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Carnivore Competition: Spatial and Dietary Implications of Gray Wolf Recolonization for Cougars in Northeast Oregon

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Elizabeth K. Orning for the degree of Doctor of Philosophy in Wildlife Science
presented on June 6, 2019.

Title: Carnivore Competition: Spatial and Dietary Implications of Gray Wolf Recolonization for Cougars in Northeast Oregon

Abstract approved:

Katie M. Dugger

After a 40-year absence from Oregon's landscape, expanding gray wolf (*Canis lupus*) populations are reestablishing elements of interspecific competition with sympatric large carnivores, like cougars (*Puma concolor*). This presents new challenges for management of large carnivores and their ungulate prey populations (e.g., elk, *Cervus canadensis nelsoni*; mule deer, *Odocoileus hemionus*) in these re-established multi-carnivore systems. Wolf range expansion and interactions with populations of sympatric cougars could alter predation on deer and elk populations in the Pacific Northwest. Competition could also affect the spatial distribution, demography, and population dynamics of cougars, the assumed subordinate predator in wolf-cougar interactions. However, the strength of competitive interactions dictate the trajectory of top-down effects and can be system specific. Coupled with a paucity of empirical data on cougar diets and space use across landscapes with and without wolves, prediction of subsequent effects to prey populations is challenging. Furthermore, the common assumption of additive predation effects when a missing predator is added back to an ecosystem may not be well-founded because elk populations have increased in some parts of the Pacific Northwest. My primary research objectives were to 1) estimate diet composition and kill rates for wolves in northeast Oregon, 2) estimate diet composition and kill rates for cougars and evaluate changes in cougar predation patterns across time periods with and without wolves, 3)

evaluate cougar home range and kill site distribution for changes relative to pre-wolf patterns, and 4) investigate the influence of wolf presence on cougar movement patterns and habitat use in northeast Oregon. In addition to addressing key ecological questions about carnivore interactions, results from my research provide information on implications of expanded predator systems for elk and mule deer populations, and will be useful to other states and Canadian provinces in western North America facing similar changes in predator guild composition and community dynamics as wolves continue to expand their range.

I implemented a 3-year study in northeast Oregon to investigate diet, kill rates, and space use of wolves and cougars in a recently re-established multi-predator, multi-prey system to better understand wolf-cougar interactions and the mechanisms by which competition may influence cougar populations. A study of cougar populations in northeast Oregon prior to wolf recolonization provided 3 years of pre-wolf cougar information (2009-2012) for comparison with similar information on cougars after wolf recolonization (2014-2016). During my research, 34 wolves and 15 adult cougars were captured and fit with Global Positioning System (GPS) collars to compare predation and space use patterns with 25 GPS-collared cougars prior to wolf recolonization. I documented predation patterns (diet composition, kill rate) for 11 wolves sympatric to GPS-collared cougars in northeast Oregon. I identified 159 predation events over winter (44 wolf-weeks) and summer (8 wolf-weeks) periods for wolves. Annually, wolf packs killed an average of 2.23 ungulates/wk (90% CI = 1.62 – 2.85). There was no evidence kill rates varied by pack ($P = 0.92$), but rates did vary by season ($P = 0.005$), with summer kill rates ($\bar{x} = 3.46$ ungulates/wk, SE = 0.52) 2.26 times higher than winter kill rates ($\bar{x} = 1.53$ ungulates/wk, SE = 0.26), consistent with increased availability of smaller neonate prey on the landscape and summer diets primarily consisting of elk calves. Biomass intake rates did not vary by pack ($P = 0.80$) or season (summer = 243 kg/wk, SE = 56; winter = 182 kg/wk, $P = 0.24$). My results quantified kill rates for wolves in northeast Oregon, and I documented that wolf predation patterns were consistent with other elk dominant systems in North America.

I compared cougar predation patterns (diet composition, kill rate, search and handling time) across periods before (2009-2012) and after (2014-2016) wolf recolonization in northeast Oregon and identified 542 predation events for cougars in the post-wolf period to compare with 1,213 cougar predation events documented before wolf recolonization. Cougar predation was different between study periods, with changes most evident in predation patterns of female cougars. Female cougars had lower proportions of mule deer in their summer diets (12%), lower summer kill rates (17% – 50%), lower biomass intake rates (14% – 61%), and longer search times (30% – 138%) than respective female cougar reproductive groups in the previous cougar study. My results quantified the dietary costs of interspecific competition for cougars in northeast Oregon.

I used locations for wolves and cougars from GPS collar data to evaluate spatial overlap and shifts in home range (HR) and kill site distribution based on kernel density estimates (KDE) generated for 1,213 cougar predation sites before (2009-2012) and 481 sites after (2014-2016) wolves recolonized northeast Oregon. I compared seasonal post-wolf cougar 50% and 95% predation ranges for overlap with density estimates from 107 wolf predation sites (2014 – 2015). I found that the distribution of cougar predation sites differed between time periods with and without wolves and relative to areas wolves frequently made kills. Based on total predation site distributions, 19% of core summer range where cougars made kills overlapped core wolf prey use areas. Over annual periods, the amount of overlap between post-wolf cougars and wolves decreased 9% at the 50% predation range scale and increased 6% at the 95% predation range scale. Cougars were responding to the presence of wolves and our results suggest the spatial scale of that response occurs within a cougars' home range. Relative to pre-wolf cougar predation sites, post-wolf cougar predation sites were higher in elevation and closer to water. Coupled with little change in cougar diet composition, distributional shifts in areas cougars frequently kill prey could signal relatively unchanged effects to prey populations in this multi-predator system. My results quantified spatial costs of interspecific competition (with wolves) for cougar populations in northeast Oregon.

I evaluated activity patterns (distance traveled, rates of travel, time of day) for cougars before (2009-2012) and for wolves and cougars after (2014-2018) wolves recolonized northeastern Oregon. I compared movement rates (km/hr) based on 42,892 and 48,723 GPS relocations of cougars from pre- and post-wolf periods, respectively. I also compared diel patterns of cougars with patterns generated from 79,437 GPS relocations of northeast Oregon wolves. Cougar movement and diel activity differed between time periods. Cougars moved shorter distances per 3-hr time step with wolves on the landscape ($\bar{x}_{\text{pre}} = 0.60$ km, 90%CI 0.49 – 0.70; $\bar{x}_{\text{post}} = 0.43$ km 90%CI 0.38 – 0.47, %P = 0.34). I observed a change in the pattern of cougar activity over the diel cycle from peak movement rates in the evening followed by night > day > morning, peak rates of activity in the evening > morning > night > day. I used step-selection functions (SSFs) and a two-stage approach to incorporate movement and evaluate individual and population level selection for three variables associated with spatial risk of wolf interaction (openness, wolf kill density, wolf intensity of use). I found that female cougars were selecting for less open habitats in winter after wolf recolonization (%P = 0). By examining individual selection I was able to demonstrate different competition mitigation strategies between male and female cougars. My results demonstrated cougars changed aspects of their activity and exemplify an optimal foraging strategy to balance fitness costs of competition.

