best scoring model (ΔAIC_c), and AIC_c weights (*W*) are given for each model. The top models ($\Delta AIC < 2$) are highlighted in **bold**.

Model	LL	*K*	AIC_c	ΔAIC_c	*W*
(a) Attacking					
snow-free area 50 m	**-94.46**	**3**	**195.06**	**0.00**	**0.16**
snow-free area 60 m	**-94.51**	**3**	**195.16**	**0.10**	**0.16**
snow-free area 40 m	**-94.60**	**3**	**195.36**	**0.29**	**0.14**
snow-free area 70 m	**-94.72**	**3**	**195.60**	**0.53**	**0.13**
snow-free area 20 m	**-94.94**	**3**	**196.02**	**0.96**	**0.10**
snow-free area 30 m	**-94.94**	**3**	**196.03**	**0.97**	**0.10**
snow-free area 80 m	**-95.15**	**3**	**196.45**	**1.38**	**0.08**
snow-free area 10 m	**-95.43**	**3**	**197.00**	**1.94**	**0.06**
snow-free area 90 m	-95.71	3	197.57	2.51	0.05
null	-97.44	2	198.95	3.89	0.02
(b) Capturing					
snow-free area 20 m	**-30.35**	**3**	**66.96**	**0.00**	**0.64**
snow-free area 10 m	-32.51	3	71.27	4.31	0.07
snow-free area 30 m	-32.81	3	71.89	4.93	0.05
snow-free area 90 m	-33.12	3	72.5	5.55	0.04
null	-34.20	2	72.54	5.58	0.04
snow-free area 40 m	-33.27	3	72.81	5.85	0.03
snow-free area 60 m	-33.33	3	72.92	5.97	0.03
snow-free area 50 m	-33.35	3	72.95	6.00	0.03
snow-free area 70 m	-33.45	3	73.16	6.21	0.03
snow-free area 80 m	-33.57	3	73.4	6.44	0.03

Table 4-2. Model-selection results for CLMMs predicting the effects of predation risk, bison group size, and wolf activity period on the probability that bison used habitats with low (0-1212 m^2), medium (1220-3870 m^2), or high (3870-7780 m^2) amounts of snow-free ground in Pelican Valley, Yellowstone National Park. Wolf presence was measured as the number of days wolves were present in the valley within 1 (a), 2 (b), 3 (c), 4 (d), 5 (e), 6 (f), and 7 (g) day(s) previous to the scan. All models include random effects for scan identity, nested within year, and the null model includes an intercept plus the random intercepts. Log-likelihood (LL), number of parameters (*K*), AIC$_c$, differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (*W*) are given for each model. The top models (ΔAIC < 2) are highlighted in **bold**. 'Wolf presence' (e.g., wolf 1, wolf 2, etc.) and 'bison group size' are continuous variables. 'Wolf activity' represents whether the scan took place during the time of day when wolves were generally inactive (0) or active (1). The number of years/scans/observations included in each analysis is 4/139/3877 (1-day), 4/136/3714 (2-days), 4/129/3459 (3-days), 4/120/3165 (4-days), 4/108/2846 (5-days), 4/92/2422 (6-days), and 4/80/2110 (7-days).

Model Set	LL	K	AICc	ΔAICc	W
(a) Wolf presence (1 day)					
bison group size + wolf activity	**-2127.04**	**5**	**4264.53**	**0.00**	**0.41**
wolf 1 + bison group size	**-2127.60**	**5**	**4265.65**	**1.12**	**0.23**
bison group size	**-2127.64**	**5**	**4265.73**	**1.20**	**0.22**
wolf 1 + bison group size + activity	-2127.01	6	4266.66	2.13	0.14
null	-2196.26	3	4398.70	134.17	0.00
wolf 1	-2196.23	4	4400.77	136.24	0.00
wolf 1 + wolf activity	-2195.75	5	4401.94	137.41	0.00
wolf activity	-2195.76	6	4404.15	139.62	0.00
(b) Wolf presence (2 days)					
bison group size + wolf activity	**-2069.74**	**5**	**4149.95**	**0.00**	**0.41**
wolf 2 + bison group size	**-2070.30**	**5**	**4151.07**	**1.12**	**0.23**
bison group size	**-2070.35**	**5**	**4151.17**	**1.22**	**0.22**
wolf 2 + bison group size + activity	-2069.71	6	4152.07	2.12	0.14
null	-2138.38	3	4282.93	132.99	0.00
wolf 2	-2138.38	4	4285.06	135.11	0.00
wolf 2 + wolf activity	-2137.90	5	4286.26	136.31	0.00
wolf activity	-2137.90	6	4288.45	138.50	0.00
(c) Wolf presence (3 days)					
bison group size + wolf activity	**-1982.43**	**5**	**3975.35**	**0.00**	**0.38**
wolf 3 + bison group size	**-1982.85**	**5**	**3976.19**	**0.84**	**0.25**
bison group size	**-1983.00**	**5**	**3976.49**	**1.14**	**0.22**
wolf 3 + bison group size + activity	**-1982.28**	**6**	**3977.26**	**1.91**	**0.15**
null	-2052.18	3	4110.55	135.20	0.00
wolf 3	-2052.18	4	4112.67	137.33	0.00
wolf 3 + wolf activity	-2051.75	5	4113.99	138.64	0.00
wolf activity	-2051.75	6	4116.19	140.84	0.00

Table 4-2 cont.

(d) Wolf presence (4 days)					
bison group size + wolf activity	**-1838.45**	**5**	**3687.42**	**0.00**	**0.41**
wolf 4 + bison group size	**-1839.04**	**5**	**3688.60**	**1.18**	**0.23**
wolf 4 + bison group size + activity	**-1838.15**	**6**	**3689.05**	**1.63**	**0.18**
bison group size	**-1839.33**	**5**	**3689.18**	**1.76**	**0.17**
null	-1902.59	3	3811.38	123.97	0.00
wolf 4	-1902.51	4	3813.36	125.94	0.00
wolf 4 + wolf activity	-1901.90	5	3814.32	126.91	0.00
wolf activity	-1901.99	6	3816.73	129.31	0.00
(e) Wolf presence (5 days)					
wolf 5 + bison group size	**-1702.37**	**5**	**3415.32**	**0.00**	**0.33**
bison group size + wolf activity	**-1702.52**	**5**	**3415.62**	**0.30**	**0.28**
wolf 5 + bison group size + activity	**-1701.46**	**6**	**3415.75**	**0.42**	**0.27**
bison group size	-1703.39	5	3417.37	2.05	0.12
wolf 5	-1756.85	4	3522.10	106.77	0.00
wolf 5 + wolf activity	-1755.97	5	3522.53	107.20	0.00
null	-1758.34	3	3522.91	107.58	0.00
wolf activity	-1757.59	6	3528.01	112.69	0.00
(f) Wolf presence (6 days)					
wolf 6 + bison group size	**-1449.51**	**5**	**2909.72**	**0.00**	**0.33**
bison group size + wolf activity	**-1449.65**	**5**	**2909.99**	**0.27**	**0.29**
wolf 6 + bison group size + activity	**-1448.63**	**6**	**2910.26**	**0.54**	**0.26**
bison group size	-1450.57	5	2911.83	2.11	0.12
wolf 6	-1495.18	4	2998.82	89.10	0.00
wolf 6 + wolf activity	-1494.49	5	2999.68	89.96	0.00
null	-1497.77	3	3001.81	92.09	0.00
wolf activity	-1497.00	6	3006.98	97.26	0.00
(g) Wolf presence (7 days)					
wolf 7 + bison group size	**-1261.99**	**5**	**2534.79**	**0.00**	**0.55**
wolf 7 + bison group size + activity	**-1261.48**	**6**	**2536.10**	**1.32**	**0.28**
bison group size + wolf activity	-1263.31	5	2537.43	2.64	0.15
bison group size	-1263.88	6	2540.91	6.13	0.03
wolf 7	-1311.11	4	2630.75	95.97	0.00
wolf 7 + wolf activity	-1310.78	5	2632.37	97.58	0.00
null	-1314.15	3	2634.62	99.83	0.00
wolf activity	-1313.73	6	2640.60	105.82	0.00

Table 4-3. Parameter estimates predicting the probability that bison used habitats with a low (0-1212 m^2), medium (1220-3870 m^2), or high (3870-7780 m^2) amount of snow-free ground in Pelican Valley, Yellowstone National Park. Estimates of β-coefficients, SEs and 95% confidence intervals were taken from the top model ($\Delta AIC_c < 2$) from each CLMM model set that included a predation risk metric (Table 4-2). Measures include the total number of days wolves were present in the valley within 1 (a), 2 (b), 3 (c), 4 (d), 5 (e), 6 (f), and 7 (g) days prior to a scan (e.g., 'wolf 1', 'wolf 2', etc.). 'Bison group size' refers to the number of bison individuals < 100 m apart.

Parameter	β	SE	*95% CI*	
(a) Wolf presence (1 day)				
wolf 1	0.05	0.18	-0.30	0.41
bison group size	0.10	0.01	0.09	0.12
intercept 1|2	2.06	0.29	1.48	2.64
intercept 2|3	3.60	0.30	3.01	4.19
(b) Wolf presence (2 days)				
wolf 2	0.04	0.12	-0.20	0.28
bison group size	0.10	0.01	0.09	0.12
intercept 1|2	2.08	0.32	1.46	2.70
intercept 2|3	3.62	0.32	2.99	4.26
(c) Wolf presence (3 days)				
wolf 3	0.06	0.11	-0.15	0.27
bison group size	0.11	0.01	0.09	0.12
intercept 1|2	2.17	0.34	1.50	2.83
intercept 2|3	3.72	0.34	3.04	4.39
(d) Wolf presence (4 days)				
wolf 4	0.09	0.11	-0.13	0.30
bison group size	0.11	0.01	0.09	0.13
intercept 1|2	2.27	0.36	1.55	2.98
intercept 2|3	3.80	0.37	3.07	4.53
(e) Wolf presence (5 days)				
wolf5	0.14	0.09	-0.03	0.32
bison group size	0.11	0.01	0.09	0.13
intercept 1|2	2.45	0.34	1.78	3.13
intercept 2|3	3.98	0.35	3.28	4.67

Table 4-3 cont.

(f) Wolf presence (6 days)				
wolf 6	0.14	0.09	-0.03	0.31
bison group size	0.11	0.01	0.08	0.13
intercept 1|2	2.58	0.41	1.79	3.38
intercept 2|3	4.11	0.41	3.30	4.92
(g) Wolf presence (7 days)				
wolf 7	0.17	0.08	0.02	0.32
bison group size	0.11	0.01	0.09	0.14
intercept 1|2	2.86	0.44	2.00	3.72
intercept 2|3	4.40	0.45	3.52	5.28

Table 4-4. Model-selection results for models predicting the effects of collinear metrics of winter temperature (a), winter precipitation (b), and summer growing conditions (c) on winter bison abundance in Pelican Valley, Yellowstone National Park (1971-2014). Log-likelihood (LL), number of parameters (*K*), AIC$_c$, differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (*W*) are given for each model. Metrics are presented as the average (AVG), minimum (MIN), maximum (MAX), or total (SUM) for each variable. Total winter precipitation was measured from 1 November through 30 April; summer growing conditions were measured the previous summer from 1 May through 31 October.

Model Set	LL	K	AIC$_c$	ΔAIC$_c$	W
(a) Winter temperature					
AVG of AVG daily temperature (°C)	-261.22	2	526.72	0.00	0.60
AVG of MIN daily temperature (°C)	-262.25	2	528.80	2.08	0.21
AVG of MAX daily temperature (°C)	-262.42	2	529.13	2.41	0.18
(b) Winter precipitation					
MAX SWE (mm)	-258.18	2	520.66	0.00	0.79
SUM winter precipitation (mm)	-260.87	2	526.03	5.37	0.05
(c) Summer growing conditions					
SUM summer precipitation (mm)	-263.00	2	530.29	0.00	0.36
MAX growing degree days for grasses	-263.11	2	530.51	0.22	0.32
SUM growing season days for grasses	-263.12	2	530.52	0.23	0.32

Table 4-5. Parameter estimates, SEs, and 95% confidence intervals from the complete time series (a), pre-wolf (b), and post-wolf reintroduction (c) models predicting winter bison abundance in Pelican Valley, Yellowstone National Park. Variables were independently centered and scaled in all models. Measures included a binary term for ‘wolf reintroduction’ (i.e., all years < 1996 = 0 and all years ≥ 1996 = 1) (a), park-wide bison abundance (Bison YNP), a quadratic term for bison abundance (Bison YNP^2) (a-b), snow water equivalent (SWE) (mm), and winter temperature (Temperature) (°C).

Parameter	β	SE	*95% CI*	
(a) Complete time series model (1971-2014)				
Intercept	6.02	0.08	5.87	6.18
Wolf reintroduction	-0.35	0.13	-0.60	-0.11
Bison YNP	0.21	0.06	0.09	0.32
Bison YNP^2	-0.16	0.04	-0.24	-0.08
SWE	-0.13	0.05	-0.23	-0.04
Temperature	0.08	0.05	-0.02	0.18
(b) Pre-wolf model (1971-1995)				
Intercept	5.91	0.04	5.82	5.99
Bison YNP	0.38	0.03	0.32	0.44
Bison YNP^2	-0.13	0.03	-0.19	-0.06
SWE	0.01	0.03	-0.05	0.07
Temperature	0.02	0.03	-0.04	0.08
(c) Post-wolf model (1996-2014)				
Intercept	5.58	0.09	5.42	5.76
Bison (YNP)	-0.06	0.09	-0.23	0.12
SWE	-0.30	0.10	-0.49	-0.10
Temperature	0.02	0.10	-0.19	0.22

Table 4-6. Model-selection results for models predicting the effects of an interaction between park-wide bison abundance and year on winter bison abundance in Pelican Valley, Yellowstone National Park (1971-2014). A model with no interaction term was also included. Log-likelihood (LL), number of parameters (*K*), AIC$_c$, differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (*W*) are given for each model. The top models (ΔAIC < 2) are highlighted in **bold**. 'Year' is a categorical binomial variable representing a breakpoint for that year (e.g., for 1980, all years < 1980 = 0 and all years ≥ 1980 = 1). Other variables include park-wide bison abundance (park-wide bison), snow water equivalent (SWE) (mm), and winter temperature (winter temp) (°C). 'Year x park-wide bison' refers to an interaction between the two variables.

Model Set	LL	K	AICc	ΔAICc	W
year, park-wide bison, SWE, winter temp	-254.41	5	520.40	14.84	0.00
year(1972) x park-wide bison, SWE, winter temp	-254.69	6	523.65	18.09	0.00
year(1973) x park-wide bison, SWE, winter temp	-253.48	6	521.23	15.67	0.00
year(1974) x park-wide bison, SWE, winter temp	-251.74	6	517.76	12.19	0.00
year(1975) x park-wide bison, SWE, winter temp	-251.94	6	518.15	12.58	0.00
year(1976) x park-wide bison, SWE, winter temp	-252.10	6	518.48	12.91	0.00
year(1977) x park-wide bison, SWE, winter temp	-250.16	6	514.60	9.04	0.00
year(1978) x park-wide bison, SWE, winter temp	-249.43	6	513.13	7.56	0.01
year(1979) x park-wide bison, SWE, winter temp	-249.60	6	513.48	7.92	0.01
year(1980) x park-wide bison, SWE, winter temp	-249.45	6	513.18	7.62	0.01
year(1981) x park-wide bison, SWE, winter temp	-249.46	6	513.19	7.63	0.01
year(1982) x park-wide bison, SWE, winter temp	-249.24	6	512.75	7.19	0.01
year(1983) x park-wide bison, SWE, winter temp	-249.21	6	512.68	7.12	0.01
year(1984) x park-wide bison, SWE, winter temp	-249.18	6	512.62	7.06	0.01
year(1985) x park-wide bison, SWE, winter temp	-248.99	6	512.25	6.69	0.01
year(1986) x park-wide bison, SWE, winter temp	-248.94	6	512.16	6.60	0.01

Table 4-6 cont.

year(1987) x park-wide bison, SWE, winter temp	-249.29	6	512.85	7.29	0.01
year(1988) x park-wide bison, SWE, winter temp	-249.52	6	513.31	7.75	0.01
year(1989) x park-wide bison, SWE, winter temp	-247.45	6	509.16	3.60	0.05
year(1990) x park-wide bison, SWE, winter temp	-247.31	6	508.88	3.32	0.05
year(1991) x park-wide bison, SWE, winter temp	-247.03	6	508.33	2.76	0.07
year(1992) x park-wide bison, SWE, winter temp	-248.46	6	511.20	5.64	0.02
year(1993) x park-wide bison, SWE, winter temp	-248.06	6	510.39	4.83	0.03
year(1994) x park-wide bison, SWE, winter temp	-248.15	6	510.57	5.01	0.02
year(1995) x park-wide bison, SWE, winter temp	**-245.65**	**6**	**505.56**	**0.00**	**0.29**
year(1996) x park-wide bison, SWE, winter temp	-247.81	6	509.90	4.34	0.03
year(1997) x park-wide bison, SWE, winter temp	-249.57	6	513.41	7.85	0.01
year(1998) x park-wide bison, SWE, winter temp	-249.57	6	513.41	7.85	0.01
year(1999) x park-wide bison, SWE, winter temp	-249.55	6	513.36	7.80	0.01
year(2000) x park-wide bison, SWE, winter temp	-249.55	6	513.36	7.80	0.01
year(2001) x park-wide bison, SWE, winter temp	-248.17	6	510.61	5.05	0.02
year(2002) x park-wide bison, SWE, winter temp	**-246.13**	**6**	**506.54**	**0.98**	**0.18**
year(2003) x park-wide bison, SWE, winter temp	-249.45	6	513.18	7.62	0.01
year(2004) x park-wide bison, SWE, winter temp	-247.71	6	509.69	4.13	0.04
year(2005) x park-wide bison, SWE, winter temp	-247.15	6	508.58	3.02	0.06
year(2006) x park-wide bison, SWE, winter temp	-249.85	6	513.96	8.40	0.00
year(2007) x park-wide bison, SWE, winter temp	-249.88	6	514.03	8.47	0.00
year(2008) x park-wide bison, SWE, winter temp	-250.29	6	514.85	9.29	0.00
year(2009) x park-wide bison, SWE, winter temp	-251.38	6	517.03	11.46	0.00
year(2010) x park-wide bison, SWE, winter temp	-250.05	6	514.38	8.82	0.00

Table 4-6 cont.

year(2011) x park-wide bison, SWE, winter temp	-250.95	6	516.16	10.60	0.00
year(2012) x park-wide bison, SWE, winter temp	-249.97	6	514.22	8.66	0.00
year(2013) x park-wide bison, SWE, winter temp	-254.96	6	524.20	18.64	0.00

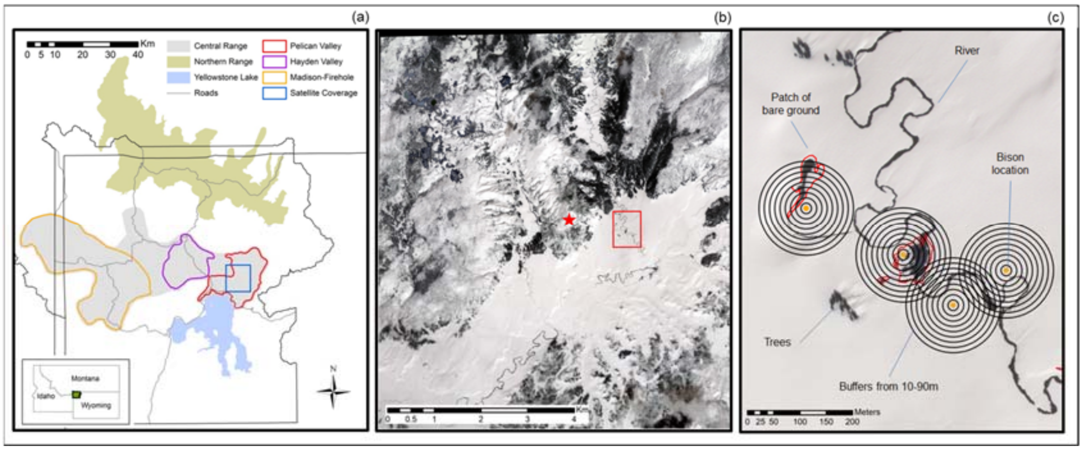


Fig. 4-1. Bison winter ranges in Yellowstone National Park (a), and a satellite image of Pelican Valley (b), including an enlarged section demonstrating the methods used to quantify the snowscape (c). Image (a) describes locations of the central (grey) winter ranges of Pelican Valley (red), Hayden Valley (purple), and the Madison/Firehole (orange), and the northern winter range (grey-green), as well as the area covered by satellite imagery (blue) (a). Field crews collected data from a central observation point in Pelican Valley, denoted with a red star (b). The enlarged section (red) of image (b) shows examples of patch location (red), bison location (orange), and the buffers used to calculate snow-free area (m^2) surrounding wolf-bison encounter and bison group locations (black) (c).

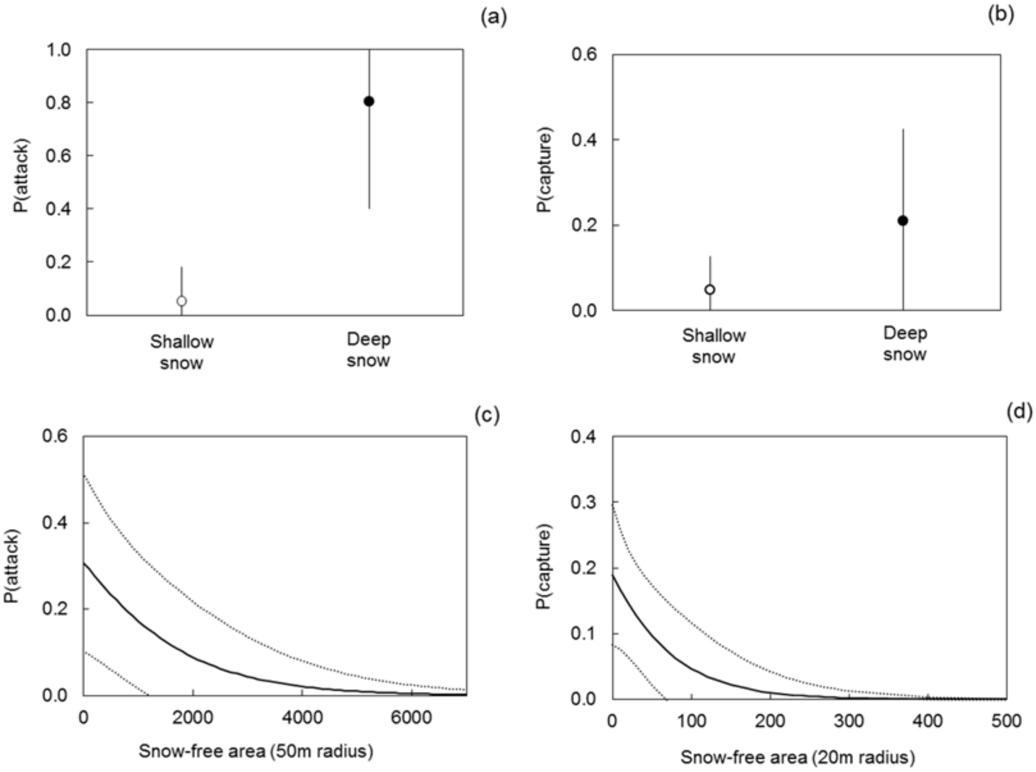


Fig. 4-2. Effects of snow depth on attacking (a) and capturing (b), and snow-free area within a 50 m and 20 m radius on attacking (c), and capturing (d), respectively. Snow depth, relative to the bison group at the location of each attempted attack and capture, is defined as either 'shallow' (e.g., no snow, packed snow, and hoof deep) or 'deep' (ankle, knee, and stomach deep). The lines are population-averaged predicted values with 95% confidence intervals from best-fit GLMM models (Table 4-1). The number of wolf-bison encounters/observations included in each analysis is 82/134 (a), 34/83 (b), 103/168 (c), and 43/97 (d).

