Impacts of Re-colonizing Gray Wolves on Mule Deer and White-tailed Deer in North-Central Washington

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Abstract

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Previous research on gray wolves (*Canis lupus*) in protected landscapes demonstrates these large carnivores can have consumptive and non-consumptive effects on prey species which lead to top-down trophic cascades. However, much remains to be known about impacts of gray wolves on prey in managed landscapes as well as how these predators influence interactions between prey species. Recent natural re-colonization of gray wolves to managed landscapes of Washington state facilitated a natural experiment wherein we explored impacts of gray wolves on multiple sympatric prey species – mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*). We compared survival, habitat use, and resource partitioning of adult mule deer and adult white-tailed deer in wolf present and wolf absent areas. Mule deer and white-tailed deer survival rates were not negatively impacted by presence of gray wolves. Season was the primary factor in explaining all predator and human-caused mortality. Our data suggests gray wolves may not have consumptive effects on native prey populations in Washington state. Next, mule deer and white-tailed deer experiencing gray wolf predation risk did exhibit shifts in habitat use relative to conspecifics in areas without gray wolves. Shifts in habitat use by mule deer and white-tailed occurred at coarse and fine-spatial scales, respectively, and were explained by divergent escape tactics of each prey species and the landscape features that promote escape of each deer species when facing gray wolf predation risk. It appears gray wolves can influence habitat use of multiple prey species and potentially at differing spatial scales depending on escape behavior of prey species and the landscape features that promote escape of prey from predation. Our results suggest gray wolves could initiate multiple top-down trophic cascades via prey species specific shifts in habitat use in response to gray wolf predation risk. Lastly, there was increased resource partitioning between mule deer and white-tailed deer in areas with gray wolves compared to resource partitioning between mule deer and white-tailed deer in areas without gray wolves. Increased resource partitioning between mule deer and white-tailed deer was again explained by divergent escape tactics of each prey species and the landscape features promoting escape of each deer species subject to wolf predation risk. However, direction and magnitude of resource partitioning between mule deer and white-tailed in areas with gray wolves compared to areas without gray wolves varied with season and scale. Our findings demonstrate that gray wolf predation risk can mediate interactions between co-occurring prey species but is context-dependent. We suggest further research on consumptive and non-consumptive effects of gray wolves on multiple prey species to better understand the potential for top-down trophic cascades in managed landscapes.

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General Introduction

Trophic cascade theory can be traced back to the 1920's when Aldo Leopold documented an irruption in a deer population, and subsequent over grazing of the plant community, on the Kiabab Plateau in Arizona following eradication of nearly all natural predators (Leopold 1943). Leopold (1943) argued that lack of predators on a landscape allows prey populations to grow beyond normal limits resulting in decreased available forage due to increased herbivory. Trophic cascade theory took another leap forward in the 1960s, when Hairston et al. (1960) argued that predators allow for the proliferation of plants by consuming herbivores. Paine (1966) contributed to the idea of predators affecting ecological interactions by demonstrating that community assemblages could be drastically altered by the presence and overall abundance of top predators that directly impact competition at lower trophic levels. Initial research on trophic cascades addressed direct effects of predation on prey species, which is the killing of prey by predators (Estes and Palmisano 1974; Carpenter et al. 1985; Power 1990). More recently non-consumptive effects of predation risk on prey has received considerable attention (Lima and Dill 1990; Schmitz et al. 1997; Ripple and Beschta 2004; Fortin et al. 2005). Non-consumptive effects are a behavioral response by prey to perceived predation risk (Lima and Dill 1990) and include, but are not limited to, changes in habitat use (Creel et al. 2005), activity budgets (Wirsing and Heithaus 2012), diet composition (Schmitz 2003), competitive interactions (Persson 1993), stress hormones (Creel et al. 2009), and overall body condition or nutritional status (Creel et al. 2013) of an individual or entire prey population (Schmitz et al. 1997). Research on non-consumptive effects has focused on behavior-mediated trophic cascades (BMTC), where changes to prey behavior induced by predation risk transmit cascading effects to lower trophic levels (Schmitz et al. 1997; Dill et al. 2003; Wilmers et al. 2003; Ripple and

Beschta 2004; Fortin et al. 2005). To date, there have been two main avenues for research concerning BMTCs: microcosm experiments and larger scale natural experiments (Schmitz et al. 1997, 2000; Ripple and Beschta 2012). Microcosm experiments involving invertebrate food webs have consistently demonstrated the ability of predation risk from top predators to shift behavior of prey species and subsequently impact plant biomass and diversity (Beckerman et al. 1997; Schmitz et al. 2004; Schmitz 2008). Given the complexity of BMTCs, larger scale natural experiments are difficult to carry out and account for all relevant variables. Few such experiments have been carried out to date, which has contributed in part to much debate about whether the top-down effects demonstrated in microcosm experiments scale up to the landscape level (Kauffman et al. 2010; Beschta and Ripple 2013; Creel et al. 2013; Middleton et al. 2013). Though no experimental design will ever fully control for all possible confounding variables, more large scale natural experiments examining BMTCs could help to elucidate to the nature of BMTCs at a landscape level.

To date, most large scale BMTC research conducted in terrestrial systems has focused on a one-to-one predator-prey relationship with emphasis on potential linkages in top-down behaviorally mediated trophic cascades (Schmitz et al. 1997, 2004; Schmitz 2003; Ripple and Beschta 2004, 2006, 2008; Fortin et al. 2005; Kauffman et al. 2011; Creel et al. 2013; Middleton et al. 2013); however, research in marine systems has investigated the indirect effects top-predators have on multiple prey species (Dill et al. 2003; Wirsing et al. 2010, 2011; Heithaus et al. 2012; Burkholder et al. 2013). In previous research the top-predator and primary prey species are focused on while non-consumptive effects of predation on secondary prey species are not addressed (Lima 2002, Ripple and Beschta 2004, 2006, 2008; Fortin et al. 2005; Wirsing et al. 2010, Kauffman et al. 2011; Creel et al. 2013; Middleton et al. 2013). This approach is understandable but predator-prey research has demonstrated that secondary prey species can be impacted by non-consumptive effects of predation, sometimes to an extent greater than the primary prey species (Gervasi et al. 2013; Latombe et al. 2014). Thus, it seems logical that BMTCs could arise from multiple predator-prey relationships including secondary prey species. Studying parallel BMTCs could offer great insight into understanding the complete landscape level effects of top-predators. For example, a BMTC involving one prey species could be canceled out by the BMTC involving another prey species (in terms of effects on plants). Alternatively, BMTCs involving multiple prey species might have additive or even multiplicative effects. Therefore great insight on top-down trophic cascades could be gained if research efforts attempted to assess non-consumptive effects of predation by studying multiple prey species. Further, BMTCs could alter overlap in resource use by sympatric prey species, therefore altering potential competitive interactions between the two prey species (Persson 1993; Chase et al. 2002).

It is likely that the evolution of most prey species has been shaped in part by predation risk from at least one predator. Each prey species must balance predation risk with various needs, such as preferred habitat, such that the anti-predator behavior of the prey species complements the terrain in which the prey species regularly occurs to minimize predation risk (Lingle 2002). Because anti-predator behavior is the means by which prey minimize predation risk, anti-predator behavior can likely serve as a possible mechanism for predicting non-consumptive effects of predation risk with respect to a given linkage in a tri-trophic (predator → prey → producer) food web (Lingle and Pellis 2002; Gervasi et al. 2013; Latombe et al. 2014). For example, a more sure-footed prey species may seek out steep, rocky slopes while a more fleet-footed prey species may seek out open terrain with high visibility to minimize predation risk from the same top-predator (Lingle 2002). It can be hypothesized that there will be differing cascading effects because differences in anti-predator behavior cause the prey species to occupy different habitats. Thus focusing on a single predator-prey interaction might only reveal part of the overall non-consumptive effects of the top-predator on productivity at lower trophic levels (Lingle 2002). Currently, few studies have examined parallel BMTCs involving non-consumptive effects of a top-predator on multiple prey species in a terrestrial landscape. This represents a current gap in our understanding of the effects of top-predators in terrestrial ecosystems and BMTCs in general.

Gray wolves (*Canis lupus*), absent from large portions of their historic range in Canada and the United States since the 1930's, are once again present in parts of their historic range due to natural re-colonization and conservation efforts (Boitani 2003). This long absence, followed by re-colonization, offers a great model system for exploring impacts of a top-predator on prey and BMTCs due to the generalist nature of gray wolves (Ripple and Beschta 2012). Currently, much of the research exploring impacts of re-colonizing gray wolves on prey and potential BMTCs has taken place in protected areas, most notably Yellowstone and Banff National Parks (Ripple and Beschta 2004; Hebblewhite et al. 2005). National parks, with their minimal human impact and intact ecosystems, are inherently ideal places for conducting research to understand fundamental ecological processes. However, given that large intact landscapes are necessary for trophic cascades to occur regularly and with the natural level of top-down attenuation (Borer et al. 2005), such landscape scale processes likely require areas larger than most protected areas (Newmark 1987). It is possible that the debate over the existence of BMTCs is ongoing because landscapes in which research efforts are trying to determine their existence are too small to support the processes in a sustained manner (Newsome and Ripple 2014). Furthermore, given that the majority of earth has been altered by humans, it is possible that findings of current research efforts have little application to managed landscapes given that BMTCs may prematurely attenuate at higher trophic levels due to human impacts (Rogala et al. 2011).

The goal of this research was to contrast top down effects of gray wolves on behavior of sympatric mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) as a first key step of evaluating for parallel trophic cascades in a managed landscape. The research took place in Washington State, where human activity is prevalent, and gray wolf recolonization allowed for a treatment/control approach of wolf present and wolf absent areas. Through this treatment/control design, we examined three potential avenues for how gray wolves might impact mule deer and white-tailed deer. Though very similar, mule deer and white-tailed deer have the potential to respond differently to gray wolf predation risk given their contrasting anti-predator behavior (Lingle 2002). First, we compared survival rates and sources of mortality of mule deer and white-tailed deer in areas with and without wolves. Further, we investigated what factors drive survival of each deer species in areas with and without wolves. Second, we examined seasonal shifts in habitat use of mule deer and white-tailed deer in areas with and without wolves. We assessed how escape tactics of each deer species predicts shifts in seasonal habitat use patterns in areas with and without wolves and at what spatial scale (coarse vs. fine) each species potentially responds to wolf predation risk. Lastly, we compared seasonal resource partitioning between mule deer and white-tailed deer in areas with versus without wolves. We again assessed how escape tactics of each deer species predicts direction of seasonal shifts in resource partitioning between deer species in areas with versus without wolves and at what spatial scale certain resources might be partitioned in response to wolf predation risk.

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Chapter 1: Impacts of recolonizing gray wolves on survival and mortality in two sympatric ungulates

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Abstract: There is growing recognition that humans may mediate the strength and nature of the ecological effects of large predators. We took advantage of ongoing gray wolf (*Canis lupus* Linnaeus, 1758) recolonization in Washington to contrast adult survival rates and sources of mortality for mule deer (*Odocoileus hemionus* Rafinesque, 1817) and white-tailed deer (*O. virginianus* Zimmermann, 1780) in areas with and without wolf packs in a managed landscape dominated by multiple human uses. We tested the hypothesis that the addition of wolves to the existing predator guild would augment predator-induced mortality rates for both ungulates. Source of mortality data from adult mule deer and white-tailed deer, respectively, revealed that wolf related mortality was low compared to that inflicted by other predators or humans. Predator-caused mortality was largely confined to winter. There was little effect of wolf presence on adult deer mortality rates, and there was no difference in mortality between the two deer species relative to wolf-free or wolf-occupied sites. Although this study occurred early in wolf recovery in Washington, our results differ from those demonstrated for gray wolves in protected areas. Thus, we encourage further investigation of effects of direct predation by recolonizing large carnivores on prey in human-dominated landscapes.

Introduction

The potential for top-down effects initiated by large predators is widely recognized (Terborgh et al. 2001; Estes et al. 2011; Ripple et al. 2014). Consequently, there is growing concern about the ecosystem impacts of ongoing global declines in these species (Estes et al. 2011; Ripple et al. 2014; Ripple et al. 2016). Despite evidence that humans can attenuate the effects of large predators (e.g., Hebblewhite et al. 2005; Rogala et al. 2011; Haswell et al. 2017; Kuijper et al. 2016), most terrestrial studies of top-down forcing to date have occurred where the anthropogenic footprint is minimal (i.e., protected areas and wilderness that still contain adequate predator populations; Newsome and Ripple 2015). Thus, questions remain about the extent to which our current understanding of the ecological roles of large predators applies to managed landscapes that have been modified by human activity and, importantly, cover the majority of the Earth’s terrestrial surface (Vucetich et al. 2005; Hamlin et al. 2008; Newsome and Ripple 2015).

Over the past few decades, some large predator species have begun to recolonize portions of their historical ranges, including many areas that are shared by humans (Chapron et al. 2014; Ripple et al. 2014). This trend facilitates natural experiments along recolonization fronts that quantify the impacts of large predator recovery on ecosystems through spatial and/or temporal comparison of areas where predators are and are not present. For example, the recovery of Eurasian lynx (*Lynx lynx* Linnaeus, 1758) in parts of Scandinavia has enabled comparative studies revealing impacts on both prey species (roe deer, *Caprelous capreolus* Linnaeus, 1758; Melis et al. 2009) and smaller mesocarnivores (red fox, *Vulpes vulpes* Linnaeus, 1758; Pasanen-Mortensen et al. 2013). The recent eastward recovery of puma (*Puma concolor* Linnaeus, 1771) populations in North America (LaRue et al. 2012; Mallory et al. 2013) offers a similar opportunity to perform natural experiments examining the ability of this large predator to affect hyperabundant prey (e.g., deer) populations and, in turn, influence plant recruitment, nutrient dynamics, and habitat succession (Cote et al. 2004; Ripple and Beschta 2008; Ripple et al. 2014).

The gray wolf (*Canis lupus* Linnaeus, 1758) is currently recolonizing large portions of western North America, and numerous studies have capitalized on this process to explore interactions between these canid predators and prey species (Metz et al. 2016). Results from these investigations are mixed, rendering it difficult to generalize about the impacts of recolonizing wolves on prey population dynamics (Messier 1994; Ballard et al. 2001; Mech and Peterson 2003; Garrott et al. 2005; Evans et al. 2006; Hamlin et al. 2008; Brodie et al. 2013, Christianson and Creel 2014). In Yellowstone National Park, for example, White and Garrott (2005) concluded that predation by wolves on adult elk (*Cervus elaphus* Erxleben, 1777) was additive because it led to marked decreases in adult survival and subsequent elk population declines. By contrast, Vucetich et al. (2005) found that gray wolf predation on adult elk in the same system was largely compensatory and that human harvest and winter weather were largely responsible for observed changes in adult elk survival. In Minnesota, factors such as winter severity were linked to decreased body condition in white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780), suggesting that at least some of the mortalities attributed to recolonizing gray wolves were compensatory (Nelson and Mech 1981). Finally, long-term research on Isle Royale has led to the conclusion that food influences moose (*Alces alces* Linnaeus, 1758) demography more than predation from gray wolves in the absence of other large carnivores (Vucetich and Peterson 2004). Most of these studies, however, have occurred in protected rather than managed landscapes, leaving open the question of whether the top-down effects of wolf predation that have been observed also manifest in areas subject to more extensive human modification. (Hebblewhite et al. 2005; Hurley et al. 2011; Brodie et al. 2013).

In 2008, gray wolves began naturally recolonizing Washington from northern Idaho and southern British Columbia, and there are now 18 confirmed packs in the state (Jimenez and Becker 2016; Maletzke et al. 2016). In areas of Washington colonized by gray wolves, average home range size, average pack size, and pack density are similar to other managed landscapes in neighboring states (Jimenez and Becker 2016; Maletzke et al. 2016), but pack size and pack density in these managed areas is low relative to protected areas (Jimenez and Becker 2016). At present, these packs are distributed heterogeneously across eastern Washington, setting the stage for natural experiments examining the effects of wolf recovery on native prey populations. In this region, mule deer (*Odocoileus hemionus* Rafinesque, 1817) and white-tailed deer dominate the ungulate prey guild (Robinson et al. 2002). Gray wolves are known to readily take both species (Nelson and Mech 1981; McNay and Voller 1995). Mule deer and white-tailed deer may differ in their vulnerability to predation by gray wolves, however, because of inherent differences in their resource selection patterns. Namely, mule deer use rocky uneven terrain whereas white-tailed deer use more rolling riparian habitat (Lingle and Pellis 2002). As coursing predators, gray wolves generally tend to select for relatively gentle terrain while hunting (Mech and Peterson 2003; Oakleaf et al. 2006). Thus, gray wolves could exert larger consumptive effects on white-tailed deer compared to mule deer because of greater overlap in habitat use patterns.

In this study we investigated effects of gray wolves on sympatric mule deer and white-tailed deer in a managed landscape in eastern Washington affected by multiple human activities such as hunting, logging, and ranching. Specifically, taking advantage of spatial heterogeneity in wolf presence, we contrasted survival rates and sources of mortality for adult mule deer and white-tailed deer in areas with and without established packs. Under the hypothesis that the extent to which gray wolves influence prey survival is mediated by habitat overlap, we predicted that any observed differences in prey mortality rates and overall survival between wolf-occupied and wolf-free areas would be exhibited by white-tailed deer to a greater extent than by mule deer. Alternatively, gray wolf predation could have little impact on ungulate survival in managed landscapes if wolf density and/or predation efficiency are limited by anthropogenic activity (Pimlott 1967; Messier 1994; Vucetich et al. 2005; Kuijper et al. 2016). Under this latter scenario, the presence of wolves would not be expected to correlate with differences in rates of predator-induced mortality and overall survival in prey populations.

Materials and Methods

Study area

The study took place from 2013-2016 in an area of eastern Washington spanning Okanogan and Ferry counties and including portions of the Okanogan-Wenatchee and Colville National Forests and the Colville Reservation (Fig. 1.1). National Forest and Colville Reservation lands cover 3,282 km^2 (28%) and 5,657 km^2 (47%), respectively, with the remaining 2,993 km^2 (25%) being privately owned. Human density averaged 2.25/km^2 (range: 0-179/km^2) over the entirety of the study area (U.S. Census Bureau 2016). Road density averaged 1.12 km/km^2 (range: 0-3.76/km^2) for primary and secondary roads combined (U.S. Census Bureau 2016).

The study area contains the Okanogan Highlands and Kettle River Range, which create a topography composed of predominantly moderate slopes on mountainous and hilly terrain with broad round summits. The Okanogan Highlands and Kettle River Range are bisected by the Sanpoil River. Elevations range from 300 to 2,065 m. Average temperatures range from 28°C during summer to -8°C in winter. Average precipitation ranges from 21 cm in summer in the form of rain to 105 cm in winter in the form of snow. Habitat types range from shrub steppe composed primarily of sagebrush (*Artemisia tridentate* Nuttall, 1841) and bitterbrush (*Purshia tridentate* Pursh) at lower elevations to ponderosa pine (*Pinus ponderosa* Lawson), Douglas-fir (*Pseudotsuga menziesii* Mirbel), and subalpine fir (*Abies lasiocarpa* Hooker) forest at higher elevations. Riparian areas, dominated by poplars (*Populus spp*. Linnaeus), are regularly dispersed along drainages that flow into the Okanogan and Sanpoil River valleys, respectively (Clausnitzer and Zamora 1987). Mule deer, white-tailed deer, elk, and moose comprise the resident ungulate community, though each deer species was ~20 and 50 times more abundant than moose and elk, respectively (Spence 2017). Coyotes (*Canis latrans* Say, 1823), bobcats (*Lynx rufus* Schreber, 1777), American black bears (*Ursus americanus* Pallas, 1780), and cougars represented the mammalian predators present at all four sites, whereas gray wolves were only present in the 'wolf' sites.

The study area was broken up into four sites, two occupied by gray wolf packs and two lacking wolves. The four sites encompassed an average of 613 km^2 (range = 550-680 km^2). The two 'wolf' sites were defined by an amalgamated 95% kernel density home range from multiple adult radio-collared wolves in each pack. The two 'non-wolf' sites were defined based on National Forest boundaries. Wolf packs first colonized the region in summer of 2010 and, over the course of the investigation, used the Colville National Forest and Colville Reservation but not the adjacent Okanogan-Wenatchee National Forest (Fig. 1.1). Specifically, wolf-occupied areas occurred on either side of the Sanpoil River. One non-wolf site was immediately south of

Aeneas Valley and north of the Colville Reservation. The other non-wolf site was located north of the other non-wolf area near Bonaparte Lake (Fig. 1.1). All four sites were consisted of similar topography and habitat types, and experience similar levels of human use in the form of cattle ranching, logging, and hunting. Cattle were present on the landscape in each year of the investigation from mid-June to mid-October. Logging occurred year round.

Hunting of both deer species on the National Forests occurs in autumn and length of season varies depending on Game Management Unit (GMU) and weapon-type. Generally, no GMU is hunted more than two full months in a year. During the study period 844 (range: 648-966) deer were harvested each year with >80% being antlered individuals. Further, an average of 4 (range: 1-7) cougars and 116 (range: 103-147) American black bears were harvested each year. Note that these cougar and bear data come from game management units that are larger than our study area (harvest data obtained from: https://wdfw.wa.gov/hunting/harvest/). Hunting of both species on the Colville Reservation occurs from June 1st to December 31st each year. There was no reporting of harvest of any kind on reservation lands. It is possible that overall harvest is comparable to off reservation lands given less people hunted the reservation but did so for a longer period of time but we cannot be certain.