Wolf recolonization simultaneously introduces elements of interspecific competition between wolves and other predators, including cougars. My results demonstrated the capacity for interspecific interactions to counter-intuitively alter top-down effects by reducing ungulate kill rates, and alter movement rates, daily activity patterns, and habitat selection of cougars. Overlooking interspecific competition between predators could result in underestimating costs to subordinate competitor species and overestimating effects of multiple predators on prey populations.

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Carnivore Competition: Spatial and Dietary Implications of Gray Wolf
Recolonization for Cougars in Northeast Oregon

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Elizabeth K. Orning

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Elizabeth K. Orning, Author

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CHAPTER 1 – GENERAL INTRODUCTION

Elizabeth K. Orning

Predator-prey interactions and the top-down effects of carnivores are among the most fundamental of ecological relationships and have been the focus of widespread scientific study since the inception of ecology (e.g., Murdoch 1966, 1994, Slobodkin et al. 1967, Skogland 1991, Messier 1994, Mech and Peterson 2003). A synthesis of simultaneously occurring bottom-up and top-down forces acting in concert with biotic and abiotic factors are inarguably affecting biological systems (Hunter and Price 1992, Garrot et al. 2009, Griffin et al. 2011, Johnson et al. 2013, Laundré et al. 2014). However, tests of theoretical predator-prey dynamics have yielded numerous studies focused on top-down influences of terrestrial carnivores based on single predator, single prey species relationships (Dale et al. 1994, Eberhardt 1997, Hayes et al. 2000, Laundré 2010), or single predator, multiple prey species relationships (Hebblewhite et al. 2003, Hebblewhite et al. 2005, Atwood et al. 2009, Knopff et al. 2010). Communities often have multiple predators and the effects of interspecific interactions between carnivores can alter competing predator densities or predation patterns in unexpected ways (Sih et al. 1998, Casula et al. 2006), and understanding these dynamics is critical to conservation and management of carnivores and their prey (Griffin et al. 2011, Eacker et al. 2016). In order to disentangle complexities and evaluate the mechanisms involved in multiple predator-multiple prey systems, an understanding of baseline information on predator types and interactions, predation risk, and criteria for defining effects are necessary (Sih et al. 1998).

Groups of species that use common resources in a similar way are commonly referred to as an ecological guild (Root 1967). Accordingly, wolves (*Canis lupus*) and cougars (*Puma concolor*) are predominant members of a carnivore guild in northeast Oregon that also includes black bears (*Ursus americana*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), foxes (*Vulpes vulpes*), badgers (*Taxidea taxus*), skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and several Mustelid species (weasel family). The most ubiquitous interaction among guild members is probably competition, commonly typified by two basic types of interspecific interactions: exploitative and interference competition (Ballard et al. 2003). Exploitative competition has been hard to demonstrate as the indirect effects produced are based on differential efficiency in accessing and utilizing shared resources. For example, competition for food is one form of exploitative competition in which outcomes are often expressed slowly (differential survival and reproduction), but may ultimately lead to evolutionary divergence or extinction (Krebs 1994). Interference competition has direct effects which are often asymmetrical (one species benefits)

and typically expressed through aggressive behavior (i.e. threat of injury or killing) that causes the immediate exclusion of a competing individual or population from a resource (Krebs 1994, Ballard et al. 2003). The principle of competitive exclusion holds that if two sympatric species have adequate niche differentiation they may coexist in a stable environment (Krebs 1994). Hence, competitive exclusion depends on the degree of dietary niche overlap, the degree of spatial overlap, and the availability of limited food and space resources (Ballard et al. 2003).

While it is well-established competition among carnivores can affect the spatial distribution, demography, and population dynamics of the weaker predator (Lawton and Hassell 1981, Tilman 1986), demonstrating competition affects through quantified measures or experiments has remained difficult (Creel et al. 2001, but see Phillips and Smith 1996, and Bartnick et al. 2013). In addition, interspecific interactions where sympatric predators compete for prey and one competitor also preys upon the other can have strong effects on the dynamics of the subordinate competitor (Connor and Bowers 1987, Holt and Polis 1997, Creel et al. 2001). This form of interference competition, known as intraguild predation (IGP), has important implications for direct and indirect effects of predator-predator interactions and any subsequent top-down effects (Holt and Polis 1997, Sih et al. 1998, Creel et al. 2001). IGP models suggest predator coexistence is more likely at low or intermediate prey densities (Holt and Polis 1997), a non-intuitive prediction important for carnivore conservation and management (Creel et al. 2001). This prediction is based on assumptions that the subordinate predator is more efficient at exploiting shared basal prey species and that competition is asymmetric (Creel et al. 2001), meaning impacts are not equal between each competing predator.

Affects to subordinate competitors from asymmetric competition can be characterized in three ways. First, the subordinate competitor may be killed outright by the dominant competitor (i.e. direct killing). Second, food acquired by the subordinate predator may be stolen by the dominant competitor (kleptoparasitism). Third, the subordinate predator might actively avoid the dominant predator to reduce the risks of food loss or direct mortality (Mills and Gorman 1997, Creel et al. 2001). Mortality and kleptoparasitism have obvious direct fitness costs, but if the dominant competitor in a system monopolizes areas of high prey density, spatial avoidance might reduce prey availability for a subordinate competitor, increase the energetic costs of hunting (Gorman et al. 1998), and reduce subordinate competitor population density via limited access to prey (Creel et al. 2001). A subordinate carnivore might also change their hunting

behavior (e.g. total amount or time of day foraging, or areas traveled to encounter prey) such that time between predation events are longer due to efforts to actively avoid encounters or direct interactions with their dominant competitor (i.e. an indirect effect from interference competition). This is typically referred to as active avoidance, and could produce measurable changes to predation patterns.

In North America, expanding large carnivore populations may be resurrecting interspecific competition and IGP effects across portions of their historical range, potentially changing the structural dynamics of entire communities. Sympatric wolves and cougars share habitat, home ranges, and prey resources (Kunkel et al. 1999, Husseman et al. 2003, Ruth 2004). Direct interactions between large carnivores have been challenging to document (cryptic behavior, occur at low densities) and most observations are anecdotal (Ballard et al. 2003). Wolf pack structure may provide wolves the advantage in wolf-cougar interactions (i.e. cougars are outnumbered), such that the likelihood that wolves can kill cougars is greater than for cougars to kill wolves (Murphy et al. 1999). Wolves can usurp cougar kills (Ruth and Hornocker 1996, Kunkel et al. 1999, Ruth et al. 2011) and occasionally kill adult cougars (Schmidt and Gunson 1985, Boyd and Neal 1992, Jimenez, unpublished data) and cougar kittens (White and Boyd 1989, Jimenez et al. 2006, M. Elbroch, pers. comm.), suggestive of asymmetric agonistic interactions in favor of wolves and cougars as the subordinate competitor in wolf-cougar systems. A recent meta-analysis of cougar dominance relative to other guild members reported that, broadly, cougars were subordinate in their interactions with at least one other apex predator in 47.5% of their North and South American range (Elbroch and Kusler 2018). However, there are cases of cougars killing wolves (Jimenez et al. 2008), and the effects of competitive interactions with wolves may be limited if cougars exploit alternate prey resources or habitats unoccupied by wolves, or if agonistic interactions are rare (Kortello et al. 2007, Atwood et al. 2009).