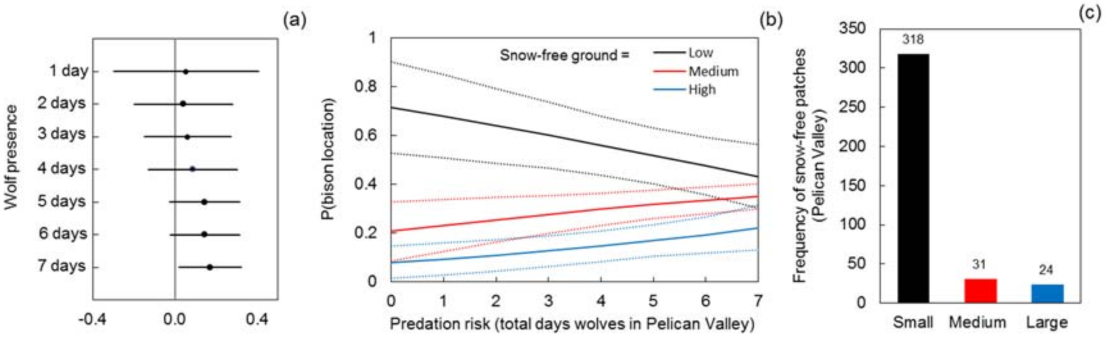


Fig. 4-3. Parameter estimates predicting bison spatial response to prior wolf presence (measured at 1-7 days) (a), the effect of wolf predation risk (i.e., the total number of days wolves were present within 7 days) on the probability that bison used habitats with a low (0-1212 m^2; black), medium (1220-3870 m^2; red), and high (3870-7780 m^2; blue) amount of snow-free ground (b), and the frequency of small (black), medium (red), and large (blue) patches (i.e., unique areas of snow-free ground) in Pelican Valley (c). Habitats with a low amount of snow-free ground (i.e., black) were riskier for bison, while habitats with a high amount of snow-free ground were safer (i.e., red and blue) (Fig. 4-2c-d). Estimates of β-coefficients and 95% confidence intervals in (a) were taken from the top model ($\Delta AIC_c < 2$) from each CLMM model set that included a predation risk metric (Table 4-2; 4-3). The lines in (b) are population-averaged predicted values and associated 95% confidence intervals from the best-fit CLMM model from the 7-day model set (Table 4-3). The number of years/scans/observations included in the 7-day analysis is 4/80/2110.

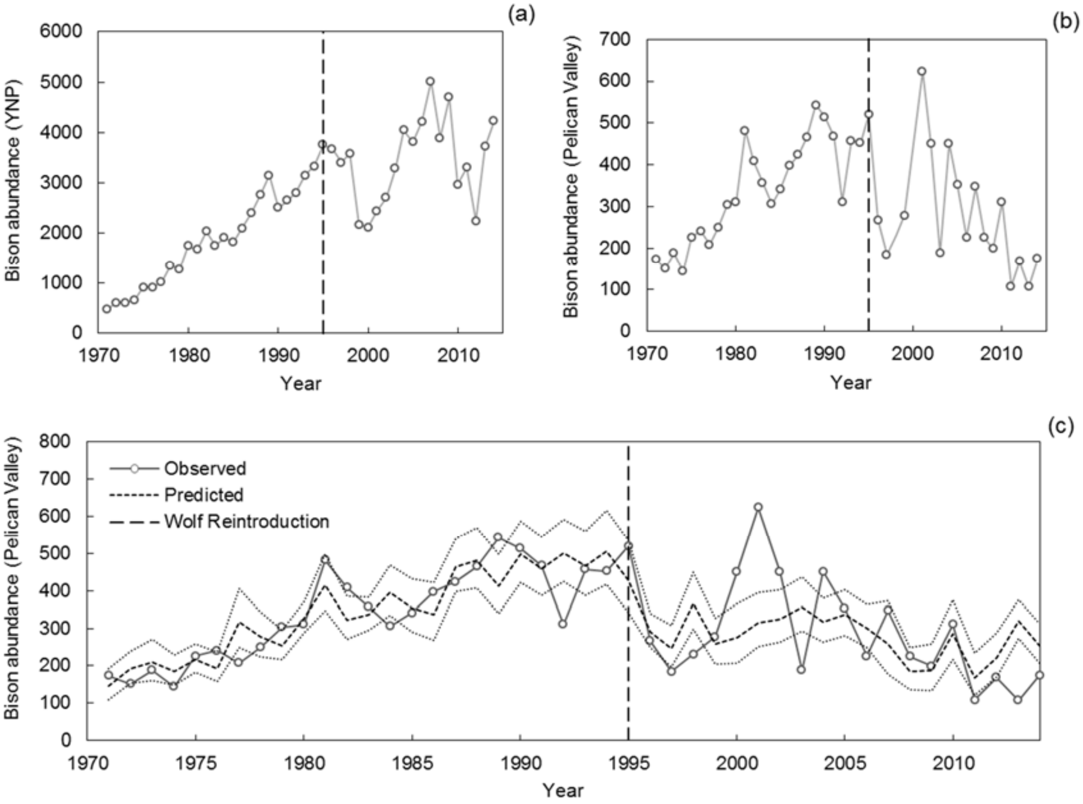


Fig. 4-4. The bison population in Yellowstone National Park (YNP) (a), winter bison abundance in Pelican Valley (b), and the observed (open circles) versus predicted (dashed line) abundance of bison wintering in Pelican Valley, 1971-2014, with associated 95% confidence intervals (c). Predictions in graph (c) are from the 'complete time series' model (i.e., 1971-2014) which included a binary term for wolf reintroduction. The vertical dashed lines represent the year that wolves were reintroduced to YNP (i.e., 1995). Open circles (a-b) are uncorrected count data for each year.

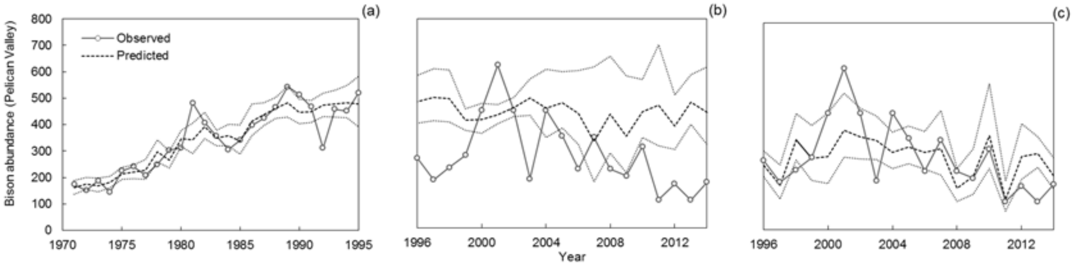


Fig. 4-5. The observed (open circles) versus predicted (dashed line) abundance of bison wintering in Pelican Valley, 1971-2014, with associated 95% confidence intervals. Predictions and 95% CI before (a) and after (b) wolf reintroduction estimated using the 'pre-wolf' model (i.e., 1971-1995). Predictions and 95% CI in graph (c) were estimated using the 'post-wolf' model (i.e., 1996-2014).

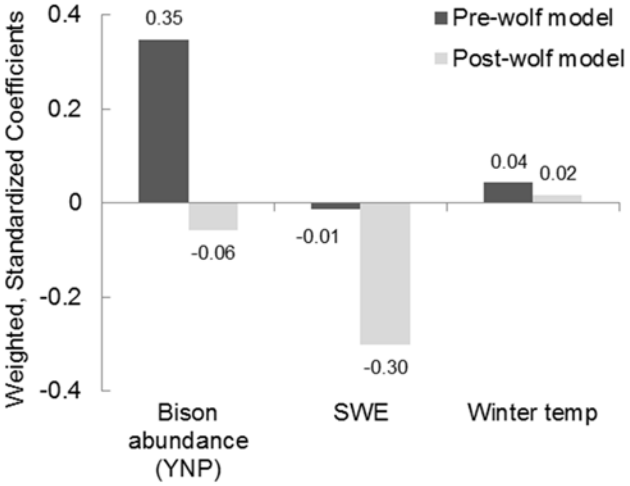


Fig. 4-6. The standardized regression coefficients, or the relative influence of park-wide bison abundance, maximum SWE (mm), and average daily winter temperature (°C) on winter bison abundance in Pelican Valley, for the 'pre-wolf' (dark grey) and 'post-wolf' (light grey) models. To facilitate comparison, park-wide bison abundance was included as a linear term in both the pre- and post-wolf models when calculating standardized regression coefficients.

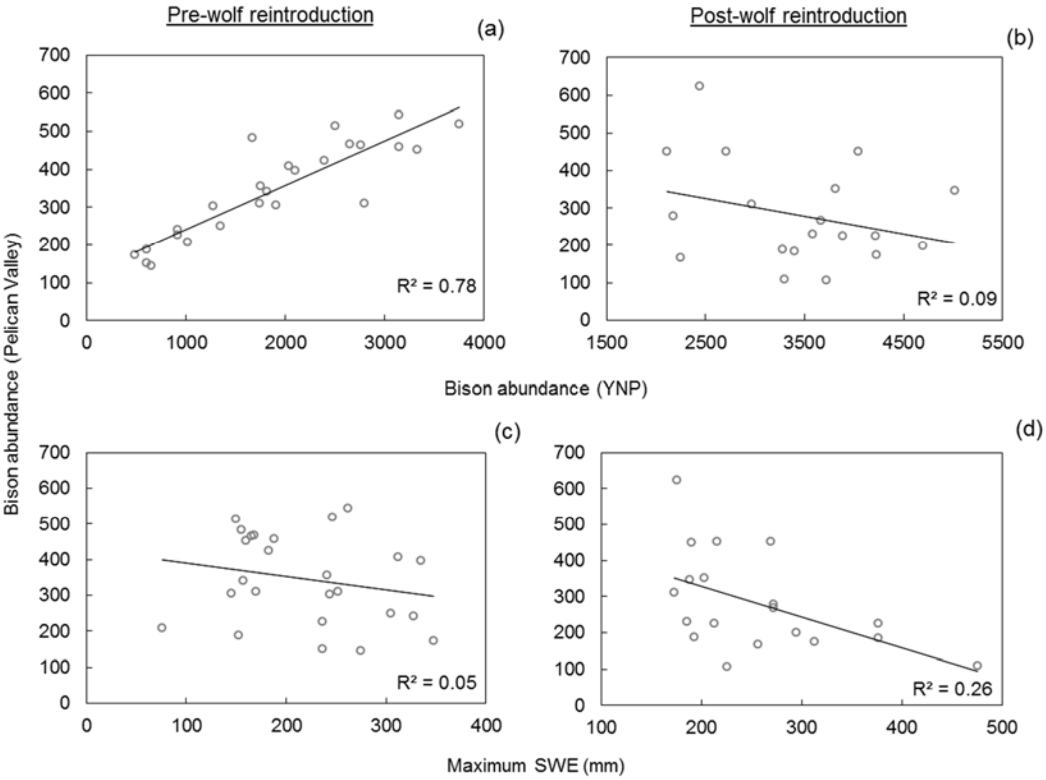


Fig. 4-7. The relationship between bison abundance in Pelican Valley and park-wide bison abundance pre- (a) and post- (b) wolf reintroduction, and between bison abundance in Pelican Valley and maximum snow water equivalent (SWE) pre- (c) and post- (d) wolf reintroduction. These graphs were generated using the raw data.

CHAPTER 5

COMPETITION BETWEEN APEX PREDATORS? BROWN BEARS DECREASE WOLF KILL RATE ON TWO CONTINENTS[3]

Abstract

Trophic interactions are a fundamental topic in ecology, but we know little about how competition between apex predators affects predation, the mechanism driving top-down forcing in ecosystems. We used long-term datasets from Scandinavia, Europe, and Yellowstone National Park, North America, to evaluate how gray wolf (*Canis lupus*) kill rate was affected by a sympatric apex predator, the brown bear (*Ursus arctos*). We used kill interval, i.e., the number of days between consecutive ungulate kills, as a proxy of kill rate. Although brown bears can monopolize wolf kills, we found no support in either study system for the common assumption that they cause wolves to kill more often. On the contrary, our results showed the opposite effect. In Scandinavia, wolf packs sympatric with brown bears killed less often than allopatric packs, during both spring, after bear den emergence, and summer. Similarly, the presence of bears at wolf-killed ungulates was associated with wolves killing less often during summer in Yellowstone. The consistency in results between the two systems suggests that brown bear presence actually reduces wolf kill rate. Our results suggest that the influence of predation on lower trophic levels may depend on the composition of predator communities.

---

[3] Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proc Roy Soc B.* 284: B20162368.

1. Introduction

Understanding the influence of top-down and bottom-up effects on ecosystem regulation is a central focus of ecology [e.g., 1, 2, 3]. Although the strength of top-down and bottom-up effects on prey abundance often varies through time [4, 5], predation is an important driver of prey population dynamics [6, 7]. The composition of predator communities can have profound effects on prey abundance [5, 8, 9] and the strength of top-down effects can be altered by competition between sympatric predators at the top level of trophic systems [10].

Interspecific interactions between predators are widespread in nature and play an important role in community structure and stability [11]. Ultimately, such interactions can either weaken or strengthen top-down effects by altering predator densities or predation patterns. Kleptoparasitism by competitors, for example, can negatively impact predator foraging efficiency [e.g., 12], limiting predator abundance and the impact of predation on prey populations [10]. Alternatively, theft of kills can result in increased predation [13, 14], potentially increasing the predator's impact on the prey population. Quantifying how competition between apex predators affects predation dynamics is an important step towards understanding the cascading ecological effects of such interactions.

Kill rate (i.e., the number of prey killed per predator per unit time) is an essential component of predation, yet we still have a limited understanding of how it is influenced by interspecific interactions between apex predators. Here, we analyzed how the kill rate of one apex predator and obligate carnivore, the gray wolf (*Canis lupus*), was affected by another, sympatric apex predator and omnivore, the brown bear (*Ursus arctos*). Brown bears are efficient, and typically dominant, scavengers of wolf-killed prey, which has motivated the assumption that wolf kill rate is higher where wolves are sympatric with brown bears [15, 16], because they are forced to hunt more often to compensate for the loss of food. Understanding how wolf kill rate is affected by bears is especially important, because these two species are largely sympatric in temperate climates [17], where wolves are usually a dominant predation force that can limit the abundance of prey populations [6].

We used data from two long-term studies in southcentral Scandinavia (SCA), Europe, and Yellowstone National Park (YNP), USA, in a first transcontinental attempt to evaluate the assumption that brown bears cause wolves to kill more often. In both systems, wolf predation has been a central research topic for over 15 years [18, 19]. We used kill interval (i.e., the number of days between consecutive ungulate kills) as a measure of kill rate and divided our analyses by season, as wolf kill rates vary throughout the year [18, 19]. We predicted that 1) kill interval of SCA wolf packs sympatric with brown bears would decrease across the spring bear den emergence period (March-May) as bears progressively emerged from winter dens; wolf packs allopatric with brown bears should exhibit no such decline. We also predicted that, during summer, 2) wolf kill interval would be lower for wolf packs that were sympatric, compared to allopatric, with bears in SCA, and 3) the presence of bears at wolf-killed ungulates would decrease wolf kill interval in YNP, where the species are sympatric.

2. Materials and Methods

(a) Study areas

Scandinavia – Sweden and Norway constitute the Scandinavian Peninsula, referred to as Scandinavia. This part of the study was conducted in south-central Scandinavia (~100,000 km², elevation 50-1000 m), which primarily consists of intensively managed boreal forest (see [20]). Breeding wolf and brown bear populations coexist only in the northern portion of the study area (61° N, 15° E); wolf packs in the southern and western parts of the study area were outside of the brown bear distribution (60° N, 13° E). The wolf population was estimated at 460 (95% CI=364-598) in the winter of 2014/2015, with their range restricted to south-central Scandinavia [21]. Here, moose (*Alces alces*) are the main prey for wolves, with roe deer (*Capreolus capreolus*) being secondary prey [18, 22]. Moose densities in Scandinavia are among the highest in the world ($\overline{x}$=2 moose/km²) [23].

The Scandinavian brown bear population was estimated at 3300 individuals in 2008 [24] and reaches a density of 3 bears/100 km2 in areas where they are sympatric with wolves [25]. During early summer, ungulate neonate calves are the primary food for Scandinavian brown bears [26], with most moose predation occurring in late May-June [27]. Bears in Scandinavia rarely prey on adult ungulates [28]. Although wolves decrease the temporal variation in ungulate biomass available to scavengers in Scandinavia [29], the extent to which wolf-killed prey contributes to brown bear diet remains unknown.

Yellowstone National Park – Yellowstone National Park (8991 km²) is a protected area in northwestern Wyoming, USA, that supports wolf and brown bear populations. The study area was limited to northern Yellowstone, known as the Northern Range (NR) (995 km², elevation 1500-2000 m). Since 2008, the NR wolf population ranged between 34-57, with the current minimum number estimated at 42 wolves (Yellowstone Wolf Project, unpublished data). Elk (*Cervus elaphus*) are the main prey for wolves in Yellowstone [19]. Secondary prey species include bison (Bison bison), deer (*Odocoileus* spp.), bighorn sheep (*Ovis canadensis*), moose and pronghorn (*Antilocapra americana*).

The brown bear population in the Greater Yellowstone Ecosystem (~37,000 km2), which encompasses YNP, was ~750 bears in 2014 [30], with NR brown bear density ranging between 5-15 bears/100 km2 [31]. Brown bears in YNP scavenge ungulate carcasses, particularly after den emergence in early spring [32]. Wolf-killed ungulates, however, provide scavenging opportunities for brown bears throughout the year [33] and contribute to the relatively high proportion of meat in their diet [34, 35]. YNP brown bears frequently usurp carcasses from wolves [36]. They also prey on neonate elk from late May-July [34, 37], but rarely kill adult ungulates [38]. American black bears (*Ursus americanus*) are also present in YNP, but there is no record of them usurping wolf-killed ungulates.

(b) Data collection

Scandinavia – Predation studies in SCA occurred during two distinct time periods, hereafter referred to as 'spring' and 'summer'. These studies were conducted from

2001-2015 on wolf packs whose territories were sympatric (N_{spring}=8; N_{summer}=4) and allopatric (N_{spring}=9; N_{summer}=8) with brown bears (Table 5-1). Wolves were aerially captured and immobilized according to accepted veterinary and ethical procedures [39, 40]. At least one breeding adult in each pack was fit with a GPS collar (Vectronic Aerospace, Germany) and followed during each study period. Kill interval was measured at the 'pack' level in SCA, where wolf packs were often small and the breeding pair was generally the main food provider. Field crews searched for carcasses within a 100 m radius of all 'clustered' GPS points and recorded cause of death, species, age, and sex of carcasses found (see [41] and Appendix 2). Time of first wolf position within the cluster was used as a proxy for the time of death of wolf-killed prey.

The number and distribution of confirmed brown bear deaths is an established index of brown bear distribution and density in Scandinavia [42, 43]. We used data on brown bear deaths, including hunter harvest estimates, to create an index of bear density across Scandinavia [see 44]. Harvest estimates are reliable because bear hunters in Scandinavia are not limited to specific hunting districts, and are required by law to report the kill sites of harvested bears. The index ranged from 0 (i.e., areas with no or sporadic bear presence) to 1 (i.e., areas with the highest bear density). Wolf territories were either located in areas with high (index >0.8) or very low (<0.1) bear density. This natural division allowed wolf territories to be categorized as either 'sympatric' or 'allopatric' with brown bears.

Prey type was categorized as adult or calf moose in spring, and neonate or non-neonate (i.e., newborn calf or adult/yearling) moose in summer. For both systems, multiple carcasses in a kill event were reduced to a single kill and assigned to the largest prey type. Spring and summer pack size estimates were based on snow tracking of GPS-collared wolves during winter. We calculated moose densities using hunter harvest statistics (number of moose harvested/km^2) generated at the municipality level in Norway and the hunting management unit in Sweden. Moose density was calculated as the weighted average density of all management units within a wolf territory, using a 1-year time lag, which has been shown to be a good predictor of moose density [45]. Snow depth measurements (m) for each spring kill date were obtained from the Swedish Meteorological and Hydrological Institute, using the meteorological station closest to each territory. Most stations were located either inside, or within 5 km, of the territory boundary, except for 2 territories where the closest station was within 35 km.

Yellowstone National Park – Studies in YNP took place during summer (1 May – 31 July) from 2008-2015 on 19 wolves in 10 packs (N=23) (Table 5-1). Monitored wolves (breeding and nonbreeding individuals) were captured and fit with a GPS collar (Lotek; Newmarket, ON, Canada) following animal handling guidelines of the American Society of Mammalogists [46] and approved by the National Park Service Institutional Animal Care and Use Committee (Permit: IMR_Yell_Smith_Wolf_ 2012). Field crews searched for carcasses within a 400 m^2 area of all clustered GPS points and recorded cause of death, species, age, and sex of carcasses found (see [47] and Appendix 2). Time of first wolf position within 100 m of the carcass site was used as a proxy for the time of death of wolf-killed prey. Kill interval was treated independently for each monitored wolf within each pack, and was thus measured at the 'wolf' level. We did so because more than one wolf per pack was followed during the YNP studies, and here, pack mates often feed at different kill sites during summer [47]. A wolf was associated with an ungulate kill if it, or its pack, killed the animal, and it was located at least twice within 100 m of the carcass one or three days after death, for a small or large ungulate, respectively [47].

We classified brown bears as 'present' at wolf kills if field crews observed a brown bear, or detected bear sign, at the carcass site. In YNP, bear sign was not diagnostic to species at 85% (N=127/149) of carcasses. For the purposes of this study, we assumed that unknown bear sign was indicative of brown bears because this species was most often sighted at wolf kills (86% (N=139/162) of bear sightings at wolf kills, 1995-2015), and most often observed interacting with wolves at carcasses (89% (N=225/254) of wolf-bear interactions, 1996-2016). Therefore, there was a low risk of attributing black bear presence to brown bear presence. Furthermore, black bears are less likely than brown bears to usurp wolf kills [15, 35], and therefore less likely to affect wolf kill interval. Thus, attributing black bear presence to brown bears is likely to underestimate any effect that brown bears might have on wolf kill interval. Prey type was categorized as either large (i.e., elk, bison, or moose ≥11 months) or small ungulate (i.e., any neonate, or adult deer, bighorn sheep, or pronghorn), or unknown. We assumed wolves were scavenging when they visited a carcass that had not been killed by their pack. A 'scavenging event' was, therefore, a carcass scavenged by a wolf between consecutive kills. Pack size was recorded as the maximum number of individuals observed during March, unless pack size declined during the study period; newborn pups were not included in summer pack size estimates for either system. Distance of the kill site to the nearest paved or gravel road, a proxy for human disturbance, was measured in kilometers for both SCA and YNP in ArcGIS Version 10.2.