Data Collection

We monitored gray wolf activity in all four sites within the study area in three ways. First, we deployed sixteen motion-activated game cameras (M880 by Moultrie®, Calera, AL, USA) year round as a grid along logging roads and game trails (1 per 5 km^2) at each site and checked the cameras every three months. Game cameras were deployed for an average of 18,173 (range: 16,409 – 19,564) trap nights over all four sites. Second, we conducted weekly track surveys along logging roads and game trails during winter months (mid-December to mid-March) using snowmobiles. Specifically, track surveys covered a minimum of 60 km each week in each site. The surveys did not always cover the same roads and trails each week; rather, we surveyed the same general area each week and the same roads and trails every two weeks. Third, GPS radio-collars deployed on at least one member of each wolf pack occupying the designated wolf areas by the Colville Confederated Tribes Fish and Wildlife Department aided in monitoring wolf presence and movements. Wolves were captured using aerial net gunning in winter and #7 double long spring rubber jawed foothold traps in summer. Foothold traps were checked mid-morning and early afternoon. Captured wolves were outfitted with Global Positioning System (GPS) radio-collars (Globalstar Survey Collars, Vectronic Aerospace Gmbh, Berlin, Germany), sexed, and weighed. To ensure only adults were collared, we did not trap <400 m from a den or rendezvous site with pups <6 months of age. The GPS collars were programmed to obtain a location every 5 hours. Combined, these three methods enabled continuous and intensive monitoring of presence/absence and the overall number of wolves present in each site. Neither non-wolf site had any documented gray wolf activity during the course of this study. Both the wolf sites were occupied continuously by individual packs, each ranging in size from 3-8 individuals throughout the study with a mean of 5 individuals for each pack for an average wolf density of 8.6/1,000 km^2. This mean pack size and wolf density is similar to that of wolves in other managed landscapes in the northwestern United States where mean pack size is ~5.7 and density is 6.3/1,000 km^2 (Jimenez and Becker 2016).

To determine survival rates and sources of mortality of mule deer and white-tailed deer, we captured individuals of each species over four winters (December – March) using aerial net gunning and baited clover trapping (Haulton et al. 2001). We outfitted clover traps with trap transmitters to alert us to captures. Trap transmitter signals were checked in the early morning and late afternoon. Captured deer were outfitted with GPS radio-collars (Globalstar Survey Collars, Vectronic Aerospace Gmbh, Berlin, Germany), ear tagged, aged, sexed, and weighed. To ensure only adults were collared, we did not collar any individual weighing < 30 kg. The GPS collars were programmed to obtain a location every 12 hours and switch to mortality mode if the deer wearing the collar exhibited no movement for a 12-hour period. GPS collars had the potential to last 4-5 years with this location fix rate but three years was the longest any deer was monitored. An individual deer was assigned to the wolf present treatment if its 95% kernel home range was completely contained within the 95% kernel home range of a wolf pack, otherwise deer were assigned to the non-wolf treatment. Given most trapping in the wolf present areas occurred within the core home range of the wolf packs (as determined from GPS collars, cameras, and track surveys) very few ($n = 4$) deer only partially overlapped with a wolf pack home range. After 12 consecutive hours of inactivity, GPS collars sent a mortality notification via email detailing the location of the likely mortality. We attempted to get to GPS-collared deer within 24 hours after receiving mortality notification to aid in identifying the proximate cause of death. We used the most recent GPS fix and VHF telemetry equipment to navigate to the site where a potential mortality took place. We used puncture marks, scat, tracks, and other signs to determine cause of death and, if predation, the species of predator (Barber-Meyer et al. 2008; Hurley et al. 2011). None of the deer that partially overlapped with wolf pack home ranges were killed by wolves. Human-related mortality included take from firearm and archery seasons as well as tribal hunts and illegal harvest. Other causes of death included accidents (e.g., falls), injury, and disease. If death could not be attributed to a specific cause, it was categorized as unknown. Individuals were censored from survival analyses following emigration from a given study site (> 10 km), collar failure, or termination of the study. All animal captures and collar deployments were conducted under the University of Washington Institutional Animal Care and Use Committee (IACUC) protocol number 4226-01 and wildlife collection permits from the Washington Department of Fish and Wildlife and the Colville Tribes Fish and Wildlife Department.

Analyses

We recorded time to mortality events or loss of contact such that the date the animal was collared was zero and every day after was additive. Accordingly, an animal monitored for exactly one year would have a monitoring period of 365 days. We used Kaplan-Meier (KM) estimates of annual survival and non-parametric cumulative incidence functions (CIF) to estimate cause-specific mortality rates of both deer species in areas with and without wolf packs (Murray 2006). We estimated CIF using a competing risks framework, whereby mortality from one source precluded mortality from other sources, to characterize the impacts of non-human predators on adult deer survival while separately accounting for the influence of human hunters (Heisey and Patterson 2006).

We also evaluated a variety of factors potentially affecting deer survival using Cox proportional hazards (CPH) regression. This approach enables rigorous evaluation of covariate effects on the instantaneous rate of death experienced by individuals due to two or more mutually exclusive sources of mortality, and can incorporate time-varying explanatory variables including time itself (Murray 2006; Hosmer et al. 2008; Murray et al. 2010). Our analysis compared hazard ratios from two competing sources of mortality, human and non-human predators, and focused on adult deer. We created multiple records for each adult deer monitored such that the number of records matched the number of competing risks. Causes of death not accounted for in the competing risks of interests were censored (Murray et al. 2010). We derived regression coefficient estimates for the competing risks based on explanatory variables considered likely to influence survival patterns: wolf presence, deer species, and season. We treated wolf presence, species, and season as binary variables. We expressed season as binary variables for autumn and winter, respectively, whereby it was 1/0 for autumn versus the rest of the year and likewise for winter. Seasonal variation was expressed this way because human-caused mortality was confined to autumn (i.e., September-November, during the hunting season) and predator-caused mortality was primarily confined to late autumn and winter (n = 17, 77.3%; November-March).

Following multiple regression we built global CPH models for each competing risk based on all of the variables above, and all potential interactions therein, with foremost interest in the main effect of wolf presence. We were also particularly interested in the interaction between wolf treatment and deer species as evidence for the hypothesis that predation by wolves would be more pronounced in white-tailed deer than mule deer. Specifically, because mule deer were assigned a ‘1’ whereas white-tailed deer were assigned a ‘0’, a negative coefficient for the deer X wolf interaction would support this hypothesis. Furthermore, significant interactions between wolf treatment and season would indicate that wolf impacts on deer survival were confined largely to a particular time of year for one or both prey species. We initially included individual site variables to test for differences between sites within a wolf treatment type; however, preliminary analyses revealed no significant difference between sites nested within wolf treatment types so sites within wolf treatment types were pooled. Causes of death not accounted for when individually assessing each competing risk of interest were censored. Global models initially included variables for wolf treatment, deer species, autumn, winter, and interactions between wolf treatment and deer species and all other variables, respectively. We used Akaike Information Criteria corrected for small sample size (AICc) to select the most parsimonious model (Heisey and Patterson 2006) for each competing risk, and restricted consideration of the most parsimonious models to those with a ΔAICc ≤ 2 relative to the top model (Hosmer et al. 2008). Sample sizes for AICc calculations were based on number of related mortalities. Finally, we verified the proportional hazards assumption for all top models by first calculating Schoenfield residuals and then performing a chi-square test to check for correlation ($\alpha \leq 0.05$; Therneau and Grambsch 2000).

Results

Across our four study sites over the course of three years, we collared 120 individual adult mule deer (*n* = 61) and white-tailed deer (*n* = 59). We based survival analyses on a total of 38 mortalities out of the 120 individuals (Table 1). The largest mortality factor was predation (*n* = 22, 53.7%), followed by hunting (*n* = 16, 39.0%) and unknown causes (*n* = 3, 7.3%). Of the 22 mortalities due to predation, cougars were the predominant predator (*n* = 12, 54.5%), followed by coyotes (*n* = 7, 31.8%), gray wolves (*n* = 2, 9.2%), and American black bears (*n* = 1, 4.5%).

Overall annual survival probability from KM analysis was 0.69 (SE = 0.04; Table 2). Annual survival for adults of both deer species was greater in the areas with versus without wolves (Table 2). Deer mortality rates due to predators were more than twice as high as human-related mortality in areas with wolves. Mortality rates due to humans were four times higher in areas without wolves compared to areas with wolves (Table 2). Cumulative Incidence Functions revealed that human-related mortality was greater than predator-related mortality for all deer species and treatment combinations except for mule deer in the non-wolf areas (Fig. 1.2). We acknowledge that the large standard errors in these and subsequent analyses potentially indicate a lack of power which could be due to low occurrence of deer being eaten by wolves.

Multiple regression coefficient estimates derived using a competing risks framework revealed that there was no significant difference in hazard ratios due to predation between wolf and non-wolf areas (Table 3). Hazard ratios due to human predation were significantly higher in autumn compared to spring and summer, whereas hazard ratios due to non-human predation were significantly higher in winter compared to all other seasons. Cox proportional hazards modeling for each competing risk demonstrated that the most parsimonious model for determining the overall and relative influences of factors driving white-tailed deer and mule deer mortality for each risk type were different (Table 4). Namely, the winter season was the main factor driving risk to deer dying because of non-human predation (CE = 2.90; SE = 0.412; $p < 0.001$). Support for this model was nearly six times greater than the next best model based on comparison of AICc weights (Table 4). By implication, deer were more at risk from non-human predation in winter than any other season. It is important to note that deer species did not show up in any of the top predator models, indicating that adults of both species experienced similar levels of risk for predator-caused mortality.

Discussion

In terrestrial ecosystems, the top-down impacts of large predators are now widely recognized and yet have received relatively little attention in managed landscapes where human modification is pervasive (Vucetich et al. 2005; White and Garrott 2005; Hamlin et al. 2008; Dorresteijn et al. 2015). Accordingly, questions remain about the extent to which our understanding of the consumptive impacts of large predators in wilderness and protected areas applies to areas with a deeper human footprint (Kuijper et al. 2016). Our results are not consistent with the idea that wolves exert strong effects on prey survival in managed landscapes, at least during the early phases of recolonization, nor do they support the hypothesis that wolves in these systems alter patterns of adult deer mortality to a degree that coincides with species-specific habitat use patterns. Rather, non-human predation hazard rates for adult mule and white-tailed deer were primarily influenced by season, with both sexes of both deer species experiencing elevated predator-caused mortality in winter irrespective of wolf treatment (Table 3; 4).

Why was the impact of wolf predation on adult deer survival so weak in our study system? One possible answer is that, in managed landscapes, gray wolves tend to be sparsely distributed relative to conspecifics in protected areas because of low pack size and/or some territories not being occupied (Jimenez and Becker 2016; Borg et al. 2015). This disparity in wolf distribution could arise from wolves avoiding anthropogenic features (e.g., roads, trails, livestock grazing allotments; Muhly et al. 2011). As a result, human-modified landscapes may offer greater amounts of wolf-free, or at least low-risk, space for prey to occupy (Mech et al. 1980; Haight et al. 1998; Kuijper et al. 2016). Indeed, recent research has demonstrated support for the 'predator shelter hypothesis', under which prey take refuge from predators in areas of increased human activity (Shannon et al. 2014). Another possible answer is that, despite overall habitat similarity between the study sites, it is possible that subtle habitat differences between sites may have contributed to differences in survival. We also acknowledge that low power owing to the small number (*n* = 2) of deer killed by wolves over the course of the investigation may have hindered our ability to detect an effect of wolves on deer survival. Importantly, however, the paucity of wolf predation events in our study is itself evidence of the weak impact of these predators on deer demography.

The wolf packs in our study region did not suffer any anthropogenic mortalities over the course of the investigation as determined from regular and close monitoring of each pack. For managed landscapes in general, however, humans are the primary driver of wolf mortality, and the combination of anthropogenic and natural mortality in these areas can result in lower overall survival than would be observed in systems where humans are not a major cause of death (Murray et al. 2010). Accordingly, another non-mutually exclusive driver of attenuated wolf impact might be increased rates of breeder loss in managed landscapes due to potentially increased likelihood of human-related mortality (e.g., vehicle strike, hunting, poaching, etc.). Such losses can fracture pack dynamics and reduce denning and recruitment rates, which are key for population growth (Brainerd et al. 2008), and may also affect pack hunting success (Borg et al. 2015).

Mule deer and white-tailed deer were not the only ungulates in the study area. Moose and elk were also present but in relatively small numbers (Washington Department of Fish and Wildlife 2014). It is therefore also possible that gray wolves selected for moose and elk given their larger body size and greater nutritional payout relative to either deer species (Griffiths 1980), rendering additive effects of wolf predation on our focal prey species less likely. However, given their generalist diet (Newsome et al. 2016), wolves would not be expected to preferentially target prey species whose relative availability is low (Huggard 1993). Furthermore, past research has shown that gray wolves often target smaller species where sympatric ungulates exist (Potvin et al. 1988; Paquet 1992; Dale et al. 1994). Indeed, a contemporary investigation of gray wolf foraging behavior using GPS clusters from collared individuals in our study system found deer at over 50% of gray wolf kill sites compared to 36% for moose and elk combined (Spence 2017).

Gray wolves in British Columbia were shown to subsist primarily on moose and secondarily on caribou (*Rangifer tarandus* Linnaeus, 1758), with which they had reduced spatial overlap relative to moose (Seip 2001). Furthermore, previous studies have revealed that patterns of predator-prey spatial overlap explain why mule deer and white-tailed deer exhibit differing levels of susceptibility to another coursing canid, the coyote (Lingle 2002; Atwood et al. 2009). Accordingly, we predicted that wolves would affect the survival of sympatric mule and white-tailed deer differentially (Lingle 2002; Gervasi et al. 2013). Specifically, we expected that white-tailed deer, which favor escape terrain that is shared by wolves, and are disproportionately preyed on by wolves in other systems (Nelson and Mech 1981; Lingle and Pellis 2002), would be more susceptible to wolf predation than mule deer. Instead, the presence of gray wolves did not result in a significant difference in mortality rates due to predation between the two deer species, either within or between treatments (Table 3). By implication, the intensity of wolf predation in managed landscapes may need to reach a certain density threshold beyond that found in our study area (8.6 wolves/1,000 km^2) and other managed landscapes (6.3 wolves/1,000 km^2 in areas of Idaho and Montana; Jimenez and Becker 2016) before manifesting differentially across prey species. By comparison, wolf densities in protected areas can exceed 40/1,000 km^2 (Smith et al. 2003). In our system, then, diminished wolf effectiveness and/or widespread low-risk gaps may have enabled white-tailed deer to avoid heavy predation in areas occupied by wolf packs despite similar habitat use patterns (Lingle and Pellis 2002; Mech and Peterson 2003; Oakleaf et al. 2006).

In our system it is interesting to note that overall deer mortality from predators and humans was nearly equal and that human-caused mortality was greater than that caused by predators for each species in each treatment with the exception of mule deer in wolf areas (Table 2). Accordingly, our results add to a growing literature implying that human-caused mortality may rival or even exceed wolf predation as a driver of ungulate survival and population trends in landscapes where human activities include hunting (White and Garrott 2005; Wright et al. 2006; Brodie et al. 2013; Dorresteijn et al. 2015). Notably, for example, a recent review of ecosystems in the western United States found that human-related factors were the primary influence on adult elk mortality, regardless of predator assemblage (Brodie et al. 2013). The relative influence of human and non-human predation on ungulate dynamics in any particular situation, however, is likely to depend on myriad factors including human density, interactions between predator species, predator and ungulate management, and landscape configuration (Kuijper et al. 2016). Thus, a more comprehensive understanding of how ungulate populations are shaped by predation in human-dominated ecosystems will require studies that rigorously address these drivers of context dependency.

Seasonal patterns of adult deer mortality, especially in relation to large carnivores, are well documented (Ballard et al. 2001; DeLGiudice et al. 2002; White and Garrott 2005; Wright et al. 2006). During summer, adult deer tend to be in relatively good condition because of access to high-quality forage and are not impeded by snow accumulation, making them hard for predators to catch and bring down. As winter approaches, however, adult deer are rendered easier to catch and bring down because their body condition decreases along with forage quality and availability and snow accumulates (Mech et al. 2001). Accordingly, wolves in the Greater Yellowstone Ecosystem were found to primarily take juvenile and older elk (Mech et al. 2001;

Wright et al. 2006), but as winter severity increased this pattern attenuated and reliance on prime-aged individuals increased (Mech et al. 2001). By inference, severe winter conditions could compound the effects of humans and wolves on ungulate populations by allowing wolves to increasingly rely on the healthy and prime-aged individuals that are typically harvested by human hunters (Brodie et al. 2013). Our study occurred over a three-year period during which winters were relatively mild. Thus, the effects of wolf predation on deer populations in our study area could grow in concert with increasing winter severity.

Collectively, our findings suggest that direct wolf predation on adult deer in ecosystems where human activity is pervasive may be too weak to markedly affect ungulate population dynamics (Gervasi et al. 2013; Kuijper et al. 2016). Accordingly, they raise questions about the extent to which results from studies of wolf-prey interactions in wilderness and protected areas apply to managed landscapes with an extensive human footprint (Hebblewhite et al. 2005; Andersen et al. 2006; Hamlin et al. 2008; Dorresteijn et al. 2015). Other studies of wolf re-colonization have revealed large and immediate impacts of wolves on prey survival and numbers (Hebblewhite et al. 2002, 2005; Christianson and Creel 2014). Given our work started several years after wolves appeared on the landscape in our study area, these studies suggest that had wolves had an impact on ungulate demography, we should have been able to detect it.

We would caution, however, that we did not investigate the impacts of gray wolves on neonate survival, which can greatly impact ungulate population dynamics (Nelson and Mech 1986). Furthermore, predator-prey interactions can vary markedly over time (Gaillard et al. 1998; Owen-Smith et al. 2005; Vucetich et al. 2005), partly because they are modified by a suite of dynamic environmental factors including catastrophic wildfires, severe winters, and drought (Vucetich et al. 2005; Barber-Meyer et al. 2008). For example, severe winters have been shown to exacerbate the effects of wolf predation on both white-tailed deer (Fuller 1991) and elk (Brodie et al. 2013). Lastly, given the brevity of our investigation, small sample size may have limited the scope of our inference and, moreover, top-down impacts on prey in our system could strengthen as wolves become more established. Thus, there remains need for longitudinal studies of consumptive predator-prey interactions in managed landscapes in general and studies capable of exploring relationships between variability in predator-prey population dynamics and abiotic and biotic conditions (Vucetich et al. 2005; Nelson et al. 2011; Brodie et al. 2013).

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Tables

Table 1.1. Sample sizes of adult mule deer (*Odocoileus hemionus*) and white-tailed deer (*O.virginianus*) that were GPS-collared and deer dying from different causes. Adult deer sample sizes (numbers collared and succumbing to specific forms of mortality) are stratified by wolf (*Canis lupus*) treatment (presence/absence), deer sex, and deer species.

Treatment	Species	Sex	Collared	Cause of Mortality					
				Cougar	Coyote	Black Bear	Gray Wolf	Human	Unknown
Wolf	White-tailed Deer	Male	6	0	0	0	0	2	0
Wolf	White-tailed deer	Female	19	1	0	0	2	0	0
Wolf	Mule Deer	Male	9	1	0	0	0	2	1
Wolf	Mule Deer	Female	18	3	2	0	0	0	0
Non-Wolf	White-tailed Deer	Male	13	1	0	1	0	6	0
Non-Wolf	White-tailed Deer	Female	21	2	3	0	0	2	1
Non-Wolf	Mule Deer	Male	12	0	1	0	0	3	0
Non-Wolf	Mule Deer	Female	22	4	1	0	0	1	1

Table 1.2. Overall annual survival rates and cause-specific mortality rates for mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*), derived from Kaplan-Meier analyses and Cumulative Incidence Functions. Survival and cause-specific mortality rates are broken out by treatment and species. Standard errors are in parentheses.

Treatment	Species	Overall Survival	Predator Related Mortality	Human Related Mortality
Both	Both	0.69 (0.04)	0.16 (0.03)	0.15 (0.03)
Wolf	Both	0.78 (0.05)	0.16 (0.04)	0.06 (0.03)
Wolf	White-tailed Deer	0.83 (0.07)	0.08 (0.05)	0.09 (0.06)
Wolf	Mule Deer	0.74 (0.07)	0.19 (0.06)	0.07 (0.04)
Non-Wolf	Both	0.60 (0.06)	0.16 (0.04)	0.24 (0.05)
Non-Wolf	White-tailed Deer	0.53 (0.09)	0.17 (0.06)	0.30 (0.08)
Non-Wolf	Mule Deer	0.67 (0.08)	0.17 (0.07)	0.16 (0.06)

Table 1.3. Cause-specific hazard coefficient estimates for the two primary (competing) sources of mortality influencing mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) mortality in northeastern Washington: non-human predators and humans. All variables were binomial: the 'Wolf' variable distinguished between wolf (*Canis lupus*; 1) and non-wolf (0) areas; the 'Species' variable contrasted mule deer (1) and white-tailed deer (0); and the 'Winter' and 'Fall' variables identified mortalities in those seasons, respectively.

Variable	Predator			Human		
	Estimate	SE	*P*	Estimate	SE	*P*
Wolf	-0.36	0.65	0.58	0.10	0.64	0.88
Species	0.14	0.56	0.80	-1.13	0.53	0.03
Fall	1.22	0.65	0.06	3.16	0.76	<0.01
Winter	3.29	0.55	<0.01	0.43	1.08	0.69

Table 1.4. Comparison of ΔAICc, AICc weights, and concordance (a measure of fit) of top cox proportional hazards models for the two primary sources of mortality influencing mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) survival in northeastern Washington: non-human predators and humans. All variables were binomial: the Wolf variable distinguished between wolf (*Canis lupus*; 1) and non-wolf (0) areas; the species variable contrasted mule deer (1) and white-tailed deer (0); and the Winter and Fall variables identified mortalities in those seasons, respectively.