Predation effects on prey populations are tied to the complexities of intraguild dynamics, as the predation risk for shared prey can vary relative to the nature of predator-predator interactions as well as based on the behavioral responses of prey to predators (Atwood et al. 2009). For example, anti-predator shifts by prey to avoid habitats preferred by a primary predator may inadvertently expose prey to direct predation by a second predator (Fraser et al. 2004, Atwood et al. 2009). Predator facilitation such as this primarily occurs when a phenotypic

response is induced by a predator that increases the prey's overall vulnerability to direct predation by another species (Soluk and Collins 1988, Burkholder et al. 2013). However, the introduction of a second predator and cumulative direct predation by multiple predators can have a variety of effects on prey beyond customary compensatory or additive models (Sih et al. 1993, Casula et al. 2006). Thus, while it is important to understand predation patterns or patterns in prey use, simple predator-prey models rely on the behavioral independence of predators from their prey, and do not capture the effects of phenotypic niche shifts, interference competition, IGP or synergistic predation (Casula et al. 2006).

Gray wolf population distribution expanded following reintroductions in central Idaho and Yellowstone National Park in 1995-1996 (US Fish and Wildlife Service), with consistent wolf sign observed in the Wallowa and Blue Mountains of northeast Oregon since 2006, and the first breeding pair documented in the state in 2009 (Oregon Department of Fish and Wildlife [ODFW] 2010). Since near extirpation in the 1960's, Oregon cougar populations have recovered to stable population levels widely dispersed throughout the state. As of 2018, eighteen to twenty wolf packs have been documented in northeast Oregon (ODFW 2018 Annual Wolf Report). The presence of two sympatric apex predators, coupled with cougar research prior to wolf recolonization (Clark 2014, Clark et al. 2014*b, a*, 2016, Davidson et al. 2014), made northeast Oregon ideally suited to examine the dynamics of intraguild competition and potential multi-predator effects to ungulate prey populations, as a second predator (wolves) recolonized an area occupied solely by cougars for the past 60 years.

The aim of my research was to provide information on wolf-cougar interactions and to investigate the competition dynamics of both carnivores in northeast Oregon. First, I wanted to provide system-specific information on wolf predation and spatial ecology. Second, and central to my research, I wanted to examine and quantify changes in cougar predation and spatial dynamics in response to expanding wolf populations. The objectives of my research were to 1) estimate diet composition and kill rates for wolves in a multi-predator-multi-prey system (Chapter 2), 2) estimate diet composition and kill rates for cougars after wolf recolonization and compare to pre-wolf cougar predation patterns (Chapter 3), estimate and compare cougar home range and kill site distributions across time periods with and without wolves (Chapter 4), estimate and compare movement patterns for wolves and cougars (Chapter 5), and finally, to identify any differences in cougar habitat selection relative to predation site characteristics or

risk of wolf interaction between time periods with and without wolves (Chapters 4 & 5). In addition to addressing key ecological questions regarding predator-predator interactions now that wolves are returning to ecosystems from which they had been extirpated, my research provides information on the affects expanding wolf populations have on cougar populations, and implications of this expanded predator system for elk and mule deer populations. Results from my research will be useful to other states and Canadian provinces in western North America facing similar changes in predator guild composition and community dynamics as wolves continue to expand their range.

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CHAPTER 2 – WOLF PREDATION PATTERNS IN NORTHEAST OREGON

Elizabeth K. Orning, Katie M. Dugger, and Darren A. Clark

ABSTRACT

Expanding gray wolf (*Canis lupus*) populations present new challenges for management of carnivore and ungulate populations (e.g., elk, *Cervus canadensis*; mule deer, *Odocoileus hemionus*) in multi-carnivore systems. We documented predation patterns (diet composition, kill rate) of wolves after wolf recolonization of the Mt. Emily Wildlife Management Unit in northeast Oregon (2014-2016). We identified 159 predation events over winter (44 wolf-weeks) and summer (8 wolf-weeks) for wolves. Annually, wolf packs killed an average of 2.23 ungulates/wk (90% CI = 1.62 – 2.85). There was no evidence kill rates varied by pack ($P = 0.92$), but rates did vary by season ($P = 0.005$), with summer kill rates ($\bar{x} = 3.46$ ungulates/wk, SE = 0.52) 2.26 times higher than winter kill rates ($\bar{x} = 1.53$ ungulates/wk, SE = 0.26), consistent with increased availability of smaller neonate prey on the landscape and summer diets primarily consisting of elk calves. Biomass intake rates did not vary by pack ($P = 0.80$) or season (summer = 243 kg/wk, SE = 56; winter = 182 kg/wk, $P = 0.24$). Our study quantified predation patterns for a re-emerging wolf population in northeast Oregon, and the predation patterns we documented were similar to other elk dominant systems in North America.

INTRODUCTION

Gray wolves (*Canis lupus*) have diverse predation patterns in North America (Dale et al. 1994, Messier 1994, Eberhardt 1997, Kunkel et al. 1999, Mech et al. 2001, Vucetich et al. 2011, Metz et al. 2012, Klaczek et al. 2016). As a result, the effects of wolves on prey populations in some systems is still intensely debated (Dale et al. 1994, Mech and Peterson 2003, Wittmer et al. 2005, Brown et al. 2007). Determining the mechanisms that link predator and prey population dynamics is fundamental to understanding the diversity of observed wolf predation patterns. Empirical studies of wolf-ungulate systems have found that while predation is affected by prey density, other factors including the type of prey species, predator-prey ratios (Vucetich et al. 2002), wolf group size (Schmidt and Mech 1997, MacNulty et al. 2011), prey vulnerability (Peterson and Allen 1974), alternative prey availability (Dale et al. 1994), snow cover (Jedzrejewski et al. 2002), and habitat heterogeneity (Kunkel and Pletscher 2000) are also important. This is by no means an exhaustive list and much of the variation in wolf predation remains unexplained (Messier 1994, Dale et al. 1995, Vucetich et al. 2002).

The characteristics and class of prey in a predator's diet composition is a key element to predicting effects on prey populations. The effects of age-specific vital rates on population growth of prey species is variable, and the vulnerability of prey to predator is also variable among age classes. If the age class preyed upon most frequently by wolves contributes little to prey population growth (Wisdom et al. 2000, Caswell 2001), the effects of wolf prey use of specific age classes may or may not be detrimental to prey populations. The type of prey killed by wolves can also be influenced by a multitude of factors (see Mech and Peterson 2003), but several overarching trends in selection patterns are recognized. Wolves are opportunistic and flexible hunters, and selection of prey is primarily based on prey size, abundance, and vulnerability (Peterson and Ciucci 2003). Fundamentally, selection patterns involve a combination of capture efficiency and profitability (biomass acquired) relative to the risk of wolves being injured/killed, both elements encompassed in the concept of prey vulnerability (Mech and Peterson 2003). There is considerable evidence (see summary by Mech 1970, Mech et al. 1998, and table 5.4 in Mech and Peterson 2003) that wolves tend to prey on less fit individuals, including a variety of more vulnerable prey classes (old, newborn, weak, diseased, injured or debilitated and juveniles lacking strength/experience; Mech and Peterson 2003).