(c) Data analysis

We estimated wolf kill interval as the number of days between consecutive ungulate kills per pack in SCA and per wolf in YNP. We calculated kill interval in SCA using moose kills only (moose account for >95% of the biomass in their diet [18, 22]), and, in YNP, using kills of all ungulate species [19]. In YNP, we included 4 kills of unknown ungulate species when calculating the time between consecutive kills (N=544). Once the kill interval was established, we subsequently excluded them from the statistical analyses.

Spring wolf kill interval in SCA – To determine how brown bear presence influenced wolf kill interval, we compared how kill interval varied across the spring den emergence period (March-May) between wolf packs that were sympatric and allopatric with bears. We assumed that the effective number of bears increased as the emergence period advanced from March to May, and tested for an interaction between kill date and bear presence. We used observations collected between 1 March – 15 May (N=17), the period when bears emerge from their den. In SCA, the mean date of den emergence was 4 April for males (6 March – 25 April) [48] and 20 April (6 March – 14 June) for females [49]. We removed one pack year from the dataset; the Kukumäki pack was affected by sarcoptic mange in 2013 and had a kill interval that was substantially longer than average during that study period. Model variables in the candidate model set included bear presence, Julian kill date (61-133), pack size (2-9), prey type, moose density (0.006-0.39), distance from the kill site to the nearest road (0.004-1.15 km), and snow depth (0-0.96 m).

Summer wolf kill interval in SCA and YNP – To determine the effect of brown bears on wolf kill interval during summer, we evaluated whether brown bear presence 1) within wolf territories in SCA and 2) at wolf-killed ungulates in YNP was an important predictor of kill interval. We used observations collected between 18 May – 15 July in SCA (N=12) and 1 May – 31 July in YNP (N=23). Inaccessibility of some clusters (2%; N=103/4962) in YNP precluded a site search. This did not bias our estimate of YNP kill interval because our calculations only considered time periods during which all clusters were searched (except for unsearched clusters near the home site; see Appendix S1). Model variables in the SCA candidate model set included bear presence, Julian kill date (139-193), pack size (2-9), prey type, moose density (0.02-0.68), and distance to nearest road (0.008-1.16 km). Model variables in the YNP candidate model set included bear presence, Julian kill date (120-211), pack size (2-15), prey type, number of scavenged carcasses between kills (0-2), and distance to nearest road (0.03-16.61 km).

We conducted all analyses in R version 3.0.1 [50] using general linear mixed models (GLMMs) using the ‘lmer’ function in the ‘lme4’ package version 1.1-7 [51]. GLMMs can account for potential correlation between multiple observations taken on an individual wolf, from each pack, and within each year; pack identity and year were fit *a priori* as crossed random effects in all models. Wolf identity was also included as a crossed random effect in YNP models. The kill interval in YNP was square root transformed to meet model assumptions. All models included a compound symmetric correlation structure, which assumed that all observations for each wolf, pack, and year were, on average, equally correlated [52]. Model parameters were estimated using maximum likelihood.

We used Akaike Information Criterion (AIC) model selection [53] to test our 3 main predictions. The best-fit model had the lowest AIC score, which was adjusted for small sample size (AIC_c). To determine the relative importance of our variables of interest, we examined whether they were retained in the top models (models with a $\Delta AIC_c < 2$ [53]). The correlation coefficients between model variables were <0.6 in all model sets; except for bear density and Julian date in the spring SCA analysis, which had a correlation coefficient of 0.7. We performed model averaging on models with $\Delta AIC_c < 2$ to estimate β coefficients, standard errors, and 95% confidence intervals (95% CI), using the 'modavg' function in the 'AICcmodavg' package version 2.0-1 [54]. Population-averaged fitted values for graphs were calculated from best-fit models using the 'PredictSE' function in the 'AICcmodavg' package.

3. Results

(a) Spring wolf kill interval in SCA

We found no evidence that kill interval decreased across the spring bear emergence period for SCA wolves sympatric with brown bears. On the contrary, all 6 top models of spring wolf kill interval in SCA (Table 5-2a) included a positive interaction between Julian date and bear presence (Table 5-3a; Figure 5-1a) (N=140 observations/12 packs/11 years). This indicates that kill interval decreased across the spring emergence period for wolves that were allopatric, rather than sympatric, with bears (Figure 5-2). The kill interval of sympatric wolves was effectively constant across the spring emergence period. Note, however, that the 95% confidence interval for this interaction included 0 (Table 5-3a). Terms for pack size, moose density, prey type, and snow depth also were retained in the top models (Table 5-2a). The best fit model (Table 5-3a) indicated that time between wolf kills decreased with increasing moose density and pack size (Figure 5-1a). Estimates from the top model that included a term for prey type and snow depth (Table 5-2a) suggested that kill interval increased when adult moose were killed compared to calves (β=0.20; SE=0.19) and decreased with increasing snow depth (β=$^{-}$0.13; SE=0.09), although the 95% CIs for these two estimates overlapped 0. Adult moose comprised 21% (N=29/140) of all kills made by wolves during spring, and 24% (N=20/84) and 16% (N=9/56) of kills in allopatric and sympatric areas, respectively.

(b) Summer wolf kill interval in SCA and YNP

The variable for bear presence was retained in 4 of 5 top models of summer wolf kill interval in SCA (Table 5-2b) (N=157 observations/10 packs/6 years), and the 95% CI around its model averaged coefficient did not overlap 0, providing strong support for the positive direction of this effect (Figure 5-1b). On average, the kill interval of sympatric packs was 12.1 ±5.6 hours longer than it was for allopatric packs (Figure 5-3a). Mean (±SE) kill interval for all packs was 1.82 ±1.33 days (43.68 ±31.92 hours), suggesting that bear presence in a wolf territory increased kill interval by about 28%. Terms for prey type, pack size, moose density, and Julian date were included in the 5 top SCA models (Table 5-2b). Kill interval increased when wolves killed non-neonate moose compared to neonates (Figure 5-1b; Figure 5-3a). During the summer, non-neonate moose constituted 12% (N=19/157) of all wolf kills in SCA, and comprised 9% (N=10/106) and 18% (N=9/51) of kills in allopatric and sympatric areas, respectively. In addition, kill interval decreased with moose density, and increased with pack size, although the 95% CIs for these estimates overlapped 0 (Figure 5-1b).

Bear sign was found at 27% (N=149/544) of the unique kills detected during summer in YNP. Although wolves killed more small ungulates (N=312/544), bears used large ungulate kills more often; bear sign was found at 14% (N=44/312) of small ungulate kills and at 45% (N=105/232) of large ungulate kills. Bear presence was retained as a predictor of wolf kill interval in all 3 top models (Table 5-2c) (N=691 observations/19 wolves/10 packs/8 years), and the 95% CI around the model averaged coefficient for bear presence did not overlap 0 (Figure 5-1c). Kill interval increased when bears were present at kills (Figure 5-3b); bear presence was associated with a 7.6 hour increase in kill interval. The mean summer kill interval was 2.19 ±1.99 days (52.7 ±47.8 hours), suggesting that bear presence increased kill interval by about 14%. Terms for prey type, scavenge events, Julian date, distance to nearest road, and pack size were also retained in the top YNP models (Table 5-2c). Kill interval in YNP increased with the number of scavenge events, over the summer season, and when large ungulates were killed compared to small ungulates (Figure 5-

1c). Kill interval also decreased with pack size and distance to the nearest road, although the 95% CIs for these estimates overlapped 0 (Figure 5-1c).

4. Discussion

Wolf kill interval was affected by several factors in both Scandinavia and Yellowstone, including prey type, wolf pack size, and Julian date (Figure 5-1). For example, wolf kill interval increased in both systems when wolves killed larger prey, as previously reported [18-19, 55] (Figure 5-1). Kill interval in Scandinavia also decreased as the abundance of wolves' primary prey, moose, increased, as previously demonstrated [55-57]. In Yellowstone, kill interval also increased as wolves scavenged more carcasses between kills. While these results highlight factors that are known to affect wolf kill interval [18-19, 55-57], we also show a novel effect of brown bear presence.

Contrary to our hypotheses, the presence of brown bears resulted in wolves killing less frequently in both Scandinavia and Yellowstone. Wolf packs sympatric with brown bears in Scandinavia killed less often than allopatric packs in both spring and summer. In Yellowstone, where brown bear and wolf distributions overlapped, the presence of bears at wolf-killed ungulates was associated with wolves killing less often during summer. These results contradict the expectation that wolves kill more often where they coexist with brown bears, because the loss of food biomass from kleptoparasitism forces additional hunting to meet energetic demands [15, 16].

The reason why brown bears are linked to increased wolf kill interval is not intuitive, but several mechanisms might cause this pattern. By definition, kill interval is the sum of time a predator spends handling (i.e., consuming) the first prey and searching for and killing the second. Interference competition can force a subordinate predator to prematurely abandon its kill, resulting in decreased handling time and, subsequently, shorter kill intervals (e.g., through kleptoparasitism [13, 14]). Conversely, it is also possible that predators might realize greater fitness benefits from lingering at the usurped carcass, striving for occasional access, rather than prematurely abandoning it to make a new kill.

Hunting large ungulates is a difficult and dangerous task for wolves. Less than 25% of elk hunts in Yellowstone are successful [58, 59] and wolves in Scandinavia succeed in killing moose about half the time (45-64% [40]). Hunts often necessitate a significant energy investment for wolves (e.g., chase distances can be long and hunting bouts can last hours [60]). Furthermore, wolves face a high risk of injury, or even death, when hunting large prey that can fight back [60, 61]. Increased kill intervals could result, therefore, if wolves waited for occasions to feed on their kill while bears remained at the carcass, or if they waited for bears to leave, instead of abandoning their kills, as do Eurasian lynx (*Lynx lynx*) [13] and mountain lions (*Puma concolor*) [14, 62]. This would be expected with larger prey, where longer time spent at the kill site could increase the potential for interactions and where more biomass is likely to remain once the kill has been relinquished by the bear.

Alternatively, exploitative competition may increase kill interval if greater time investment, or superior search efficiency, by one predator diminishes the supply of a shared prey, thus leading to an increase in search time for a second predator and lengthening kill interval [63]. In many systems where they occur, brown bears are the most significant predator of neonate ungulates [64]. In Scandinavia, bears accounted for ~90% of total neonate moose mortality when allopatric with the wolf population [65]. In Yellowstone, predators accounted for 94% of all neonate elk mortality within the first 30 days of life; brown and black bears accounted for 69% of those deaths, whereas wolves accounted for 12% [37]. Therefore, successive depletion of neonate prey by both brown bears and wolves could have caused increased search times and, subsequently, an increased wolf kill interval, during summer in both systems.

It is also possible that facilitation, rather than competition, from brown bears increased wolf kill interval. Frequent predation by bears could increase scavenging opportunities for wolves, thereby lengthening wolf kill interval. However, there is little evidence for this mechanism in Scandinavia or Yellowstone. Although bears are important predators of neonates during early summer in both systems [37, 65], neonates are small and quickly consumed, with little or no biomass remaining for scavengers. To date, there have been no confirmed cases of adult wolves utilizing neonate bear kills in Scandinavia [66]. Furthermore, brown bears in Scandinavia and Yellowstone rarely kill adult ungulates [28, 67], whose carcasses would be more likely to retain useable biomass.

During spring in Scandinavia, it is more likely that interference competition caused increased kill intervals, as wolves and bears do not predate on the same resource (i.e., neonate moose) at this time of year, as compared to early summer. However, neonate moose represented the majority of wolf kills made by both sympatric (82%) and allopatric packs (91%) during the summer in Scandinavia. Although we controlled for variation in moose density, we were unable to account for brown bear-induced changes to neonate prey density during summer, which could have explained the observed difference in kill interval between sympatric and allopatric packs in summer. In Yellowstone, small ungulate prey, including neonates, accounted for ~57% of 544 of the kills, although 70% of the detected bear sign was at large ungulate kills. Whereas wolves in Yellowstone kill neonate ungulates frequently during summer, large ungulates supply the majority of acquired biomass [19]. Thus, it is possible that increased summer wolf kill interval was the result of multiple mechanisms; bears reducing densities of neonate ungulates (i.e., exploitative competition) and wolves loitering at larger, usurped kills (i.e., interference competition). Future research should tease apart the relative role of interference and exploitative competition between apex predators in driving seasonal predation patterns in different ecosystems.

Although we used two large datasets at a transcontinental scale to improve our understanding of competition between two apex predators, there were some limitations with our study. For instance, bear 'presence' was differentially defined in Scandinavia and Yellowstone, and kill interval was calculated at different levels (i.e., pack versus individual) in the two systems. However, our results were consistent across seasonal and transcontinental scales; bear presence increased wolf kill interval (i.e., decreased kill rate) in both Scandinavia and Yellowstone during spring and summer. These findings suggest that competition between brown bears and wolves actually extended the kill interval of wolves in Scandinavia (Figure 5-1a-b; Figure 5-2; Figure 5-3a) and Yellowstone (Figure 5-1c; Figure 5-3b).

Our results challenge the conventional view that brown bears do not affect the distribution, survival, or reproduction of wolves [68]. For example, extended wolf kill intervals in areas sympatric with bears may help explain why wolf pair establishment in Scandinavia was negatively related to bear density, among other intraspecific and environmental factors [44]. Although the outcome of interactions between bears and wolves at carcasses varies, bears often dominate, limiting wolves' access to food [15, 16, 36]. Furthermore, our findings suggest that wolves do not hunt more often to compensate for the loss of food to brown bears. In combination, this implies that bears might negatively affect the food intake of wolves, such that wolf populations that are sympatric with brown bears might suffer fitness consequences. Determining the energetic costs of these interactions (e.g., food biomass lost and energy expended by wolves) and linking them to predator population dynamics will ultimately help us understand the costs of sympatry among apex predator populations.

Although bears seemingly caused fewer prey to be killed by wolves, it is difficult to ascertain how this ultimately affected the cumulative predation rate of the respective ungulate populations, as we only examined wolf predation. Whereas predation by brown bears on neonates is well understood, and can be additive to other predator-induced mortality [64], our results suggest the possibility that the total impact of wolves and brown bears on non-neonate prey may be less than the sum of their individual impacts. If so, the outcome of interactions between wolves and bears may mitigate, rather than exacerbate, the influence of these carnivores on ungulate population dynamics.

Our results provide new information about the consequences of competition between apex predators that is relevant to understanding how large predator diversity affects trophic interactions in natural systems. Interspecific interactions between apex predators can either relax or strengthen their cumulative effect on prey populations and overall ecosystem functioning [9, 10]. Ignoring such interactions may result in underestimating the effect that interspecific competition between predators can have on predator populations, as well as overestimating the impact of multiple predators on prey population dynamics.

References

1. Hairston N.G., Smith F.E., Slobodkin L.B. 1960 Community structure, population control, and competition. *American Naturalist* **94**(879), 421-425. (doi: 10.1086/282146).
2. Sinclair A.R.E., Krebs C.J. 2002 Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philos T Roy Soc B* **357**(1425), 1221-1231. (doi:10.1098/rstb.2002.1123).
3. Steneck R. 2005 An ecological context for the role of large carnivores in conserving biodiversity. In *Large Carnivores and the Conservation of Biodiversity* (eds. Ray J., Redford K.H., Steneck R., Berger J.), pp. 9-33. Washington D.C., Island Press.
4. Meserve P., Kelt D., Milstead W., Gutiérrez J. 2003 Thirteen years of shifting top-down and bottom-up control. *BioScience* **53**(7), 633-646.

5. Peterson R.O., Vucetich J.A., Bump J., Smith D.W. 2014 Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *The Annual Review of Ecology, Evolution, and Systematics* **45**, 325-345.
6. Vucetich J.A., Hebblewhite M., Smith D.W., Peterson R.O. 2011 Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *The Journal of animal ecology* **80**(6), 1236-1245. (doi:10.1111/j.1365-2656.2011.01855.x).
7. Terborgh J., Lopez L., Nunez P., Rao M., Shahabuddin G., Orihuela G., Riveros M., Ascanio R., Adler G.H., Lambert T.D., et al. 2001 Ecological meltdown in predator-free forest fragments. *Science* **294**(5548), 1923-1926. (doi:10.1126/science.1064397).
8. Finke D., Denno R. 2004 Predator diversity dampens trophic cascades. *Nature* **429**, 407-410.
9. Bruno J., Cardinale B. 2008 Cascading effects of predator richness. *Frontiers in Ecology and the Environment* **6**(10), 539-549.
10. Ives A., Cardinale B., Snyder W. 2005 A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecology letters* **8**, 102-116.
11. DeVault T.L., Rhodes O.E., Shivik J.A. 2003 Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**(2), 225-234. (doi: 10.1034/j.1600-0706.2003.12378.x).

12. Carbone C., Du Toit J.T., Gordon I.J. 1997 Feeding success in African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group size? *Journal of Animal Ecology* **66**(3), 318-326.
13. Krofel M., Kos I., Jerina K. 2012 The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* **66**(9), 1297-1304. (doi:10.1007/s00265-012-1384-6).
14. Elbroch L., Lendrum P., Allen M., Wittmer H. 2014 Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology* **00**, 1-8.
15. Ballard W.B., Carbyn L.N., Smith D.W. 2003 Wolf interactions with non-prey. In *Wolves: Behavior, Ecology, and Conservation* (eds. Mech L.D., Boitani L.), pp. 259-271. Chicago and London, The University of Chicago Press.
16. Boertje R.D., Gasaway W.C., Grangaard D.V., Kelleyhouse D.G. 1988 Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. *Can J Zool* **66**(11), 2492-2499.
17. Ripple W.J., Estes J.A., Beschta R.L., Wilmers C.C., Ritchie E.G., Hebblewhite M., Berger J., Elmhagen B., Letnic M., Nelson M.P., et al. 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**(6167). (doi:ARTN 1241484.10.1126/science.1241484).
18. Sand H., Wabakken P., Zimmermann B., Johansson O., Pedersen H.C., Liberg O. 2008 Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia* **156**(1), 53-64. (doi:10.1007/s00442-008-0969-2).

19. Metz M.C., Smith D.W., Vucetich J.A., Stahler D.R., Peterson R.O. 2012 Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* **81**(3), 553-563. (doi:10.1111/j.1365-2656.2011.01945.x).
20. Ordiz A., Stoen O.G., Saebo S., Sahlen V., Pedersen B.E., Kindberg J., Swenson J.E. 2013 Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology* **50**(2), 306-314. (doi:10.1111/1365-2664.12047).
21. Svensson L, Wabakken P, Maartmann E, Åkesson M, Ø. F. 2015 The wolf in Scandinavia and Finland: final report from wolf monitoring in 2014-2015. (pp. 1-52, Hedmark University College and Viltskadecenter, Swedish University of Agricultural Sciences.
22. Sand H., Zimmermann B., Wabakken P., Andren H., Pedersen H.C. 2005 Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin* **33**(3), 914-925. (doi: 10.2193/0091-7648(2005)33[914:Ugtagc]2.0.Co;2).
23. Lavsund S., Nygren T., Solberg E.J. 2003 Status of moose populations and challenges to moose management in Fennoscandia. *Alces* **39**, 109-130.
24. Kindberg J., Swenson J.E., Ericsson G., Bellemain E., Miquel C., Taberlet P. 2011 Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* **17**(2), 114-123. (doi:10.2981/10-100).
25. Solberg K.H., Bellemain E., Drageset O.M., Taberlet P., Swenson J.E. 2006 An evaluation of field and non-invasive genetic methods to estimate brown bear

(*Ursus arctos*) population size. *Biological Conservation* **128**(2), 158-168. (doi:10.1016/j.biocon.2005.09.025).

26. Stenset N.E., Lutnæs P.N., Bjarnadóttir V., Dahle B., Fossum K.H., Jigsved P., Johansen T., Neumann W., Opseth O., Rønning O., et al. 2016 Seasonal and annual variation in the diet of brown bears (*Ursus arctos*) in the boreal forest of southcentral Sweden. *Wildlife Biology* **22**, 107-116.
27. Rauset G.R., Kindberg J., Swenson J.E. 2012 Modeling female brown bear kill rates on moose calves using global positioning satellite data. *Journal of Wildlife Management* **76**(8), 1597-1606. (doi:10.1002/jwmg.452).
28. Dahle B., Wallin K., Cederlund G., Persson I.L., Selvaag L., Swenson J.E. 2013 Predation on adult moose *Alces alces* by European brown bears *Ursus arctos*. *Wildlife Biology* **19**(2), 165-169.
29. Wikenros C., Sand H., Ahlqvist P., Liberg O. 2013 Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. *PloS one* **8**(10), e77373. (doi:10.1371/journal.pone.0077373).
30. Haroldson M.A., Van Manen F.T., Bjornlie D.D. 2015 Estimating number of females with cubs In *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2014* (eds. Van Manen F.T., Haroldson M.A., Soileau S.C.), pp. 11-20. Bozeman, MT USA, U.S. Geological Survey.
31. Bjornlie D.D., Van Manen F.T., Ebinger M.R., Haroldson M.A., Thompson D.J., Costello C.M. 2014 Whitebark pine, population density, and home-range size of grizzly bears in the Greater Yellowstone Ecosystem. *PloS one* **9**(2). (doi:ARTN e88160 10.1371/journal.pone.0088160).

32. Green G.I., Mattson D.J., Peek J.M. 1997 Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *Journal of Wildlife Management* **61**(4), 1040-1055. (doi: 10.2307/3802101).
33. Wilmers C.C., Crabtree R.L., Smith D.W., Murphy K.M., Getz W.M. 2003 Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* **72**(6), 909-916. (doi: 10.1046/j.1365-2656.2003.00766.x).
34. Fortin J.K., Schwartz C.C., Gunther K.A., Teisberg J.E., Haroldson M.A., Evans M.A., Robbins C.T. 2013 Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of Wildlife Management* **77**(2), 270-281. (doi:10.1002/jwmg.483).
35. Hebblewhite M., Smith D.W. 2010 Wolf Community Ecology: Ecosystem effects of recovering wolves in Banff and Yellowstone National Parks. In *The World of Wolves: New perspectives on ecology, behavior and management* (eds. Musiani M., Boitani L., Paquet P.C.), pp. 69-122. Calgary, Alberta, Canada, University of Calgary Press.
36. MacNulty D.R., Varley N., Smith D.W. 2001 Grizzly bear, *Ursus arctos*, usurps bison calf, *Bison bison*, captured by wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. *Canadian Journal of Zoology* **115**(3), 495-498.
37. Barber-Meyer S.M., Mech L.D., White P.J. 2008 Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* **169**, 1-30. (doi:10.2193/2008-004).