Source	**Model**	**ΔAICc**	**Weights**	**Concordance**
Predator	Winter	0.00	0.77	0.81
	Winter x Wolf	3.63	0.13	0.85
	Null	4.25	0.09	0.66
	Wolf	8.85	0.01	0.58
Human	Fall	0.00	0.93	0.76
	Fall x Species	6.08	0.04	0.75
	Wolf	7.85	0.02	0.61
	Null	10.35	0.01	0.30

Figures

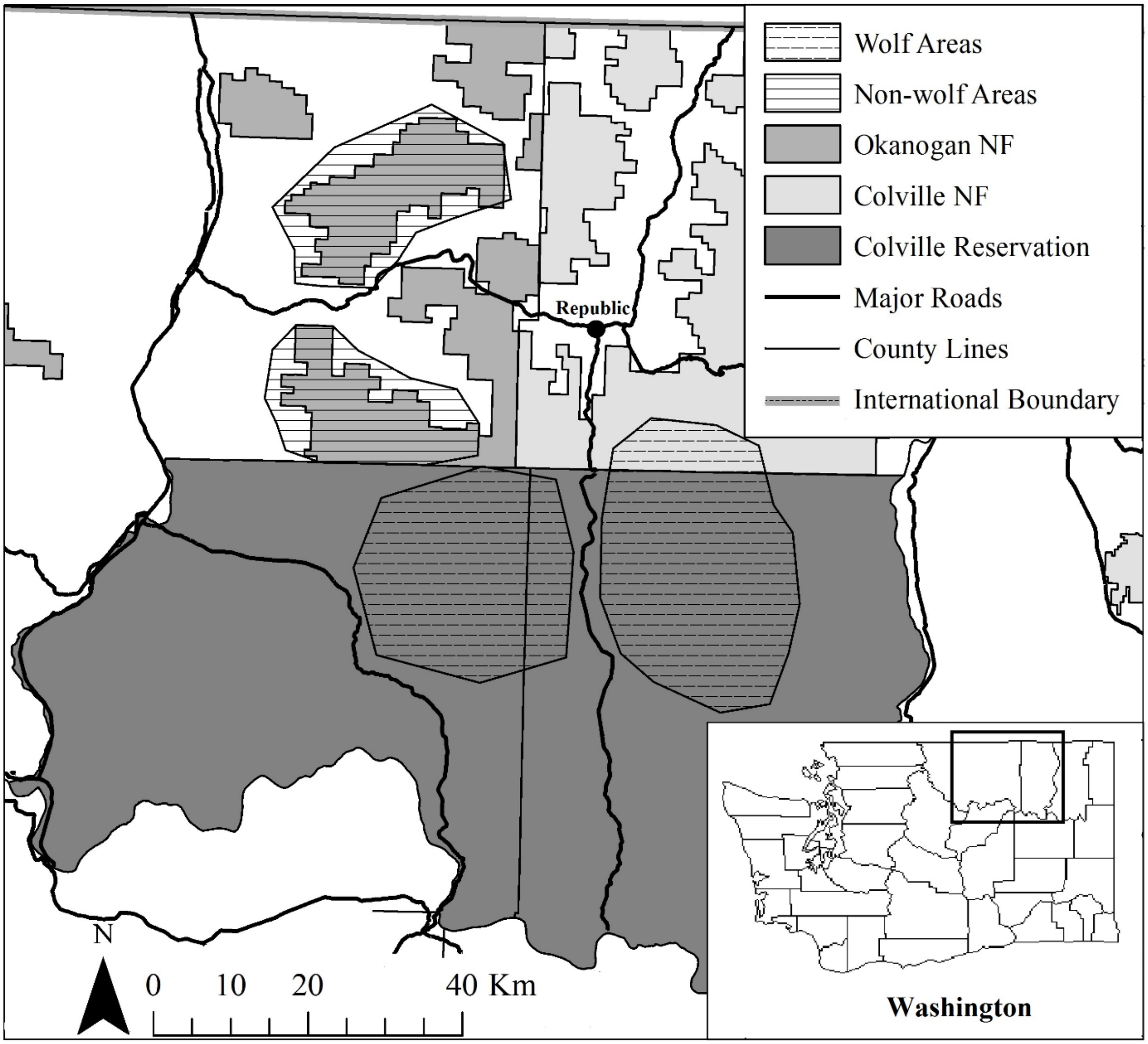

Figure 1.1. Location of the study area (11N 372208 E, 5389786 N) in Washington, USA, which included two areas occupied by gray wolves (*Canis lupus*) that fell primarily within the Colville Reservation and two wolf-free areas in the Okanogan-Wenatchee National Forest.

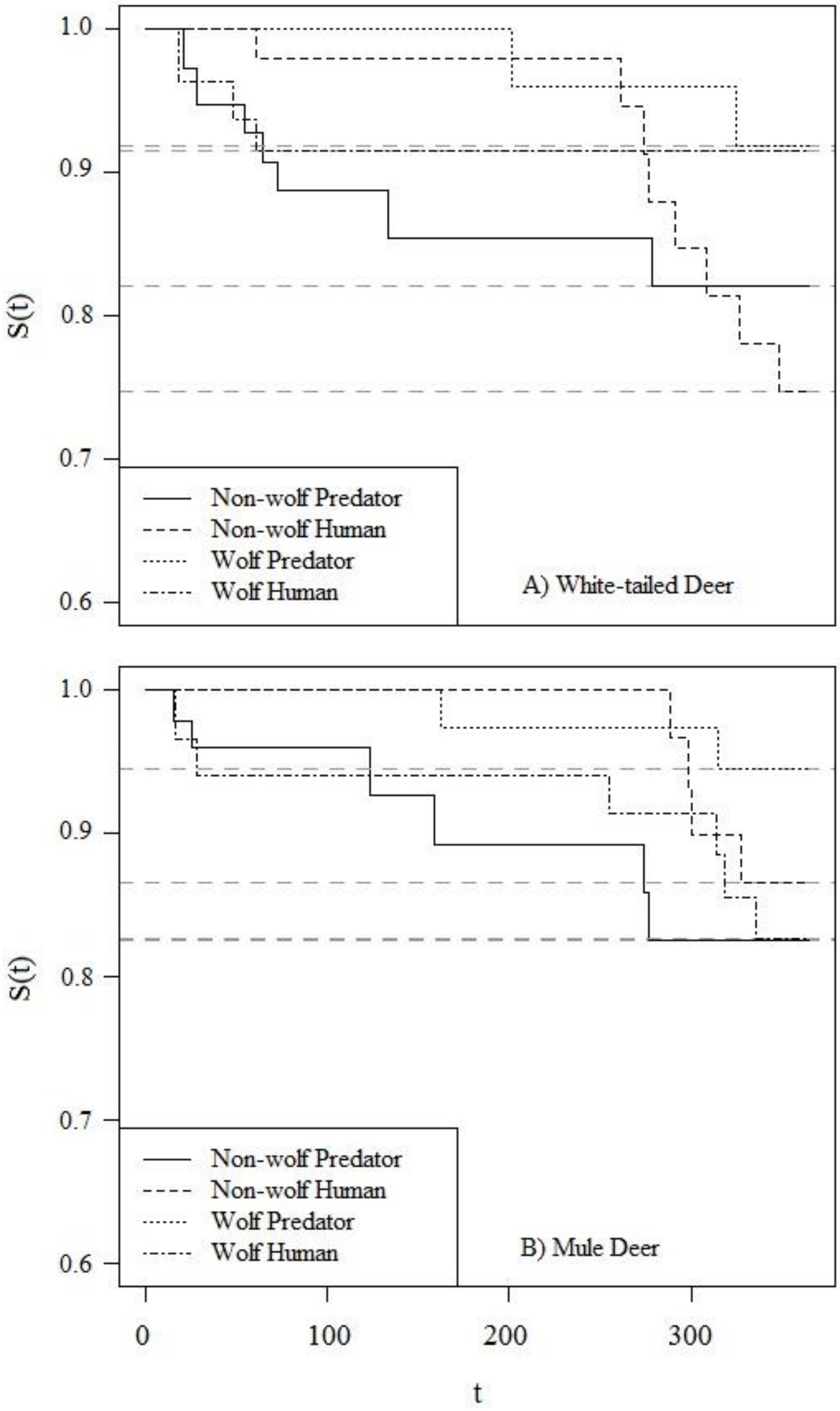

Figure 1.2. Cumulative Incidence Functions (CIF) estimating cause-specific mortality rates for a) white-tailed deer (*Odocoileus virginianus*) and b) mule deer (*O. hemionus*) in wolf (*Canis lupus*) and non-wolf areas. The Y-axis presents time in Julian days within a year and the x-axis depicts survival over time.

Chapter 2: Escape behavior predicts divergent anti-predator responses of sympatric prey to recolonizing gray wolves

*In review as: Dellinger JA, Shores CR, Craig A, Heithaus MR, Ripple, WJ, Wirsing AJ. Escape behavior predicts divergent anti-predator responses of sympatric prey to recolonizing gray wolves.

Abstract: There is growing appreciation for the role prey escape behavior can play in shaping non-consumptive effects of predators. We took advantage of ongoing gray wolf recolonization in eastern Washington, USA to contrast habitat use patterns of two sympatric prey species with different escape tactics – mule and white-tailed deer – at sites with and without established wolf packs. Under the hypothesis that the nature and scale of responses by these ungulates to wolf predation risk hinge on their escape behavior, we predicted that (1) mule deer would avoid encounters with wolves with coarse-scale spatial shifts to rugged terrain, where their stotting (bounding) and active-defense escape tactics are most effective; and that (2) white-tailed deer would not seek to avoid wolves but rather manage wolf risk with fine-scale spatial shifts toward gentle terrain facilitating their sprinting escape mode. Resource selection functions based on 61 mule deer and 59 white-tailed deer equipped with GPS radio-collars from 2013-2016 revealed that habitat use patterns for each species were altered by wolf presence, but in divergent ways that supported our predictions. More broadly, our findings add to a growing literature highlighting escape behavior as a key driver of contingency in prey responses to predation risk across multiple ecosystem types and, consequently, suggest that predators could initiate multiple direct and indirect non-consumptive effects (trophic cascades) in the same ecosystem that are transmitted by divergent responses of sympatric prey with different escape modes.

Introduction

Behavioral responses of prey to predators often take the form of shifts in habitat use, which in turn may influence how prey exploit resources and interact with co-occurring species (Lima and Dill 1990; Fortin et al. 2005; Thaker et al. 2011; Latombe et al. 2014). Prey individuals are typically assumed to avoid their predators (Laundre et al. 2010), diminishing their ecological effects (e.g., foraging pressure) where predators are more numerous, while increasing their impacts where predators are relatively scarce (Ripple and Beschta 2012). A growing literature, however, suggests that prey responses to predators hinge on key features of the interaction such as predator hunting mode and landscape context and, as a result, that anti-predator habitat shifts and their consequences will not always follow this pattern (Schmitz 2008; Heithaus et al. 2009; Wirsing et al. 2010). For example, Schmitz (2008) found that the hunting mode of sympatric spider predators (sit-and-wait versus active) dictated whether herbivorous grasshoppers (*Melanopuls femurrubrum*) foraged in refuge or exposed grassland habitat and, as a result, promoted either increased or reduced plant diversity. Working in a coral reef ecosystem, Catano et al. (2016) observed that landscape heterogeneity mediated avoidance of a predator decoy by herbivorous fishes, with reef complexity apparently enhancing avoidance because it impedes both predator detection and escape. By implication, efforts to identify the factors that determine how prey use space when threatened with predation are crucial to the development of a general framework for predicting the effects of predators on their prey and, ultimately, ecosystems.

Escape behavior has been proposed as an important driver of context dependence in predator-prey relationships that interacts with predator hunting mode and landscape features to determine prey spatial responses to predation risk (Lingle 2002; Heithaus et al. 2009; Wirsing et al. 2010). Overall predation risk can be decomposed into the probability of encountering a predator (pre-encounter risk) and the probability of death as a result of the encounter (post-encounter risk) (Lima and Dill 1990; Hebblewhite et al. 2005). Thus, prey individuals with certain escape tactics might actually benefit from minimizing post-encounter risk by using space where predators are relatively abundant but less lethal, whereas prey species with escape behaviors that do not facilitate surviving an encounter with a predator should seek to minimize pre-encounter risk by avoiding the predator altogether (Heithaus et al. 2009; Wirsing et al. 2010). In a given ecosystem, the hunting mode of the predator and the structure of the landscape will determine the spatial pattern of predator lethality experienced by each prey species and, consequently, which prey species might benefit from managing pre- versus post-encounter risk (Heithaus et al. 2009; Wirsing et al. 2010). This framework has implications for the spatial scale at which prey species should respond to the risk of predation. Namely, prey species whose escape behavior facilitates surviving an encounter should be expected to manifest fine-scale habitat shifts when exposed to the threat of predation, whereas those seeking to minimize pre-encounter risk should exhibit coarse-scale shifts in habitat use in response to the predator (Kauffman et al. 2007). To date, few studies have tested whether escape behavior can predict contrasting spatial responses of different prey species to a shared predator in the same landscape. Accordingly, we examined the possibility that recolonizing gray wolves (*Canis lupus*) in eastern Washington, USA elicit divergent habitat shifts by two sympatric herbivores – mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) – with different modes of escape.

In 2008, gray wolves began naturally recolonizing Washington from southern British Columbia, Canada and northern Idaho, and there are now 20 confirmed packs in the state (Jimenez and Becker 2016). At present, these packs are distributed heterogeneously across eastern Washington, setting the stage for natural experiments examining the effects of gray wolf recolonization on prey populations, including habitat use patterns, by contrasting areas with and without resident wolves. In this region, mule deer and white-tailed deer dominate the ungulate guild (Robinson et al. 2002), and gray wolves are known to primarily consume both species (making up ≥50% of wolf diet depending on the pack) within this region (Spence 2017). Mule deer and white-tailed deer may differ in their responses to presence of wolves, however, because their respective escape tactics are most effective in different habitat types (Lingle and Pellis 2002). Specifically, mule deer stot (i.e., bound) and exhibit active defense, and both of these escape tactics are facilitated by uneven terrain, especially against coursing canid predators (Lingle 2002). White-tailed deer, by contrast, are better equipped to escape canids on relatively gentle terrain because they flee predators and rely on early detection (Lingle and Pellis 2002). As coursing predators, gray wolves tend to select for relatively gentle terrain while hunting (Supplementary Material 2.1; Mech and Peterson 2003; Oakleaf et al. 2006). Thus, we might expect mule deer to exhibit coarse-scale habitat shifts from gentle to rugged terrain that reduce the likelihood of encounters with gray wolves (i.e., pre-encounter risk) while also promoting escape in the event of an attack. Conversely, white-tailed deer exposed to wolves should be more likely to remain in areas dominated by gentle terrain, given the presumed lethality associated with encountering predators in rugged areas, and exhibit finer-scale shifts in habitat use that enhance the possibility of escaping a predator encounter.

Here, taking advantage of spatial heterogeneity in wolf presence, we contrasted both coarse- and fine-scale habitat use patterns of adult mule deer and white-tailed deer in areas with and without established packs. We hypothesized that the nature and scale of anti-predator responses of these two deer species to wolves are mediated by escape behavior. Under this hypothesis, we expected mule deer to seek to avoid wolf encounters by increasing their use of rugged terrain and, consequently, that differences in habitat use patterns of this prey species in wolf-present and wolf-absent areas would be greatest at a relatively coarse spatial scale (Wirsing et al. 2010). Specifically, we predicted that, relative to conspecifics in wolf-absent areas, mule deer in wolf-present areas would exhibit increased use of space: 1) with greater slope (Lingle and Pellis 2002); 2) farther from roads (due to roads being graded/flatter surfaces that facilitate coursing movements; Whittington et al. 2011); and 3) closer to cover (i.e., more forested habitat to avoid detection; Hernandez and Laundre 2005) (Table 1). By contrast, because escape success of white-tailed deer has been shown to correlate spatially with terrain that is typically hunted by wolves, we predicted that differences in habitat use patterns of this prey species in wolf-present and wolf-absent areas would be greatest at relatively fine spatial scales (Heithaus et al. 2009; Wirsing et al. 2010). Specifically, we predicted that, relative to conspecifics in wolf-absent areas, white-tailed deer in wolf-present areas would show increased use of space: 1) with reduced slope (Lingle and Pellis 2002); 2) closer to roads (fewer obstacles on roads to inhibit escape; Kunkel and Pletscher 2001); and 3) farther from cover (i.e., more open shrub habitat to aid in early detection; Kittle et al. 2008; Table 1).

Materials and methods

Study area

This study took place from 2013-2016 in an area of eastern Washington spanning Okanogan and Ferry Counties and including portions of the Okanogan-Wenatchee and Colville National Forests and the Colville Reservation (Fig. 2.1). The study area contains the Okanogan Highlands and Kettle River Range. These areas are composed of similar topography with predominantly moderate slopes on mountainous and hilly terrain (Supplementary Material 2.2). The Sanpoil River is the main drainage that bisects the Okanogan Highlands and Kettle River Range. Elevation in the area ranges from 300 to 2,065 m. Shrub steppe habitats composed primarily of sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) makeup most of the habitat at lower elevations, whereas ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*) forest dominate at higher elevations. Riparian areas, composed primarily of poplars (*Populus spp*.), are regularly dispersed along drainages (Clausnitzer and Zamora 1987). Mule deer, white-tailed deer, elk (*Cervus elaphus*), and moose (*Alces alces*) comprise the resident ungulate community, though each deer species is 20 and 50 times more abundant than moose and elk, respectively (Spence 2017). Coyotes (*Canis latrans*), bobcats (*Lynx rufus*), American black bears (*Ursus americanus*), and cougars (*Puma concolor*) represent the larger mammalian predators present throughout the study area.

We broke the study area into four separate sites, two occupied by gray wolf packs and two lacking wolves. The four sites encompassed an average of 613 km^2 (range = 550-680 km^2). In areas of Washington that have been recolonized by gray wolves, average home range size, average pack size, and pack density are similar to those documented in other managed landscapes in neighboring states (Jimenez and Becker 2016), but pack size and pack density in all of these managed areas are low relative to protected areas (Jimenez and Becker 2016). Wolf packs were first detected in the region in the summer of 2010 and, over the course of the investigation, were found to occupy the Colville National Forest and Colville Reservation but not the adjacent Okanogan-Wenatchee National Forest (Fig. 2.1). Specifically, wolf-present areas were situated immediately east (Nc'icn Pack) and west (Strawberry Pack) of the Sanpoil River and State Highway 21. One wolf-absent site, named ‘Aeneas’, was immediately south of Aeneas Valley and State Highway 20, and north of the Colville Reservation. The other wolf-absent site, named ‘Bonaparte’, was located near Bonaparte Lake and north of State Highway 20 (Fig. 2.1). No site was more than 30 km from the three other sites. All four sites experience similar levels of human use in the form of cattle ranching, logging, and hunting. Cattle grazed freely on the landscape in each year of the investigation from approximately mid-June to mid-October. Logging occurred year round with variable harvest intensity and cut block size. Hunting of both deer species on the National Forests occurs in autumn and length of season varies depending on Game Management Unit (GMU) and weapon-type. Generally, no GMU is hunted more than two full months in a year during autumn. Both wolf-absent areas primarily occurred in GMU 204. Hunting of both species on the Colville Reservation primarily occurs during the autumn months.

Data Collection

We monitored gray wolf activity in all four sites within the study area in three ways. First, we deployed sixteen motion-activated game cameras (M880 by Moultrie®, Calera, AL, USA) year round as a grid (1 per 5 km^2) along logging roads and game trails at each site, and checked the cameras every three months. Second, we conducted weekly track surveys at each study site along logging roads and game trails during winter months (mid-December to mid-March) using snowmobiles. Third, radio-collars deployed on at least two members of each wolf pack occupying the designated wolf areas by the Colville Confederated Tribes Fish and Wildlife Department aided in monitoring wolf presence, movements, and pack size. Combined, these three methods enabled continuous and intensive monitoring of occupancy and overall number of wolves present in each site. Neither wolf-absent site had any documented gray wolf activity during the course of this study, whereas both of the wolf-present sites were occupied by packs ranging in size from 3-8 individuals over the course of the investigation.

To determine habitat use patterns of mule and white-tailed deer, we captured individuals of each species over three consecutive winters (December – March) using aerial net gunning and baited clover trapping (Haulton et al. 2001). We outfitted clover traps with trap transmitters to alert us to captures. Trap transmitter signals were checked daily in the early morning and late afternoon. Captured deer were equipped with Global Positioning System (GPS) radio-collars (Globalstar Survey Collars, Vectronic Aerospace Gmbh, Berlin, Germany), ear tagged, aged, sexed, and weighed. To ensure that only adults were collared, we did not instrument any individual weighing < 30 kg (Haulton et al. 2001). The GPS collars were programmed to obtain a location every 12 hours and five minutes, in the interest of obtaining an even distribution of locations throughout the day, and to switch to mortality mode if the instrumented deer exhibited no movement for a 24-hour period. All animal captures and collar deployments were conducted under University of Washington Institutional Animal Care and Use Committee (IACUC) protocol number 4226-01 and wildlife collection permits from the Washington Department of Fish and Wildlife and the Colville Tribes Fish and Wildlife Department.

Analyses

We used GPS data from radio-collared mule deer and white-tailed deer to examine patterns of resource use with a use-availability framework that compared landscape attributes associated with used locations to those at regularly generated available locations (Benson 2013). We analyzed resource use at two spatial scales. First, we created a 95% minimum convex polygon (MCP) home range estimate for each radio-collared deer. Regularly spaced points occurring every 30 m (minimum pixel size of spatial data used in analyses) within each 95% MCP home range served as used locations. Then we created a 95% MCP encompassing all deer GPS locations to represent available habitat for a second-order resource use analysis examining the drivers of home range establishment across the landscape by mule and white-tailed (Johnson 1980). Regularly spaced points occurring every 30 m within the study area, but not within individual deer home ranges, served as available locations for this coarse-scale analysis (Johnson 1980; Benson 2013). We then compared regularly spaced points within individual deer home ranges to regularly spaced points within the study area to quantify any differences in home range establishment (i.e., coarse-scale habitat use) for both deer species in wolf-present and wolf-absent areas. Second, we used the 95% MCP home range estimates for each radio-collared deer above as the basis for a third-order resource use analysis that explored drivers of space use within the home range (Johnson 1980). Regularly spaced points occurring every 30 m within each individual deer home range served as available locations for this relatively fine-scale habitat use analysis (Johnson 1980; Benson 2013). We then compared GPS fix locations to available locations within each individual home range to determine differences in resource use patterns of both deer species in wolf-present and wolf-absent areas at a fine spatial scale. We developed resource selection functions (RSFs) for both deer species, at both spatial scales, by estimating coefficients for landscape attributes from a binomial logistic regression of used versus available locations (Manly et al. 2002; Johnson et al. 2006). We accounted for the influence of GPS fix success on RSF estimates by including weights for detection depending on habitat type (Nielson et al. 2009). We included a random effect for individual in the model building process to account for among-individual variance in habitat use patterns that we could not specifically address with fixed effects. RSFs resulting from this approach yield coefficient estimates that can be used to understand relative probability of use of areas along a gradient of habitat attributes for species of interest (Boyce et al. 2002).