The functional response (i.e. number of prey killed per predator per unit time), more commonly referred to as kill rate, is one of the basic elements that structure the population biology of predation (Holling 1959, Taylor 1984). Kill rates are documented for wolves in several systems (Vucetich et al. 2002, Hebblewhite et al. 2003, Sand et al. 2005, 2008, Metz et al. 2012), but contradictory results regarding the factors most strongly influencing wolf kill rates are well-documented (Therberge 1990, Dale et al. 1994, Vucetich et al. 2002, 2005, 2011, Peterson et al. 2003, Vucetich and Peterson 2004, Jost et al. 2005, Zimmermann et al. 2015), and could reflect variability in methodology or among systems, and thus, the need for continued study. Global positioning system (GPS) advancements have aided efforts, providing a new platform to evaluate predation patterns and we are beginning to gain insight into the causes of observed effects and consequences of wolf population expansion (Sand et al. 2008, Metz et al. 2011, 2012, Tallian et al. 2017). For management strategies of both wolves and their prey to be effective, reliable estimates of system-specific kill rates and information on diet composition are necessary to predict community-level effects.

As part of a larger research effort to investigate apex carnivore competition associated with wolf recolonization in Oregon, we documented kill rates and prey use for a sample of wolves over 3 years (2014-2016). Our primary objective for this study was to examine generalized wolf predation patterns as established in other multi-predator multi-prey systems (DeCesare 2012a, Metz et al. 2012), and for comparison with predation patterns of other competing carnivores. We characterize the system in northeast Oregon by estimating: 1) the number and frequency with which wolves kill ungulates, and 2) the proportion of specific sex and age classes of prey in wolf diets. We also evaluated whether 3) wolf kill rates varied by season, and 4) whether predation patterns were consistent among wolf packs. We predicted that wolf prey use would correspond to variability in seasonal availability of vulnerable prey classes, and that those patterns would be consistent across packs. We expected wolves to use the most vulnerable prey classes available (reproductive vulnerability; Lima and Dill 1990), which would manifest as different proportions of various age classes and sexes of ungulates in wolf diet composition over different seasons, as found in other wolf-ungulate systems (Kunkel et al. 1999, Kunkel and Pletscher 2000, Smith et al. 2004, Metz et al. 2012). Generally, the basic pattern of ungulate vulnerability follows that newborns are most vulnerable during their first weeks of life and continue to be more vulnerable than adults during their first months of life as juveniles, adult males are vulnerable before, during and after the rut, and adult females are most vulnerable in late spring prior to parturition. Given that individual vulnerability to predation can also vary relative to individual fitness (i.e. nutritional condition, injury, age), we expected higher proportions of inexperienced (juvenile) and less fit (poor body condition) individuals would comprise the overall diet of wolves regardless of season (Mech and Peterson 2003).

METHODS

Study Area

The study area was located in the Blue Mountain Range of northeast Oregon (Fig. 1), and contained a mixture of private, public, and tribal lands (Confederated Tribes of the Umatilla Indian Reservation; CTUIR) covering 1,992 km². The U.S. Forest Service (USFS; Wallowa Whitman and Umatilla National Forests) and the State of Oregon manage public lands within the

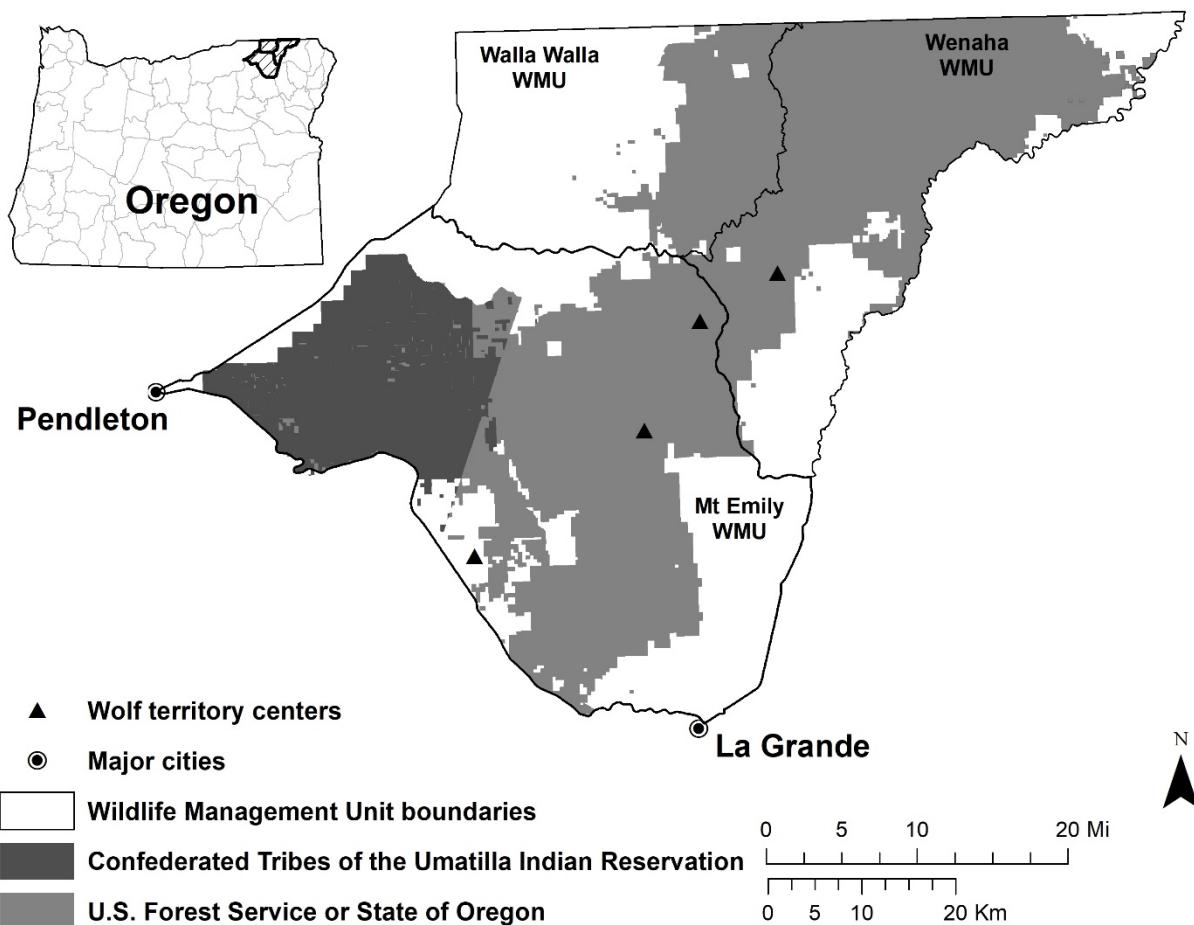


Figure 2.1. Location of Wildlife Management Units (Mt. Emily, Wenaha, Walla Walla) in northeast Oregon, USA, and approximate territory center points of wolf packs monitored with global positioning system (GPS) collars to determine prey use and kill rates (2014 – 2016).