38. Evans S., Mech D., White P.J., Sargeant G. 2006 Survival of adult female elk in Yellowstone following wolf restoration. *Journal of Wildlife Management* **70**(5), 1372-1378.
39. Arnemo J.M., Fahlman Å. 2007 Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. (pp. 1-18. Tromsø, Norway, Norwegian School of Veterinary Science.
40. Sand H., Wikenros C., Wabakken P., Liberg O. 2006 Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour* **72**(4), 781-789. (doi:10.1016/j.anbehav.2005.11.030).
41. Zimmermann B., Wabakken P., Sand H., Pedersen H.C., Liberg O. 2007 Wolf movement patterns: a key to estimation of kill rate? *Journal of Wildlife Management* **71**(4), 1177-1182. (doi:10.2193/2006-306).
42. Swenson J.E., Sandegren F., Soderberg A. 1998 Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* **67**(5), 819-826. (doi: 10.1046/j.1365-2656.1998.00248.x).
43. Kindberg J., Ericsson G., Swenson J.E. 2009 Monitoring rare or elusive large mammals using effort-corrected voluntary observers. *Biological Conservation* **142**(1), 159-165. (doi:10.1016/j.biocon.2008.10.009).
44. Ordiz A., Milleret C., Kindberg J., Månsson J., Wabakken P., Swenson J.E., Sand H. 2015 Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere* **6**(12), 284. (doi: 10.1890/ES15-00243.1).

45. Ueno M., Solberg E.J., Iijima H., Rolandsen C.M., Gangsei L.E. 2014 Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. *Ecosphere* **5**(2). (doi:Artn 13 10.1890/Es13-00083.1).
46. Sikes R., Gannon W., Amer Soc M. 2011 Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **92**, 235-253.
47. Metz M.C., Vucetich J.A., Smith D.W., Stahler D.R., Peterson R.O. 2011 Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PloS one* **6**(3), e17332. (doi:10.1371/journal.pone.0017332).
48. Manchi S., Swenson J.E. 2005 Denning behaviour of Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* **11**(2), 123-132. (doi: 10.2981/0909-6396(2005)11[123:Dbosbb]2.0.Co;2).
49. Friebe A., Swenson J.E., Sandegren F. 2001 Denning chronology of female brown bears in central Sweden. *Ursus* **12**, 37-45.
50. R Core Team. 2014 R: A Language and Environment for Statistical Computing. (3.1.1 ed. Vienna, Austria, R Foundation for Statistical Computing.
51. Bates D., Maechler M. 2014 Package 'lme4': Linear mixed-effects models using S4 classes. 1.1-7 ed.
52. Weiss R. 2005 *Modeling longitudinal data*. New York, NY, Springer.
53. Burnham K.P., Anderson D.R. 2002 *Model selection and multimodal inference, a practical information theoretic approach*. 2nd ed. New York, Springer-Verlag.

54. Mazerolle M.J. 2014 Package 'AICcmodavg': Model selection and multimodel inference based on (Q)AIC(c). 2.0 ed.
55. Vucetich J.A., Peterson R.O., Schaefer C.L. 2002 The effect of prey and predator densities on wolf predation. *Ecology* **83**(11), 3003-3013.
56. Messier F. 1994 Ungulate population-models with predation - a case-study with the North-American moose. *Ecology* **75**(2), 478-488. (doi: 10.2307/1939551).
57. Sand H., Vucetich J.A., Zimmermann B., Wabakken P., Wikenros C., Pedersen H.C., Peterson R.O., Liberg O. 2012 Assessing the influence of prey-predator ratio, prey age structure and packs size on wolf kill rates. *Oikos* **121**(9), 1454-1463. (doi:10.1111/j.1600-0706.2012.20082.x).
58. Smith D.W., Mech L.D., Meagher M., Clark W., Jaffe R., Phillips M.K., Mack J.A. 2000 Wolf-bison interactions in Yellowstone National Park. *Journal of Mammalogy* **81**(4), 1128-1135.
59. MacNulty D.R., Smith D.W., Mech L.D., Vucetich J.A., Packer C. 2012 Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology* **23**(1), 75-82. (doi:10.1093/beheco/arr159).
60. Mech L.D., Smith D.W., MacNulty D.R. 2015 *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. USA, University of Chicago Press.
61. MacNulty D.R. 2002 The predatory sequence and the influence of injury risk on hunting behavior in the wolf, The University of Minnesota.
62. Smith J., Wang Y., Wilmers C.C. 2015 Top carnivores increase their kill rates on prey as a response to human-induced fear. *P Roy Soc B-Biol Sci* **282**. (doi:20142711).

63. Holt R., Grover J., Tilman D. 1994 Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* **144**(5), 741-771.

64. Griffin K., Hebblewhite M., Robinson H., Zager P., Barber-Meyer S., Christianson D., Creel S., Harris N., Hurley M., Jackson D., et al. 2011 Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology* **80**, 1246-1257.

65. Swenson J.E., Dahle B., Busk H., Opseth O., Johansen T., Soderberg A., Wallin K., Cederlund G. 2007 Predation on moose calves by European brown bears. *Journal of Wildlife Management* **71**(6), 1993-1997. (doi:10.2193/2006-308).

66. Milleret C. 2011 Estimating wolves (*Canis lupus)* and brown bear (*Ursus arctos)* interactions in central Sweden. Does the emergence of brown bears affect wolf predation patterns?, Annee Universitaire.

67. Mattson D.J. 1997 Use of ungulates by Yellowstone grizzly bears. *Biological Conservation* **81**, 161-177.

68. Servheen C., Knight R.R. 1993 Possible effects of a restored gray wolf population on grizzly bears in the Greater Yellowstone Area. *Scientific Monograph* **22**, 28-37.

Tables and Figures

Table 5-1. Summary of predation studies carried out in spring (a) and summer (b) in Scandinavia and summer in Yellowstone National Park (c). The sex (M/F) of the followed wolf is indicated at the end of each wolf ID number.

(a) Scandinavia – Spring

Wolf Territory	Wolf Followed	Study Period	Duration of Study (Days)	Sympatric with Bears
Gråfjell	M0109M	12/11/01 - 04/21/02	132	No
Gråfjell	M0109M	02/17/03 - 04/20/03	63	No
Tyngsjö	M0204F	01/31/02 - 04/24/02	84	No
Bograngen	M0009M	02/17/03 - 04/20/03	63	No
Nyskoga	M0007M	02/13/04 - 03/16/04	33	No
Djurskog	M0306M	02/01/04 - 03/28/04	56	No
Jangen	M0404M	02/02/04 - 04/01/04	60	No
Gräsmark	M0611M / M0610F	02/18/07 - 04/09/07	50	No
Kloten	M0910M	02/11/08 - 03/31/08	50	No
Fulufjället	M0904M	02/15/09 - 04/08/09	52	Yes
Fulufjället	M0904M	04/01/10 - 06/01/10	61	Yes
Tenskog	M1002M	02/13/10 - 04/11/10	57	Yes
Tenskog	M1003M	03/14/11 - 05/16/11	63	Yes
Tandsjön	M1103M	02/20/12 - 05/14/12	84	Yes
Kukumäki	M1302M	02/25/13 - 04/28/13	62	Yes
Tandsjön	M1103M	03/19/14 - 04/25/14	37	Yes
Kukumäki	M1302M	03/03/14 - 04/25/14	53	Yes
Kukumäki	M1301F	03/04/15 - 04/24/15	51	Yes

(b) Scandinavia – Summer

Wolf Territory	Wolf Followed	Study Period	Duration of Study (Days)	Sympatric with Bears
Nyskoga	M0007M	06/02/03 - 06/10/03	8	No
Gråfjell	M0109M	06/02/03 - 07/14/03	42	No
Bograngen	M0009M	06/02/03 - 07/14/03	42	No
Halgån	M0206F	06/21/03 - 07/14/03	23	No
Djurskog	M0306M	06/21/04 - 07/12/04	21	No
Koppang	M0402M	06/14/04 - 07/05/04	21	No
Gråfjell	M0109M	06/14/04 - 07/05/04	21	No
Kloten	M0918M	06/13/09 - 07/11/09	28	No

Table 5-1 cont.

Tenskog	M1002M	05/30/11 - 06/26/11	27	Yes
Tandsjön	M1103M	05/19/14 - 06/21/14	33	Yes
Kukumäki	M1302M	05/19/14 - 06/22/14	34	Yes
Kukumäki	M1301F	05/18/15 - 06/29/15	42	Yes

(c) Yellowstone – Summer

Wolf Territory	**Wolf Followed**	**Study Period**	**Duration of Study (Days)**
Leopold	624F	05/01/08 - 08/01/08	92
Leopold	625F	05/01/08 - 08/01/08	92
Oxbow Creek	626F	05/01/08 - 08/01/08	92
Oxbow Creek	627M	05/01/08 - 08/01/08	92
Blacktail	692F	05/01/09 - 08/01/09	92
Blacktail	693F	05/01/09 - 08/01/09	92
Everts	684M	05/01/09 - 08/01/09	92
Everts	685M	05/01/09 - 08/01/09	92
Blacktail	642F	05/01/10 - 08/01/10	92
Blacktail	752F	05/01/10 - 08/01/10	92
Agate Creek	775M	06/01/11 - 06/30/11	29
Blacktail	777M	05/01/11 - 08/01/11	92
Blacktail	777M	05/01/12 - 05/28/12	27
Blacktail	829F	05/01/12 - 08/01/12	92
Junction Butte	777M	05/31/12 - 08/01/12	62
8 Mile	SW763M	05/01/13 - 08/01/13	92
889F/890M Group	889F	05/01/13 - 06/27/13	57
889F/890M Group	890M	05/01/13 - 08/01/13	92
911M Group	911M	05/13/14 - 07/01/14	49
Junction Butte	890M	05/01/14 - 07/01/14	61
Junction Butte	907F	05/01/14 - 07/01/14	61
Junction Butte	911M	05/01/14 - 05/13/14	12
Prospect Peak	964M	05/01/15 - 08/01/15	92

Table 5-2. *A priori* GLMM model sets predicting wolf kill interval (days between consecutive kills) during spring (a) and summer (b) in Scandinavia and summer in Yellowstone National Park (c). The null models contain the intercept and crossed random effects for pack ID and year (a-b) and pack ID, wolf ID and year (c). Log-likelihood (LogLike), number of parameters (K), AIC$_c$, differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (Wi) are given for each model. The top models (ΔAIC < 2) are highlighted in bold. Bear presence was defined as wolves being either allopatric or sympatric with brown bears in Scandinavia (a-b), or brown bears being absent or present at a wolf kill in Yellowstone National Park (c). Continuous variables were centered and scaled in all models. Categorical variables for prey type were: adult or calf moose (a), neonate and non-neonate moose (b), and small and large ungulate (c). Other independent variables included wolf pack size, Julian date of the kill, snow depth (m) in the territory at kill date, moose density (average number of moose harvested/km^2), the number of carcasses scavenged between kills, and distance (km) from the kill site to the nearest road. 'Bear presence x Julian date' refers to an interaction between the two variables (a).

(a) Scandinavia - Spring

Model Set	LogLike	K	AICc	ΔAICc	Wi
Bear Presence x Julian Date + Moose Density + Pack Size	**-183.90**	**9**	**387.19**	**0.00**	**0.12**
Bear Presence x Julian Date + Pack Size + Moose Density + Snow Depth	**-182.86**	**10**	**387.43**	**0.24**	**0.11**
Bear Presence x Julian Date + Pack Size	**-185.23**	**8**	**387.56**	**0.37**	**0.10**
Bear Presence x Julian Date + Prey Type + Pack Size + Moose Density	**-183.39**	**10**	**388.48**	**1.29**	**0.07**
Bear Presence x Julian Date + Prey Type + Pack Size	**-184.63**	**9**	**388.64**	**1.45**	**0.06**
Bear Presence x Julian Date + Pack Size + Snow Depth	**-184.68**	**9**	**388.75**	**1.56**	**0.06**
Bear Presence x Julian Date	-187.17	7	389.19	2.00	0.05
Bear Presence x Julian Date + Prey Type + Pack Size + Moose Density + Snow Depth	-182.64	11	389.34	2.14	0.04
Bear Presence x Julian Date + Snow Depth	-186.18	8	389.45	2.26	0.04
Bear Presence x Julian Date + Prey Type	-186.53	8	390.17	2.98	0.03
Bear Presence x Julian Date + Prey Type + Pack Size + Moose Density + Road	-183.07	11	390.20	3.00	0.03
Bear Presence x Julian Date + Moose Density + Snow Depth	-185.41	9	390.20	3.01	0.03
Bear Presence x Julian Date + Prey Type + Pack Size + Snow Depth	-184.28	10	390.27	3.08	0.03
Bear Presence x Julian Date + Prey Type + Pack Size + Road	-184.36	10	390.42	3.23	0.02
Bear Presence x Julian Date + Road	-186.73	8	390.57	3.38	0.02
Bear Presence x Julian Date + Moose Density	-186.86	8	390.81	3.62	0.02
Bear Presence x Julian Date + Prey Type + Pack Size + Moose Density + Snow Depth + Road	-182.24	12	390.93	3.74	0.02
Bear Presence x Julian Date + Prey Type + Snow Depth	-185.81	9	391.00	3.81	0.02
Moose Density + Pack Size	-189.19	6	391.02	3.82	0.02
Moose Density + Pack Size + Snow Depth	-188.11	7	391.07	3.88	0.02
Bear Presence x Julian Date + Prey Type + Road	-186.20	9	391.79	4.60	0.01
Bear Presence x Julian Date + Moose Density + Prey Type	-186.26	9	391.90	4.71	0.01
Bear Presence x Julian Date + Prey Type + Moose Density + Snow Depth	-185.16	10	392.03	4.84	0.01
Prey Type + Pack Size + Moose Density	-189.04	7	392.92	5.73	0.01
Moose Density + Snow Depth	-190.25	6	393.13	5.94	0.01
Prey Type + Pack Size + Moose Density + Snow Depth	-188.03	8	393.17	5.97	0.01
Moose Density	-191.48	5	393.41	6.22	0.01
Bear Presence x Julian Date + Prey Type + Moose Density + Road	-185.90	10	393.50	6.31	0.01
Julian Date + Moose Density + Snow Depth	-189.72	7	394.28	7.09	0.00
Prey Type + Pack Size + Moose Density + Road	-188.78	8	394.67	7.48	0.00
Prey Type + Pack Size + Moose Density + Snow Depth + Road	-187.71	9	394.81	7.62	0.00
Null (Intercept Only)	-193.31	4	394.92	7.72	0.00
Prey Type + Moose Density + Snow Depth	-190.13	7	395.12	7.92	0.00

Table 5-2 cont.

Moose Density + Prey Type	-191.26	6	395.15	7.96	0.00
Julian Date + Prey Type + Pack Size + Moose Density	-189.03	8	395.16	7.97	0.00
Julian Date + Prey Type + Pack Size + Moose Density + Snow Depth	-187.91	9	395.21	8.02	0.00
Julian Date + Moose Density	-191.44	6	395.51	8.32	0.00
Pack Size	-192.59	5	395.63	8.44	0.00
Julian Date + Prey Type + Moose Density + Snow Depth	-189.66	8	396.41	9.22	0.00
Prey Type	-193.01	5	396.47	9.28	0.00
Snow Depth	-193.02	5	396.50	9.30	0.00
Julian Date + Prey Type + Pack Size + Moose Density + Road	-188.78	9	396.95	9.75	0.00
Julian Date	-193.29	5	397.03	9.83	0.00
Prey Type + Pack Size	-192.32	6	397.28	10.09	0.00
Julian Date + Moose Density + Prey Type	-191.22	7	397.30	10.10	0.00
Pack Size + Snow Depth	-192.41	6	397.45	10.25	0.00
Prey Type + Road	-192.70	6	398.03	10.84	0.00
Prey Type + Snow Depth	-192.82	6	398.26	11.07	0.00
Julian Date + Snow Depth	-192.85	6	398.33	11.13	0.00
Julian Date + Prey Type	-192.98	6	398.59	11.40	0.00
Prey Type + Pack Size + Road	-192.04	7	398.93	11.74	0.00
Prey Type + Pack Size + Snow Depth	-192.21	7	399.26	12.07	0.00
Julian Date + Prey Type + Pack Size	-192.32	7	399.50	12.30	0.00
Julian Date + Pack Size + Snow Depth	-192.36	7	399.57	12.38	0.00
Julian Date + Prey Type + Snow Depth	-192.65	7	400.15	12.96	0.00
Julian Date + Prey Type + Pack Size + Road	-192.04	8	401.18	13.98	0.00
Julian Date + Prey Type + Pack Size + Snow Depth	-192.17	8	401.43	14.24	0.00

(b) Scandinavia - Summer

Model Set	LogLike	K	AICc	ΔAICc	Wi
Bear Presence + Prey Type	**-213.77**	**6**	**440.10**	**0.00**	**0.15**
Bear Presence + Moose Density + Prey Type	**-213.20**	**7**	**441.16**	**1.06**	**0.09**
Bear Presence + Prey Type + Pack Size	**-213.35**	**7**	**441.46**	**1.36**	**0.08**
Prey Type	**-215.75**	**5**	**441.89**	**1.79**	**0.06**
Bear Presence + Prey Type + Julian Date	**-213.64**	**7**	**442.02**	**1.93**	**0.06**
Prey Type + Road	-214.93	6	442.43	2.33	0.05
Prey Type + Moose Density + Julian Date	-213.88	7	442.51	2.42	0.05
Moose Density + Prey Type	-215.01	6	442.59	2.49	0.04
Bear Presence + Moose Density + Prey Type + Road	-212.81	8	442.60	2.50	0.04
Prey Type + Julian Date	-215.08	6	442.72	2.63	0.04
Bear Presence + Prey Type + Pack Size + Road	-212.90	8	442.78	2.68	0.04
Prey Type + Moose Density + Road	-214.06	7	442.86	2.77	0.04
Bear Presence + Moose Density + Prey Type + Julian Date	-213.01	8	442.99	2.90	0.04
Bear Presence + Prey Type + Pack Size + Moose Density	-213.10	8	443.17	3.07	0.03
Bear Presence + Prey Type + Pack Size + Julian Date	-213.28	8	443.52	3.43	0.03
Prey Type + Pack Size	-215.69	6	443.94	3.84	0.02
Prey Type + Pack Size + Road	-214.73	7	444.21	4.12	0.02
Bear Presence + Moose Density + Prey Type + Pack Size + Road	-212.66	9	444.55	4.45	0.02
Prey Type + Pack Size + Julian Date	-214.95	7	444.65	4.56	0.02
Prey Type + Pack Size + Moose Density + Julian Date	-213.88	8	444.73	4.64	0.02
Prey Type + Pack Size + Moose Density	-215.01	7	444.77	4.67	0.01
Prey Type + Pack Size + Moose Density + Road	-214.01	8	444.99	4.90	0.01
Bear Presence + Moose Density + Prey Type + Pack Size + Julian Date	-212.95	9	445.13	5.03	0.01
Prey Type + Pack Size + Moose Density + Road + Julian Date	-213.11	9	445.44	5.35	0.01
Bear Presence + Prey Type + Pack Size + Moose Density + Road + Julian Date	-212.54	10	446.58	6.48	0.01
Bear Presence	-218.27	5	446.94	6.84	0.00
Bear Presence + Moose Density	-217.83	6	448.23	8.13	0.00
Bear Presence + Road	-217.92	6	448.40	8.30	0.00
Bear Presence + Pack Size	-218.06	6	448.67	8.57	0.00
Null (Intercept Only)	-220.40	4	449.07	8.97	0.00
Moose Density	-219.89	5	450.18	10.08	0.00
Bear Presence + Pack Size + Julian Date	-217.73	7	450.20	10.11	0.00
Moose Density + Road	-219.03	6	450.63	10.53	0.00
Moose Density + Pack Size + Julian Date	-218.22	7	451.19	11.09	0.00
Pack Size	-220.40	5	451.20	11.10	0.00

Table 5-2 cont.

Bear Presence + Moose Density + Pack Size + Julian Date	-217.35	8	451.67	11.57	0.00
Bear Presence + Moose Density + Pack Size + Road	-217.41	8	451.80	11.70	0.00
Moose Density + Pack Size	-219.77	6	452.11	12.01	0.00
Moose Density + Pack Size + Road	-219.01	7	452.78	12.68	0.00

(c) Yellowstone - Summer

Model Set	LL	K	AICc	Delta_AICc	AICcWt
Bear Presence + Prey Type + Scavenge + Julian Date	**-555.63**	**9**	**1129.52**	**0.00**	**0.40**
Bear Presence + Prey Type + Scavenge + Julian Date + Road	**-555.42**	**10**	**1131.16**	**1.64**	**0.18**
Bear Presence + Prey Type + Pack Size + Scavenge + Julian Date	**-555.56**	**10**	**1131.45**	**1.93**	**0.15**
Prey Type + Scavenge + Julian Date	-558.07	8	1132.35	2.83	0.10
Bear Presence + Prey Type + Pack Size + Scavenge + Julian Date + Road	-555.36	11	1133.10	3.58	0.07
Prey Type + Scavenge + Julian Date + Road	-557.83	9	1133.92	4.40	0.04
Prey Type + Pack Size + Scavenge + Julian Date	-557.97	9	1134.20	4.68	0.04
Prey Type + Pack Size + Scavenge + Julian Date + Road	-557.73	10	1135.79	6.26	0.02
Bear Presence + Prey Type + Scavenge	-561.25	8	1138.72	9.19	0.00
Bear Presence + Prey Type + Pack Size + Scavenge	-561.03	9	1140.33	10.81	0.00
Bear Presence + Prey Type + Scavenge + Road	-561.14	9	1140.53	11.01	0.00
Bear Presence + Prey Type + Pack Size + Scavenge + Road	-560.92	10	1142.17	12.64	0.00
Prey Type + Scavenge	-564.33	7	1142.82	13.30	0.00
Bear Presence + Pack Size + Scavenge + Julian Date	-562.44	9	1143.14	13.62	0.00
Bear Presence + Scavenge	-564.84	7	1143.84	14.32	0.00
Prey Type + Pack Size + Scavenge	-564.04	8	1144.28	14.76	0.00
Prey Type + Scavenge + Road	-564.19	8	1144.59	15.07	0.00
Bear Presence + Pack Size + Scavenge + Julian Date + Road	-562.19	10	1144.70	15.17	0.00
Bear Presence + Pack Size + Scavenge	-564.77	8	1145.74	16.22	0.00
Prey Type + Pack Size + Scavenge + Road	-563.91	9	1146.08	16.56	0.00
Bear Presence + Pack Size + Scavenge + Road	-564.60	9	1147.47	17.94	0.00
Pack Size + Scavenge + Julian Date	-569.10	8	1154.41	24.89	0.00
Scavenge	-571.17	6	1154.46	24.94	0.00
Pack Size + Scavenge + Julian Date + Road	-568.78	9	1155.82	26.30	0.00
Pack Size + Scavenge	-571.09	7	1156.34	26.82	0.00
Pack Size + Scavenge + Road	-570.86	8	1157.93	28.41	0.00
Bear Presence + Prey Type + Julian Date	-598.52	8	1213.25	83.73	0.00
Bear Presence + Prey Type + Pack Size + Julian Date	-597.84	9	1213.94	84.42	0.00
Prey Type + Julian Date	-600.41	7	1214.98	85.46	0.00
Bear Presence + Prey Type	-600.59	7	1215.35	85.82	0.00
Prey Type + Pack Size + Julian Date	-599.66	8	1215.53	86.01	0.00
Bear Presence + Prey Type + Pack Size	-599.68	8	1215.57	86.05	0.00
Bear Presence + Prey Type + Pack Size + Julian Date + Road	-597.68	10	1215.69	86.17	0.00
Bear Presence + Prey Type + Road	-600.49	8	1217.18	87.66	0.00
Prey Type + Pack Size + Julian Date + Road	-599.49	9	1217.24	87.72	0.00
Bear Presence + Prey Type + Pack Size + Road	-599.57	9	1217.41	87.89	0.00
Prey Type	-602.84	6	1217.81	88.28	0.00
Prey Type + Pack Size	-601.83	7	1217.83	88.31	0.00
Prey Type + Road	-602.72	7	1219.61	90.09	0.00
Prey Type + Pack Size + Road	-601.72	8	1219.64	90.12	0.00
Bear Presence	-605.97	6	1224.07	94.55	0.00
Bear Presence + Pack Size	-605.50	7	1225.16	95.64	0.00
Bear Presence + Julian Date	-605.71	7	1225.59	96.06	0.00
Bear Presence + Pack Size + Julian Date	-605.32	8	1226.85	97.32	0.00
Bear Presence + Pack Size + Road	-605.33	8	1226.88	97.36	0.00
Julian Date	-611.49	5	1233.07	103.55	0.00
Null	-611.67	5	1233.42	103.90	0.00
Pack Size	-611.20	6	1234.52	104.99	0.00
Pack Size + Road	-610.99	7	1236.14	106.62	0.00
Pack Size + Julian Date	-611.09	7	1236.34	106.81	0.00

Table 5-3. Parameter estimates from the top models predicting wolf kill interval (days between consecutive kills) for spring (a) and summer (b) in Scandinavia and summer in Yellowstone National Park (c) (Table 5-2). Model-averaged estimates of β-coefficients, SEs and 95% confidence intervals were taken from the top models ($\Delta AIC_c < 2$) for (b) and (c). Interaction terms precluded model averaging, so estimates are reported from the top model for (a). Continuous variables were centered and scaled in all models, and parameter estimates are on the square root scale for (c). The reference group for categorical variables is listed first in parentheses. Bear presence was defined as wolves being either allopatric (A) or sympatric (S) with brown bears in Scandinavia (a-b), or brown bears being absent (A) or present (P) at a wolf kill in Yellowstone National Park (c). Categorical variables for prey type included neonate (N) and non-neonate (NN) moose in Scandinavia (b), and small (S) and large (L) ungulate in Yellowstone National Park (c). 'Bear presence x Julian date' refers to an interaction between the two variables (a). Other independent variables included wolf pack size, Julian date of the kill (a-c), moose density (average number of moose harvested/km^2) (a-b), and number of scavenged carcasses between kills and distance (km) from the kill site to the nearest road (c).