We included the following landscape attributes as explanatory variables in the global RSFs (i.e., the base models from which the above predictions were tested) for each deer species and spatial scale combination (four total): 1) distance to habitat type in meters (forest and shrub); 2) landscape attributes (slope and distance to nearest road); 3) wolf presence/absence; and 4) season. We classified season by noting the date of each GPS location and then using binary coding (0/1), with winter (October – March) set as the reference season (0). Binary classification of season allowed for simplistic representation of snow presence (present versus absent) on the landscape. Wolf presence was also expressed as a binary effect (0/1), whereby radio-collared deer in areas without wolves present served as the reference treatment. We included a two-way interaction between wolf and season to investigate differences in deer behavior among various combinations of treatment (wolf-present and wolf-absent) and season (summer and winter). We also included two-way interactions between wolf and season, respectively, and each other variable (habitat types and landscape attributes). If deer in wolf-present and wolf-absent areas behaved divergently, then both the binary wolf presence/absence variable and at least one of the two-way interactions including the wolf variable would be significant. Furthermore, we included three-way interactions involving wolf presence/absence, season, and each other variable. These three-way interactions allowed for discerning potential differences in habitat use between mule deer and white-tailed deer as a function of various combinations of treatment (wolf-present and wolf-absent) and season (summer and winter). We obtained raw data for habitat types from the Washington GAP (Geospatial Analysis Project) raster habitat layer (United States Geological Survey 2011), and for secondary roads and landscape attributes from the Washington State GIS data clearinghouse (https://wagda.lib.washington.edu/data/geography/wa_state/; accessed 11/15/2016). We analyzed all spatial data at a 30 x 30 m resolution. We assessed habitat type and landscape attributes using a Euclidean Distance Analysis (EDA) framework (Benson 2013). Briefly, we estimated the straight-line distance from each pixel (at 30 x 30 m resolution) to the nearest secondary road, forest cover, or shrub habitat. We then standardized these EDA distance values by subtracting each value by the mean and then dividing by the standard deviation to render coefficient estimates derived from these variables easier to interpret (Benson 2013). Initially, we also included deer sex for both ungulate species as a fixed effect in our RSFs. However, preliminary analyses revealed little effect of sex on differences in habitat use patterns between deer of either species in wolf-present and wolf-absent areas and between seasons at either spatial scale. Accordingly, in order to maximize sample size, we pooled the sexes in subsequent models (Table 2). We assessed performance of RSFs using cross-validation procedures (Supplementary Material 2.3; Johnson et al. 2006; Benson 2013; Dellinger et al. 2013).

We used Program R version 3.1.2 (R Core Team, 2014) for all statistical analyses, and ArcView GIS version 10.2 Geographic Information System (GIS; ESRI, Redlands, California) and Geospatial Modeling Environment version 0.7.4.0 (Beyer 2015) for spatial analyses. In all analyses, we considered $P \leq 0.05$ to be statistically significant.

Results

Across our four study sites over the course of three years, we collared 120 adult deer (n = 61 mule deer, n = 59 white-tailed deer; Table 2). We collected an average of 700 locations (±

562 sd) per radio-collared individual, with an average successful GPS fix rate of 81% (75-88%). Individuals were monitored for an average of 433 days (± 275 sd).

Overall, model-averaged coefficient estimates for mule deer demonstrated greater disparity in resource use patterns as a function of wolf presence at a coarse spatial scale (i.e., with respect to second-order resource use; Table 3; Fig. 2). Furthermore, differences in use of particular resources by mule deer in wolf-present and wolf-absent areas generally supported the prediction that this species would manage wolf predation risk with habitat shifts that facilitate encounter avoidance (Tables 1, 3). Specifically, relative to conspecifics in wolf-absent areas, mule deer in wolf-present areas exhibited (i) a lower probability of using areas close to secondary roads at the coarse-scale of analysis; (ii) a lower probability of using areas with low slope at the coarse-scale; and (iii) a higher probability of using areas close to forested habitat at the coarse-scale. Mule deer in wolf-present and wolf-absent areas selected shrub habitat in a similar manner at both coarse and fine spatial scales. Mule deer exhibited some seasonality in habitat use patterns at the coarse-scale. Namely, use of space relative to roads varied between seasons, with mule deer manifesting increased use of areas close to roads in wolf-absent areas during winter and the opposite pattern in the wolf-present areas. Furthermore, at the coarse-scale mule deer in wolf-present areas selected for forest more in winter compared to summer. Fine-scale habitat use patterns of mule deer in wolf-present versus wolf-absent areas were more similar in summer than in winter. For example, mule deer in wolf-present areas more readily avoided areas as distance to forest and shrub cover increased, respectively, compared to mule deer in wolf-absent areas during winter (Fig. 2).

Overall, model-averaged coefficient estimates of white-tailed deer demonstrated greater disparity in resource use patterns as a function of wolf presence at a relatively fine spatial scale (i.e., with respect to third-order resource use; Table 3; Fig. 3). Moreover, differences in use of particular resources by white-tailed deer in wolf-present and wolf-absent areas generally supported the prediction that this species would manage predation risk from wolves with habitat shifts that facilitate post-encounter escape (Table 1, 3). Specifically, relative to conspecifics in wolf-absent areas, white-tailed deer in wolf-present areas exhibited (i) a higher probability of using areas close to secondary roads at the fine spatial scale of analysis; (ii) a higher probability of using areas with low slope at the fine spatial scale; and (iii) a higher probability of using areas close to shrub habitat at the fine spatial scale. White-tailed deer in wolf-present and wolf-absent areas selected forested habitat similarly at both the coarse and fine spatial scales of analysis. White-tailed deer exhibited some seasonality in habitat use patterns. Namely, in all study areas white-tailed deer selected areas with lower slope in summer compared to winter at the fine spatial scale. Coarse-scale habitat use patterns of white-tailed deer in wolf-present areas versus white-tailed deer in wolf-absent areas were more similar in summer than in winter (Fig. 2). For example, at the coarse spatial scale white-tailed deer in wolf-present areas responded more to increasing distance from shrub cover during winter relative to summer compared to conspecifics in wolf-absent areas (Fig. 3). Cross-validation of model-averaged coefficient estimates revealed good predictive ability of resource use by mule and white-tailed deer at both coarse and fine spatial scales (Supplementary Material 2.3).

Discussion

There is now broad agreement that predators can influence prey populations and community dynamics by eliciting anti-predator behavior (Lima 2002; Hernandez and Laundre 2005; Creel and Christianson 2008). Yet, predicting the responses of prey to particular predators, and by extension the nature of non-consumptive predator indirect effects in communities, remains a challenge (Heithaus et al. 2009). Predator recolonization events set the stage for natural experiments that contrast responses of sympatric prey in areas with and without the returning predator and thereby allow examination of the factors driving divergent anti-predator responses both within and among prey species (Wirsing et al. 2010; Dorresteijn et al. 2015). Taking advantage of the return of grey wolves to a multi-prey landscape in eastern Washington, USA, we found support for the hypothesis that the nature and scale of prey responses to predation risk are mediated by escape behavior. Specifically, mule deer at risk from wolves exhibited coarse-scale spatial shifts that suited their escape tactic (stotting) and resulted in wolf avoidance, whereas white-tailed deer manifested fine-scale shifts that facilitated their escape mode (sprinting) but resulted in spatial overlap with wolves. Our results offer new insights into the way these ungulates manage their risk of predation from wolves both spatially and temporally. More broadly, they validate the use of escape behavior in conjunction with predator hunting mode and landscape structure to predict prey responses to predation risk (Heithaus et al. 2009; Wirsing et al. 2010) and suggest that predators with certain hunting modes could trigger multiple indirect non-consumptive effects in the same ecosystem owing to divergent responses of sympatric prey with different escape tactics.

Mule deer exhibit active defense and stotting as anti-predator behaviors (Lingle 2002), both of which are fostered by sloped, uneven terrain with obstacles (Lingle and Pellis 2002). Namely, obstacles and broken ground can reduce angles of attack, in-turn helping to focus defensive behavior, and favor bounding over running around impediments to movement for quickly and efficiently covering ground (Lingle 2002). Given that the anti-predator behaviors of mule deer putatively inhibit escaping wolves in areas that these canids frequent (i.e., areas with gentle and rolling terrain), we predicted that this prey species would avoid encounters with and reduce the probability of being detected by wolves (Atwood et al. 2009; Wirsing and Ripple 2011) by manifesting coarse-scale shifts toward more rugged uplands with increased slopes (i.e., uneven ground; Wirsing et al. 2010; Whittington et al. 2011; Table 1). In accord with this prediction, differences in resource use by mule deer were best captured by the coarse-scale analysis, and individuals exhibited patterns of use that are consistent with encounter avoidance. Specifically, when exposed to wolf predation risk, mule deer shifted into forest cover where detection by cursorial predators like wolves was less likely (Fortin et al. 2005). Mule deer at risk from wolves also avoided areas with gentle terrain, which wolves use heavily for hunting (Mech and Peterson 2003; Oakleaf et al. 2006), and roads and trails, which wolves often use as travel routes (Supplementary Material 2.1; Kunkel and Pletscher 2001). We also predicted that at the coarse-scale mule deer in wolf-present areas would avoid areas close to shrub habitat to a greater extent than conspecifics in wolf-absent areas because shrub habitat facilitates being detected by wolves. We found, however, that mule deer in wolf-present areas showed no significant difference in use of areas close to shrub habitat compared to mule deer in wolf-absent areas, perhaps indicating the foraging benefits of shrub habitat for mule deer (Pierce et al. 2004). Nevertheless, our results overall are strikingly consistent with the idea that mule deer anti-predator responses to wolves are governed by their escape mode. In accord with our study, Lingle (2002) found that mule deer at risk from coyotes on the Alberta prairie responded by shifting to rugged terrain, and Bowyer (1987) suggested that mule deer fawns select steeper slopes to avoid coyotes. Notably, however, all of these studies were conducted in areas characterized by topographical complexity. Accordingly, the manner in which mule deer respond to the threat of predation from coursing canids in areas with less topographical variation remains to be determined. We also recognize that mule deer use of more gentle terrain and areas closer to roads in the non-wolf areas relative to the wolf areas may be an attempt to decrease predation risk from cougars (Pierce et al. 2004), whereas the habitat use pattern we observed in the wolf areas could reflect risk from both predators (Atwood et al. 2009). We were unable to explore these possibilities, underscoring the value of future studies capable of discriminating between the effects of these two predators on mule deer.

White-tailed deer use flight and early detection as anti-predator tactics (Lingle 2002), and both of these countermeasures are generally facilitated by gentle, open terrain with good visibility and few obstacles (Lingle and Pellis 2002). Given that the anti-predator behaviors of white-tailed deer actually promote escaping wolves in areas where wolves hunt, we predicted that this species would not avoid wolves but rather exhibit fine-scale shifts facilitating running and vigilance (Wirsing et al. 2010; Wirsing and Ripple 2011; Table 1). In accord with this prediction, differences in resource use by white-tailed deer were best captured by the fine-scale analysis (Kuijper et al. 2015), and individuals exhibited patterns of use that are consistent with facilitating post-encounter escape (Lingle 2002). Namely, white-tailed deer at risk from wolves selected areas close to roads, which in our study area bisect relatively flat areas with few obstacles to hinder escape, areas with little to no slope (i.e., areas characterized by level ground that facilitate sprinting), and more open habitats offering greater visibility. (Kunkel and Pletscher 2001; Lingle and Pellis 2002). Our results agree with previous research suggesting that white-tailed deer minimize predation risk from coursing predators by relying on early detection, which is facilitated by use of open habitats and avoidance of dense cover (e.g., Kunkel and Pletscher 2001). They are also consistent with work by Kittle et al. (2008), who found that white-tailed deer in Ontario, Canada selected for sheltered deer yards with low snowfall in winter that placed them in close proximity to hunting wolves, and with previous studies demonstrating that, following detection, white-tailed deer are more vulnerable to coursing predators where escape is impeded by obstacles (e.g., deep snow) or not facilitated via use of roads or established trails (Nelson and Mech 1991). Collectively, these investigations support the notion that, rather than avoiding canids like mule deer, white-tailed deer at risk from these coursing predators select resources that promote their sprinting mode of escape.

Mule deer and white-tailed deer in areas with wolves exhibited greater seasonality in resource use patterns at the predicted spatial scales of their responses to wolves than conspecifics in areas without wolves. Specifically, at the coarse-scale mule deer in wolf-present areas had a higher probability of selecting areas close to forest cover in winter versus summer (Table 1; Fig. 2). This pattern might be the result of adult mule deer making more of an effort to avoid encounters with wolves in winter, the season during which cervid vulnerability to predation tends to be greatest (Nelson and Mech 1991). At the fine-scale, white-tailed deer in wolf areas showed a higher probability of selecting areas close to open shrub in winter versus summer, possibly as a means of more efficiently detecting and escaping wolves during the most dangerous time of year. Adult white-tailed deer and mule deer in other systems have been found to exhibit seasonal differences in habitat use patterns in relation to predation risk, most notably in response to hunting whereby both deer species selected for cover to decrease detection by human hunters (Swenson 1982; Kilgo et al. 1998). To date, however, seasonal differences in habitat use patterns of either species in relation to non-human predation risk remain largely unexplored. Our results highlight the seasonality that can characterize mule and white-tailed deer responses to wolves and, by extension, imply that studies with limited temporal scope may underestimate or miss effects of predators on these ungulates. More broadly, they show that consideration of spatiotemporal patterning can strengthen insights into predator-prey interactions by revealing context specific processes that influence how prey behaviorally manage predation risk (Padie et al. 2015).

The conceptual framework underlying this study was originally developed as a result cross-fertilization of research in aquatic and terrestrial environments (Lima 2002; Heithaus et al. 2009; Wirsing et al. 2010) and then invoked in a marine ecosystem (Heithaus et al. 2012; Catano et al. 2016). Our findings add to a growing literature (e.g., Crowell et al. 2016; Martin and Owen-Smith 2016) showing that it also applies in terrestrial settings. Accordingly, they underscore the value, irrespective of eco-domain, of considering the three-way interaction between prey escape behavior, predator hunting mode, and landscape structure when predicting or explaining prey responses to predation risk. For example, large roving predators such as gray wolves (Middleton et al. 2013) and African wild dogs (*Lycaon pictus*; Thaker et al. 2011) have been posited as having weak non-consumptive impacts on prey relative to ambush predators because their spatially diffuse risk signature minimizes the effectiveness of anti-predator behaviors such as habitat shifts. Other studies, however, have found that roving predators can influence prey behavior to a greater extent than their ambushing counterparts (e.g., Creel et al. 2014). Insofar as they bear out predictions from the aforementioned framework, our findings suggest that this disparity likely owes to context dependence. That is, rather than exerting uniformly weak non-consumptive effects, roving predators like wolves may elicit marked behavioral changes when and where the setting allows members of prey species with certain escape tactics the scope to manage their risk. More broadly, our results suggest that at least some aspects of predator-prey interactions in aquatic and terrestrial systems operate under a similar set of ecological ‘rules’, the recognition of which could foster a more general understanding of predator-prey interactions that encompasses a diversity of systems and taxa (Terborgh and Estes 2010; Wirsing and Ripple 2011; Wirsing et al. 2014).

A growing literature suggests that the effects of top predators can be attenuated in human-dominated ecosystems (Hebblewhite et al. 2005; Gervasi et al. 2013; Ripple et al. 2014; Kuijper et al. 2016). Indeed, we found that wolves in our study system, where human activity is pervasive, had weak effects on survival of adult mule and white-tailed deer (Chapter 1). Yet, here we detected marked behavioral responses in both deer species to recolonizing wolves. By implication, wolves in our human-managed system might not be numerous enough to kill many prey individuals (Jimenez and Becker 2016), but their presence may still be sufficient to cause prey to invest in defensive behavior. Microcosm experiments with invertebrate predator-prey systems have demonstrated that even when the ability of predators to consume prey is removed (i.e., consumptive effects equal zero), prey may maintain defensive countermeasures similar those exhibited by conspecifics exposed to predators capable of killing them (Schmitz et al. 1997; Nelson et al. 2004). Building on these small-scale experiments, our findings add support to the idea that non-consumptive predator effects can operate even when direct predation is negligible (Schmitz et al. 1997; Nelson et al. 2004; Creel and Christianson 2008). Our results are also relevant to the debate over whether recolonizing predators can trigger cascading effects to lower trophic levels by imposing risk in managed landscapes (Hebblewhite et al. 2005; Gervasi et al. 2013; Dorresteijn et al. 2015; Kuijper et al. 2016). The mule and white-tailed deer anti-predator responses we observed mean that wolves have the potential to exert behavior-mediated indirect effects on plant communities in our system. There remains need, however, for studies asking whether these responses are strong enough to affect lower trophic levels and examining the possibility that the effects of wolves on deer in managed landscapes could be superseded in some circumstances by risk effects imposed by human predators (Lone et al. 2014; Dorresteijn et al. 2015).

In conclusion, our results demonstrate that escape behavior influences the nature and spatial scale of prey responses to predation risk and thereby highlight the potential for top predators to impact multiple sympatric prey species at varying spatial scales via risk effects because of differences in prey escape behavior (Latombe et al. 2014; Padie et al. 2015; Catano et al. 2016; Makin et al. 2017). By implication, top predators could trigger multiple indirect non-consumptive effects in the same ecosystem by inducing divergent responses of sympatric prey with different escape tactics (Wirsing et al. 2010). Accordingly, we encourage further exploration of direct and indirect effects of predators with shared prey that exhibit divergent escape behavior in the interest of better understanding the non-consumptive pathways by which top-down forcing can occur in ecosystems. Given that prey escape responses can depend on predator hunting mode and landscape context (Lingle 2002; Heithaus et al. 2009; Wirsing et al. 2010; Latombe et al. 2014), studies in systems with multiple predator and prey species interacting across heterogeneous landscapes are likely to be especially revealing. Finally, from a conservation standpoint our findings emphasize the important roles played by predators in all landscapes rather than just protected areas (Heithaus et al. 2012; Dorresteijn et al. 2015; Kuijper et al. 2016). In particular, our results suggest that even if predators do not inflict much mortality in human-modified ecosystems, their recovery might at least partly restore key processes such as defensive investment by prey species (Kuijper et al. 2016) with the potential to generate multiple trophic cascades (Ripple and Beschta 2012).

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Supplementary Material

Supplementary Material 2.1.

Our predictions with respect to how mule and white-tailed should respond to wolf presence were based on the assumption that wolves and white-tailed deer share a tendency to select low-lying and gentle terrain in our study system. This tendency has been demonstrated for the two species independently in other systems (Kunkel and Pletscher 2001; Atwood et al. 2007). Nevertheless, we wanted to ensure its validity in our study area. Hence, using GPS radio-collar location data from wolves in both packs (~ 2,000 combined locations), we generated mean estimates and associated 95% confidence intervals for wolf locations in relation to distance to nearest secondary road, distance to forest habitat, distance to shrub-steppe habitat, and slope. We then compared these estimates to those for regularly spaced points occurring every 30 m across the wolf-occupied landscape.

Analysis of resource use by GPS radio-collared wolves confirmed our key assumption with respect to their space-use behavior. Namely, wolves were more likely to occur in areas closer to secondary roads and with reduced slope compared to what was available, whereas 95% confidence intervals for used and available distance to forest cover and open shrub overlapped (Supplementary Material Figure 2.1).