study area, and private land management was dominated by commercial agriculture and forest habitat, managed either as industrial forests or grazed rangelands. Elevation ranged from 360 – 1,850 m, with vegetation strongly influenced by topography, aspect, and elevation. On the west side of the study area low elevation sites were dominated by exposed upland slopes and riparian areas comprised of hawthorn (*Crataegus columbiana*), willow (*Salix* spp.), and blackberry (*Rubus armeniacus*) with scattered ponderosa pine (*Pinus ponderosa*), and black cottonwood (*Populus trichocarpa*). Mixed-conifer stands with exposed southern aspects characterized high elevation sites in the central and eastern part of the study area with common species including ponderosa pine, douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), and lodgepole pine (*P. contorta*).

Oregon Department of Fish and Wildlife (ODFW) manage wildlife populations using discretely bounded areas known as Wildlife Management Units (WMUs). We focused our study of wolf predation on the Mt. Emily WMU because this unit had cougar (*Puma concolor*) predation patterns characterized for the area prior to wolf recolonization and allowed for comparison of predation patterns over periods before and after 3 packs were documented in the WMU (2014-2016; see Chapter 3). Wolf predation was monitored for two packs that primarily used the Mt. Emily WMU and two packs that used portions of Mt. Emily and adjacent WMUs (Wenaha, Walla Walla).

A number of potential large prey species inhabit the Blue Mountains, with the most abundant ungulates being elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Moose, (*Alces alces*), bighorn sheep (*Ovis canadensis*), and occasionally, mountain goat (*Oreamnos americanus*) were present in small, localized populations. Feral horse (*Equus ferus caballus*) were present on CTUIR lands and potentially available as prey to wolves (C. Scheeler, CTUIR, pers. comm.). Additionally, livestock (e.g. cattle and sheep) were present throughout the year on private property and seasonally available on USFS and CTUIR managed grazing allotments or other privately owned lands. Many types of smaller prey were also available in the study area (e.g. ground squirrel (*Spermophilus* spp.), snowshoe hare (*Lepus americanus*), badger (*Taxidea taxus*), beaver (*Castor canadensis*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*), but we focused on large ungulates in our system as they were most likely to be accurately represented in diets of wolves (Sand et al. 2005). In addition to wolves, cougar, black bear (*Ursus americanus*), coyote (*Canis latrans*),

bobcat (*Lynx rufus*), and fox (*Vulpes vulpes*) were other predators that commonly occurred in the study area and may also be preyed on by wolves.

Wolf Capture and Monitoring

Wolves were captured and radio collared by ODFW as part of their annual wolf population monitoring program and followed procedures approved by USDA Forest Service – Starkey Experimental Forest and Range Institutional Animal Care and Use Committee (IACUC No. 92-F-0004). In the spring and fall, wolves were captured using rubber-jawed foot-hold traps (McBride EZ grip # 7 traps [Livestock Protection Company, LPC, Alpine, TX]) and a helicopter was used to aid capture of wolves in winter. Captured wolves were immobilized with Telazol (100 mg/mL; Fort Dodge Animal Health, Fort Dodge, IA) delivered to large muscle masses (i.e. rear hind quarter or shoulder) by jab stick or dart injection (R. Morgan, ODFW, pers. comm.). ODFW biologists recorded the weight and sex of each wolf, and obtained estimates of age from tooth eruption, replacement, and wear (Van Ballenberghe et al. 1975, Fuller and Keith 1980, Fritts and Mech 1981). Wolves were classified as breeding or non-breeding and by age class as yearlings (12-24 months old) or adults (> 24 months; Haight et al. 2002). Yearling and adult wolves > 40 lbs were fitted with GPS collars (GPS PLUS II or Vertex Survey [Vectronic Aerospace GmbH, Berlin, Germany]). Collars were scheduled to collect 8 locations per day (0300, 0600, 0900, 1200, 1500, 1800, 2100, 2400 hours) annually. Fix schedules were increased to collect locations every 30 minutes (48 locations/day) during summer predation study periods. GPS collars used an Iridium platform which allowed location data to be retrieved after a pre-set number of acquired locations via Iridium satellite link communication.

Kill Site and Prey Remain Identification

We processed locations from GPS collars every 7-12 days and identified potential kill sites for wolves using the PYTHON (Python Software Foundation, Hampton, NH) rule-based algorithm developed by Knopff et al. (2009) to generate clusters of GPS locations based on carnivore-specific criteria (Anderson and Lindzey 2003, Sand et al. 2008, DeCesare 2012a). This algorithm was designed to identify predation sites for prey > 8 kg in size for cougar (Knopff et al. 2009), but has been successfully used to identify sites with prey remains for wolves (DeCesare 2012a). Applying cluster methodology to wolves required the assumption they spend

≥ 1 hour in proximity to a carcass (Sand et al. 2008, Metz et al. 2011). We implemented increased fix schedules over summer monitoring periods for wolves to overcome decreased search and handling time, and variation in wolf presence at predation sites that require increased fix rates (Zimmermann et al. 2007, Webb et al. 2008, Metz et al. 2011, DeCesare 2012b). Each potential wolf predation site cluster was defined as sets of ≥ 2 locations within 300 m and 4 days of each other.

We investigated potential kill sites over two seasons: 1) summer (14 days each in Jun, Jul, and Aug) and 2) winter (1 Jan – 31 Mar). In summer, wolf activity often centers on den or rendezvous sites, where pups are confined until they are mobile enough to travel with the pack, distinguishable in GPS collar data by repeated travel movements to these sites from non-consecutive locations and clusters. We used ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA, USA) to map the algorithm-generated location clusters to identify rendezvous sites. We did not search potential predation sites when they were within 1 km of den or rendezvous sites, or when collared wolves were within 1 km of the area to be searched to minimize disturbance to wolf behavior. We navigated to the geometric cluster centers using handheld GPS units and systematically searched for prey remains following methods described in Clark et al. (2014a). Searches were conducted by walking a grid-like pattern of transect lines spaced 5-10 m apart (i.e. dependent on variability in terrain visibility) from the generated cluster center to the radius extent. Even after an initial carcass was detected we continued to search grids to the radius extent to identify multiple carcasses.