Parameter	β	SE	*95% CI*	
(a) Scandinavia – Spring				
Intercept	0.74	0.62	-0.67	2.21
Bear Presence (A:S)	-0.74	0.90	-2.45	0.83
Julian Date	-0.01	0.01	-0.03	0.004
Bear Presence x Julian Date	0.02	0.01	-0.003	0.04
Pack Size	-0.21	0.08	-0.39	-0.03
Moose Density	-0.18	0.10	-0.42	-0.03
(b) Scandinavia – Summer				
Intercept	-0.19	0.12	-0.42	0.04
Bear Presence (A:S)	0.39	0.17	0.05	0.73
Julian Date	-0.05	0.09	-0.23	0.14
Prey Type (N:NN)	0.71	0.23	0.26	1.17
Pack Size	0.07	0.08	-0.08	0.22
Moose Density	-0.09	0.08	-0.24	0.07

Table 5-3 cont.

(c) Yellowstone – Summer

Intercept	1.40	0.06	1.29	1.51
Bear Presence (A:P)	0.11	0.05	0.01	0.20
Julian Date	0.07	0.02	0.03	0.12
Prey Type (S:L)	0.18	0.05	0.08	0.27
Pack Size	-0.01	0.04	-0.09	0.06
Scavenge	0.20	0.02	0.16	0.24
Road	-0.01	0.02	-0.06	0.03

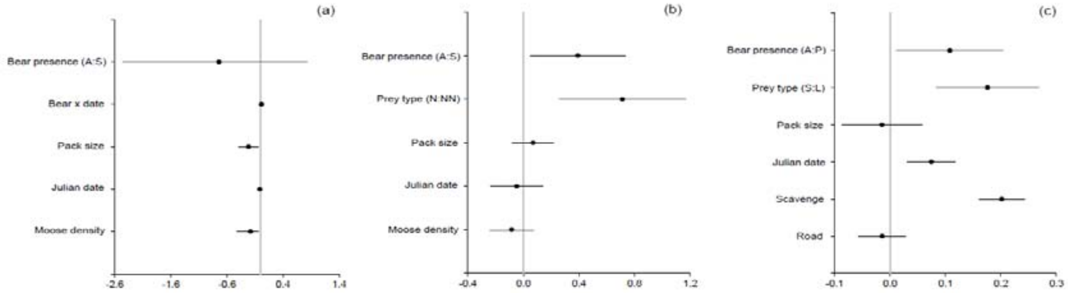


Figure 5-1. Parameter estimates from the top models predicting wolf kill interval (days between consecutive kills) for spring (a) and summer (b) in Scandinavia and summer in Yellowstone National Park (c) (Table 5-2). Model averaged estimates of β-coefficients, SEs, and 95% confidence intervals were taken from the top models ($\Delta AIC_c < 2$) for (b) and (c) (Table 5-3b-c). Interaction terms precluded model averaging, so estimates are reported from the top model for (a) (Table 5-3a). Continuous variables were centered and scaled in all models, and parameter estimates are on the square root scale for (c). The reference group for categorical variables is listed first in parentheses. Bear presence was defined as wolves being either allopatric (A) or sympatric (S) with brown bears in Scandinavia (a-b), or brown bears being absent (A) or present (P) at a wolf kill in Yellowstone National Park (c). Categorical variables for prey type included neonate (N) and non-neonate (NN) moose in Scandinavia (b), and small (S) and large (L) ungulate in Yellowstone National Park (c). 'Bear x date' refers to an interaction between bear presence and Julian date (a). Other independent variables included wolf pack size, Julian date of the kill (a-c), moose density (average number of moose harvested/km^2) (a-b), and number of carcasses scavenged by wolves between kills and distance (km) from the kill site to the nearest road (c).

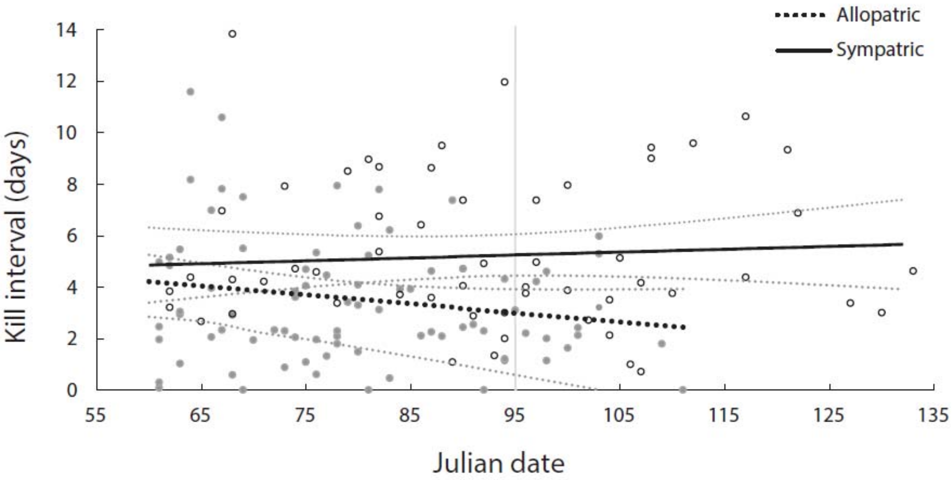


Figure 5-2. Effect of bear presence on the time interval (in days) between consecutive wolf-killed moose during the spring in wolf territories in Scandinavia. The black lines indicate the population-averaged fitted values, with associated 95% confidence intervals (light grey dotted lines), from the best-fit GLMM of kill interval (Table 5-3a). Open and filled circles represent the data for wolf kills in sympatric and allopatric wolf-bear areas, respectively. The vertical gray line indicates the mean date of den emergence for male brown bears in Scandinavia (4 April).

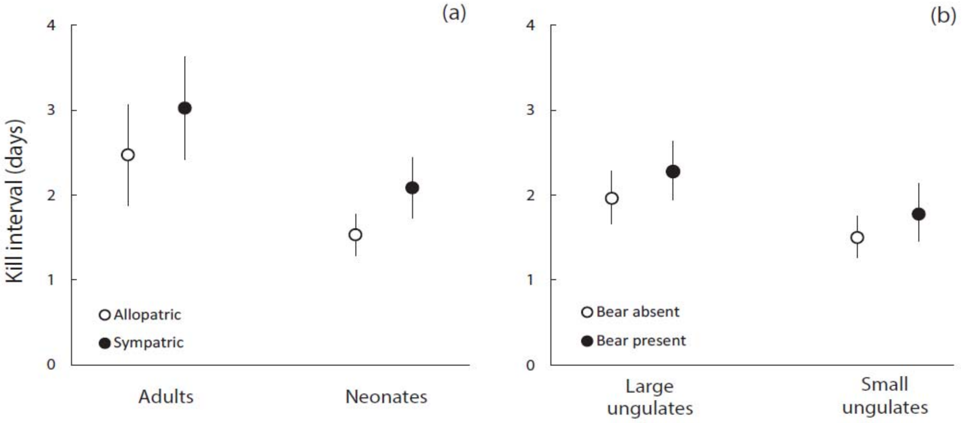


Figure 5-3. Effect of bear presence in a wolf territory in Scandinavia (a) and bear presence at a wolf kill in Yellowstone National Park (b) on the time interval (in days) between consecutive wolf kills in the summer. Open and closed circles are population-averaged fitted values with 95% confidence intervals from the best-fit GLMMs of kill interval (Table 5-3b-c).

CHAPTER 6

CONCLUSION

Since the reintroduction of wolves to Yellowstone National Park in 1995-1997, researchers have collected information on wolf (*Canis lupus*) predation and wolf-bison (*Bison bison*) and wolf-elk (*Cervus elaphus*) interactions. I used these data to evaluate 1) the role of cooperative hunting in the ability of predators to hunt dangerous prey, 2) how predator preference for differentially dangerous prey species changes in relation to their relative abundance, 3) the ability of cursorial predators to drive large-scale, landscape level shifts in prey habitat use. Furthermore, I collaborated with Scandinavian ecologists to 4) evaluate how wolf predation was affected by a sympatric apex predator, the brown bear (*Ursus arctos*), on two continents.

In chapter 2, I found that wolves were more cooperative when hunting bison, their most dangerous prey (Carbyn, Oosenbrug & Anions 1993; Mech & Peterson 2003), than when hunting elk. My results show that the success of wolves hunting bison increased over large group sizes, a pattern that is consistent with cooperation. This is contrary to previous research demonstrating that in many group-hunting taxa hunting success fails to increase over larger group sizes, despite apparent cooperation among hunters (Packer & Ruttan 1988; Boesch & Boesch 1989; Boesch 1994; Rose 1997; Kim, Krafft & Choe 2005; MacNulty *et al.* 2012). I attribute the increase in bison capture success across large group sizes to enhanced cooperation motivated by the very low capture rate of a single hunter when hunting dangerous prey.

Although improved ability to capture formidable prey is not an obvious driver of grouping patterns in Yellowstone wolves, these results demonstrate the potential for such an effect. This is an important finding because most empirical studies of group-size specific hunting success imply that the formation and maintenance of large predator groups is unrelated to prey capture. This chapter clarifies that the benefit of improved hunting success could favor large groups in populations and species that hunt large, dangerous prey.

In chapter 3, I linked individual level behavioral mechanisms with population level patterns to show how prey switching is inhibited by life history and behavioral traits that constrain predator hunting ability. Prey switching occurs when a generalist predator kills disproportionately more of an abundant prey species and correspondingly spares a rare species (Murdoch 1969; Murdoch & Oaten 1975). However, my results suggest that wolves in northern Yellowstone attacked and killed disproportionately more of the rarer, but safer species. Wolves maintained a strong preference against bison even when this species was more than twice as abundant as elk. There was also evidence that wolf aversion to killing bison strengthened as their relative abundance increased. Analyses of wolf-bison behavioral interactions indicate that wolf preference against bison reflected an inability to consistently overcome bison antipredator defenses, which included herding together and aggressively confronting wolves. The ability of wolves to capture bison was limited to a narrow set of conditions involving larger wolf packs (>11 animals) pursuing smaller bison herds (10-20 animals) that included calves; wolves were 11-18 times more likely to capture calves than adults.

My results suggest that prey switching is an unlikely stabilizing mechanism in predator-prey systems where the alternative prey is dangerous. This is because the potentially severe fitness costs of attacking dangerous prey causes predator preference for different prey species to vary in relation to relative prey vulnerability, which is, in turn, a function of the predator and prey traits that determine the outcome of interactions. This is a departure from classic theory which maintains that prey preference is primarily a function of relative prey abundance (Murdoch 1969; Murdoch & Oaten 1975). These results are important for understanding the dynamics of dangerous prey systems because incorrectly assuming prey switching overestimates the stability of ecological communities (van Leeuwen *et al.* 2013). I encourage future studies of dangerous prey systems to explore alternative stabilizing mechanisms, including facultative shifts between hunting and scavenging.

In chapter 4, I evaluated the potential for cursorial predators to affect the large-scale habitat use of prey in free-living systems. This study presents several lines of evidence suggesting wolves are a plausible mechanism behind recent decreased bison preference for Yellowstone's high elevation winter range. First, extensive snow cover in the valley predisposed bison to wolf predation. Second, when wolves were present, bison utilized rare snow-free habitats, decreasing the likelihood of predation. Third, the influence of snow cover on bison use of the Pelican Valley winter range was 30 times stronger after wolf reintroduction than before. In mountainous areas, ungulate predation risk in winter increases as a function of elevation due to progressively greater snow depths that hinder the ability to escape from predators. Because snow is an index of risk, I think this enhanced sensitivity reflects a response to wolf predation risk. Finally, a model that predicted how bison wintering numbers might have been realized after wolf reintroduction, had wolves never been reintroduced, predicted a fairly stable wintering bison population instead of the declining one that I observed.

This chapter provides rare evidence of large-scale shifts in prey habitat use in response to predation risk from a cursorial predator. My results imply that bison could have shifted their preference to lower elevation winter ranges in response to wolf predation risk. These findings are contrary to the prevailing assumption that decreased bison preference for high-elevation winter range in the park's interior is unrelated to wolves. (e.g., Bjornlie & Garrott 2001; Bruggeman *et al.* 2009; Fuller, Garrott & White 2009; Geremia *et al.* 2011; Geremia, Wallen & White 2015). Cursorial predators are expected to incite weak spatial responses by prey. However, this study suggests that even coursing predators can produce consistent risk cues when their hunting success is directly coupled with landscape characteristics.

In Chapter 5, I collaborated with Scandinavian ecologists to determine how wolf predation was affected by a sympatric apex predator, the brown bear. These results suggest brown bear presence resulted in wolves killing less frequently in both Scandinavia and Yellowstone. Wolf packs that were sympatric with brown bears in Scandinavia killed less often than allopatric packs in both spring and summer. In Yellowstone, where brown bear and wolf distributions fully overlapped, bear presence at wolf kills was correlated with an increase in time to the next kill. These results are contrary to the traditional expectation that wolves kill more often where they coexist with brown bears because the loss of food biomass from kleptoparasitism forces additional hunting to meet energetic demands (Boertje *et al.* 1988; Ballard, Carbyn & Smith 2003).

The reason why brown bears are linked to increased wolf kill interval is not intuitive, but several mechanisms might cause this pattern. Interference competition can force a subordinate predator to prematurely abandon its kill, resulting in decreased handling time and, subsequently, shorter kill intervals (e.g., through kleptoparasitism (Krofel, Kos & Jerina 2012; Elbroch *et al.* 2014)). However, it is also possible that predators might realize greater fitness benefits from lingering at the usurped carcass, striving for occasional access, rather than prematurely abandoning it to make a new kill. In addition, exploitative competition may increase kill interval if greater time investment, or superior search efficiency, by one predator diminishes the supply of a shared prey. This would lead to an increase in search time for a second predator and lengthen kill interval (Holt, Grover & Tilman 1994). My results provide new information about the consequences of competition between apex predators that is relevant to understanding how large predator diversity affects trophic interactions in natural systems. Interspecific interactions between apex predators can either relax or strengthen their cumulative effect on prey populations and overall ecosystem functioning (Ives, Cardinale & Snyder 2005; Bruno & Cardinale 2008). These results suggest that ignoring such interactions may result in underestimating the effect that interspecific competition between predators can have on predator populations, as well as overestimating the impact of multiple predators on prey population dynamics.

This study contributes to the current body of work addressing the effects of wolf reintroduction in Yellowstone National Park. My research is unique because it focuses on wolf-bison interactions, which are a little-studied aspect of this system. Wolf-bison systems were almost completely wiped out during the turn of the 19th century, and the recovery and conservation of both species is an on-going objective of both government agencies and non-government organizations. Understanding the life-history traits that allow wolves to successfully hunt bison, the ability of wolves to incorporate bison into their diet, the spatial response of bison to wolf predation, and how competition between apex predators affects predation patterns provides new insight into how wolf-bison systems function. This information can help guide restoration and recovery efforts of these once iconic and wide-spread species.

Wolf-bison interactions also represent an ideal case study to understand relationships between predators and dangerous prey in carnivore-ungulate systems, which are classic model systems for studying predator-prey interactions. However, few studies have measured the behavioral relationships between predators and their most formidable and dangerous prey species. The results from this study suggest that both species traits and landscape characteristics regulate the ability of predators to hunt dangerous prey. For example, predators may be more successful at hunting dangerous prey when predator groups are more cooperative, or in habitats that inhibit prey antipredator defenses. However, in systems where the alternative prey are dangerous, predators may be fundamentally constrained in their ability to prey switch, which can alter the form of a predator’s functional response (Holling 1959), the stability of predator prey systems (Murdoch & Oaten 1975), the strength of apparent competition between prey species (Holt 1977), and the strength of top-down forcing (Sinclair, Mduma & Brashares 2003). Yet, interactions between predator and prey that do not result in death can still elicit strong behavioral responses (Werner & Peacor 2003), and even relatively invulnerable prey may avoid habitats associated with increased harassment. Understanding how predators modify their foraging behavior to cope with dangerous prey species is important for understanding the dynamics of natural systems (Mukherjee & Heithaus 2013). This study contributes to a growing body of theory on this important type of predator-prey interaction: predators that hunt dangerous prey.

References

Ballard, W.B., Carbyn, L.N. & Smith, D.W. (2003) Wolf interactions with non-prey. *Wolves: Behavior, Ecology, and Conservation* (eds L.D. Mech & L. Boitani), pp. 259-271. The University of Chicago Press, Chicago and London.

Bjornlie, D.D. & Garrott, R.A. (2001) Effects of winter road grooming on bison in Yellowstone National Park. *The Journal of Wildlife Management,* **65,** 560-572.

Boertje, R.D., Gasaway, W.C., Grangaard, D.V. & Kelleyhouse, D.G. (1988) Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **66,** 2492-2499.

Boesch, C. (1994) Cooperative hunting in wild chimpanzees. *Animal Behaviour,* **48,** 653-667.

Boesch, C. & Boesch, H. (1989) Hunting behavior of wild chimpanzees in the Taï National Park. *Am J Phys Anthropol,* **78,** 547-573.

Bruggeman, J.E., Garrott, R.A., White, P.J., Bjornlie, D.D., Watson, F.G. & Borkowski, J. (2009) Bison winter road travel: facilitated by road grooming or a manifestation of natural trends. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 604-621. Elesevier, San Diego, CA.

Bruno, J. & Cardinale, B. (2008) Cascading effects of predator richness. *Frontiers in Ecology and the Environment,* **6,** 539-549.

Carbyn, L.N., Oosenbrug, S. & Anions, D. (1993) *Wolves, Bison and the Dynamics Related to the Peace-Athabaska Delta in Canada's Wood Buffalo National Park*. Circumpolar Research Series Number 4; Canadian Circumpolar Institute, Edmonton, Alberta.

Elbroch, L., Lendrum, P., Allen, M. & Wittmer, H. (2014) Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology,* **00,** 1-8.

Fuller, J.A., Garrott, R.A. & White, P.J. (2009) Emigration and density dependence in Yellowstone bison. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G. Watson), pp. 237-254. Elsevier Inc., San Diego, CA.

Geremia, C., Wallen, R.L. & White, P.J. (2015) Population dynamics and adaptive management of Yellowstone bison. National Park Service, Yellowstone National Park, Mammoth, WY.

Geremia, C., White, P.J., Wallen, R.L., Watson, F.G., Treanor, J.J., Borkowski, J., Potter, C.S. & Crabtree, R.L. (2011) Predicting bison migration out of Yellowstone National Park using bayesian models. *PLoS One,* **6,** e16848.

Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist,* **91,** 293-320.

Holt, R. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Popularion Biology,* **12,** 197-229.

Holt, R., Grover, J. & Tilman, D. (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist,* **144,** 741-771.

Ives, A., Cardinale, B. & Snyder, W. (2005) A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecol Lett,* **8,** 102-116.

Kim, K.W., Krafft, B. & Choe, J.C. (2005) Cooperative prey capture by young subsocial spiders. *Behavioral Ecology and Sociobiology,* **59,** 92-100.

Krofel, M., Kos, I. & Jerina, K. (2012) The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology,* **66,** 1297-1304.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2012) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology,* **23,** 75-82.

Mech, L.D. & Peterson, R.O. (2003) Wolf-Prey Relations. *Wolves: Behavior, Ecology and Conservation* (eds L.D. Mech & L. Boitani), pp. 131-160. The University of Chicago Press, Chicago, IL.

Mukherjee, S. & Heithaus, M.R. (2013) Dangerous prey and daring predators: A review. *Biological Reviews,* **88,** 550-563.

Murdoch, W. (1969) Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs,* **39,** 335-354.

Murdoch, W. & Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research,* **9,** 1-131.

Packer, C. & Ruttan, L. (1988) The evolution of cooperative hunting. *Am Nat,* **132,** 159-198.

Rose, L.M. (1997) Vertebrate Predation and Food-Sharing in Cebus and Pan. *International Journal of Primatology,* **18,** 727-765.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. (2003) Patterns of predation in a diverse predator–prey system. *Nature,* **425,** 288-290.

van Leeuwen, E., Brännströmb, Å., Jansen, V.A.A., Dieckmann, U. & Rossberg, A.G. (2013) A generalized functional response for predators that switch between multiple prey species. *Journal of Theoretcial Biology,* **328,** 89-98.

Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology,* **84,** 1083-1100.