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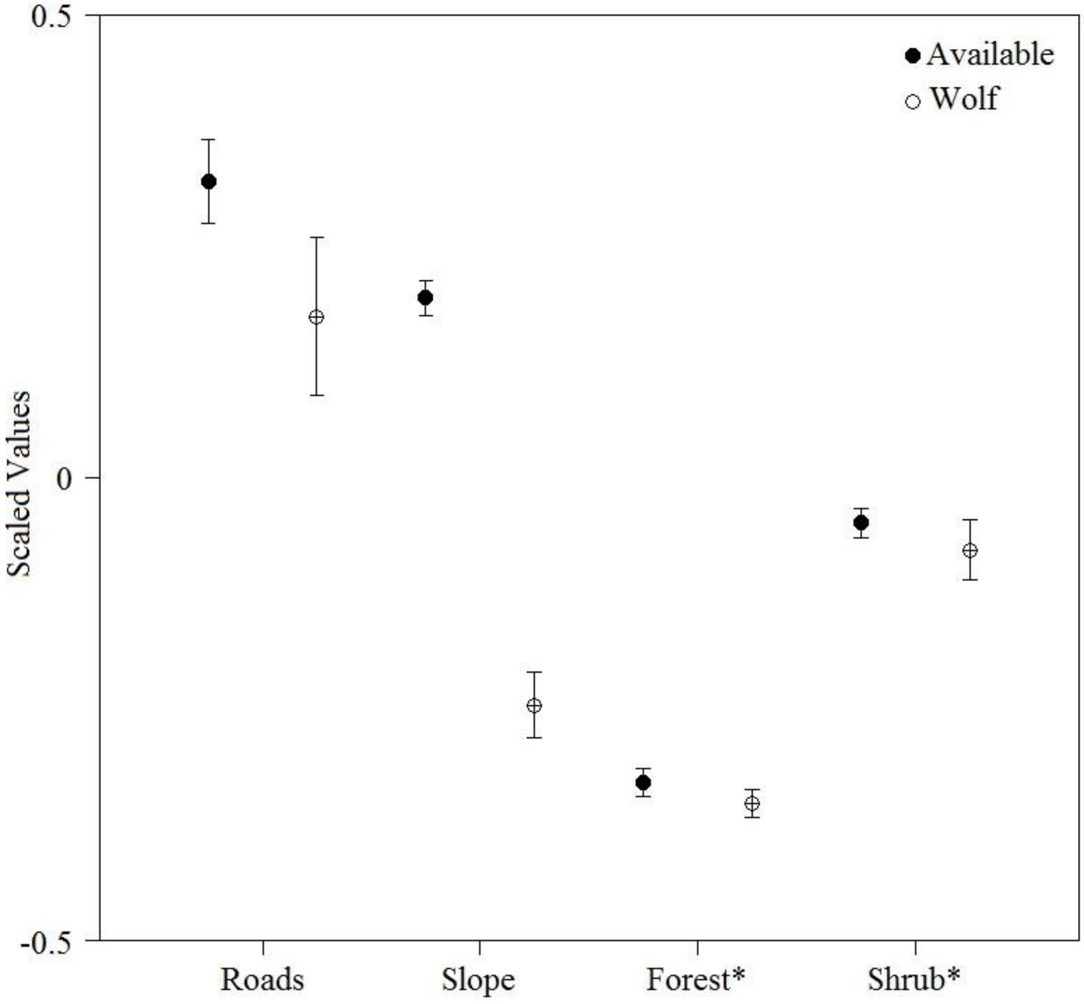
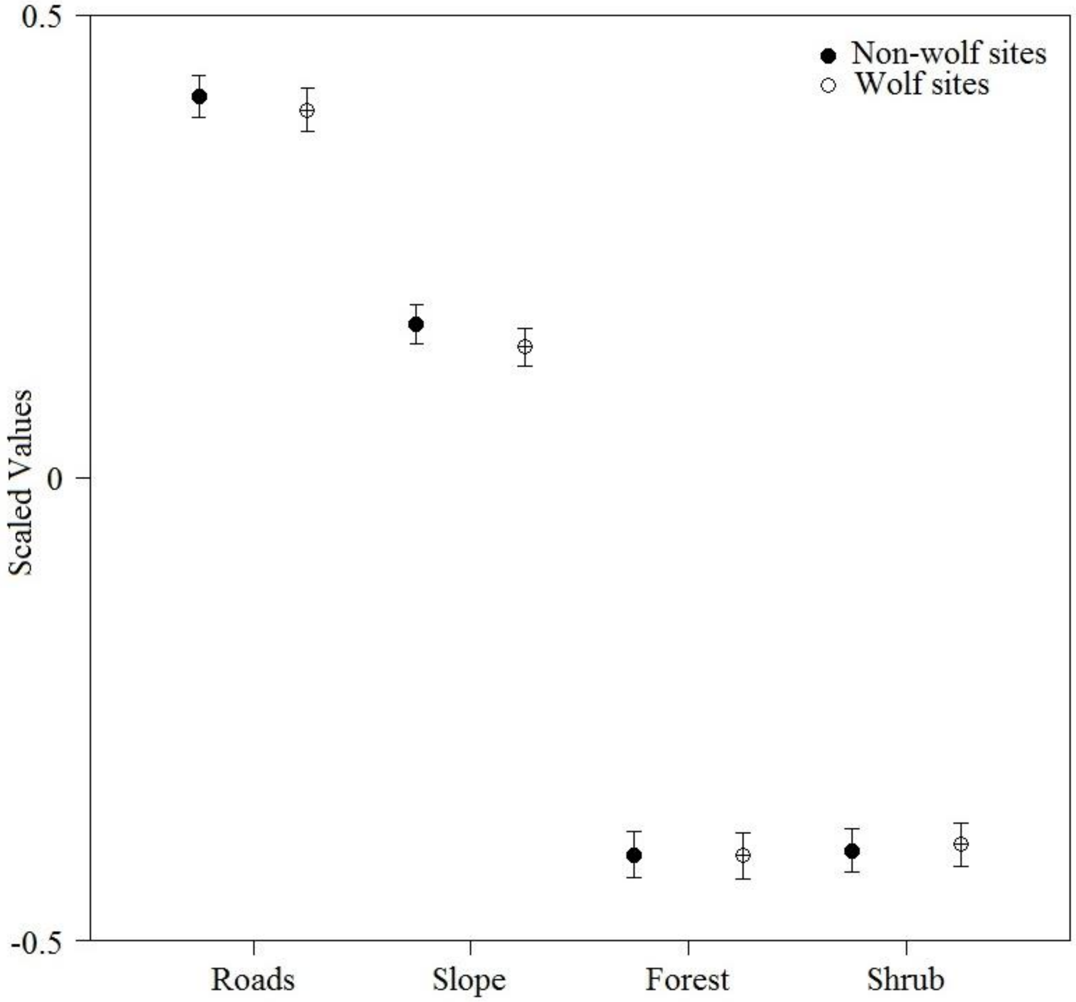


Supplementary Material Figure 2.1. Comparison of mean and 95% confidence interval values for landscape and habitat variables associated with gray wolf GPS locations and points regularly spaced across the study area (i.e., the area defined by the two wolf pack territories). Regularly spaced points indicated availability with respect to landscape and habitat variables. Asterisks indicate variables with overlapping 95% confidence intervals. Road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Forest and Shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively. All values were scaled by subtracting the by mean and diving by the standard deviation.

Supplementary Material 2.2.

We wanted to verify that deer of both species in wolf-present and wolf-absent areas had access to the same range of habitat and landscape variables. Accordingly, we compared mean values and associated 95% confidence intervals between the wolf-present and wolf-absent sites for all habitat and landscape variables used in the RSFs based on measures from the regularly spaced points occurring every 30 m (minimum pixel size of spatial data used in analyses) within the study area.

The wolf-present and wolf-absent study areas were similar with respect to the habitat and landscape variables used in the analyses of deer space use (distance to roads, distance to forest, distance to open shrub, and slope; Supplementary Material 2.2).



Supplementary Material Figure 2.2. Comparison of mean and 95% confidence interval values for landscape and habitat variables associated with regularly spaced points across the wolf-present and wolf-absent study areas. Regularly spaced points indicated availability with respect to landscape and habitat variables. All 95% confidence intervals overlap, indicating no difference in availability. Road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Forest and Shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively. All values were scaled by subtracting the by mean and diving by the standard deviation.

Supplementary Material 2.3.

We performed a binning procedure whereby five different data bins were created for building models. In each bin, we randomly selected 80% of the used and available data points for building RSF models and used the remaining 20% to cross-validate the model created from the data in that bin (Benson 2013). We repeated this procedure five times such that all data were used for building and cross-validating RSF models. Cross-validation uses linear regression to compare the proportion of expected to the proportion of observed (used) locations that occur in each of a predetermined number of proportional probability of use classes (k) (Johnson et al. 2006; Dellinger et al. 2013). We averaged coefficient estimates from the global RSFs across the different bins to come up with model-averaged coefficient estimates (Buckland et al. 1997). Significance of model-averaged coefficient estimates was used to test the predictions described above. For example, if forest and all interactions containing forest (forest x wolf; forest x season; forest x wolf x season) were significant for mule deer, then we could conclude that mule deer use of forest habitat differed between treatment and each season within each treatment. Furthermore, if shrub and only the two-way interactions containing shrub (shrub x wolf; shrub x season) were significant for white-tailed deer, then we could conclude that white-tailed deer use of shrub habitat differed between treatments but only varied seasonally for the wolf-absent areas because the three-way interaction involving shrub was non-significant.

Cross-validation of model-averaged coefficient estimates revealed good predictive ability of resource use by mule and white-tailed deer at both coarse and fine spatial scales. The slope of the linear regression of proportion of observed versus expected locations, based on k (= 10) number of probability of use classes for each model-averaged RSF, was significantly different from zero, but not significantly different from one for each of the four model-averaged RSFs

(Supplementary Material Figure 2.3). By implication, the model-averaged coefficient estimates for each RSF were proportional to the probability of habitat use by both deer species, and both deer species did not use resources in proportion to availability but rather demonstrated habitat selection Furthermore, the y-intercept of the linear regression was not significantly different from zero for each of the four model-averaged RSFs (Supplementary Material Figure 2.3), again indicating that the model-averaged RSFs were proportional to the probability of habitat use by both deer species and at each spatial scale. Agreement between the proportions of observed and expected locations within each probability of use class was high, with all Spearman rank correlation coefficient values ≥ 0.95 ($p < 0.01$), demonstrating that each model-averaged RSF was able to predict habitat use for the respective deer species and spatial scale for individual deer other than those used to build the RSFs.

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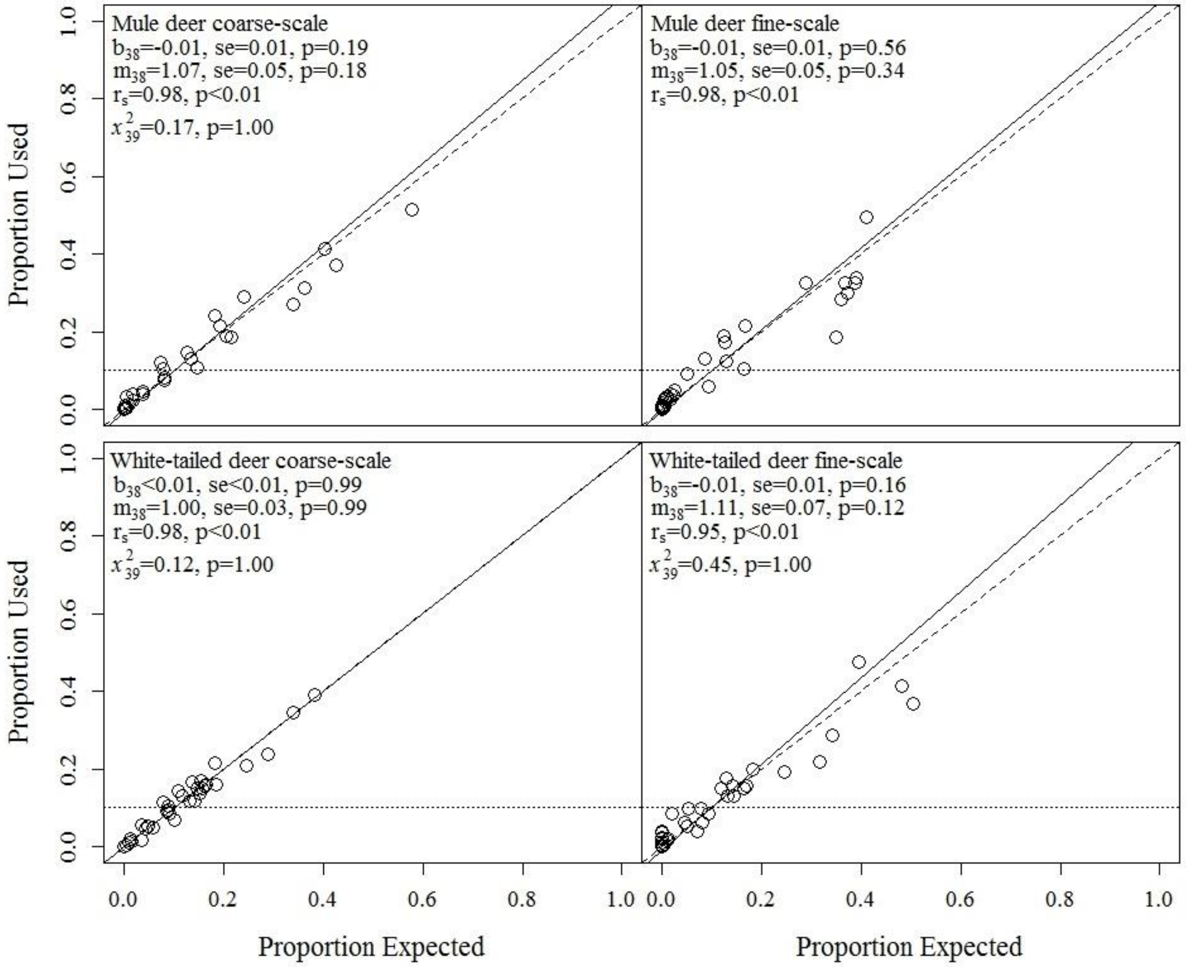

Supplementary Material Figure 2.3. Cross validation statistics for assessing performance of model-averaged RSF coefficient estimates for mule deer and white-tailed deer at coarse and fine spatial scales, respectively. Cross validation examined the proportion of used GPS locations versus the proportion of expected number of random points in each of 10 ordinal classes for both deer species and each spatial scale. For a model with strong predictive ability, y-intercept estimates (b) should not be significantly different from zero and slope estimates (m) should not be significantly different from 1. Further, Spearman correlation coefficients (r_s) should be near 1 and significant whereas chi-square coefficients (χ^2) should be non-significant. Random selection of resources would be displayed as observed values set to 0.1 (i.e., given there were k=10 number of bins for cross-validation and maximum proportion of use [1] divided by k equals 0.1), whereas selection of resources proportional to probability of selection (selected = expected) would occur along a line with slope = 1 and y-intercept of 0. Linear regression results are represented by solid lines.

Tables

Table 2.1. Predicted and observed impacts of gray wolves on patterns of habitat selection by mule and white-tailed deer across multiple spatial scales and seasons. Negative symbols signify either 1) an increasing relationship between selection and a distance variable or 2) an inverse relationship between selection and slope for deer in wolf-present areas relative to deer in wolf-absent areas. Positive symbols signify either 1) an inverse relationship between selection and a distance variable or 2) an increasing relationship between selection and slope for deer in wolf-present areas relative to deer in wolf-absent areas. Double arrows indicate no significant difference in selection for a specified variable for deer in wolf-present areas relative to those in wolf-absent areas. Distance to road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Distance to forest and shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively.

Species	Scale	Variable	Season	Predicted	Result
Mule Deer	Coarse	Distance to Road	Winter	-	-
			Summer	-	-
		Slope	Winter	+	+
			Summer	+	+
		Distance to Forest	Winter	+	+
			Summer	+	+
		Distance to Shrub	Winter	-	+
			Summer	-	-
Mule Deer	Fine	Distance to Road	Winter	↔	+
			Summer	↔	↔
		Slope	Winter	↔	+
			Summer	↔	↔
		Distance to Forest	Winter	↔	+
			Summer	↔	↔
		Distance to Shrub	Winter	↔	+
			Summer	↔	↔
White-tailed Deer	Coarse	Distance to Road	Winter	↔	↔
			Summer	↔	↔
		Slope	Winter	↔	-
			Summer	↔	↔
		Distance to Forest	Winter	↔	↔
			Summer	↔	↔
		Distance to Shrub	Winter	↔	+

			Summer	↔	↔
White-tailed Deer	Fine	Distance to Road	Winter	+	+
			Summer	+	+
		Slope	Winter	-	-
			Summer	-	-
		Distance to Forest	Winter	-	-
			Summer	-	-
		Distance to Shrub	Winter	+	+
			Summer	+	+

Table 2.2. Adult deer sample sizes and numbers of GPS locations by wolf presence/absence, sex, and species.

Treatment	Species	Sex	Collared	# GPS Locations
Wolf-present	White-tailed Deer	Male	6	2,081
Wolf-present	White-tailed Deer	Female	19	12,339
Wolf-present	Mule Deer	Male	9	5,825
Wolf-present	Mule Deer	Female	18	20,740
Wolf-absent	White-tailed Deer	Male	13	6,436
Wolf-absent	White-tailed Deer	Female	21	11,969
Wolf-absent	Mule Deer	Male	12	10,403
Wolf-absent	Mule Deer	Female	22	14,197
		Total	**120**	**83,990**

Table 2.3. Model-averaged fixed effect coefficient estimates and standard errors for each set of models grouped by deer species and spatial scale. Also included are model-averaged random effect variance and standard deviations for each set of models grouped by deer species and spatial scale. Coefficient estimates were derived from resource selection functions in a use/available framework. Asterisks (*) indicate 95% confidence intervals include zero.

Fixed Effects	Species							
	Mule Deer				White-tailed Deer			
	Coarse-scale		Fine-scale		Coarse-scale		Fine-scale	
	ß	SE	ß	SE	ß	SE	ß	SE
Intercept	-2.050	0.013	-1.709	0.013	-2.353	0.023	-2.090	0.025
Wolf	-1.756	0.049	-1.020	0.052	-0.218	0.037	0.208	0.038
Season	-0.163	0.019	0.325	0.020	-0.116	0.029	-0.158	0.033
Dist to Road	-0.039	0.006	0.092	0.009	-0.302	0.014	0.032	0.015
Slope	0.174	0.011	0.471	0.013	-0.483	0.018	-0.349	0.017
Dist to Forest	-0.049	0.020	-0.418	0.023	-1.158	0.052	-0.611	0.061
Dist to Shrub	-0.266	0.018	-0.368	0.018	0.266	0.014	0.173	0.014
Wolf:Season	1.280	0.055	0.916	0.059	0.085*	0.049	0.330	0.051
Wolf:Dist to Road	0.046	0.009	0.054	0.013	-0.176	0.024	-0.650	0.027
Wolf:Slope	0.290	0.016	-0.229	0.017	0.263	0.024	-0.133	0.023
Wolf:Dist to Forest	-2.452	0.109	-0.737	0.119	-0.047*	0.078	0.739	0.078
Wolf:Dist to Shrub	-1.155	0.038	-0.965	0.038	-0.895	0.034	-0.720	0.037
Season:Dist to Road	-0.028	0.010	-0.093	0.015	-0.046	0.020	-0.162	0.024
Season:Slope	-0.259	0.016	-0.218	0.019	-0.474	0.026	-0.416	0.025
Season:Dist to Forest	0.199	0.026	0.129	0.030	0.496	0.061	0.856	0.073
Season:Dist to Shrub	-0.504	0.029	-0.151	0.029	-0.093	0.021	0.021*	0.019
Wolf:Season:Dist to Road	0.084	0.013	0.119	0.019	-0.052*	0.035	0.102	0.038
Wolf:Season:Slope	0.277	0.022	0.241	0.024	0.002*	0.036	-0.069	0.035
Wolf:Season:Dist to Forest	1.163	0.121	0.982	0.131	-0.299	0.097	-0.377	0.102
Wolf:Season:Dist to Shrub	1.141	0.049	0.910	0.049	0.661	0.044	0.647	0.047
Random Effects	Variance	SD	Variance	SD	Variance	SD	Variance	SD
Individual	<0.001	0.024	0.682	0.826	<0.001	<0.001	0.845	0.919

Figures

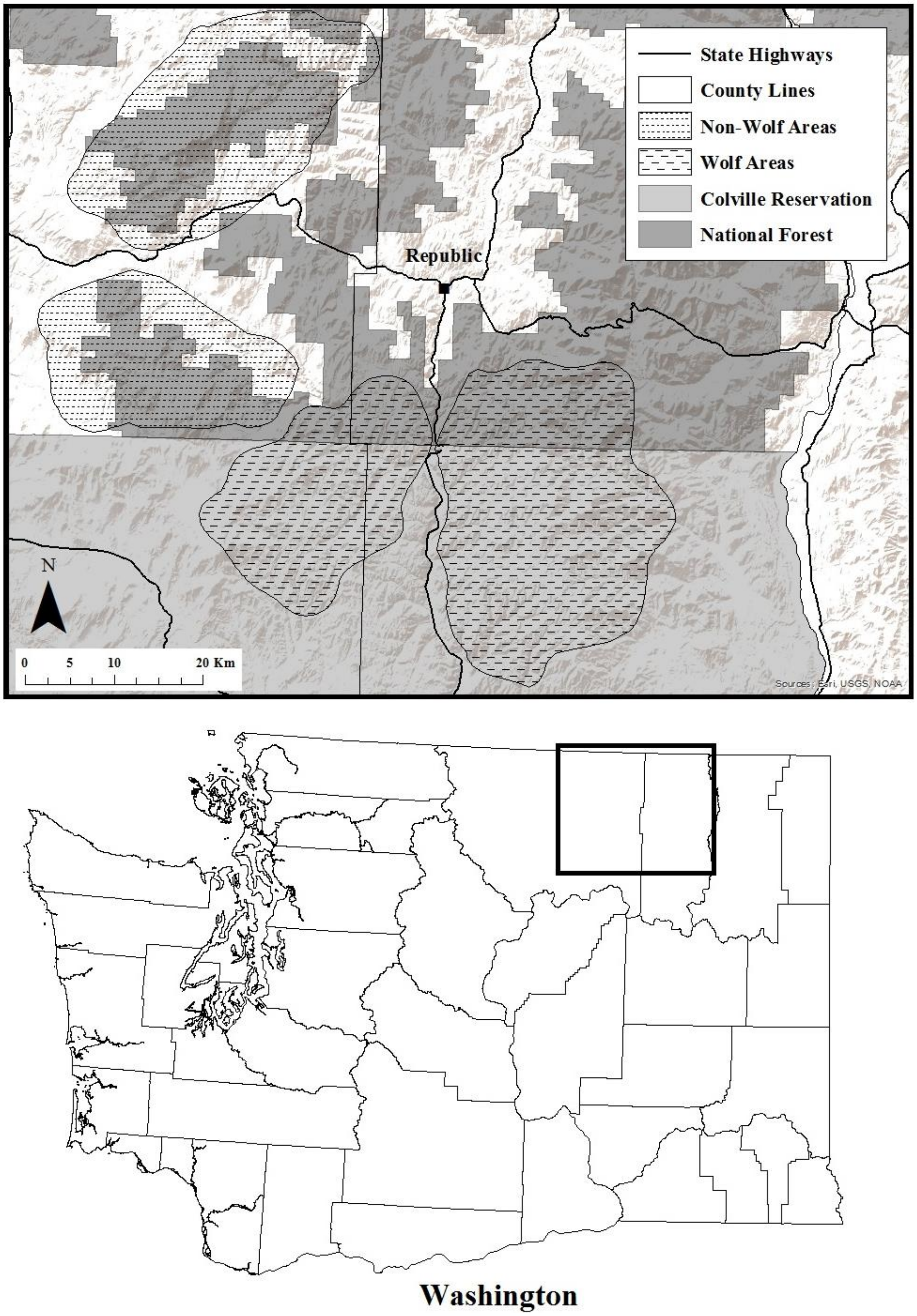

Figure 3.1. Location of the study area in Washington, USA (UTM 11 N 372231 E 5589670), which included the two study sites occupied by gray wolf packs primarily within the Colville Reservation (Nc'icn and Strawberry) and two nearby wolf-free areas in the Okanogan-Wenatchee National Forest (Aeneas and Bonaparte).