Once remains of prey were located, we used characteristics described by Ruth and Buotte (2007) to evaluate evidence at the site including signs of a struggle, drag marks, tufts of fur, broken branches, predator tracks or scat, cached or covered carcass remains, and chase trails to verify which carnivore likely made the kill or whether prey were scavenged. Scavenging behavior was determined using carcass characteristics (discarded harvest gut piles, remains with clear knife cut marks, severe trauma and proximity to roads or highways, age relative to cluster start dates), site evidence, and timing of other predators at the site. We determined prey species using skeletal, anatomical, and pelage characteristics (Moore et al. 1974, Verts and Carroway 1998, Jacobson 2003), and age of prey using body size, tooth eruption and wear patterns (Robinnette et al. 1957, Schroeder and Robb 2005), or skull size. When present, we also collected an incisor from ungulate individuals > 2.5 years old for aging prey via analysis of

cementum annuli (Low and Cowan 1963; Matson's Laboratory, Milltown, MT). We used the presence of antler pedicels or pelvic characteristics (Edwards et al. 1982) to determine sex of non-juvenile deer and elk. Prey were classified into three age classes: juvenile (< 1 year), yearling (1 year), and adult (≥ 2 years). We examined prey remains for physical abnormalities and collected femur and/or mandible marrow, when present, for marrow fat analysis. Marrow fat can be used as an index of prey condition at time of death by providing a measure of pre-starvation absolute physical condition (Mech and Delgiudice 1985, Atwood and Gese 2007). Because marrow fat is a 1-way indicator of nutritional condition (i.e. can infer poor condition from low fat values, but high fat values do not necessarily equate to good condition), no minimum value can be set as a reliable cutoff for declaring poor vs. fit prey classifications. On a relative scale, any fat loss in marrow suggests poorer condition (see Mech and Delgiudice 1985), so we used a marrow fat content of $\leq 50\%$ as a conservative threshold to define the poorest condition ungulates preyed upon in our study. We removed and weighed a 5 – 7 cm marrow sample from the central portion of a bone (femur, humerus, or mandible if long bones were unavailable) from ungulate prey > 6 months of age. Samples were oven-dried at 60° C for 48 hours and reweighed to calculate the dry-to-wet mass of the fat (Neiland 1970, Atwood and Gese 2007). We adjusted mandible fat values to femur fat equivalents for elk (following Husseman et al. 2003) when only mandibles were available to sample.

Marrow fat of prey were not normally distributed, therefore we used Mann-Whitney U-tests to compare relative condition of wolf-killed prey across summer and winter seasons. We estimated carcass biomass for deer and elk as described by Clark et al. (2014a; see appendix 1 for list of age/weights) based on capture data from northeast Oregon (B. Johnson, ODFW, unpublished data).

Wolf Probability of Attendance

Individual members of a wolf pack do not forage cohesively at all times, especially in the summer when many of the prey taken are smaller (e.g. ungulate neonates). Subsequently, because GPS collared members of a pack may not be present at all predation events associated with the total number of ungulates preyed on over a given time period, the ability to detect and reliably estimate the number of carcasses depends on wolf probability of attendance (PA; Metz et al. 2011). Our ability to detect whether a wolf had attended a carcass was comparable to

probability of detection and we used the double-count methodology first described by Metz et al. (2011) to quantify wolf PA at any given predation event. Using Eq. 1, with the number of carcasses detected by observer A (N_A), the number detected by observer B (N_B), and the number detected by both A and B (N_{AB}), the total number of carcasses for packs that included a pair of GPS collared wolves was estimated over winter and summer periods,

$$N_{total} = ((N_A + 1)(N_B + 1) / (N_{AB} + 1)) - 1, \quad (1)$$

and the probability of detection (PD) for observer A and B as follows,

$$PD_A = N_{AB} / N_B \quad (2a)$$

$$PD_B = N_{AB} / N_A \quad (2b)$$

Under this premise, each collared wolf was treated as observers A and B, and a carcass was considered detected if that wolf's GPS locations met the spatial and temporal constraints of carcass detection (i.e. cluster generation criteria described above). We used estimates of PD (Eq. 2) to calculate the number of carcasses for packs with only a single GPS collared wolf. In this case, the total number was calculated as,

$$N_{total} = N_{detected} / E[PD], \quad (3)$$

where $N_{detected}$ was the number of carcasses detected and $E[PD]$ was the probability of detection expected for a single GPS collared wolf using the mean PD acquired from multiple collared wolf packs.

Prey Composition

We calculated species and age composition of prey as the frequency of predation events where these prey characteristics were known for all individual collared wolves and wolf packs, and 2) a proportion of predation events for collective packs. We used ANOVA and Tukey's honest significance difference adjustment for multiple comparisons (Day and Quinn 1989)

between groups known or suspected to influence wolf predation patterns to account for differences based on 1) pack, and 2) season. For our assessment of seasonal differences we defined predation events that occurred from Jun – Aug as summer kills, and events from Jan – Mar as winter kills. We considered $P \leq 0.10$ as evidence of effect. All statistical analyses were carried out in R (R Core Team 2017).

Kill Rates and Inter-Kill Intervals

We estimated kill rates (KR) for wolves as both the number and live weight biomass of ungulate prey killed per wolf and pack, per unit time (week). We estimated both frequency and biomass metrics to quantify ungulate kill and biomass intake rates using a ratio estimator with the total monitoring time as the denominator and both the number and kilograms of prey as numerators (no./wk or kg/wk). While ratio estimators require longer monitoring intervals to obtain reasonably precise estimates for cougar (Knopff et al. 2009, 2010), little differences have been observed in short monitoring periods (down to 11 days) for wolves using ratio estimators (Metz et al. 2012), and they are less biased and more conservative than other methods (Hebblewhite et al. 2003). We assigned predation events to the first collared wolf in attendance of a carcass (when multiple wolves were collared), pooled data for individual wolves in the same pack (when collared wolves of the same pack attended separate carcasses), and calculated kill rates for wolf packs continuously monitored for ≥ 14 days in a given season. We used the number of wolves reported in annual pack counts (2014 – 2017 Annual Wolf Reports, ODFW) to obtain per wolf biomass intake (kg/wk/w) as a function of overall pack ungulate predation and pack size (kg/wk/p). The number of wolves in a pack was not monitored daily, and pups counts occurred at the end of each year, therefore we did not include pups in our estimates of per wolf summer rates and may have biased estimates of per wolf biomass intake high over short time periods.

We also calculated intervals between first location fixes of consecutive ungulate predation events (intervals were assigned to the month in which they ended) for each wolf pack to quantify inter-kill intervals (IKI) and the frequency of ungulate predation events. We used IKI to avoid problems estimating rates over very short monitoring periods (e.g. a few days), and because variation in interval length was of primary interest. It also allowed us to include a larger sub-sample of predation events from wolves with truncated monitoring periods due to capture or

collar performance issues (e.g. missed transmissions, failures). For our assessment of intervals, we used each predation event as the unit of analysis and tested for differences in average IKI. We also controlled for season, as described above, to isolate variation from other factors and determine if these factors varied between packs.