APPENDICES

Appendix 1 – Estimating Elk Abundance

We used a state-space model, constructed from the known time series of elk count data, to infer the most likely population size for years in which no survey occurred. State-space models can, in some cases, separate process error (i.e. variation arising from ecological processes) from observation error (i.e. variation arising from imperfect sampling) which makes this an appealing method when dealing with imprecise count data (de Valpine & Hastings 2002; Buckland *et al*. 2004; Clark & Bjornstad 2004). The inferred population size is conditional on the full time series of data and constrained by a population growth model (Clark & Bjornstad 2004). To constrain population growth, we used a state-space formulation of the Gompertz population growth model because 1) it accurately portrays density-dependent population growth (Dennis *et al*. 2006) and 2) convenience (i.e., by taking the natural logarithm of each term in the model, it becomes a simple linear equation). Although state-space models can be implemented using both Bayesian and likelihood approaches, we opted to use a Bayesian approach because of the ease in which they incorporate missing data (Kery & Schaub 2012).

Gompertz population growth model - We specify that the true population size at time t (N_t) is a function of the population size in the previous year (N_{t-1}) multiplied by growth rate. In turn, we specify growth rate as the exponential sum of β_0 and $\beta_1 * N_{t-1}$ (equation 1). Here, β_0 is equivalent to $r_{\max}$, i.e. the maximum growth rate that a given species' population could attain if resources were unlimited. β_1 estimates the strength of density dependence, i.e., the degree to which $r_{\max}$ is influenced by population density. In most cases, $\beta_1 < 0$, indicating that as population size increases, population growth rate becomes less than r_{max}. By taking the logarithm of both sides of equation 1, a simple additive linear model is obtained (equation 2), where $x_t = \log(N_t)$. For shorthand, we refer to the Gompertz equation as $f(x_{t-1})$.

$$\text{Equation 1: } N_t = N_{t-1} * e^{(\beta_0 + \beta_1 * \log(N_{t-1}))}$$

$$\text{Equation 2: } x_t = x_{t-1} + \beta_0 + \beta_1 * x_{t-1} = f(x_{t-1})$$

State-space model - To represent the Gompertz equation as a state space model, we must link the process model (equation 2) to an observation model in order to separate process error (σ_p^2) from observation error (σ_o^2). This is achieved through the following set of equations

$$\text{Equation 3: } x_t = f(x_{t-1}) + \varepsilon_t$$

$$\text{Equation 4: } y_t = g(x_t) + w_t$$

in which equation 3 is the process (i.e. Gompertz) model from above, with a normally distributed error term [$\varepsilon_t \sim N(0, \sigma_p^2)$] which accounts for variation not explained by the Gompertz model; and equation 4, in which y_t represents the log number of observed elk during each survey, and is linked to the underlying state by the observation model $g(x_t)$, plus a normally distributed error term [$w_t \sim N(0, \sigma_o^2)$] to account for observation error.

In Bayesian analyses, prior distributions must be provided for all random variables. We chose vague priors for variables for which we had no prior data, i.e. σ_p^2

and σ_o^2. However, we provided more informative priors for parameters which could be reliably estimated from ecological theory, i.e. β_0 and β_1. Providing informative priors in cases when it is appropriate results in greater identifiability of other model parameters, such as the separation of process and observation error (Lebreton & Gimenez 2013). Following Koons *et al.* (2015), we estimated an informative Gaussian prior distribution for β_0 ($\bar{x} = 0.263$, $SD = 0.09$) from estimates of $r_{\max}$ in elk (Caughley 1977; Houston 1982; Hennemann 1983; Eberhardt 1987; Gogan & Barrett 1987; McCorquodale, Eberhardt & Eberhardt 1988) as cited within Duncan, Forsyth & Hone (2007), and defined a zero mean Gaussian prior distribution for β_1 truncated at -2, 2.

The full model, including prior distributions, is provided below:

$$\mathrm{P}\left[N_t, \boldsymbol{\beta}, \sigma_p^2, \sigma_o^2 \,\middle|\, y_t\right] \propto$$

Process model:

$$\prod_{i=1}^{T} \mathrm{Normal}\left(x_t \middle| f\,(x_{t-1}; \boldsymbol{\beta}), \sigma_p^2\right) \times$$

Observation model:

$$\prod_{i=1}^{T} \mathrm{Normal}\left(y_t \middle| g(x_t), \sigma_o^2\right) \times$$

Parameter models:

Inverse Gamma$\left(\sigma_p^2 \middle| 0.001, 0.001\right)$ ×

Inverse Gamma$(\sigma_o^2|0.001, 0.001)$ ×

Normal$\left(\beta_0 \middle| 0.263,\ 0.09^2\right)$ ×

Normal$\left(\beta_1 \middle| 0,2^2\right)$T(-2, 2)

Model implementation - We conducted Markov Chain Monte Carlo (MCMC) simulations in JAGS (v. 3.4.0; Plummer 2012) via Program R and the R2jags package (Su & Yajima 2012) to estimate posterior distributions of the parameters of interest. For each model, we ran three chains each consisting of 100,000 iterations with the first 50,000 discarded as burn-in, and thinned the sample to retain every 50th simulation. Model convergence was assessed visually using traceplots and by ensuring each parameter of interest had a $\widehat{R}$ value < 1.05 (Gelman 1996). We assessed model goodness-of-fit using posterior predictive checks (Gelman *et al*. 2004; Kery & Schaub 2012; Hobbs & Hooten 2015; Hooten & Hobbs 2015). To achieve this, we generated hypothetical count data (i.e. $Y.new_t$) from the model and used a squared discrepancy statistic to compare observed and expected values from the original and new datasets at every MCMC iteration, i.e. $(Y_t - N_t)^2$and $(Y.new_t - N_t)^2$, respectively. Calculating the proportion of iterations in which the discrepancy statistics arising from the original and hypothetical datasets are more extreme than one another provides a measure of goodness-of-fit; a value of 0.5 would indicate perfect fit, while values close to 0 or 1 suggest a lack-of-fit.

Sightability model – Next, we used a model constructed by Singer and Garton (1994) to correct for bias due to elk visibility during surveys in northern Yellowstone National Park. Their model corrected for elk group size, vegetation cover type at the count location, and elk activity. Due to data limitations, we used a reduced version of that model that corrected for elk group size only. We corrected surveys that did not include group size information by using an average sightability estimated from the nearby years. Total and park winter range elk numbers were estimated from survey UTM data, where it was available. Where it was not available, elk numbers were estimated using an average from nearby years.

Table A1. Number of elk counted in the total and park winter ranges during annual aerial winter surveys in northern Yellowstone. State-space model predictions, or the inferred elk count for years when no survey occurred, for the total and park elk winter ranges are below in **bold**. Sightability corrected counts for the total and park elk winter ranges, which were used for analysis, are below in *italics*.

Year	Survey Date	Total Elk Count	Park Elk Count	Corrected Total Elk Count	Corrected Park Elk Count
1995	12/21/1994	16791	13097	*22189*	*17740*
1996	NA	**15062**	**11748**	*19904*	*15913*
1997	NA	**13459**	**10498**	*17786*	*14219*
1998	1/18/1998, 1/27/1998	11736	9137	*15509*	*12376*
1999	1/30/1998, 2/11/1999	11742	8807	*15517*	*11928*
2000	12/27/1999	14539	10904	*19106*	*16372*
2001	12/21/2000	13400	10050	*17609*	*15089*
2002	12/21-23/2001	11969	8446	*15729*	*12278*
2003	12/24/2002	9215	6759	*12662*	*9846*
2004	12/18/2003	8335	6094	*10724*	*8275*
2005	1/5/2005	9545	6175	*12808*	*8831*
2006	NA	**7992**	**3405**	*10192*	*5045*
2007	12/30/2006	6738	4331	*8913*	*5997*
2008	2/14/2008	6279	2281	*8309*	*3701*
2009	1/30/2009, 2/9/2009	7109	3576	*9771*	*5643*
2010	2/26/2010	6070	2698	*7601*	*3959*

2011	12/21/2010	4635	2399	*6398*	*3609*
2012	3/7/2012	4174	1440	*5248*	*2029*
2013	2/18/2013	3915	915	*5268*	*1585*
2014	NA	**4400**	**1012**	*5749*	*1561*
2015	1/20/2015	4844	1130	*6090*	*1853*
2016	1/2/2016	4912	1154	*6422*	*1832*

References for Appendix 1

Buckland, S.T., Newman, K.B., Thomas, L. & Koesters, N.B. (2004) State-space models for the dynamics of wild animal populations. *Ecological Modelling*, 171, 157–175.

Caughley, G. (1977). *Analysis of vertebrate populations*. John Wiley and Sons, London, UK.

Clark, J.S. & Bjørnstad, O.N. (2004) Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology*, 85, 3140–3150.

de Valpine, P. & Hastings, A. (2002). Fitting population models incorporating process noise and observation error. *Ecological Monographs*, 72, 57–76.

Dennis, B., Ponciano, J.M., Lele, S.R., Taper, M.L. & Staples, D.F. (2006) Estimating density dependence, process noise, and observation error. *Ecological Monographs*, 76, 323–341.

Eberhardt, L.L. (1987). Population projections from simple models. *Journal of Applied Ecology*, 24, 103–118.

Gelman, A. (1996) Inference and monitoring convergence. *Markov chain Monto Carlo in practice*, (eds W.R. Gilks, S. Richardson, & D.J. Spiegelhalter), pp. 131–143. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Gelman, A. (2004) Exploratory data analysis for complex models. *Journal of Computational and Graphical Statistics*, 13, 755–779.

Gogan, P.J.P. & Barrett, R.H. (1987). Comparative dynamics of introduced tule elk populations. *The Journal of Wildlife Management*, 51, 20–27.

Hennemann, W.W. III. (1983) Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. *Oecologia*, 56, 104–108.

Hobbs, N.T. & Hooten, M.B. (2015) *Bayesian models: a statistical primer for ecologists*. Princeton University Press.

Hone, J., Duncan, R.P. & Forsyth, D.M. (2010) Estimates of maximum annual population growth rates (rm) of mammals and their application in wildlife management. *Journal of Applied Ecology*, 47, 507–514.

Hooten, M.B. & Hobbs, N.T. (2015) A guide to Bayesian model selection for ecologists. *Ecological Monographs*, 85, 3–28.

Houston, D.B. (1982). *The northern Yellowstone elk*. Macmillan, New York, New York, USA.

Kéry, M. & Schaub, M. (2011) *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press, London, UK.

Koons, D.N., Colchero, F., Hersey, K. & Gimenez, O. (2015) Disentangling the effects of

climate, density dependence, and harvest on an iconic large herbivore's population dynamics. *Ecological Applications*, 25, 956–967.

Lebreton, J.D. & Gimenez, O. (2013) Detecting and estimating density dependence in wildlife populations. *The Journal of Wildlife Management*, 77, 12–23.

McCorquodale, S.M., Eberhardt, L.L. & Eberhardt, L.E. (1988). Dynamics of a colonizing elk population. *The Journal of Wildlife Management*, 52, 309–313.

Plummer, M. (2012) JAGS version 3.4.0 user manual. http://mcmcjags.sourceforge.net/

Singer, F.J. & Garton, E.O. (1994) Elk sightability model for the Super Cub. *Aerial survey; user's manual with practical tips for designing and conducting aerial big game surveys*. Idaho Department of Fish and Game, Boise, ID.

Su, Y.S., & Yajima, M. (2012) R2jags: a package for running JAGS from R.

https://cran.r-project.org/web/packages/R2jags/R2jags.pdf

Appendix 2 - Cluster Searches and Carcass Cause of Death.

Field crews searched for carcasses within a 100 m radius of all ‘clustered’ GPS points in Scandinavia, and within a 400 m^2 area of all clustered GPS points in Yellowstone. Upon carcass detection, we determined cause of death by searching each carcass and carcass site for signs of predation such as blood trails, subcutaneous hemorrhaging, canine punctures, vegetation disturbance, scat, tracks, and hair. We designated predator species using scat, tracks, and hair, and predator-specific patterns of consumption (e.g., location of canine punctures, separation of rumen from the carcass, disarticulation of the ungulate skeleton, or burial of the carcass). Furthermore, we classified carcasses as wolf-killed if its state of decomposition and suspected time of death matched spatially and temporally with GPS positions from collared wolves. All carcasses were classified into 3 categories: 1) definite wolf-killed prey, 2) probable wolf-killed prey, and 3) died from other causes (e.g., other predators, other natural causes, etc.). We assumed wolves were scavenging when they visited a carcass that had not been killed by their pack (i.e., time of death matched spatially and temporally with GPS positions from wolves in a different pack, or the ungulate died from other causes).

Brown bears rarely prey on adult ungulates (i.e., adult moose in Scandinavia and adult elk, bison, or moose ≥11 months in Yellowstone) in either system (Evans *et al.* 2006; Dahle *et al.* 2013). Evidence of bear presence at a carcass included bear scat, tracks, or hair, or characteristic signs of bear consumption (e.g., twisted remains, and crushed large bones such as femur and skull, and carcass covered with soil and vegetation). We assumed that neonate carcasses located at cluster positions (i.e., > 2 GPS positions) were killed by wolves, unless we found evidence that the kill was made by another predator. Neonate prey are consumed quickly by bears and wolves (Barber-Meyer, Mech & White 2008), and we surmised that if wolves spent enough time at a neonate carcass to create a cluster, this represented a kill. In the areas where bears and wolves overlapped in Scandinavia, we detected bear sign at, or near, 21% of 33 neonate moose kills. Note that bear sign was recorded for 3 out of 4 study packs that overlapped bear territory. In Yellowstone, bear sign was found at, or near, 14% of 312 small ungulate wolf-kills.

References for Appendix 2

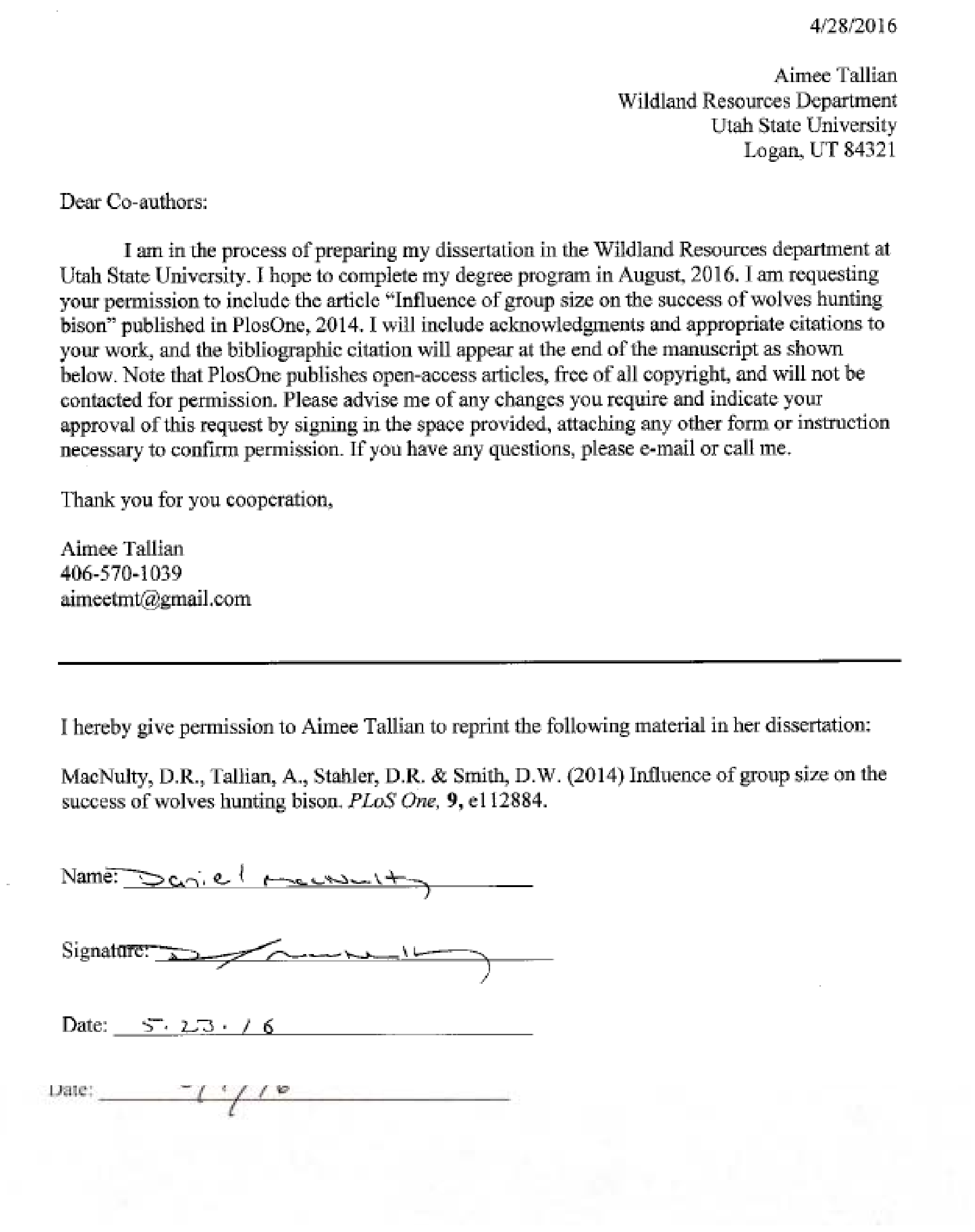
Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs,* **169,** 1-30.

Dahle, B., Wallin, K., Cederlund, G., Persson, I.L., Selvaag, L. & Swenson, J.E. (2013) Predation on adult moose *Alces alces* by European brown bears *Ursus arctos*. *Wildlife Biology,* **19,** 165-169.

Evans, S., Mech, D., White, P.J. & Sargeant, G. (2006) Survival of adult female elk in Yellowstone following wolf restoration. *Journal of Wildlife Management,* **70,** 1372-1378.

Singer, F.J. & Garton, E.O. (1994) Elk sightability model for the Super Cub. *Aerial survey; user's manual with practical tips for designing and conducting aerial big game surveys*. Idaho Department of Fish and Game, Boise, ID.

Appendix 3 – Permission Letters PlosOne



4/28/2016

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I hope to complete my degree program in August, 2016. I am requesting your permission to include the article "Influence of group size on the success of wolves hunting bison" published in PlosOne, 2014. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that PlosOne publishes open-access articles, free of all copyright, and will not be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

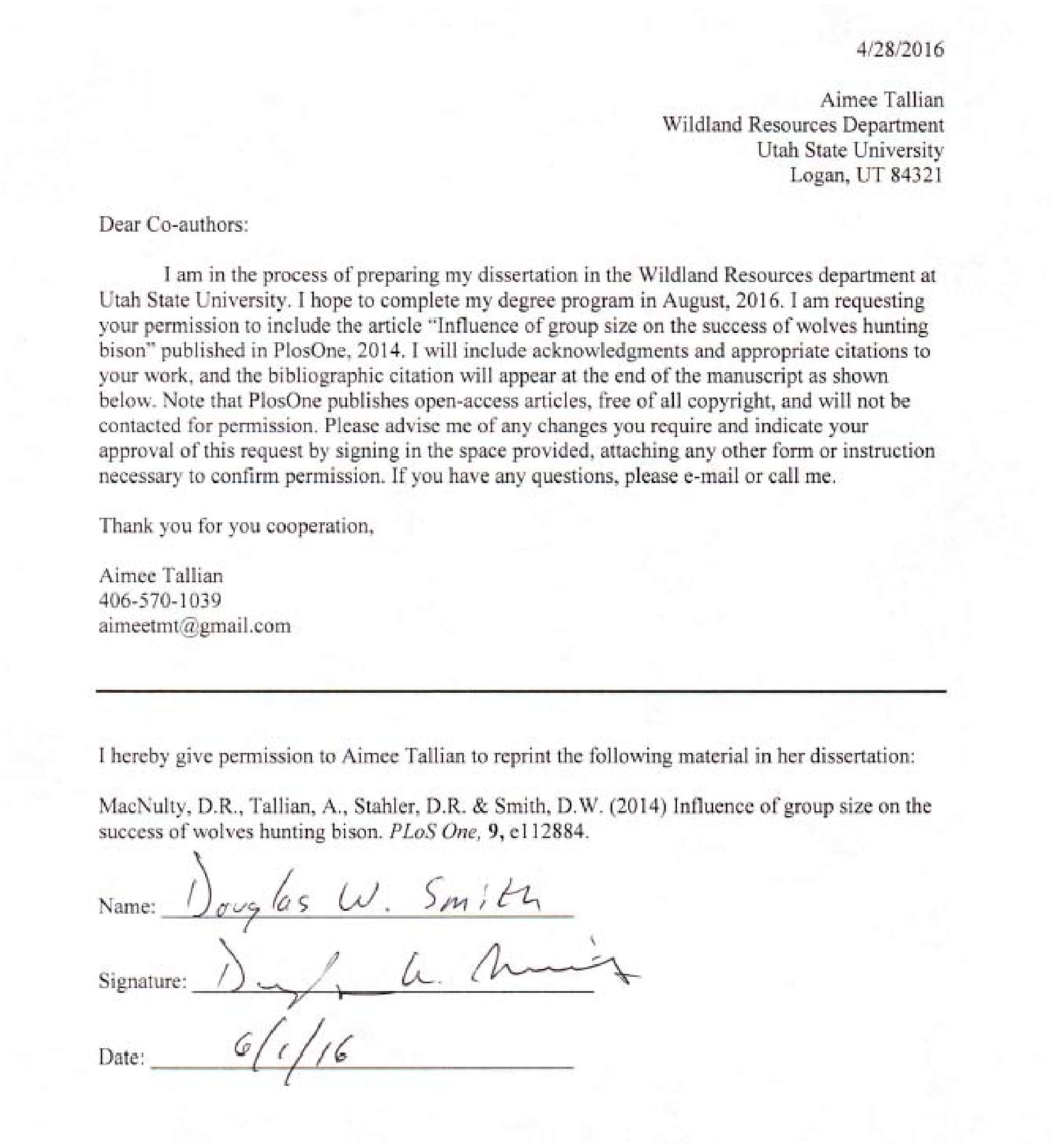
MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W. (2014) Influence of group size on the success of wolves hunting bison. *PLoS One,* **9,** e112884.