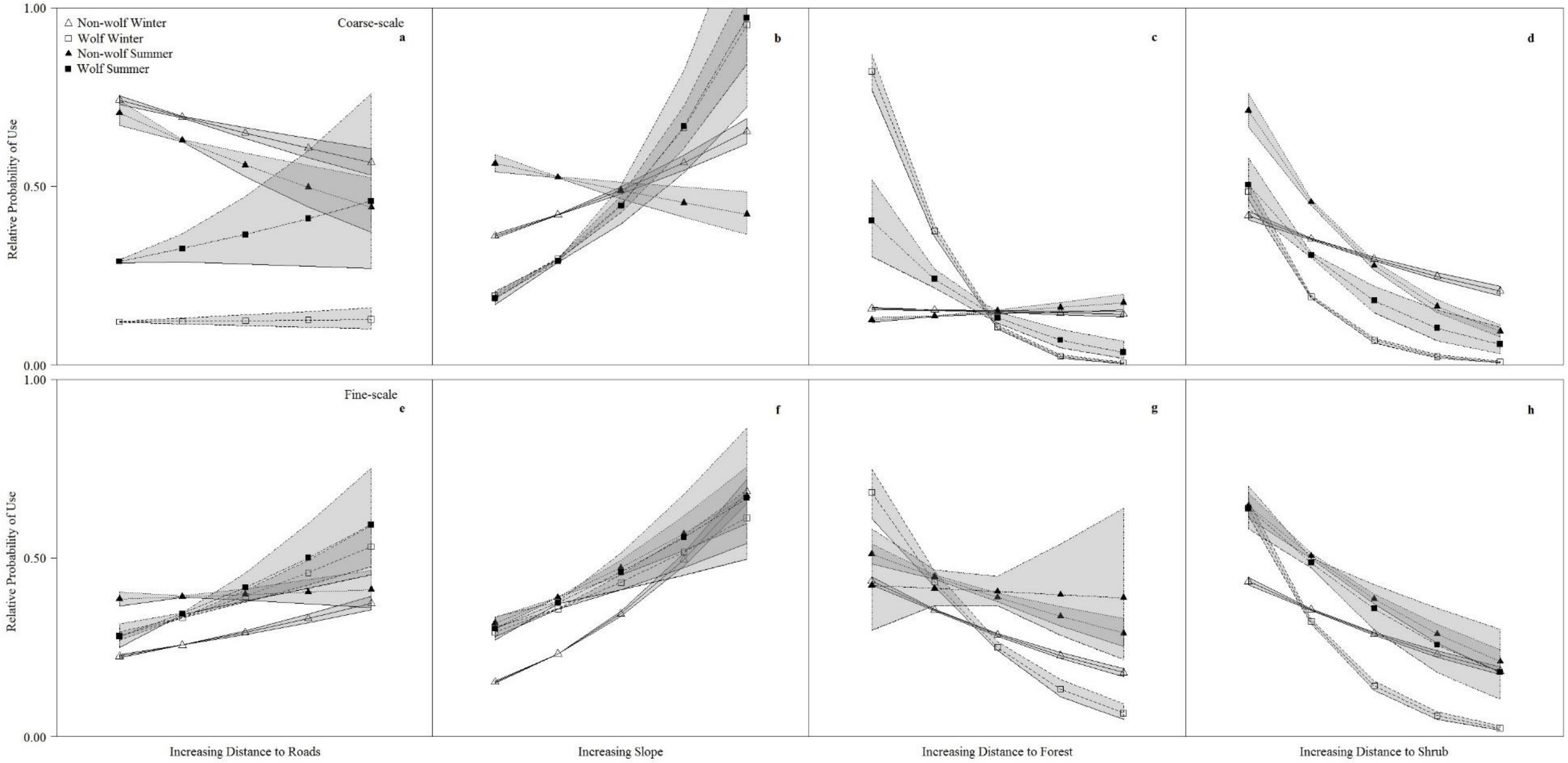

Figure 3.2. Mule deer relative probability of use (symbols connected by lines) and associated 95% confidence intervals (gray shading bounded by lines) of landscape and habitat variables. Relative probabilities of use of landscape and habitat variables are broken down by wolf presence/absence and season, respectively, for coarse scale (a-d) and fine scale (f-h) habitat use patterns. Relative probabilities were derived from coefficient estimates from resource selection functions in a use/available framework. Distance to road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Distance to forest and shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively. X-axes are the scaled values of respective variables. Scaled values were derived by subtracting the mean from all values and then diving by the standard deviation.

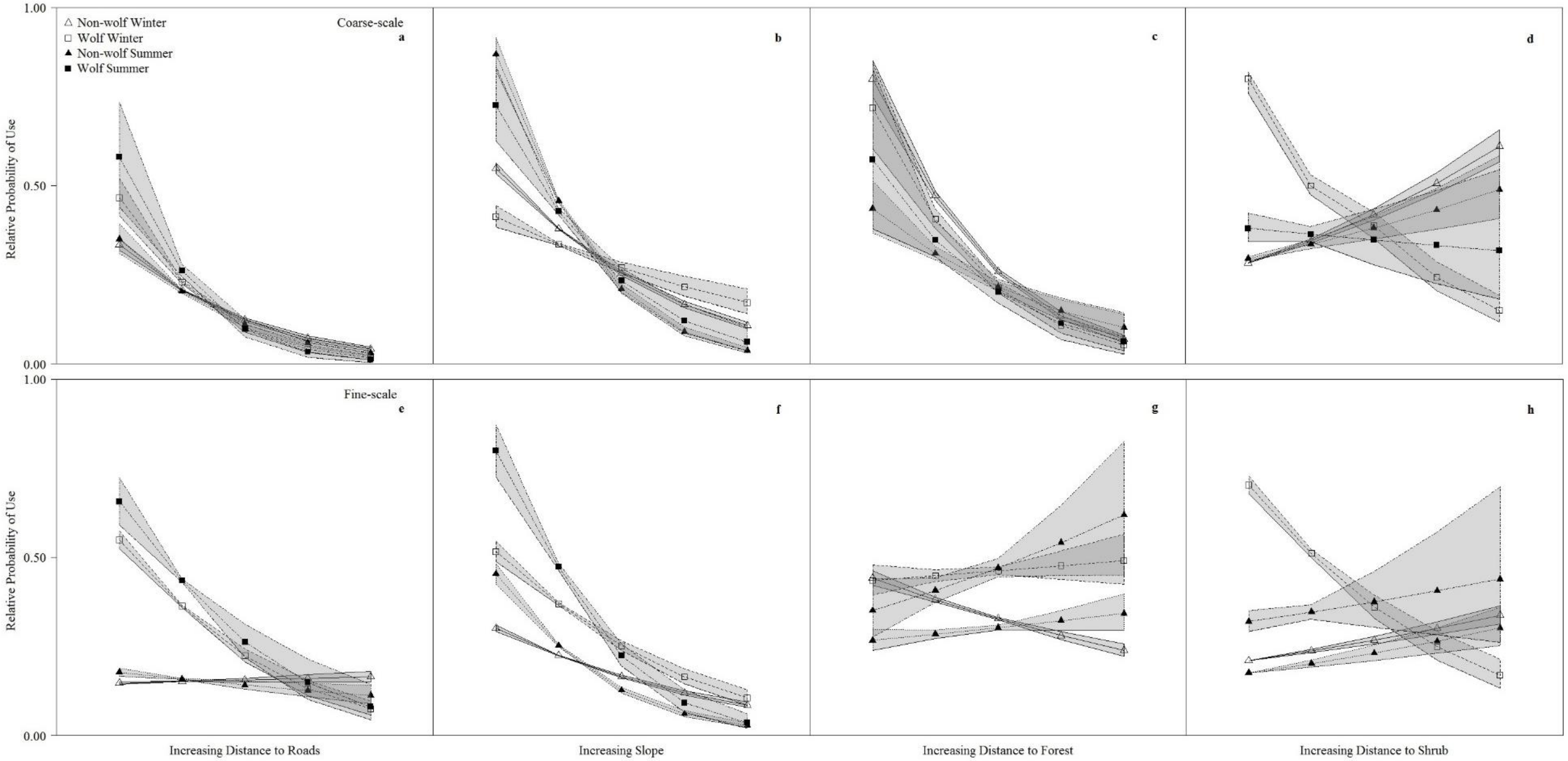

Figure 3.3. White-tailed deer relative probability of use (symbols connected by lines) and associated 95% confidence intervals (gray shading bounded by lines) of landscape and habitat variables. Relative probabilities of use of landscape and habitat variables are broken down by wolf presence/absence and season, respectively, for coarse scale (a-d) and fine scale (f-h) habitat use patterns. Relative probabilities were derived from coefficient estimates from resource selection functions in a use/available framework. Distance to road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Distance to forest and shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively. X-axes are the scaled values of respective variables. Scaled values were derived by subtracting the mean from all values and then diving by the standard deviation.

Chapter 3: Do recolonizing gray wolves impact resource partitioning among sympatric prey species?

*Pending submission

Abstract: There is increasing recognition of the role predators can play in shaping patterns of prey resource use. Yet, our understanding of the impacts of predation risk on resource overlap between co-occurring prey species remains limited, despite the long-appreciated potential for these impacts to influence patterns of competition and biodiversity. Here, we took advantage of ongoing gray wolf (*Canis lupus*) recolonization in northeastern Washington, USA, to contrast patterns of resource partitioning between sympatric mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) at sites with and without resident wolf packs. Mule and white-tailed deer have different modes of escaping canid predation (stotting and running, respectively) whose disparate efficacy on flat terrain appears to contribute to species-specific shifts in resource use in response to wolf predation risk. Thus, under the hypothesis that wolf exposure influences their resource overlap, we predicted that features of the landscape relating divergently to the probability of escaping wolves for the two deer species (e.g., slope, proximity to roads) would be partitioned to the greatest degree. Given that resource partitioning can manifest at multiple spatial scales, our analysis employed complimentary approaches to explore partitioning between the prey species as a function of wolf presence at coarse and fine scales. Redundancy analysis based on 61 mule deer and 59 white-tailed deer outfitted with GPS radio-collars from 2013-2016 revealed that wolf presence corresponded with the greatest reductions in coarse-scale overlap along gradients of slope, distance to water, distance to secondary roads, and distance to forest cover during both summer and winter. Moreover, the ways in which resources were partitioned at this scale were largely consistent with the two prey species seeking to promote their chances

of escape. Latent selection difference models revealed greater fine-scale partitioning of forest cover in wolf versus non-wolf areas during both seasons, and the manner in which this resource was partitioned was consistent with species-specific escape facilitation. Thus, our findings support the idea that wolf predation risk mediates resource partitioning between sympatric deer species and, insofar as coarse-scale partitioning of slope was especially strong in the wolf-impacted areas, suggest that escape behavior may play an important role in shaping how predators alter patterns of resource overlap among their prey. Yet, the magnitudes and directions of difference in resource overlap between the wolf-affected and wolf-free areas depended on the resource, season, and scale. By implication, our understanding of the relationship between predation risk and prey resource partitioning will benefit from a framework that accounts for these sources of context-dependency.

Introduction

Predators have the potential to promote biodiversity by altering competition among co-occurring species at lower trophic levels (Paine 1966; Hall et al. 1970; Caswell 1978; Holt 1984; Sivy et al. 2017). Paine (1966) highlighted the capacity of predators to mediate competition between sympatric prey species under field conditions. Namely, by experimentally manipulating the presence of the top predator, the ochre starfish (*Pisaster ochraceus*), in an intertidal invertebrate community, he showed that predator removal reduced prey species diversity by releasing competitively dominant California mussels (*Mytilus californianus*). Beyond this pioneering work, however, most field studies of predator effects on interspecific interactions among sympatric prey species have focused on apparent competition, whereby one relatively abundant prey species facilitates increased predation on a less common prey species by supporting increased abundance and distribution of a shared predator (Robinson et al. 2002;

DeCesare et al. 2010; Johnson et al. 2013; Wittmer et al. 2013). Accordingly, there remains need for studies examining how predators shape other types of competitive interactions between co-occurring prey species under field conditions.

Owing to the challenge of measuring competition directly, most studies seeking to examine competition instead use resource overlap as a proxy (Colwell and Futuyama 1971; Pianka 1974; Abrams 1980; Jenkins and Wright 1988). In a classic study, MacArthur (1958) inferred that five congeneric warbler species are able to coexist despite the potential for strong interspecific competition by dividing up shared resources. Similarly, Pianka (1974) used indices of resource overlap to draw inferences about how competition between lizard species was mediated by environmental variability. More recently, Smith et al. (2018) demonstrated how human activity mediated competition between co-occurring coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and gray foxes (*Urocyon cinereoargenteus*) by comparing habitat use and dietary overlap along a gradient of human activity. Accordingly, we examined patterns of resource overlap between co-occurring mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) in Washington, USA, to understand how their competitive relationship might be influenced by recolonizing gray wolves (*Canis lupus*).

Interactions between gray wolves and their prey in temperate regions of North America and Europe are well explored (e.g., Mech and Peterson 2003; Ripple and Beschta 2012; Garrott et al. 2013; Fleming et al. 2017; Winnie and Creel 2017). Only a few studies, however, have examined their effects on competition between co-occurring prey. In Yellowstone National Park, for example, direct predation by wolves significantly reduced the abundance and altered the behavior of elk (*Cervus elaphus*; Fortin et al. 2005; Evans et al. 2006), resulting in a decrease in forage overlap between elk and bison (*Bison bison*) that subsequently appears to have allowed bison numbers to increase (Ripple et al. 2011). Wolf predation risk was also shown to alter spatial distribution and foraging behavior of elk (Creel et al. 2005; Hernandez and Laundre 2005) and foraging behavior of bison (Laundre et al. 2001), resulting in decreased overlap in resource use (i.e., food and space) between the two ungulate prey species. In this system, however, the ability of gray wolves to mediate overlap in resource use between elk and bison hinges on elk predation (Hernandez et al. 2005) because bison are primarily killed by wolves when elk are scarce or absent (Smith et al. 2000) and generally only react to wolf predation risk when under immediate threat (Carbyn and Trottier 1987). By contrast, few studies to date have examined the capacity of gray wolves to mediate competitive interactions between sympatric prey species whose susceptibility to predation is more equivalent (e.g., species with more similar body size and defensive armament).

Previous research shows that mule and white-tailed deer can exhibit considerable forage and spatial overlap where they co-occur (Kramer 1973; Whittaker and Lindzey 2004; Brunjes et al. 2006). However, mule deer tend to select for more open terrain at higher elevations whereas white-tailed deer are more strongly associated with lower elevation habitats that offer greater concealment (Brunjes et al. 2006). Thus, co-occurrence of the two species is thought to be promoted by a mosaic of open and dense cover (Brunjes et al. 2006). In regions where population sizes of the two deer species are asymmetrical, the more abundant species typically occurs in areas primarily utilized by the other (Whittaker and Lindzey 2004). Under these circumstances, it is possible that the more abundant species might out compete the other because of exploitation of shared resources (Kramer 1973) and, further, that wolves could mediate this process by modifying the extent of prey resource partitioning. To date, however, the impact of wolves on the competitive relationship between mule deer and white-tailed deer has not been addressed.

Gray wolves began naturally recolonizing Washington state, USA, from northern Idaho and southern British Columbia, Canada, in 2008. There are currently more than 20 confirmed packs that are distributed heterogeneously across eastern Washington (Washington Department of Fish and Wildlife et al. 2017). This patchy wolf distribution enables natural experiments that contrast prey traits in proximal areas with and without resident packs. Taking advantage of this opportunity, we quantified patterns of resource overlap between adult mule deer and white-tailed deer in areas with and without established wolf packs. Mule deer and white-tailed deer have different escape gaits – stotting (bounding) and running, respectively – whose efficacy is believed to be promoted by divergent sets of landscape characteristics (Lingle 2002). Namely, stotting by mule deer is thought to best facilitate predator evasion in areas featuring obstacles and broken, uneven terrain (Geist 1981), whereas running is believed to allow white-tailed deer to flee most effectively from predators in areas with gentle terrain that facilitate unobstructed movement (Kunkel and Pletscher 2001; Kittle et al. 2008). Accordingly, in a previous analysis we found that mule and white-tailed deer in our study system appear to use space differently in response to the presence of wolves (Chapter 2). Specifically, relative to conspecifics in wolf-free areas, mule deer increased their use of two landscape features - steep slopes and areas removed from roads – that would be expected to enhance the effectiveness of (or reduce the costs associated with employing) stotting as a means of escape. By contrast, white-tailed deer at risk from wolves selected gentler slopes and areas more proximal to roads, both of which would be expected to facilitate fleeing. Given the putative link between these contrasting space use patterns and gray wolf predation risk, we hypothesized that the presence of wolves might mediate patterns of resource overlap between sympatric mule and white-tailed deer populations, with landscape features relating divergently to the probability of escaping wolves for the two prey species being partitioned to the greatest degree. Under this hypothesis, we predicted that increases in partitioning between mule and white-tailed deer in wolf-occupied versus wolf-free areas would be most pronounced along gradients of slope and proximity to roads, with mule deer at risk from wolves shifting away from gentle terrain and roads and the opposite pattern characterizing white-tailed deer.

Materials and Methods

Study Area

This study took place from 2013-2016 in Okanogan and Ferry Counties of eastern Washington and included portions of the Okanogan-Wenatchee and Colville National Forests and the Colville Indian Reservation (See Fig. 1 from Chapter 1). We divided the study area into four sites, two occupied by gray wolf packs and two that had yet to be colonized, as described in Chapters 1 and 2. Patterns of habitat composition, human activity, and plant and wildlife species assemblages within the study area are described in detail in Chapters 1 and 2 and were similar across the four sites.

Data Collection

We monitored gray wolf activity in all four sites within the study area as described in Chapters 1 and 2. Briefly, we regularly surveyed roads and game trails for sign, deployed remote cameras in grid fashion across the landscape (16 cameras per site), and took advantage of positional data from GPS radio-collars deployed within known wolf packs by the Colville Indian Reservation Fish and Wildlife Department. None of these monitoring methods revealed any gray wolf pack activity in either wolf-absent site during the course of the study, though we did detect lone wolves intermittently on our remote game cameras (n = 5 individual detections) that likely represented dispersing individuals.

To determine coarse- and fine-scale resource partitioning between mule and white-tailed deer, we captured individuals using a combination of aerial net gunning and baited clover traps (Haulton et al. 2001) and then outfitted them with GPS radio-collars as described in Chapters 1 and 2. All GPS data were stratified into temporal bins for winter (October-March; i.e., months with snow cover) and summer (April-September) and spatial bins representing areas where wolf packs were present versus absent. All animal captures and collar deployments were conducted under University of Washington Institutional Animal Care and Use Committee (IACUC) protocol number 4226-01 and wildlife collection permits from the Washington Department of Fish and Wildlife and the Colville Tribes Fish and Wildlife Department.

Analyses

We estimated mule deer and white-tailed deer partitioning of a number of covariates serving as potential resources based on previous work (Whittaker and Lindzey 2004; Brunjes et al. 2006) and matching those we used in Chapter 2. These covariates included elevation (measured in meters, m), slope (measured in degrees), aspect, distance to nearest secondary road (m), distance to water (m), and distance to habitat type (m; forest and shrub steppe). Spatial data on the covariates were obtained from pertinent online data warehouses as described in Chapter 2. We originally compiled all resource data at a 30 x 30 m resolution (finest resolution possible in a GIS). We assessed habitat type, secondary roads, and water using a Euclidean Distance Analysis (EDA) framework (Benson 2013). We estimated the straight-line distance from each pixel (at 30 x 30 m resolution) to the nearest secondary road, year-round water source, forest cover, or shrub steppe habitat. We then standardized these EDA distance values, as well as elevation and slope, by subtracting each value by the mean and then dividing by the standard deviation to render coefficient estimates derived from these variables easier to interpret (Benson 2013). We did not standardize aspect because this covariate ranged from 0 to ≤1.

We anticipated that wolves might mediate patterns of resource overlap between the deer species at multiple spatial scales based on the results presented in Chapter 2. Thus, we first examined resource overlap between mule deer and white-tailed deer in wolf and non-wolf areas at a coarse spatial scale (i.e., 1 km^2 cells; the scale of home range establishment; Peters et al. 2013). We examined large-scale overlap as a function of a suite of resource covariates by analyzing mule deer and white-tailed deer GPS locations across the study area using the ordination method of redundancy analysis (RDA; Bowman et al. 2010; Peters et al. 2013). Examination of coarse-scale resource overlap corresponds to measuring inter-specific overlap between habitat use patterns at the second order scale described by Johnson (1980). Given that we subsetted the GPS data according to season (summer/winter) and wolf presence/absence, there were four separate RDA analyses. We classified winter as October-March (i.e., months with snow cover) and summer as April-September. In RDA, the ordination axes for the species matrices are constrained linear combinations of the independent variable matrices that result in the best linear combination of resource covariates that maximize resource partitioning between the species (ter Braak 1995). Thus, in our case RDA revealed where the two deer species occurred along gradients of the resource covariates under investigation and attempted to define a niche space for each within the study area. The RDA analysis resulted in two ordination axes. The first represented resource covariates that explained separation between species whereas the second represented resource covariates that explained association between species (Bowman et al. 2010; Peters et al. 2013). Negative coefficient estimates on either ordination axis for any subset were interpreted such that increasing values of those resource covariates were associated with mule deer. Conversely, positive coefficient estimates on either ordination axis for any subset were interpreted such that increasing values of those resource covariates were associated with white-tailed deer (Peters et al. 2013). Thus, within each treatment subset the deer species with the smallest difference between their own species score and the coefficient estimates for any particular resource covariate (Table 1) primarily utilized that resource compared to the other deer species (Peters et al. 2013). A resource covariate derived using EDA was interpreted such that an increasing value actually meant getting farther from the resource of interest (e.g., higher values for distance to secondary road mean increasing distance to secondary road; Benson 2013). Therefore, the deer species with the largest difference between their own species score and an EDA-derived coefficient estimate for a resource covariate was positioning itself closer to the resource.