RESULTS

ODFW's wolf monitoring program captured and fit 11 wolves with GPS collars from 4 packs from June 10, 2012 to February 20, 2015. We monitored predation for 6 wolves (adult = 3, subadult = 2, yearling = 1) from 3 packs and one newly formed pair over 489 winter wolf-days and for 4 wolves from 2 packs over 64 summer wolf-days ($n = 553$ total wolf-days) from July 10, 2014 to Jan 8, 2016. Average fix success was 92.4% (range 77.8 – 97.2%) for collared wolves monitored. Each wolf pack was monitored for a mean of 70 days (range 8 – 97 days) and 16 days (range 14 – 17 days) in winter and summer, respectively. We investigated 656 GPS location clusters and identified the remains of 159 potential prey at 152 clusters. Median number of days between cluster generation and field investigation for sites with prey remains was 6 days ($\bar{x} = 6$ days, SD = 3) in summer and 70 days ($\bar{x} = 92$ days, SD = 66) in winter.

We monitored predation for two packs with multiple GPS collared wolves (2 and 3 GPS collars, respectively) and one pack with a single GPS collared wolf that dispersed from her natal pack and formed a new pair during monitoring. Mean PA for wolves was 86% in winter (PA = 0.86 ± 0.03 SE) and 70% in summer (PA = 0.70 ± 0.04 SE).

Diet Composition, Prey Use, and Scavenging

Wolf Diet Composition. – Of the 134 wolf-killed prey, 94.7% were native ungulates and the remaining 5.3% were other small mammals (ground squirrel, flying squirrel (*Glaucomys sabrinus*), snowshoe hare, and feral horse; see Table B1 and Appendix B for detailed diet description). Elk were the primary ungulate prey we identified at wolf predation sites in both winter and summer monitoring periods (60.6% and 74.2%, respectively). Wolves tended to prey on younger individuals, with elk calves being the most prevalent age class of known age ungulate prey in both seasons (36.1% and 63.3% for winter and summer, respectively), however, adult elk (30.6%) were observed nearly as often as elk calves in winter wolf diets. Females made up the majority of winter (73.9%) and summer (100%) wolf predation of adult elk where we

determined sex ($n = 23$ and $n = 3$, respectively). The age of ungulate prey varied by season ($F_{1,99} = 3.96, P = 0.05$), but not between packs (Table B2, Appendix B; $F_{3,97} = 1.04, P = 0.38$), but median prey ages were < 1 year in both seasons (summer = 0.05 years, winter = 0.83 years). The age of adult prey at wolf predation sites did not vary by pack ($F_{3,31} = 0.39, P = 0.76$) or season ($F_{1,33} = 0, P = 0.99$), and the median age was 8 years. There were no seasonal differences in the marrow condition of wolf-killed ungulates between winter ($\bar{x} = 78.1\%, 90\% \text{ CI} = 72.2 - 84.0$) and summer ($\bar{x} = 72.7\%, 90\% \text{ CI} = 58.3 - 87.1$; $W = 149, P = 0.46$), but marrow fat content of winter wolf-killed prey was 1.24 times higher than the marrow condition of a road-killed sample of ungulates collected over similar winter conditions ($n = 11, \bar{x} = 62.7\%, 90\% \text{ CI} = 48.5 - 77.0$; $W = 349, P = 0.04$). Of the wolf-killed ungulates for which we determined marrow condition to be $\leq 50\%$ ($n = 7$), the majority were from the calf ($n = 4; 66.7\%$) age class.

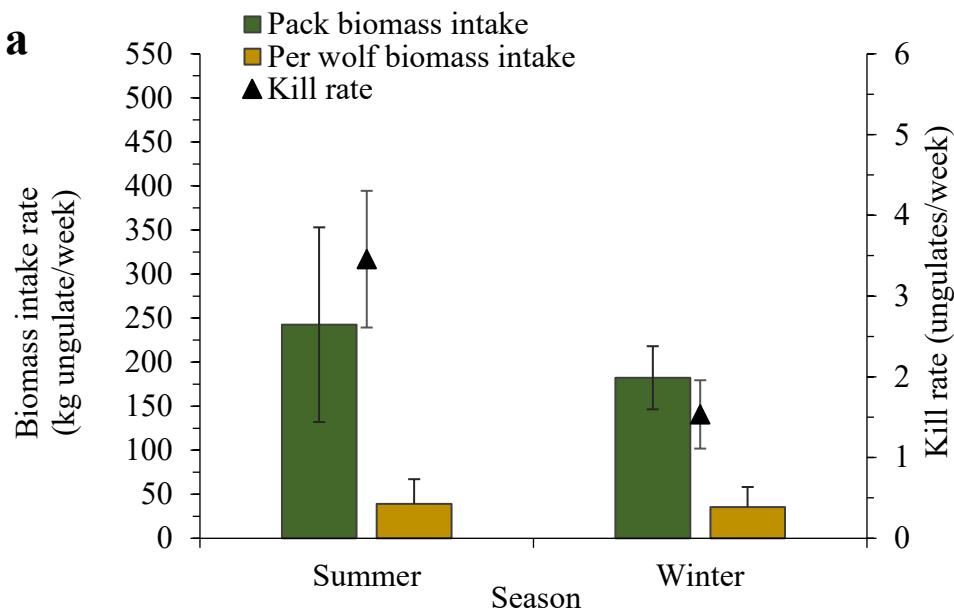
Wolf Scavenging. – We documented 18 cases of collared wolves scavenging, which represented 11.3% of all prey remains. All collared wolves engaged in at least one scavenging event and 77.8% of scavenged remains were of native ungulates (14 of 18). Non-ungulate prey items included domestic sheep ($n = 3$) and feral horse ($n = 1$). We identified scavenging events during both winter ($n = 10$) and summer ($n = 8$). Our short summer monitoring periods did not allow for direct seasonal comparison of scavenging, but suggest increased scavenging in summer (8 cases over 8 wolf-weeks in summer, 10 cases over 44 wolf-weeks in winter). We identified 3 cases in which wolves usurped prey remains from cougars still actively feeding (kleptoparasitism events), 7 cases in which wolves scavenged kills made by other predators (cougar = 6, bear = 1), and 4 cases in which wolves visited a cougar cache sites but scavenging could not be determined.

Wolf Kill Rates and Intervals

We used the 134 ungulate predation events, representing 11 pack and season-specific monitoring intervals ≥ 14 days (summer $\bar{x} = 16$ days; winter $\bar{x} = 54$ days) to calculate wolf kill rates. Annually, wolf packs killed a mean of 2.23 ungulates/week (90% CI = 1.62 – 2.85) and mean per wolf KR was 0.37 ungulates/wk/w (90% CI = 0.24 – 0.530). There was no evidence that kill rates varied by pack (Table B2, Appendix B; $F_{3,7} = 0.17, P = 0.92$), but they did vary by season ($F_{1,9} = 14.13, P = 0.005$), with kill rates 2.26 times higher in summer than winter (Fig. 2a). Total biomass intake rates did not vary by pack (Fig. 2b; $F_{3,7} = 0.34, P = 0.80$) or season ($F_{1,9} = 1.60, P = 0.24$). There was no evidence that per wolf biomass intake rates varied

seasonally ($F_{1,9} = 0.04, P = 0.86$), however, per wolf rates varied by pack (Fig. 2b; $F_{3,7} = 7.08, P = 0.02$). These differences were explained by a pair (smallest group of wolves monitored), where individual biomass intake rates for these wolves were 4 and 6 times higher than individuals of Mt. Emily (7-8 wolves) and Wenaha (11-12 wolves) packs, respectively (Table B2 and Fig. B3, Appendix B; $P = 0.02$).