Name: Daniel MacNulty

Signature:

Date: 5.23.16

Date: 7/1/16



4/28/2016

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I hope to complete my degree program in August, 2016. I am requesting your permission to include the article "Influence of group size on the success of wolves hunting bison" published in PlosOne, 2014. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that PlosOne publishes open-access articles, free of all copyright, and will not be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

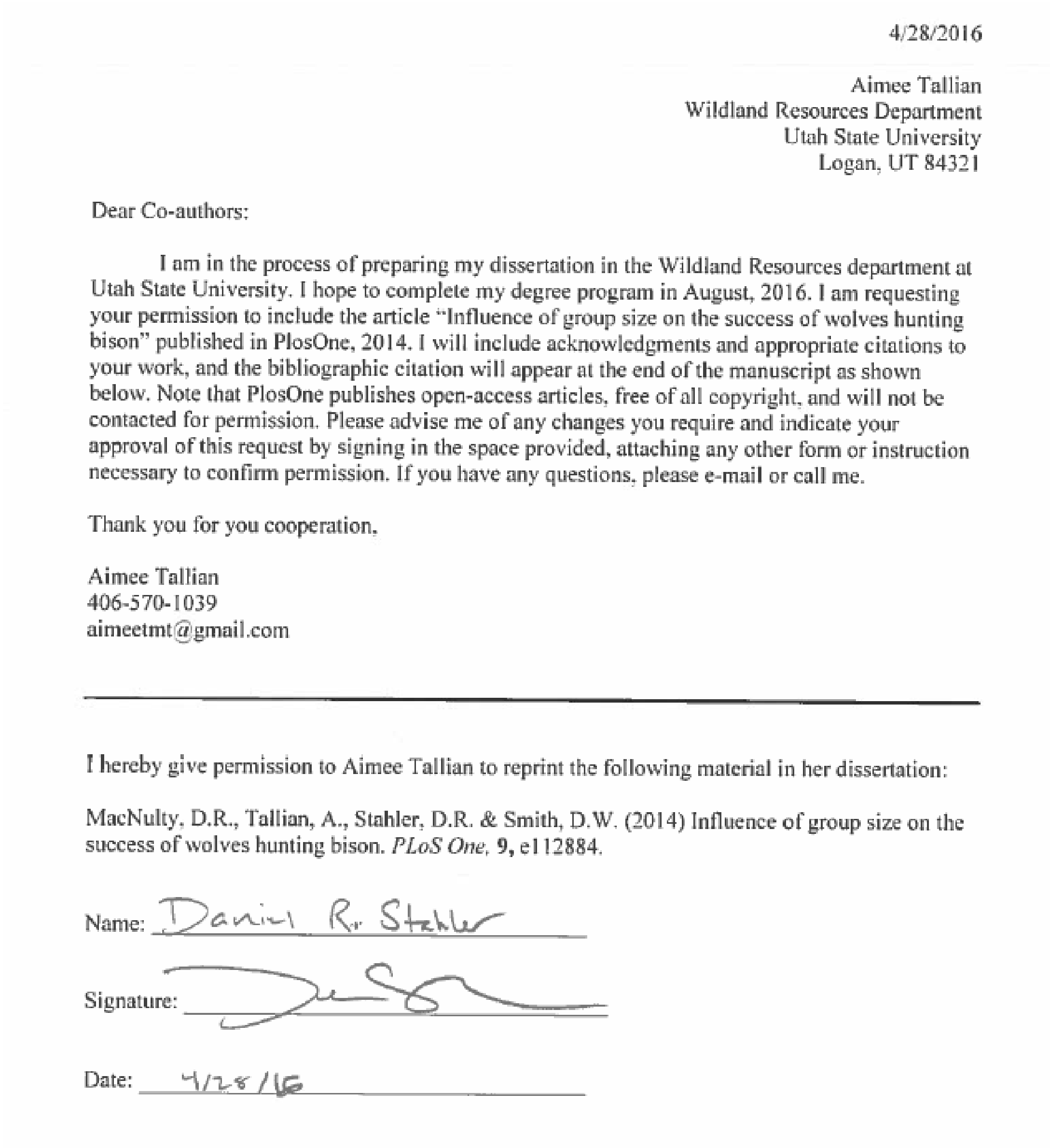
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W. (2014) Influence of group size on the success of wolves hunting bison. *PLoS One,* **9,** e112884.

Name: Douglas W. Smith

Signature:

Date: 6/1/16



4/28/2016

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I hope to complete my degree program in August, 2016. I am requesting your permission to include the article "Influence of group size on the success of wolves hunting bison" published in PlosOne, 2014. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that PlosOne publishes open-access articles, free of all copyright, and will not be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

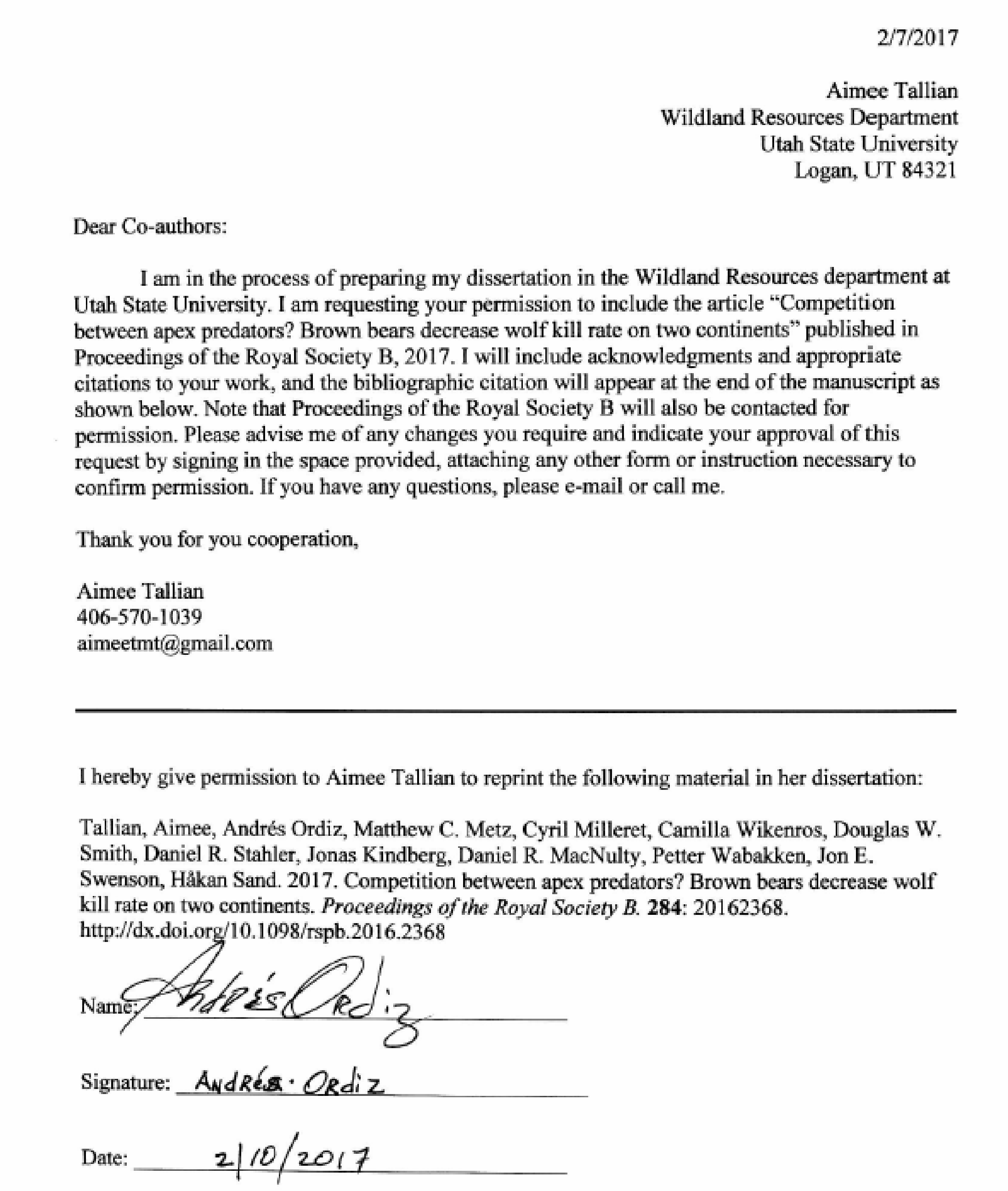
MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W. (2014) Influence of group size on the success of wolves hunting bison. *PLoS One*, **9**, e112884.

Name: Daniel R. Stahler

Signature:

Date: 4/28/16

Appendix 4 – Permission Letters Proceedings of the Royal Society B



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

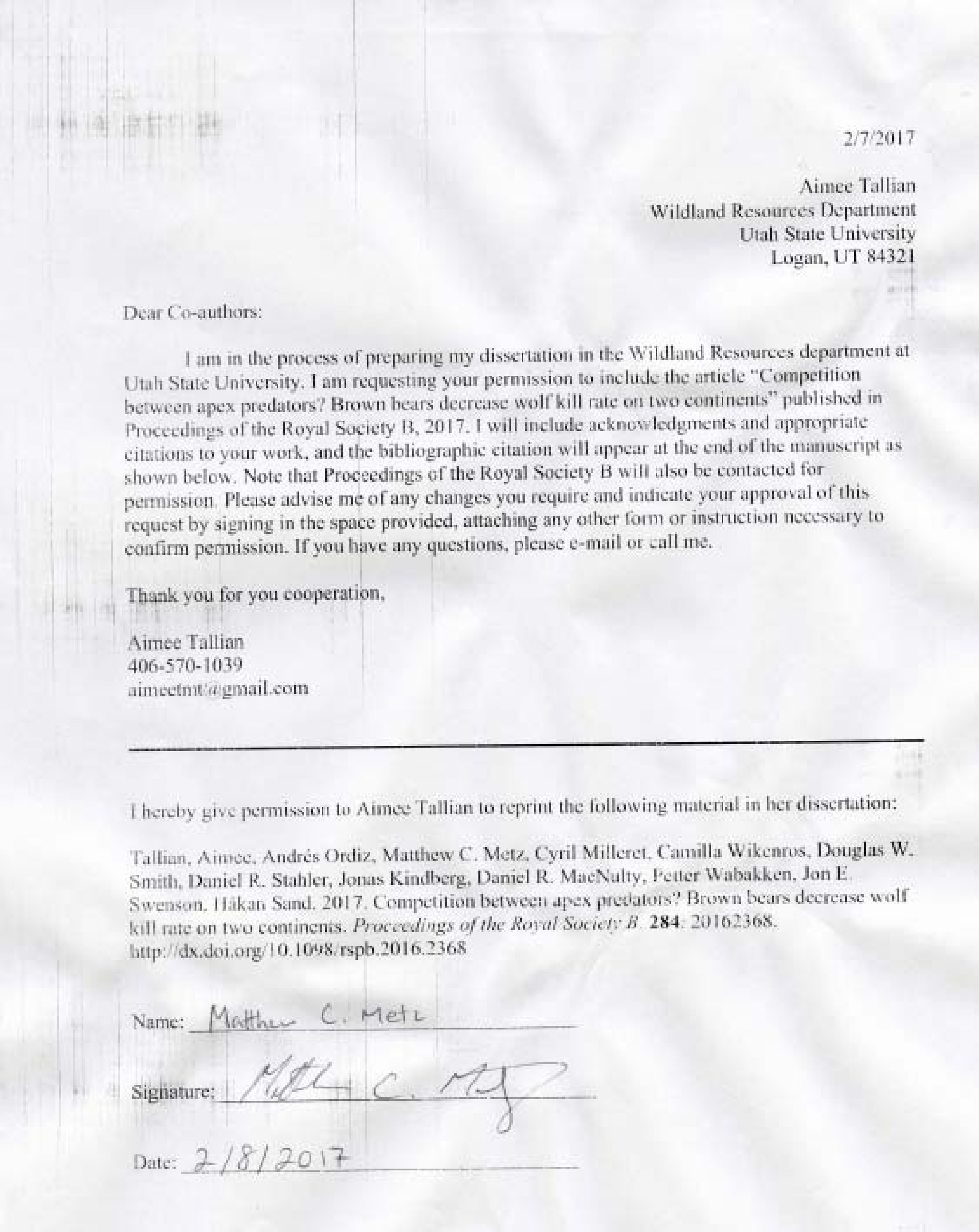
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Andrés Ordiz

Signature: AndRés · ORdiz

Date: 2/10/2017



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

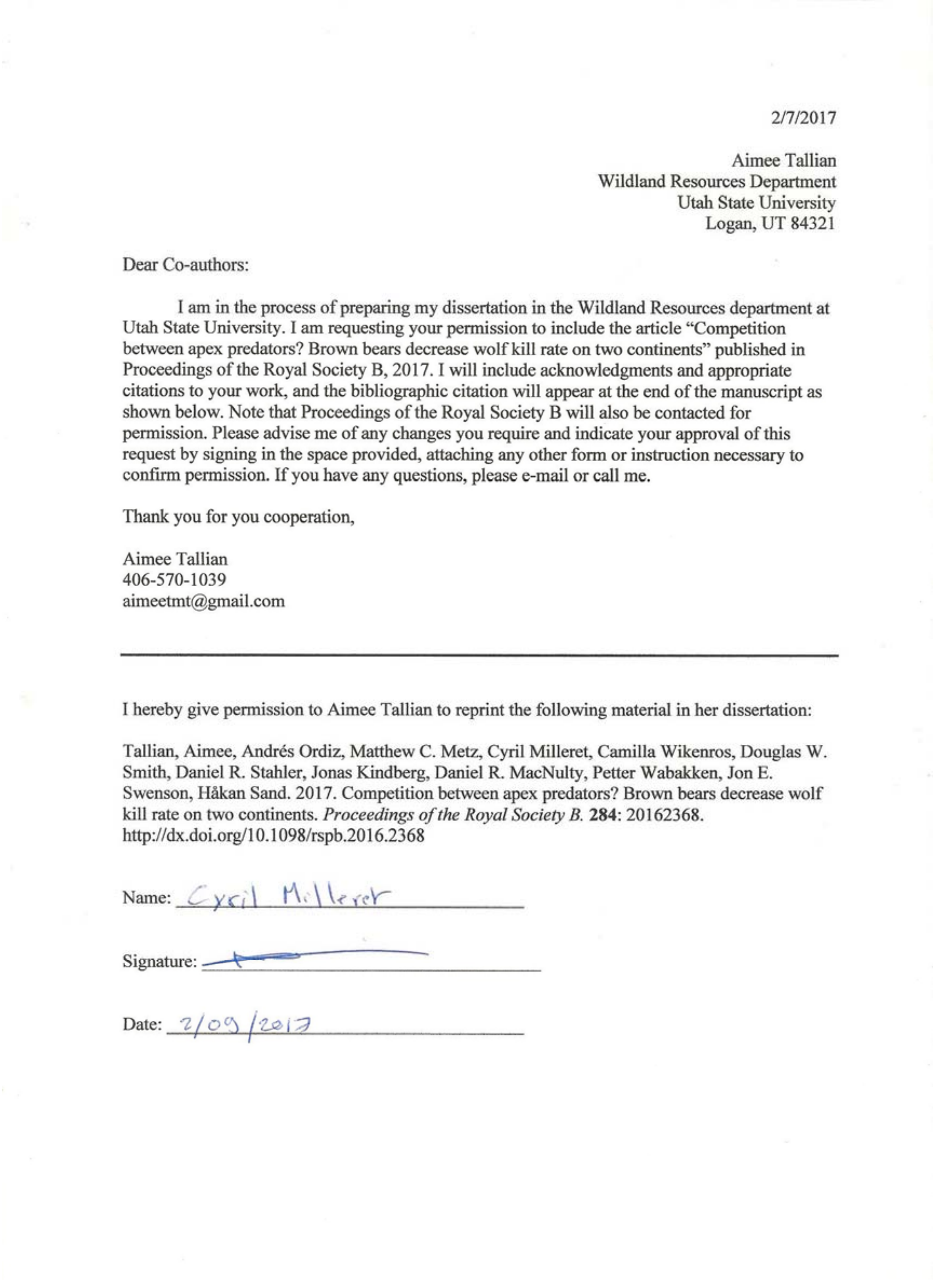
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B*. **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Matthew C. Metz

Signature:

Date: 2/8/2017



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Cyril Milleret

Signature:

Date: 2/09/2017

2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

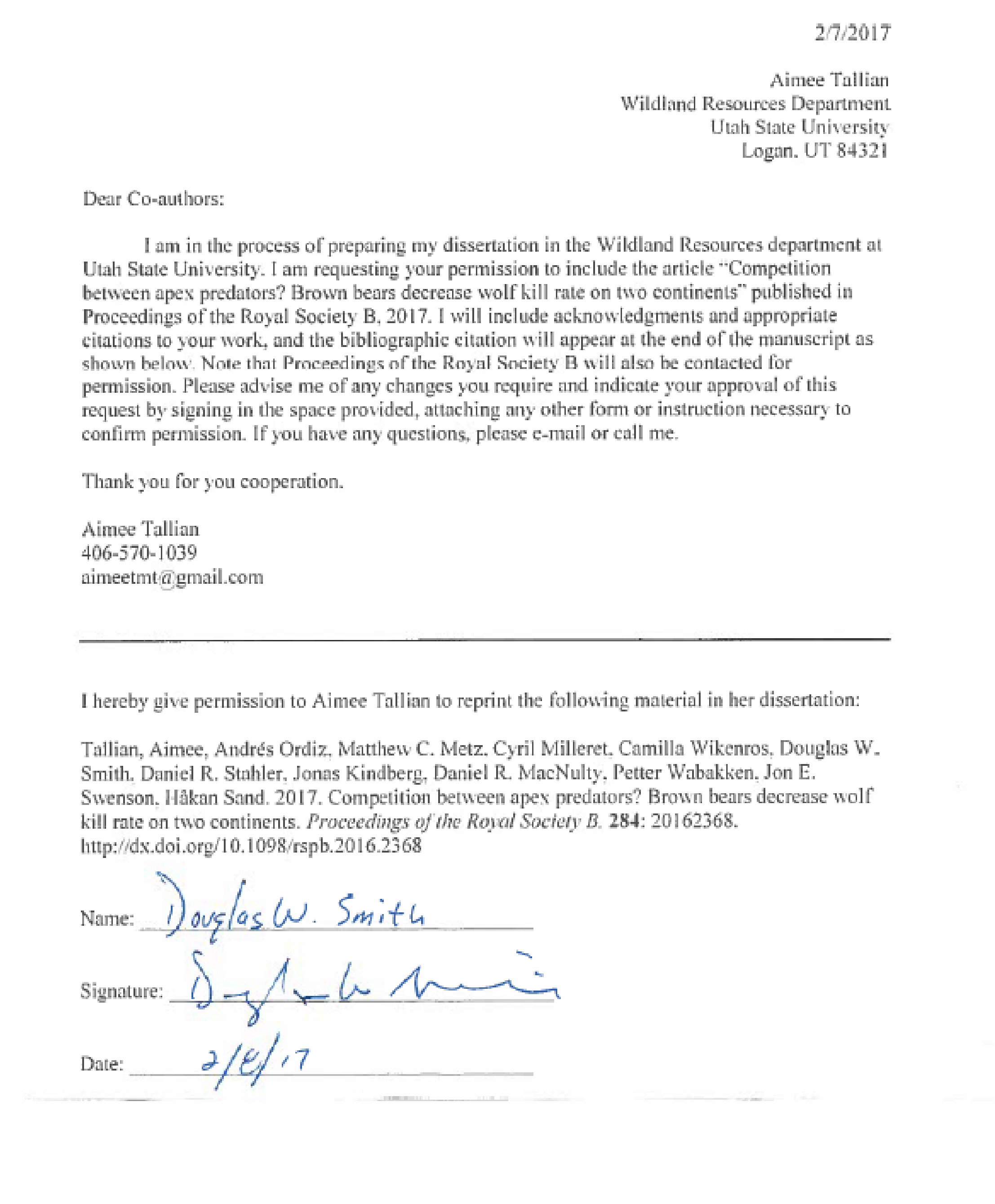
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Camilla Wikenros

Signature: Camilla Wi

Date: 2/9/2017



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation.

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

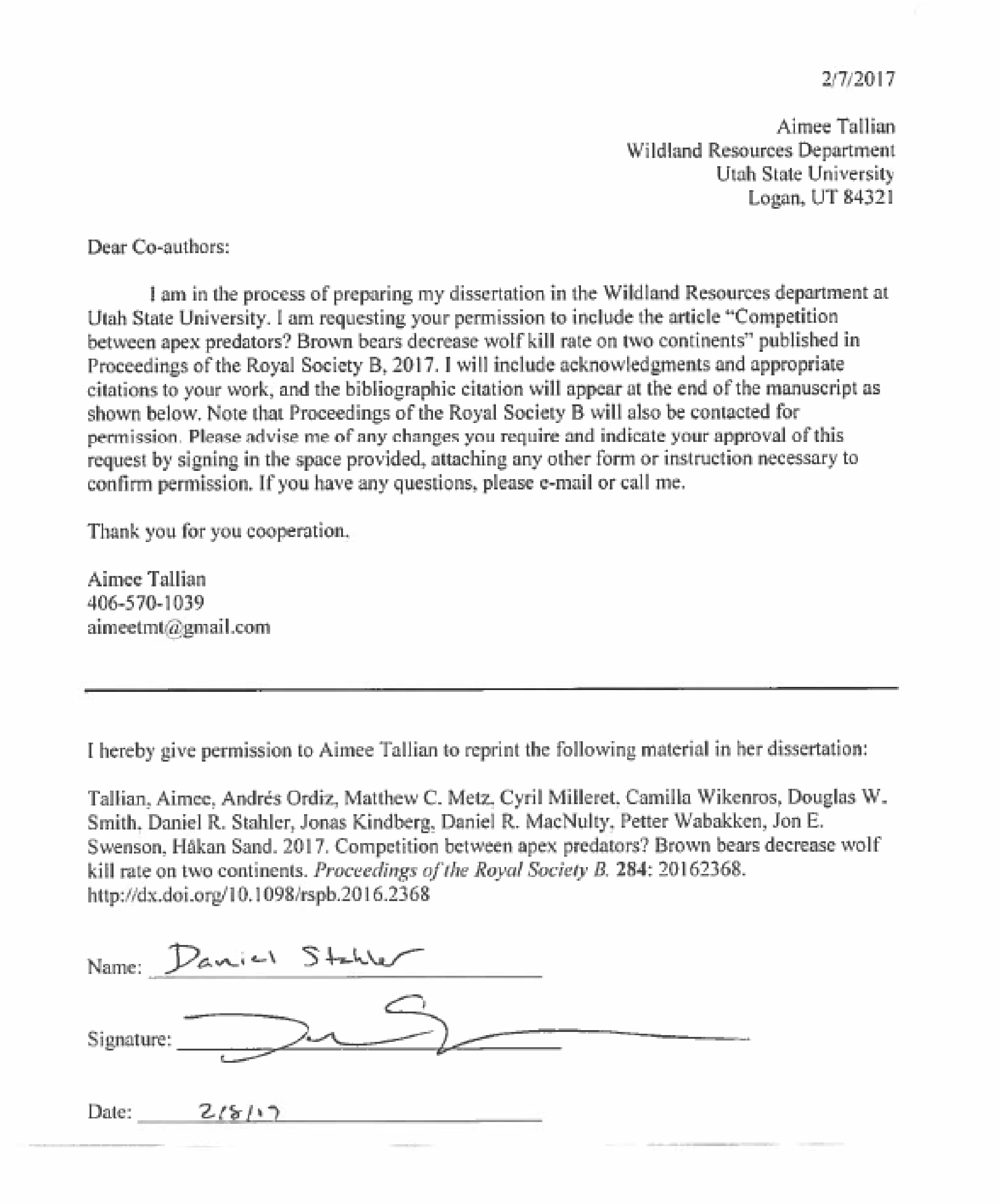
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B*. **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Douglas W. Smith

Signature:

Date: 2/8/17



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation.