We conducted RDA analyses by overlaying a 1 x 1 km sampling grid onto our study region and determining presence and number of GPS locations of each deer species in each grid cell for each season and wolf treatment. We excluded null values resulting from grid cells that did not contain any GPS locations. Because all resource covariates were continuous, we averaged values for each resource variable within each grid cell. We used Monte Carlo permutation tests to assess the significance of each deer species being constrained to a linear combination of the resource covariates (999 permutations, $\alpha = 0.05$; ter Braak 1995). Because RDA species matrices are constrained to be linear combinations of independent variable matrices, we evaluated the degree to which the constrained variance accounted for all the variance between the two deer species and the resource covariates. We report the coefficient estimate of each resource covariate as it relates to each deer species and the scores for each species (Bowman et al. 2010; Peters et al. 2013). Lastly, we calculated the graphical distance between scores for each deer species and coefficient estimates for each resource covariate, respectively. We compared these differences between the two deer species to determine whether they increased or decreased along coarse-scale resource gradients as a function of wolf treatment within each season (Ramette 2007). For example, an increased difference between each species' score and distance to forest cover, respectively, in wolf versus non-wolf areas would indicate increased partitioning of forest cover in the wolf-occupied areas.

We next examined fine-scale resource partitioning between mule deer and white-tailed deer in wolf and non-wolf areas by using logistic regression (Hosmer and Lemeshow 2000) to estimate coefficients for latent selection difference (LSD) functions (Mueller et al. 2004; Latham et al. 2011; Peters et al. 2013). Examination of fine-scale resource partitioning corresponds to exploring differences in resource overlap at the third-order scale (i.e., use of resources within the home range) described by Johnson (1980). For this analysis, we coded mule deer used locations as 1 and white-tailed deer used locations as 0 (Latham et al. 2011) and intersected locations with spatial data at the 30 x 30 m resolution. As with RDA analyses, we subsetted the data according to season (summer/winter) and wolf presence/absence to examine impacts of wolf presence on seasonal resource partitioning. Given that we subsetted the data, there were four separate LSD functions modeled. We estimated degree of resource partitioning using the β coefficients from LSD functions. Negative coefficients indicated greater use by white-tailed deer compared to mule deer and positive coefficients indicated greater resource use by mule deer compared to white-tailed deer (Latham et al. 2011). For example, a positive coefficient estimate for elevation would indicate greater use of higher elevations by mule deer relative to white-tailed deer. However, EDA derived coefficients had to be interpreted differently. Namely, a negative coefficient estimate for distance to secondary road would indicate greater use of areas farther from secondary roads by white-tailed deer relative to mule deer. Once coefficient estimates were derived, the resulting value of e^{β} for each positive coefficient estimate indicated that with every unit increase in the value of or distance to a given resource, the amount of partitioning of that resource between mule deer and white-tailed deer increased or decreased, respectively, by x%. Conversely, negative coefficient estimates were transformed using $-[1-e^{\beta}] \times 100$ and quantified the extent of partitioning of resources between white-tailed deer and mule deer (Czetwertynski 2007). We plotted these χ% relative resource partitioning differences to visually assess seasonal differences in fine-scale resource partitioning between mule deer and white-tailed deer in wolf and non-wolf areas. A potential outcome supporting our main prediction would be an increase in percent resource partitioning of sloped terrain or areas close to roads between mule deer and white-tailed deer in wolf-occupied areas relative to non-wolf areas.

Using 80% of the GPS locations, we built global LSD functions for each of the four data subsets according to season and wolf treatment using all individual resource covariates mentioned above at a 30 x 30m resolution (i.e., the finest resolution possible). We screened all resource covariates for collinearity using the Pearson's correlation coefficient threshold of $r > 0.5$, retaining the collinear variable with the higher log-likelihood and lowest p-value as determined using univariate logistic regression analysis. We then used Akaike's Information Criterion corrected for small sample size (AICc) to determine the most parsimonious LSD models (Anderson and Burnham 2002). Following model building, we used the remaining 20% of the GPS locations to test the predictive capabilities of LSD models for mule deer and white-tailed deer resource overlap (Boyce et al. 2002; Johnson et al. 2006; Benson 2013; Dellinger et al. 2013). To complete this step, we translated coefficient estimates of our most parsimonious LSD models predicting mule deer and white-tailed deer fine-scale resource overlap into spatial predictive maps (Hirzel and Le Lay 2008) using Raster Calculator in ArcMap (ESRI, Redlands, California). We used the raster layers of resource covariates mentioned above to aid in deriving the spatial predictive maps of resource partitioning. The resulting maps contained pixels with values ranging from 0-1, which represented predicted resource partitioning by mule deer or white-tailed deer. In our predictive maps, values closer to 1 indicated increased resource partitioning with mule deer primarily utilizing the resources at the given area and, conversely, values closer to 0 indicated increased resource partitioning with white-tailed deer primarily utilizing the resources at the given area. Thus, extreme values (i.e., near 1 or 0) indicated areas of little resource overlap between the two deer species whereas intermediate values (e.g., 0.3-0.7) indicated areas of increased resource overlap between the two deer species (Peters et al. 2013). We then classified the predicted probabilities of mule and white-tailed deer use across the study area into 10 equal-sized bins (0-0.1, 0.1-0.2, etc.; Boyce et al. 2002), and used the test data to assess Spearman's correlation between expected and observed number of GPS locations of each deer species in each bin (Johnson et al. 2006). Lastly, we counted the frequency of GPS locations by each species in each bin. This served as cross-validation of the most parsimonious LSD models (Peters et al. 2013). Predictive ability of the most parsimonious models should result in: 1) high correlation between expected and observed numbers of GPS locations of each deer species in each bin; 2) a high proportion of mule deer GPS locations in the bins containing higher values (i.e., 0.8-1); and 3) a high proportion of white-tailed deer GPS locations in the bins containing lower values (i.e., 0.1-0.3).

We used Program R version 3.1.2 (R Core Team 2017) for all statistical analyses, and ArcView GIS version 10.2 Geographic Information System (GIS; ESRI, Redlands, California) and Geospatial Modeling Environment version 0.7.4.0 (Beyer 2015) for spatial analyses. In all analyses, we considered $P \leq 0.05$ to be statistically significant.

Results

Over the course of three years, we collared 120 adult deer (n = 61 mule deer, n = 59 white-tailed deer). We collected an average of 700 locations (± 562 sd) per radio-collared individual and monitored individuals for an average of 433 days (± 275 sd).

Using RDA analysis, we found that the suite of resources covariates significantly defined coarse-scale resource overlap between mule deer and white-tailed deer. The relationship between the resource overlap of mule deer and white-tailed deer and the resources covariates was significant for all season by wolf treatment subsets (wolf winter: $F_{8, 1031} = 12.22$, $p < 0.01$; non-wolf winter: $F_{7, 1217} = 7.84$, $p < 0.01$; wolf summer: $F_{8, 1203} = 9.59$, $p < 0.01$; non-wolf summer: $F_{7,1424} = 14.38$, $p < 0.01$). The first RDA ordination axis primarily explained the constrained variance of the linear species-resource covariate relationship for each subset of data (Table 1), whereas the second RDA ordination axis explained relatively little. Thus, the resource covariates we used better explained resource partitioning between the two species rather than their association (Peters et al. 2013).

For each season by wolf treatment subset, RDA analyses revealed coarse-scale resource partitioning between mule deer and white-tailed deer. In each instance, relative species scores for first ordination axes were largely opposite one another, indicating resource partitioning between the two prey species. Coefficient estimates for elevation, slope, proximity to water, and roads were negative for all subsets, meaning mule deer primarily utilized higher elevations, steeper slopes and areas farther away from secondary roads and year-round water sources, respectively, relative to white-tailed deer. Given the smaller difference between the mule deer species score and the coefficient estimate for elevation, relative to the difference between the white-tailed deer species score and elevation, resource partitioning at higher elevations primarily favored mule deer relative to white-tailed deer in all treatment subsets (Table 1, Table 2). Proximity to secondary road, year-round water, forest cover, and shrub steppe habitat had negative coefficient estimates on the first ordination axis, meaning that increasing values of those resource covariates were associated with mule deer, or in other words that mule deer distanced themselves from these resources and vice versa.

Elevation and slope were most closely associated with mule deer in all RDA analyses, whereas proximity to year-round water and secondary roads were most closely associated with white-tailed deer (Tables 2, 3). Differences between mule deer and white-tailed deer species scores, respectively, and coefficient estimates for resource covariates revealed that there was less overall coarse-scale niche overlap between the two species in wolf versus non-wolf areas (Table 3). Partitioning was greatest along a gradient of slope in the wolf areas during both seasons. Increased partitioning of distance to year-round water and secondary roads, respectively, was also marked in wolf relative to non-wolf areas in both seasons. The directions of partitioning for slope and distance to secondary roads in wolf relative to non-wolf areas supported our prediction that reduced overlap would reflect shifts that facilitated escape probability (Table 2). Overall, niche overlap between deer species in wolf and non-wolf areas, respectively, was reduced in winter. However, overlap between deer species was not always lower in wolf areas for a given resource covariate. For example, mule deer and white-tailed deer niches overlapped more with respect to aspect and proximity to shrub steppe in non-wolf versus wolf areas in both seasons (Table 2).

Using LSD analysis, we found that the suite of resource covariates significantly predicted fine-scale resource partitioning between mule deer and white-tailed deer. All resource covariates were included in the most parsimonious models for wolf sites in winter and non-wolf sites in summer (Table 3). Distance to secondary roads was not in the most parsimonious model for non-wolf sites in winter and aspect was not in the most parsimonious model for wolf sites in summer. Resource partitioning of higher elevations, steeper slopes, and areas closer to year-round water and shrub steppe habitat, respectively, favored mule deer relative to white-tailed deer in all subsets. Resource partitioning between the deer species varied with wolf treatment and season. In non-wolf areas, resource partitioning of more exposed aspects (i.e., south-southwest) favored mule deer and partitioning of more sheltered aspects (i.e., north-northeast) favored white-tailed deer, respectively, in both seasons. This relationship was opposite in wolf areas in winter such that resource partitioning of exposed aspects favored white-tailed deer whereas partitioning of sheltered aspects favored mule deer. Furthermore, in non-wolf areas resource partitioning of areas farther from forest cover favored mule deer in both seasons. Again, that relationship was opposite in wolf areas in both seasons, with mule deer selecting for areas close to forest cover relative to white-tailed deer, which shifted into the open. Fine-scale partitioning of slope revealed that mule deer utilized steeper slopes relative to white-tailed deer in all treatments and seasons. However, increased partitioning of slope in wolf relative to non-wolf areas only occurred in summer and the difference in overlap during this season was modest (i.e., it increased from 3.50% to 3.95% as a function of wolf presence; Fig. 1, Table 4). Lastly, fine-scale partitioning of secondary roads revealed that mule deer utilized areas farther from secondary roads relative to white-tailed deer in all treatments and seasons except non-wolf areas in summer. Increased partitioning of secondary roads in wolf relative to non-wolf areas only occurred in winter and the difference in overlap during this season was modest (i.e., it increased from 1.02% to 3.31% as a function of wolf presence; Fig. 1, Table 4). Thus, fine-scale directions and magnitudes of partitioning of slope and distance to secondary roads in wolf relative to non-wolf areas did not support our prediction of escape facilitation (Table 4). In winter, overall fine-scale resource partitioning between mule deer and white-tailed deer was greater in wolf versus non-wolf sites. In summer, overall fine-scale resource portioning between mule deer and white-tailed deer was more similar between wolf treatments but the amount of partitioning of individual resources between the two deer species varied between wolf treatments (Fig. 1, Table 4).

The most-parsimonious LSD models for each data subset had good predictive ability. All of the most-parsimonious LSD models had high Spearman correlation coefficients (wolf winter: average $r_s = 0.97$, $p < 0.01$; non-wolf winter: average $r_s = 0.99$, $p < 0.01$; wolf summer: average $r_s = 0.99$, $p < 0.01$; non-wolf summer: average $r_s = 0.98$, $p < 0.01$). By implication, withheld GPS location data agreed with expected number of GPS locations in each bin derived from the most parsimonious LSD models. Furthermore, high proportions of mule deer and white-tailed deer GPS locations from the test data were contained within the bins containing higher and lower probability of use values, respectively (Fig. 2), demonstrating a high ability to predict resource partitioning between the two deer species in wolf present/absent areas and season.

Discussion

Taking advantage of the return of grey wolves to a multi-prey landscape in the American west, we found support for the hypothesis that wolf predation risk mediates patterns of resource overlap between sympatric ungulate prey. Specifically, during winter, coarse-scale resource partitioning between mule deer and white-tailed deer increased in areas with gray wolves relative to wolf-free sites for all resources except aspect and distance to shrub steppe, and fine-scale resource partitioning increased in the presence of wolves for all resources save slope. Accordingly, our results suggest that gray wolves may structure competitive interactions among prey in large-mammal communities. Moreover, the direction of partitioning of some resources in the wolf-impacted areas, notably slope and roads at the coarse spatial scale of analysis, putatively facilitated the respective escape modes of the two deer species, suggesting that prey escape behavior could play an important role in shaping how predators alter patterns of resource overlap among their prey. Yet, in summer, both coarse- and fine-scale resource partitioning between the prey species did not change markedly in response to wolf presence, and the magnitude and direction of differences in resource partitioning between the wolf-occupied and wolf-free areas varied with spatial scale. Indeed, partitioning of some resources such as shrub-steppe habitat and aspect was unchanged or even decreased in the presence of wolves at the coarse-scale. By implication, the relationship between predation risk and prey resource partitioning is resource-specific and hinges on spatiotemporal context.

A number of studies have demonstrated the ability of bottom-up and abiotic processes like seral stage and fire to mediate resource overlap between ungulates (Brunjes et al. 2006; Sittler et al. 2015). Along with research in the Greater Yellowstone Ecosystem (e.g., Laundre et al. 2001; Creel et al. 2005; Hernandez and Laundre 2005), our findings suggest that top-down processes like predation risk from wolves can also mediate resource overlap between co-occurring ungulate prey. To the extent that patterns of resource overlap reflect competition, then, wolves may help to structure large mammal communities by influencing competition among their ungulate prey species. Notably, the wolves in our study system existed at densities that are comparable to other human-modified ecosystems and lower than those more typical of protected areas (Jimenez and Becker 2016). Nevertheless, we detected an apparent relationship between wolf predation risk and resource overlap between mule and white-tailed deer, hinting at the potential for even stronger wolf impacts on prey competition where their numbers and distribution are not constrained by humans (Kuijper et al. 2015). We acknowledge, however, that our results are correlative, preventing us from controlling for other possible environmental drivers of resource partitioning between the prey species. Accordingly, there remains need for studies capable of simultaneously examining bottom-up and top-down forcing of prey resource partitioning and, by extension, competition.

Previous research in eastern Washington revealed that white-tailed deer exhibit higher survival and population growth rates than sympatric mule deer (Robinson et al. 2002). Moreover, in a case of apparent competition, increasing spatial overlap between mule and white-tailed deer with expansion of the latter species has apparently led to elevated cougar (*Puma concolor*) predation on mule deer (Robinson et al. 2002). Thus, high resource overlap between the two species could negatively affect mule deer populations in Washington. Insofar as wolves drive resource partitioning between mule and white-tailed deer, then, continued expansion of this top predator in Washington could not only alter competition between these two deer species but also reduce cougar predation on mule deer stemming from apparent competition. It is also possible, however, that mule deer shifts away from low-lying areas hunted by wolves could place them at greater risk of predation by cougars, which tend to target prey in areas offering stalking cover and rugged terrain (Atwood et al. 2009). Thus, there is need for studies aimed at discriminating between these two possible scenarios.

We predicted that mule and white-tailed deer at risk from wolves would be especially likely to increase their partitioning of landscape features with divergent effects on their modes of escape. For example, we expected mule and white-tailed deer in the presence of wolves to increase their partitioning of slope because steeper slopes inhibit wolf travel and white-tailed deer sprinting but facilitate mule deer stotting (Lingle 2002; Mech and Peterson 2003; Oakleaf et a. 2006). In support of this expectation, mule deer and white-tailed deer increased their partitioning of slope in wolf versus non-wolf areas except during winter at the fine spatial scale. When faced with wolf predation risk, mule deer utilized steeper slopes and white-tailed deer utilized more gentle terrain (Table 2, Table 4). Similarly, we expected that mule and white-tailed deer at risk from wolves would increase their partitioning of roaded areas because roads tend to be established in gentle, low-lying areas that facilitate sprinting by white-tailed deer but reduce the effectiveness of stotting (Kunkel and Pletscher 2001; Lingle 2002). Again supporting this expectation, mule deer and white-tailed deer increased their partitioning of roaded areas in wolf versus non-wolf areas save during summer at the fine spatial scale. Specifically, mule deer utilized areas farther from roads whereas white-tailed deer utilized areas closer to roads in wolf relative to non-wolf areas (Tables 2, 4). In general, therefore, we suggest that a framework incorporating the relationship between prey escape behavior and landscape features should aid in predicting how patterns of prey resource partitioning are likely to be shaped by spatiotemporal variation in predation risk.

In a previous analysis (Chapter 2), we found that only mule deer altered their use of forest cover when at risk from wolves relative to conspecifics in wolf-free areas. Here, therefore, we did not expect to observe strong changes in partitioning of forest cover between deer species in wolf versus non-wolf areas. Yet, where wolves were present we also observed increased partitioning of distance to forest cover at both scales and in all seasons, with white-tailed deer moving out of cover and mule deer moving into cover (Table 2, Table 4). For ungulates, dense cover can decrease the likelihood of detection by wolves but hinders fleeing (Hernandez and Laundre 2005; Kittle et al. 2008). Thus, this pattern could reflect mule deer seeking forest cover to decrease detection by wolves and avoid having to flee and white-tailed deer seeking areas more removed from forest cover that allow for more rapid movement (Kunkel and Pletscher 2001; Kittle et al. 2008; Kuijper et al. 2015). Across their respective ranges, mule deer are often more associated with open areas than are white-tailed deer (Brunjes 2006). By implication, the presence of wolves may in some cases modify the pattern of forest partitioning that has typically been observed between these two ungulates.

In some cases we found limited and even decreased resource partitioning between the deer species in wolf versus non-wolf areas. For example, the presence of wolves corresponded with decreased partitioning along gradients of shrub steppe habitat at coarse scale in both seasons (Tables 1, 2). The nature of this decrease in partitioning from non-wolf to wolf areas was such that mule deer in wolf areas utilized shrub-steppe more similarly to conspecifics in non-wolf areas compared to white-tailed deer. In other words, mule deer seemed to utilize shrub-steppe similarly across wolf treatments whereas white-tailed deer in wolf areas shifted to utilizing more shrub-steppe habitat relative to conspecifics in non-wolf areas. This coarse-scale pattern could reflect mule deer needing to utilize shrub steppe habitat for foraging and consequently having limited scope for altering their utilization of this resource in response to predation risk (Whittaker and Lindzey 2004) and white-tailed deer increasing their use of this habitat type to aid in early detection of gray wolves in wolf areas (see results from Chapter 2), thereby limiting the potential for increased partitioning of shrub-steppe between deer species in presence of wolves. Similarly, aspect was partitioned more in non-wolf than wolf areas at the coarse spatial scale in both seasons and there was no difference in partitioning between treatments at the fine-scale in summer. As with shrub-steppe habitat, the nature of this decrease in partitioning of aspect from non-wolf to wolf areas was such that mule deer in wolf areas utilized aspects more similarly to conspecifics in non-wolf areas compared to white-tailed deer (Table 1, Table 2). Again, mule deer appeared to utilize aspects similarly across wolf treatments whereas white-tailed deer in the wolf-impacted areas shifted to utilizing more southerly aspects that feature relatively open habitat. This coarse scale pattern could reflect the typical association between mule deer being and open habitats that offer their preferred forage (Brunjes et al. 2006; Whittaker and Lindzey 2004). Furthermore, white-tailed deer may attempt to detect wolves early in an encounter to allow increased time to flee (see results from Chapter 2) and, consequently, use southerly aspects when at risk from wolves. Thus, decreased partitioning of aspect in wolf versus non-wolf areas at the coarse scale likely relates to an increase in overlap in areas characterized by more southerly aspects, where mule deer are normally found, by white-tailed deer. In general, then, the extent to which gray wolves mediate partitioning of any given resource by deer species appears to depend on how the resource in question is used for risk management versus other purposes (Haswell et al. 2017).

Previous studies demonstrate variable resource partitioning between co-occurring ungulates as a function of spatial scale (Whittaker and Lindzey 2004; Peters et al. 2013). For example, caribou (*Rangifer tarandus*) and moose (*Alces alces*) in Alberta, Canada, were shown to have high resource partitioning at the coarser scale but demonstrated substantial resource overlap at the finer scale because of similar utilization of open early seral stage habitat (Peters et al. 2013). We also found that partitioning of particular resources by mule and white-tailed deer in wolf versus non-wolf sites was not consistent across the two scales of analysis. For example, at the coarse-scale, increased resource partitioning between the deer species in the wolf areas occurred along gradients of slope, distance to year-round water, secondary roads, and forest cover in all seasons. However, at the finer scale, increased resource partitioning in wolf versus non-wolf areas only occurred for distance to forest cover in all seasons (Fig. 1, Table 4). This disparity could owe to the different scales at which the two deer species make resource use and anti-predator decisions. Namely, mule deer have been shown to prioritize foraging needs over predation risk (Pierce et al. 2004). Like other ungulates, mule deer feeding decisions are normally made at fine spatial scales because energetic benefit and palatability vary from plant to plant (Whittaker and Lindzey 2004). Furthermore, in our study system, mule deer appear to manage predation risk from wolves at the coarse scale (Chapter 2). Conversely, white-tailed deer are thought to prioritize predation risk over foraging needs (Whittaker and Lindzey 2004) and, in our system, appear to account for predation risk by wolves at the fine scale (Chapter 2). Thus, we might expect wolf-mediated partitioning patterns at the coarse scale to reflect mule deer anti-predator adjustments and overlap patterns at the finer scale to be more a product of the interplay between mule deer feeding choices and white-tailed deer risk management. More broadly, because many sympatric prey species likely prioritize foraging needs differently and respond to predation risk at differing spatial scales, our findings suggest that studies addressing a single spatial scale may miss key predator effects on prey resource partitioning. Accordingly, future research should consider multiple scales simultaneously when investigating impacts of predators on competitive interactions between multiple co-occurring prey species.