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Daniel Stahler

Signature:

Date: 2/8/17

2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

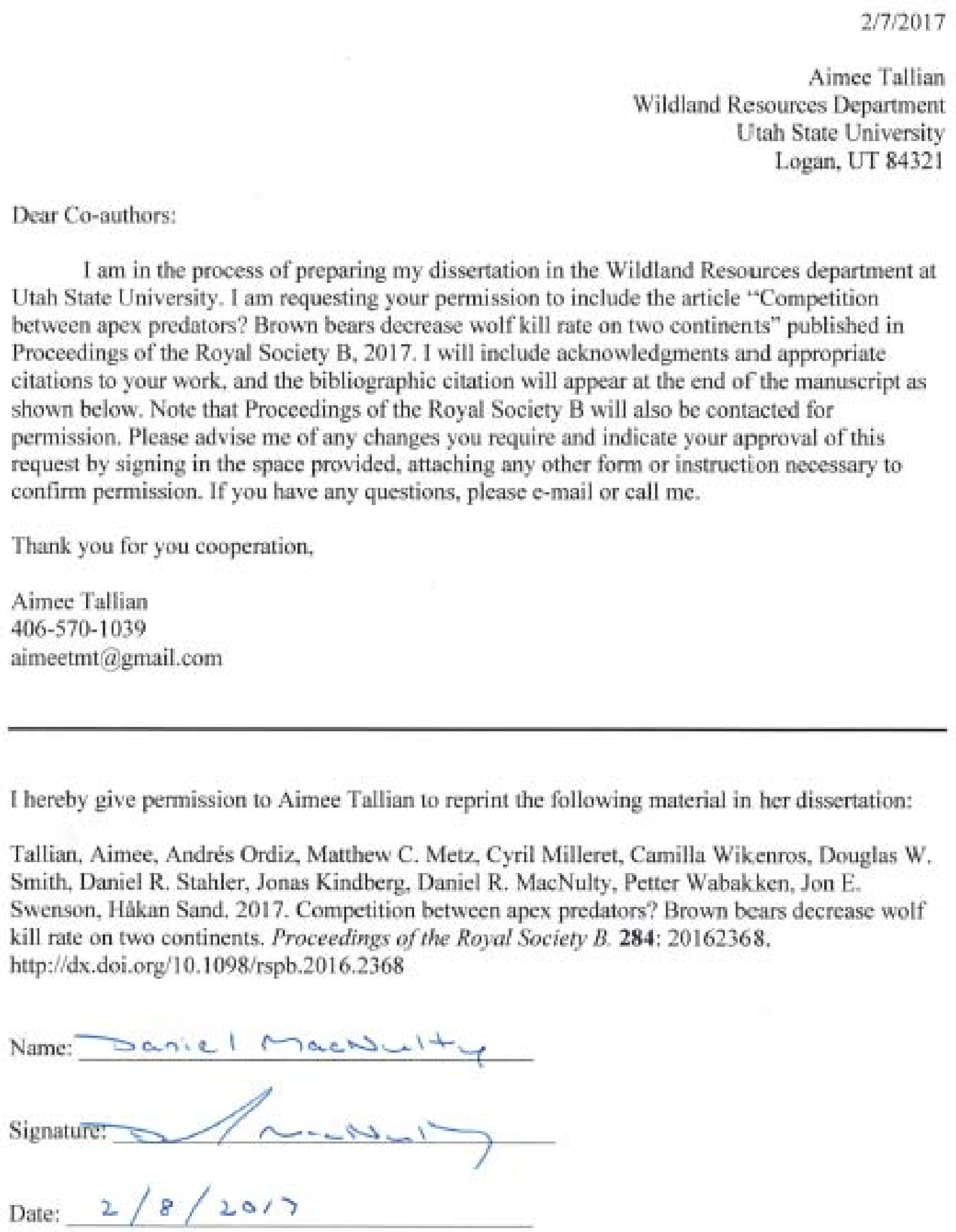
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Jonas Kindberg

Signature: ______________________

Date: 10 February 2017



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

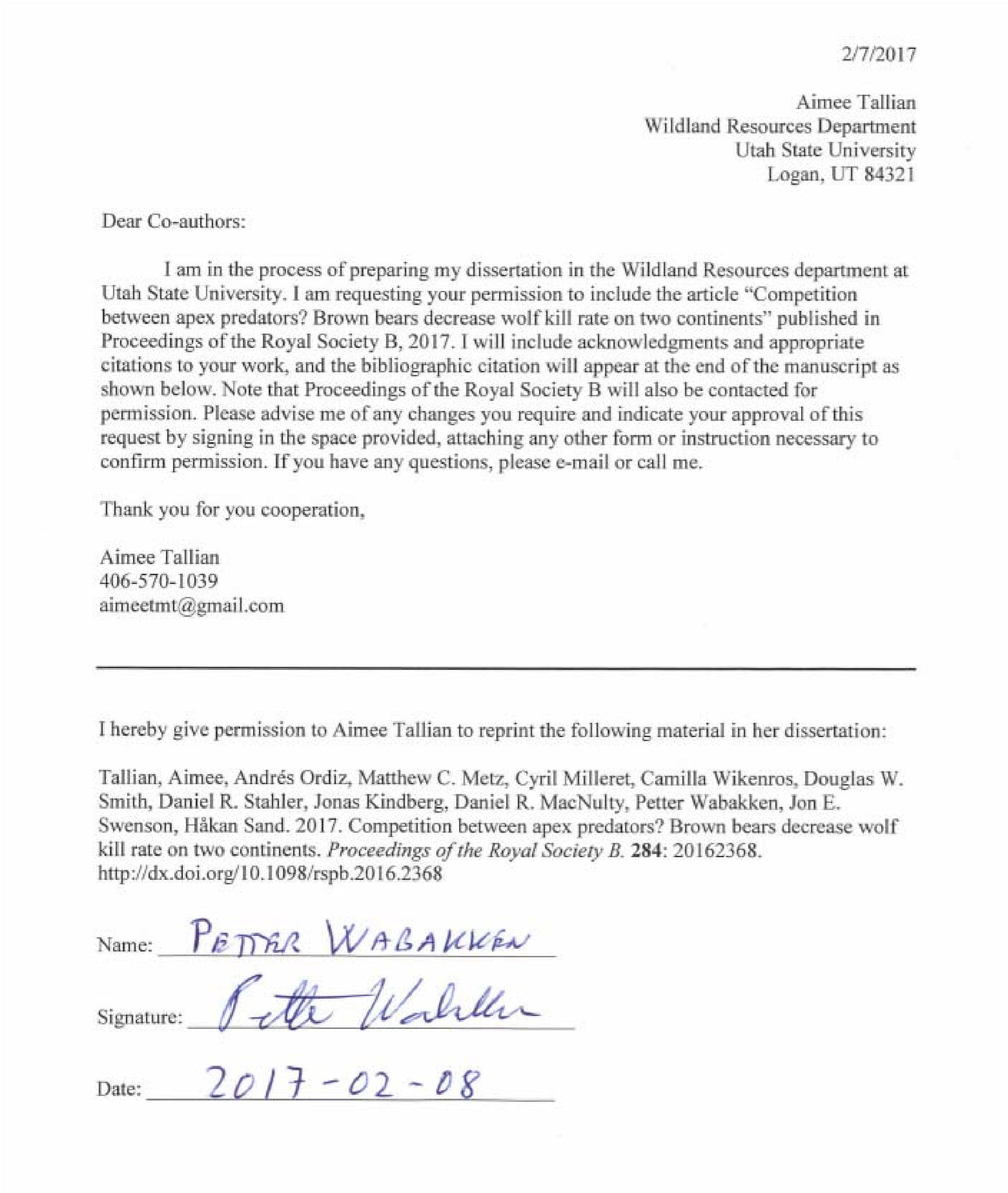
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Daniel MacNulty

Signature: MacNulty

Date: 2/8/2017



2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: PETTER WABAKKEN

Signature: Petter Wabakken

Date: 2017-02-08

2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B*. **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Jon E. Swenson

Signature:

Date: 9 February 2017

2/7/2017

Aimee Tallian
Wildland Resources Department
Utah State University
Logan, UT 84321

Dear Co-authors:

I am in the process of preparing my dissertation in the Wildland Resources department at Utah State University. I am requesting your permission to include the article "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" published in Proceedings of the Royal Society B, 2017. I will include acknowledgments and appropriate citations to your work, and the bibliographic citation will appear at the end of the manuscript as shown below. Note that Proceedings of the Royal Society B will also be contacted for permission. Please advise me of any changes you require and indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please e-mail or call me.

Thank you for you cooperation,

Aimee Tallian
406-570-1039
aimeetmt@gmail.com

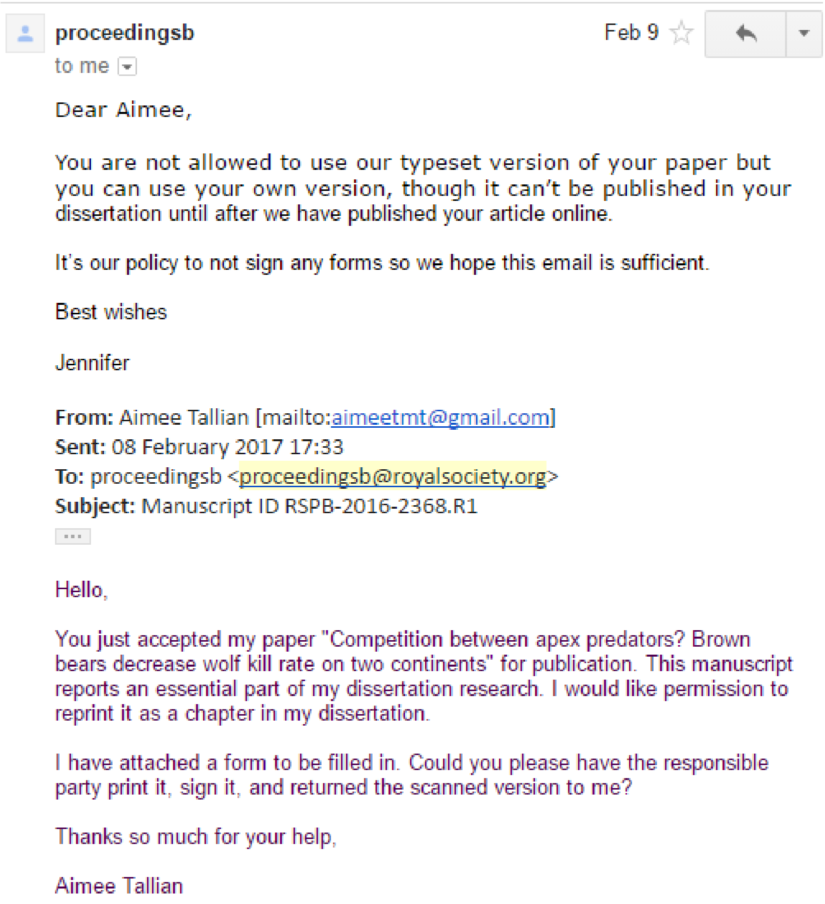
I hereby give permission to Aimee Tallian to reprint the following material in her dissertation:

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* **284**: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Name: Håkan Sand

Signature: Håkan Sand

Date: 2017-02-09



proceedingsb
to me

Feb 9

Dear Aimee,

You are not allowed to use our typeset version of your paper but you can use your own version, though it can't be published in your dissertation until after we have published your article online.

It's our policy to not sign any forms so we hope this email is sufficient.

Best wishes

Jennifer

From: Aimee Tallian [mailto:aimeetmt@gmail.com]
Sent: 08 February 2017 17:33
To: proceedingsb <proceedingsb@royalsociety.org>
Subject: Manuscript ID RSPB-2016-2368.R1

Hello,

You just accepted my paper "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" for publication. This manuscript reports an essential part of my dissertation research. I would like permission to reprint it as a chapter in my dissertation.

I have attached a form to be filled in. Could you please have the responsible party print it, sign it, and returned the scanned version to me?

Thanks so much for your help,

Aimee Tallian

CURRICULUM VITAE

Aimee G. Tallian

Department of Wildland Resources and the Ecology Center
5230 Old Main Hill - Utah State University
Logan, Utah 84322-5230
Lab: Natural Resources 221
Email: aimeetmt@gmail.com
Phone: (406) 570-1039

EDUCATION

Ph.D., Utah State University – Logan, UT 2017
Major: Ecology, Wildlife Ecology GPA: 4.0
Advisor: Dr. Daniel MacNulty

B.A., Montana State University - Bozeman, MT 2009
Major: Biological Sciences, Ecology: Ecology and Evolution
GPA: 4.0 (Highest Honors)
Advisor: Dr. Scott Creel

PROFESSIONAL EXPERIENCE

(a) Teaching

Swedish University of Agricultural Sciences – Guest Lecturer
Wildlife Biology (Fall 2015)

Utah State University – Teaching Assistant
Ecology of Animal Populations (Fall 2013)

Utah State University – Teaching Assistant / Guest Lecturer
Wildland Animal Ecology and Identification (Fall 2012/2013)

Tracker Academy – Teaching Assistant
South African College for Tourism – South Africa (July, 2011 – March, 2012)

Montana State University – Teaching Assistant
Comparative Vertebrate Anatomy (Spring 2009)

(b) Research

Undergraduate Research

Degradation rates of adrenal glucocorticoid in bear scat in Yellowstone National Park
Montana State University – Senior Research Project (2009)
Collaborators: Montana State University, Yellowstone National Park

Collaborative Research Projects

Brown bear-wolf interactions in Yellowstone and Scandinavia
Funders: National Science Foundation – GRFP & GROW
Collaborators: Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Norwegian University of Life Sciences, Hedmark University of Applied Sciences, Norwegian Institute for Nature Research, University of Montana, Yellowstone National Park

Introduction effort, species traits and establishment success in reptiles
Funders: National Science Foundation – GRFP
Collaborators: Utah State University, University of Melbourne

(c) Work

Utah State University – Museum Coordinator College of Natural Resources Specimen Collection	2012-2014
Bear Management Office – Biological Technician Yellowstone National Park – Summer Seasonal Position	2006-2011
MS252 Canyon - Deepwater Horizon Oil Spill National Park Service Resource Advisor – 1 Month Emergency Detail	2010
Bison Ecology and Management Office – Biological Technician Yellowstone National Park – Winter Seasonal Position	2009-2011
Resource Management – Lead Biological Technician Yellowstone National Park – Summer Seasonal Position	2001-2005

(d) Volunteer

Tracker Academy - Researcher South African College for Tourism, South Africa	2011-2012

Conservation and Research Volunteer 2011
Samara Private Game Reserve, South Africa

Wolf Office – Winter Study Volunteer 2009-2010
Yellowstone National Park

Student Conservation Association – Americorps 2001
Yellowstone National Park – Resource Management

PUBLICATIONS

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B.* B 284: 20162368. http://dx.doi.org/10.1098/rspb.2016.2368

Tallian, Aimee, Douglas W. Smith, Daniel R. Stahler, Matthew C. Metz, Rick Wallen, Chris Geremia, C. Travis Wyman, Joel Ruprecht, Daniel R. MacNulty (*in review)*. Predator foraging response to a resurgent dangerous prey. *Functional Ecology.*

Milleret, Cyril, Andrés Ordiz, Harry Peter Andreassen, Jonas Kindberg, Johan Månsson, **Aimee Tallian**, Petter Wabakken, Camilla Wikenros, Barbara Zimmermann, Jon E Swenson, and Håkan Sand (*in review*). Not in my back yard; habitat selection and niche overlap between two sympatric apex predators, brown bears and gray wolves. *Ecography*.

Tingley, Reid, Peter Mahoney Andrew Durso, **Aimee Tallian**, Alejandra Morán-Ordóñez, Karen Beard (2016). Threatened and invasive reptiles are not two sides of the same coin: Extinction and invasion risk in reptiles. *Global Ecology and Biogeography.*

Mahoney, Peter J., Karen H. Beard, Andrew M. Durso, **Aimee G. Tallian**, A. Lexine Long, Ryan J. Kindermann, Nicole E. Nolan, Daniel Kinka, and Harrison E. Mohn (2015). Introduction effort, climate matching, and species traits as predictors of global establishment success in non-native reptiles. *Diversity and Distributions* 21(1):64-74.

MacNulty, Daniel R., **Aimee G. Tallian**, Daniel R. Stahler, Douglas W. Smith (2014). Influence of group size on the success of wolves hunting bison. *PlosOne* 9(11):1-8.

Van den Heever, Alex, **Aimee G. Tallian** (2012). Spoor Identification and Wildlife Tracking in Southern Africa: A Training Manual. Bound and printed for exclusive use by the Tracker Academy.

ORAL AND POSTER PRESENTATIONS

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand (2016) "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" 24th International Conference on Bear Research and Management – Oral Presentation (15 minute) *received Truman Award for best student oral presentation

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand (2016) "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" Wildland Resources Seminar, Utah State University, Logan, UT – Oral Presentation (1 hour)

Tallian, Aimee, Andrés Ordiz, Matthew C. Metz, Cyril Milleret, Camilla Wikenros, Douglas W. Smith, Daniel R. Stahler, Jonas Kindberg, Daniel R. MacNulty, Petter Wabakken, Jon E. Swenson, Håkan Sand (2016) "Competition between apex predators? Brown bears decrease wolf kill rate on two continents" Predator Prey Interaction Conference, Ventura, CA – Poster Presentation

Tallian, Aimee G., Daniel R. MacNulty, Daniel R. Stahler, Douglas W. Smith (2015) "Wolf-bison interactions in Yellowstone National Park", Grimsö Wildlife Research Station, Sweden – Oral Presentation (1 hour)

Tallian, Aimee G., Daniel R. MacNulty, Daniel R. Stahler, Douglas W. Smith (2015) "The role of bison sex and group size in wolf-bison interactions" 7th European Congress of Mammalogy, Stockholm, Sweden – Oral Presentation (20 minute)

Tallian, Aimee, Reid Tingley, Karen Beard, Peter Mahoney, Andrew Durso, Alejandra Morán-Ordónez. (2015) "Extinction and invasion risk are not two sides of the same coin, at least not for reptiles". International Congress for Conservation Biology, Montpellier, France – Oral Presentation (15 minute)

Beard, Karen H., Peter J. Mahoney, Andrew M. Durso, **Aimee G. Tallian**, A. Lexine Long, Ryan J. Kindermann, Nicole E. Nolan, Daniel Kinka, and Harrison E. Mohn (2015) "Drivers of non-native reptile establishment success: managing event and location-level factors" Society for Conservation Biology Conference, Missoula, MT – Oral Presentation (20 minute)

Tallian, Aimee G., Daniel R. MacNulty, Daniel R. Stahler, Douglas W. Smith (2014) "Group size effects on predator (wolf) attack decision and hunting success of a formidable prey species (bison)" Ecological Society of America Conference, Sacramento, CA – Oral Presentation (20 minute)

Tallian, Aimee G., Daniel R. MacNulty, Daniel R. Stahler, Douglas W. Smith (2014) "Are wolves more cooperative when hunting formidable prey?" Predator Prey Interaction Conference, Ventura, CA – Poster Presentation

Tallian, Aimee G., Daniel R. MacNulty, Daniel R. Stahler, Douglas W. Smith (2013) "Preliminary findings: Wolf-bison hunting behavior in Yellowstone National Park" Biannual Collaborative Wolf Research Meeting – Yellowstone Center for Resources – Oral Presentation (30 minute)

Tallian, Aimee G. (2013) "A history of wildlife management in Yellowstone National Park" Utah State University College of Natural Resources Ecology Luncheon – Oral Presentation (1 hour)

Tallian, Aimee G. (2013) "Dynamics of predator-prey space use in a wolf-bison system" Utah State University Pre-project Symposium Presentation – Oral Presentation (15 minute)

Tallian, Aimee G. (2010) "Grizzly and black bear ecology and management" Yellowstone National Park Interpretive Training Seminar; presented to a variety of staff and public assemblies between 2006 and 2010 – Oral Presentation (1 hour)

Tallian, Aimee G., Scott Creel (2008) "Degradation rates of adrenal glucocorticoid in bear scat in the Lake District of Yellowstone National Park" – Undergraduate Scholars Conference at Montana State University – Poster Presentation

PUBLIC OUTREACH

(a) Presentations and Volunteering

Presentation – USU – Department of Wildland Resources 2013
"Wildlife research at Utah State University – Getting involved"
Public outreach and college recruitment presentation – 10 oral presentations (50 minute) given to high schools in NW Indiana

Presentation – Career Day at Cedar Ridge Middle School 2013
"What it means to have a career in science"
Four talks of 20 minutes each to 7th grade classes

Coach – Envirathon Team Wildlife Sciences 2013
“Topics in wildlife sciences”
One coaching session for their national competition

Guest Author – Londolozi Private Game Reserve Blog 2012
“Tracking lion” and “Training with the Tracker Academy”

(b) Media Coverage (Print and Online)

Billings Gazette, 2/9/17, “Carcass-stealing by grizzlies doesn’t mean wolves kill more”

New Scientist, 2/8/17, “Why grey wolves kill less prey when brown bears are around”

PhysOrg, 2/7/17, “Wolfing it down: Brown bears reduce wolf kill rates”

Salt Lake City Tribune, 11/12/14, “New research shows Yellowstone wolves pick their prey based on pack size”

PhysOrg, 11/12/14, “The more the merrier: Ecologists say larger group aids wolves' bison hunting”

GRANTS, SCHOLARSHIPS AND AWARDS

2016

Truman Award for best student oral presentation – 24th International Conference on Bear Research and Management - **$250**
USU School of Graduate Studies Dissertation Fellowship - **$8000**
USU Seely-Hinckley Fellowship - **$3000**
USU Ecology Center Dissertation Grant - **$2000**
USU Ecology Center Travel Support Award - **$300**
USU Quinney College of Natural Resources Travel Support Award - **$300**
USU School of Graduate Studies Travel Support Award - **$300**

2015

USU Ecology Center Research Award - **$2000**
USU Ecology Center ARTsySTEM Grant “Our World of Wildlife” Children’s Book Series - **$1800**

2014

NSF Graduate Research Opportunities Worldwide (GROW) - Swedish Research Council Stipend Award - **$24,000**
NSF GROW – NSF Travel Grant - **$5000**
USU Ecology Center Research Award - **$1500**
USU Ecology Center Travel Support Award - **$600**
USU Quinney College of Natural Resources Travel Support Award - **$600**
USU School of Graduate Studies Travel Support Award - **$600**
USU Department of Wildland Resources Travel Support Award - **$600**

2012

NSF Graduate Research Fellowship Program (GRFP) – Stipend Award – **$102,000**
NSF GRFP – Cost of Education Award - **$36,000**

2008

Montana State University Undergraduate Scholars Program Research Grant – **$3000**

2006

National Park Service Monetary Award for Exceptional Performance - **$1800**

JOB RELATED SKILLS

- *Practical Conservation Skills:*
  My practical experience includes Nordic skiing in the remote backcountry including long exposure to extreme winter conditions, carrying a heavy backpack, and camping for multiple nights. I am also trained and experienced at driving a snowmobile in severe winter conditions. I have extensive backcountry hiking and backpacking experience which includes; long hours spent at high elevations in extreme hot, cold, and wet climatic conditions, carrying heavy gear (over 50 lbs.), hiking long distances in steep terrain and rugged terrain and camping outside overnight in adverse conditions.
- *Computer Skills*:
  I have experience with software including Microsoft applications, STATA, R, ArcMap, and maintaining large Access and Excel Databases.
- *Training/Certificates*
  - First Aid/CPR/AED
  - USGS Firearms Qualification
  - Backcountry/Bear Safety Training (120 hours)
  - Interagency Bear Immobilization Training (120 hours)
  - Ungulate Immobilization Training (40 hours)
  - Whitewater Rescue Technician Level I (40 hours)