Past research has revealed seasonal variability in resource partitioning between mule deer and white-tailed deer. For example, females of both species were shown to decrease partitioning of densely-vegetated areas in summer for fawning purposes while increasing partitioning of this resource in winter (Brunjes et al. 2006). Similarly, we found that the magnitude and direction of resource partitioning between mule deer and white-tailed deer in wolf versus non-wolf areas were season-dependent at both spatial scales. In particular, resource partitioning between the deer species was greatest in wolf areas in winter at both scales. For example, resource partitioning between the deer species was greater in wolf versus non-wolf areas in winter at both spatial scales for elevation, distance to year round water, distance to secondary roads, and distance to forest cover (Table 2, Table 4). By contrast, there was not a consensus difference in magnitude and direction of resource partitioning between deer species in summer in wolf versus non-wolf areas, respectively, at either scale. For example, there was increased partitioning of four out of seven resources in wolf versus non-wolf areas at the coarse scale (Table 2), and of only three out of seven resources at the fine scale (Table 4). Given that wolves are linked to dens and rendezvous sites in summer, their movements and associated predation risk are likely more predictable to prey during this season (Hebblewhite and Merrill 2007). Thus, differences in partitioning as a function of wolf presence might be weaker in summer because of lower perceived (or more manageable) wolf predation risk. By contrast, increased and consistent resource partitioning in winter at multiple scales in our study could owe to a general increase in vulnerability of prey in winter related to snow presence and depth (Latombe et al. 2014). This notion of increased vulnerability of prey to predation in winter is supported by increased partitioning of variables in wolf versus non-wolf areas with demonstrated influence on escape likelihood like slope and distance to road (save for slope at the fine scale). Accordingly, future research should consider seasonality when seeking to understand how predators might mediate interactions between multiple co-occurring prey species.

The natural experimental nature of our investigation and similarity of the four study sites in terms of habitat type and topography support our interpretation that the observed patterns of resource partitioning were at least partly a response to wolf predation risk. Nevertheless, given that our findings are correlative, we acknowledge the possibility of alternative explanations for our results including plant dynamics, weather patterns, and human activity (Brunjes et al. 2006; Peters et al. 2013; Smith et al. 2018). If variation in plant species heterogeneity (i.e., mixing of plant species) and/or phenology coincided with wolf presence at one or both spatial scales, for instance, then the partitioning differences we attributed to wolf predation risk could have instead derived from deer species-specific responses to divergent effects of these bottom-up factors. Similarly, although the four study sites were in same geographic region, it is possible that localized differences in weather features (e.g., snowfall) coinciding spatially with wolf presence could have influenced deer space use and, by extension, contributed to the differences in partitioning between the wolf-occupied and wolf-free sites. Lastly, patterns of human disturbance with the potential to alter deer resource use (e.g., hunting or logging; Kuijper et al. 2015) could have varied across the sites as a function of wolf presence and thereby confounded our ability to examine differences in partitioning in relation to variation in wolf predation risk.

A growing literature has helped refine our understanding of prey responses to predators by highlighting how the context of predator-prey interactions can help predict their outcome (Schmitz 2008; Heithaus et al. 2009; Wirsing et al. 2010). This emerging framework highlights how a single predator species can have differential non-consumptive effects on multiple prey species (Heithaus et al. 2012; Latombe et al. 2014). Our findings suggest that it could be extended beyond bilateral predator-prey relationships to include more complex non-consumptive interactions between prey species responding to a shared predator. For example, resource overlap between two sympatric prey species with a shared predator is likely to depend on similarity in their escape behavior, which dictates how prey will position themselves spatially to reduce predation risk (Laundre et al. 2014). Furthermore, the presence of multiple shared predators with different hunting modes could influence resource partitioning between sympatric prey species to the extent that different landscape features facilitate prey escape/capture and predator success/failure. Accordingly, we encourage further work that explores prey resource partitioning under predation risk while explicitly accounting for drivers of context dependence including how specific resources relate to escape behavior, scale, and temporal heterogeneity.

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Tables

Table 3.1. Summary of redundancy analysis (RDA) for coarse-scale resource overlap between mule deer and white-tailed, 2013-2016, and a suite of resource covariates in northeastern Washington broken down by season (winter: October - March; summer: April - September) and wolf presence/absence. Eigenvalues, percent total variance explained by constrained variance, percent constrained variance explained by ordination axis, species scores, and coefficient estimates of resource covariates are listed.

	Non-wolf Winter		Wolf Winter		Non-wolf Summer		Wolf Summer	
	RDA 1	RDA 2	RDA 1	RDA 2	RDA 1	RDA 2	RDA 1	RDA 2
Eigenvalues	0.235	0.012	0.135	0.052	0.116	0.023	0.110	0.021
% Total variance explained by constrained variance	0.118	0.006	0.068	0.026	0.058	0.011	0.055	0.011
% Constrained variance explained by axis	0.951	0.049	0.722	0.278	0.835	0.165	0.837	0.163
Mule deer scores	-1.789	0.365	-0.481	1.045	-1.261	0.543	-1.013	0.568
White-tailed deer scores	1.613	0.405	1.685	0.298	1.221	0.561	1.288	0.447
Resource covariates	Covariate coefficient estimates							
Elevation (m)	-0.673	0.563	-0.624	-0.098	-0.554	0.416	-0.227	-0.413
Slope (°)	-0.331	0.244	-0.489	0.357	-0.388	-0.279	-0.923	0.112
Aspect (0-1 with 0 being NNE and 1 being SSW)	-0.561	-0.582	0.227	0.181	-0.663	-0.109	0.107	0.512
Distance to year-round water (m)	-0.031	0.035	-0.311	0.448	-0.037	-0.362	-0.215	0.412
Distance to secondary road (m)	-0.229	-0.061	-0.338	0.004	-0.207	-0.339	-0.412	-0.091
Distance to forest cover (m)	-0.112	-0.767	0.514	0.011	-0.093	-0.426	0.021	0.532
Distance to shrub habitat (m)	0.256	0.568	-0.124	-0.661	0.379	0.499	0.074	-0.920

Table 3.2. Graphical distance between species scores for mule deer and white-tailed deer, respectively, and coefficient estimates for each resource covariate. Graphical distances were determined from redundancy analysis (RDA) of mule deer and white-tailed deer presence using GPS locations of each deer species collected from 2013-2016 in northeastern Washington. Data was broken down by season (winter: October - March; summer: April - September) and wolf presence/absence. Bold values indicate greater difference between each deer species score and associated resource covariate relative to the opposite wolf treatment within the same season. For example, there was greater resource partitioning between mule deer and white-tailed in wolf areas in winter with respect to elevation and slope as compared to mule deer and white-tailed deer in non-wolf areas.

Resource Covariates	Non-wolf Winter			Wolf Winter		
	Mule Deer	White-tailed deer	Difference	Mule Deer	White-tailed deer	Difference
Elevation (m)	1.133	2.291	1.158	1.152	2.343	**1.191**
Slope (°)	1.463	1.951	0.488	0.688	2.175	**1.487**
Aspect (0-1 with 0 = NNE and 1 = SSW)	1.551	2.388	**0.837**	1.117	1.463	0.346
Distance to year-round water (m)	1.789	1.685	0.104	0.621	2.002	**1.381**
Distance to secondary road (m)	1.617	1.900	0.283	1.051	2.044	**0.993**
Distance to forest cover (m)	2.023	2.085	0.062	1.435	1.206	**0.229**
Distance to shrub habitat (m)	2.055	1.367	**0.688**	1.743	2.047	0.305
		Total	3.619		Total	**5.627**

Resource Covariates	Non-wolf Summer			Wolf Summer		
	Mule Deer	White-tailed deer	Difference	Mule Deer	White-tailed deer	Difference
Elevation (m)	0.718	1.781	**1.063**	1.257	1.743	0.485
Slope (°)	1.199	1.815	0.616	0.465	2.236	**1.772**
Aspect (0-1 with 0 = NNE and 1 = SSW)	0.885	2.000	**1.115**	1.121	1.183	0.062
Distance to year-round water (m)	1.522	1.560	0.038	0.813	1.503	**0.690**
Distance to secondary road (m)	1.374	1.688	0.314	0.892	1.783	**0.891**
Distance to forest cover (m)	1.518	1.643	0.126	1.035	1.270	**0.235**
Distance to shrub habitat (m)	1.641	0.844	**0.796**	1.843	1.828	0.015
		Total	4.067		Total	**4.150**

Table 3.3. Top two most parsimonious latent selection difference (LSD) models for each season by wolf treatment subset of data according to delta AICc scores ad AICc weights. LSD models were built coding mule deer as 1 and white-tailed as 0 within a binary logistic regression framework wherein deer GPS locations were regressed against resource covariates. LSD models were built for understanding relative differences in fine-scale resource partitioning between the two species. GPS locations of each deer species were collected from 2013-2016 in northeastern Washington wherein data was broken down by season (winter: October - March; summer: April - September) and wolf presence/absence. Resource covariates include: Elevation (Elev), Slope, Aspect, distance to year-round water (D2W), distance to secondary road (D2R), distance to forest cover (D2F), and distance to shrub habitat (D2S).

Most Parsimonious Models by Treatment	ΔAICc	Weights	Parameters
Non-wolf Summer			
Elev + Slope + Aspect + D2W + D2R + D2F + D2S	0.00	0.98	7
Elev + Slope + Aspect + D2W + D2F + D2S	7.95	0.02	6
Wolf Summer			
Elev + Slope + D2W + D2R + D2F + D2S	0.00	0.53	6
Elev + Slope + Aspect + D2W + D2R + D2F + D2S	0.25	0.47	7
Non-wolf Winter			
Elev + Slope + Aspect + D2W + D2F + D2S	0.00	0.41	6
Elev + Slope + Aspect + D2W + D2R + D2F + D2S	0.18	0.37	7
Wolf Winter			
Elev + Slope + Aspect + D2W + D2R + D2F + D2S	0.00	>0.99	7
Elev + Slope + D2W + D2R + D2F + D2S	13.11	<0.01	6

Table 3.4. Coefficient estimates, standard errors, and resource partitioning (RP) difference of the most parsimonious latent selection difference (LSD) models comparing fine-scale resource partitioning between mule deer and white-tailed deer in northeastern Washington, 2013-2016. GPS location data for LSD models was subset by season (winter: October - March; summer: April - September) and wolf presence/absence. Resource covariates include: Elevation (Elev), Slope, Aspect, distance to secondary road (D2R), distance to year-round water (D2W), distance to forest cover (D2F), and distance to shrub habitat (D2S). For coefficient estiamtes > 0, RP should be interpreted as: with every unit increase in the resource or for every unit increase in distance to the resource, the RP of such a resource by mule deer compared with white-tailed deer is increased by x%. For coefficient estimates < 0, RP should be interpreted as: with every unit increase in the resource or for every unit increase in distance to the resource, the RP of such a resource by mule deer compared with white-tailed deer is decreased by x%. Bold values indicate increased resource partitioning between the two deer species for the associated resource covariate relative to the opposite wolf treatment within the same season. For example, there was greater resource partitioning between mule and white-tailed deer in wolf areas in relation to distance to forest relative to deer in non-wolf areas for both seasons.

Covariates	Treatment											
	Non-wolf Summer			Wolf Summer			Non-wolf Winter			Wolf Winter		
	Coef. Est.	SE	RP %[a]	Coef. Est.	SE	RP %	Coef. Est.	SE	RP %	Coef. Est.	SE	RP %
Elev	2.148	0.040	**8.57**	1.015	0.036	2.76	2.634	0.043	13.92	3.074	0.061	**21.63**
Slope	1.253	0.032	3.50	1.373	0.028	**3.95**	0.946	0.032	**2.58**	0.832	0.028	2.30
Aspect	1.363	0.064	3.91	-0.040[b]	0.061	3.92	0.716	0.080	2.05	-0.589	0.082	**44.51**
D2W	-0.635	0.022	**46.98**	-0.176	0.024	16.14	-0.042	0.032	4.11	-0.481	0.034	**38.16**
D2R	-0.082	0.029	**7.91**	0.914	0.027	2.49	0.017[b]	0.027	1.02	1.196	0.038	**3.31**
D2F	1.596	0.056	4.93	-0.367	0.094	**30.72**	2.609	0.085	13.58	-3.682	0.238	**97.48**
D2S	-0.684	0.038	49.56	-0.779	0.041	**54.13**	-0.713	0.038	50.96	-0.728	0.065	**51.70**

[a] Resource partitioning was calculated using coefficient estiamtes (b) such that relative selection = exp(b) when $b > 0$ and [1 – exp (b)] × 100 when $b < 0$.

[b] Non-significant

Figures

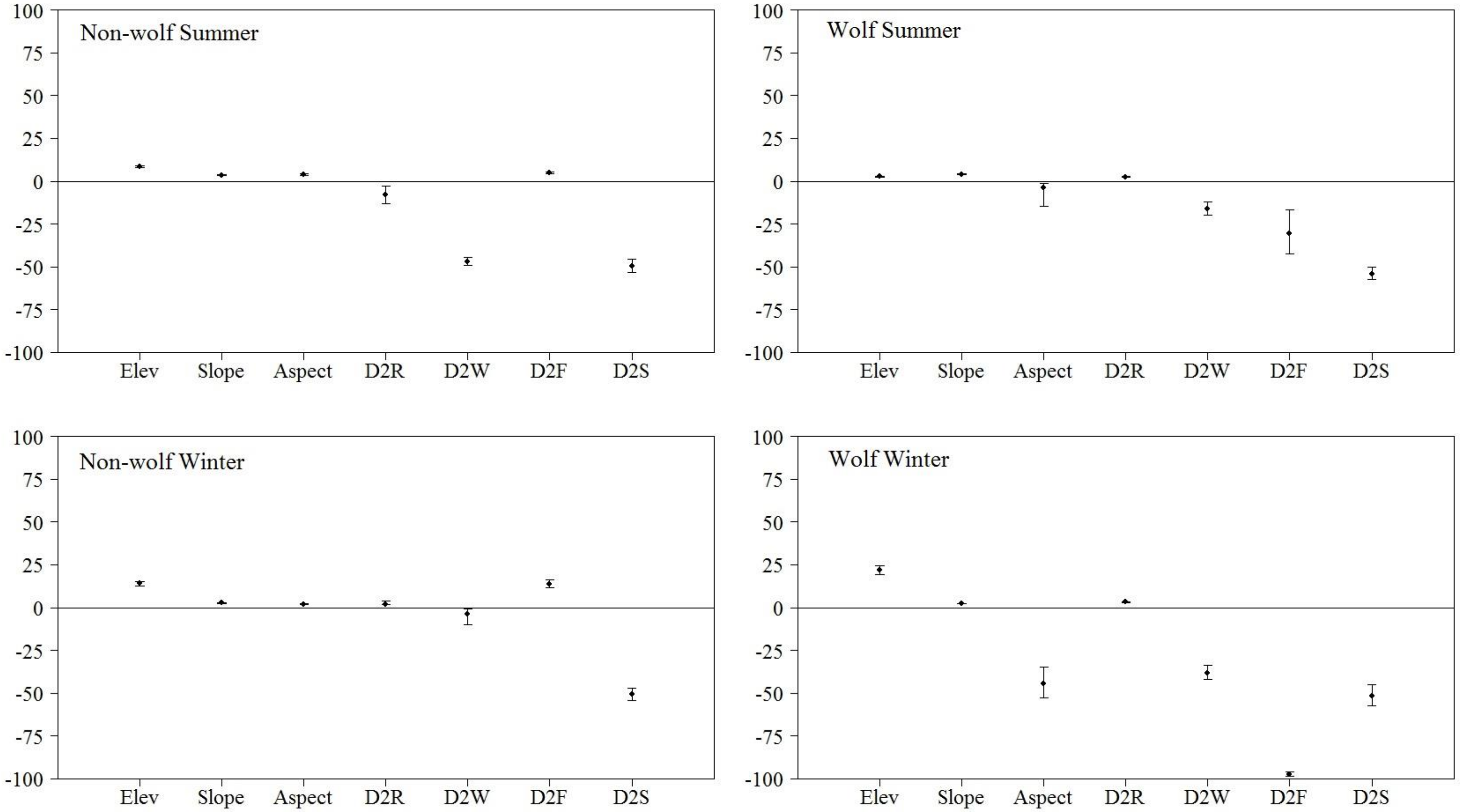

Figure 3.1. Resource separation plots resulting from Latent Selection Difference (LSD) models for understanding relative differences in resource use between mule deer and white-tailed deer at a fine spatial scale (30 x 30 m). Resource separation plots correspond to data being subsetted by season (winter: October – March; summer: April – September) and gray wolf presence/absence. Resources include: elevation (m; elev.); Slope (°); Aspect (0-1 with 0 being NNE and 1 being SSW); distance to secondary road (D2R); distance to year-round water (D2W); distance to forest cover (D2F); and distance to shrub steppe habitat (D2S). Values < 0 indicate white-tailed deer primarily utilized the resource while values > 0 indicate mule deer primarily utilized the resource.

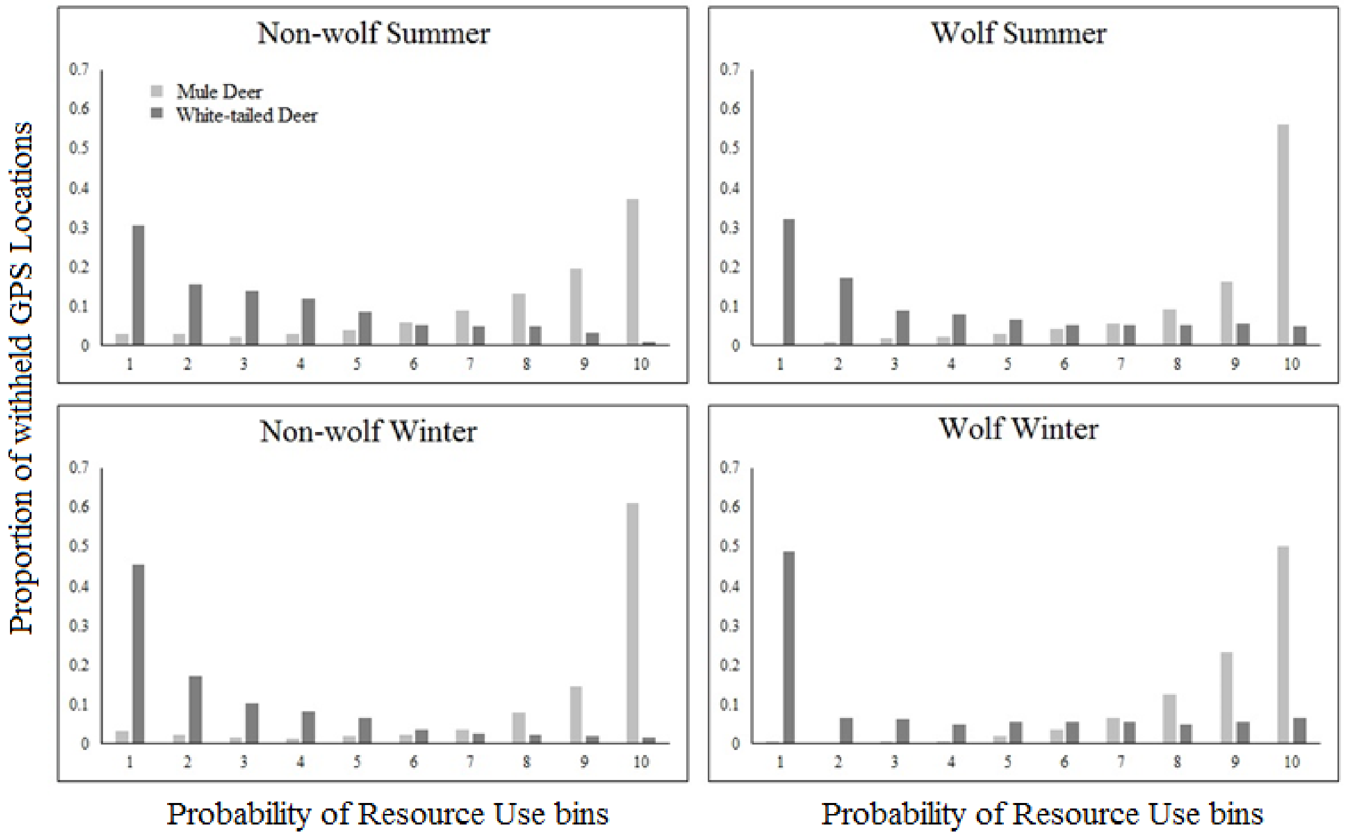

Figure 3.2. Cross-validation of the most parsimonious Latent Selection Difference (LSD) models of mule deer and white-tailed deer fine-scale resource overlap derived from deer GPS location data from northeastern Washington from 2013-2016. The most parsimonious LSD models were projected in ArcMap using raster calculator to create predictive spatial maps ranging from 0-1 in value. Values closer to 0 indicate increased probability of use by white-tailed deer relative to mule deer while values closer to 1 indicate increased probability of use by mule deer relative to white-tailed deer. Intermediate values (e.g., 0.3-0.7) indicate overlap in resource use by the two deer species. Spatial maps were broken up into 10 equal sized bins based on value (e.g., bin 1 = 0-0.1; bin 2 = 0.1-0.2, etc.). The GPS location data withheld in the LSD model building process were intersected with the spatial maps above and binned accordingly. Models with good predictive ability should have a high proportion of withheld mule deer GPS locations in the bins containing higher values (i.e., 0.8-1) and a high proportion of withheld white-tailed deer GPS locations in the bins containing lower values (i.e., 0.1-0.3).