Generally, the wolf packs we monitored killed at least once per week ($\bar{x} = 3.2$ days, SE = 0.28), but the longest interval we documented between ungulate predation events was 16 days. Seasonal ($F_{1,122} = 9.87, P = 0.002$) and monthly (Fig. 2c, $F_{6,117} = 2.17, P = 0.05$) differences in ungulate IKI were evident, where mean IKI of wolves was 3.7 (SE = 0.33) and 1.6 (SE = 0.34) days in winter and summer, respectively. There was no evidence IKI varied by pack (Table B2, Appendix B; $F_{3,120} = 0.71, P = 0.55$).



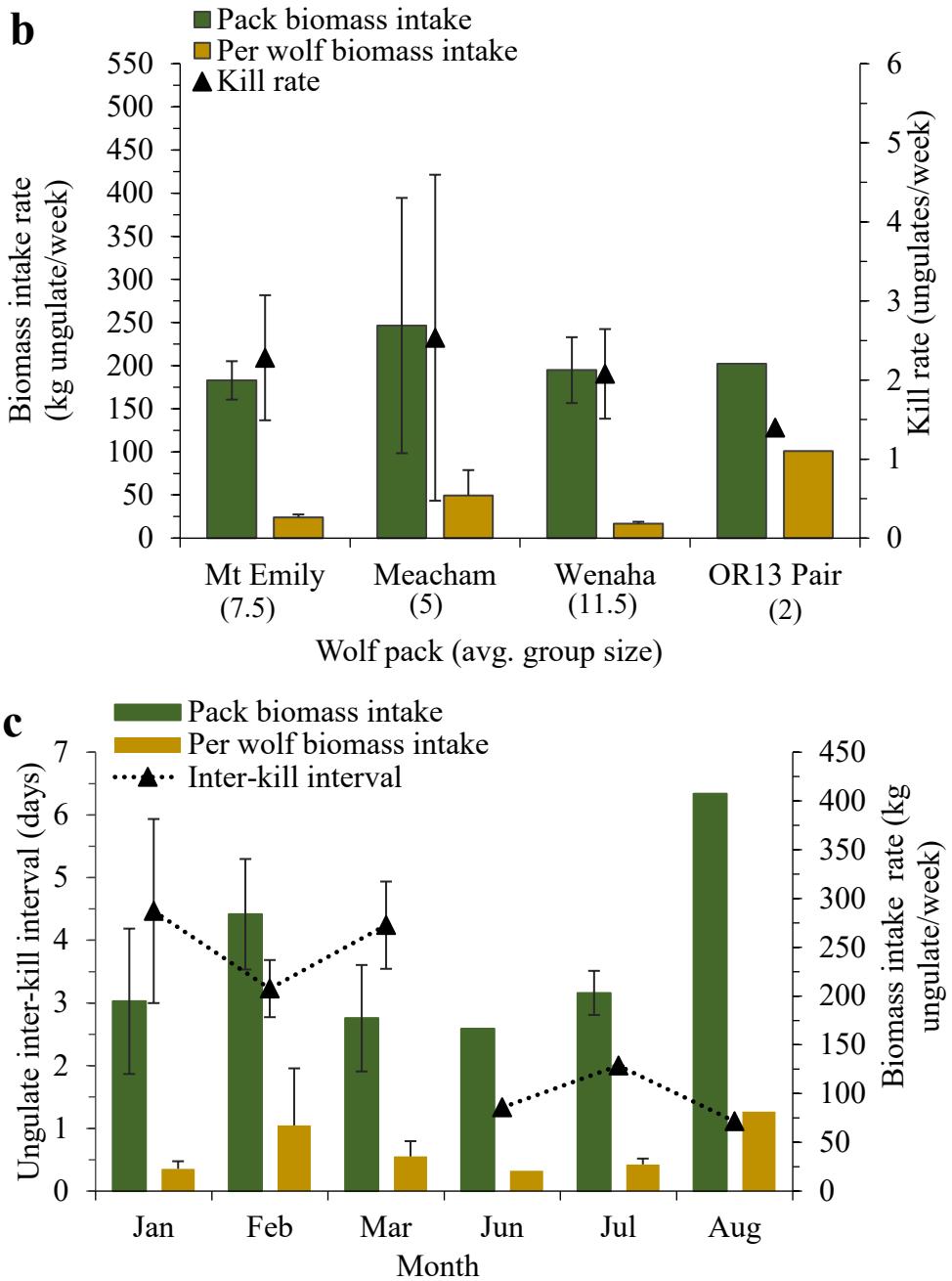


Figure 2.2. Estimates of mean wolf kill rate (ungulates/week/pack) and ungulate inter-kill interval (days), pack biomass intake (kg ungulate/week/pack), per wolf biomass intake (kg ungulate/week/wolf), and associated 90% confidence intervals by season (a), pack (b), and month (c). We estimated intervals and derived mean biomass intake rates for wolf packs from estimated weights of prey at 134 consecutive wolf predation events in northeast Oregon, USA from 2014 – 2016. Per wolf biomass intake rates were derived by dividing mean pack biomass

intake by each packs' average group size. We estimated kill rates using data from 6 wolves with ≥ 14 day monitoring intervals over winter (Jan – Mar) and summer (Jun – Aug) seasons.

DISCUSSION

Wolves in northeast Oregon preyed primarily on elk, and secondarily on deer, similar to other elk dominant systems with multiple ungulate species available to wolves as potential prey (Husseman et al. 2003, Smith et al. 2004, Atwood et al. 2007, Kortello et al. Metz et al. 2012). Our results are also consistent with other studies of wolf predation, in that wolves tended to prey on seasonally available classes of vulnerable prey (Husseman et al. 2003, Smith et al. 2004, Atwood et al. 2007, Kortello et al. Metz et al. 2012). We expected juvenile ungulates to make up the majority of wolf summer diets due to the influx of inexperienced neonates available on the landscape associated with ungulate birth pulse. Deer fawns are likely underrepresented in our wolf diet results and other studies using GPS location cluster methods to identify wolf predation sites. Increased fix rates (e.g. 5 - 10 minute fix intervals) might be able to detect very short handling times associated with prey as small as 4 kg (average deer fawn size). However, field effort required to search the increased number of generated clusters coupled with low site evidence left by wolves that can quickly subdue, consume and/or transport prey as small as neonate deer fawns, currently limits accurate documentation of small prey during summer.

Winter kill rates for wolf packs documented in our study (1.29 – 2.08 ungulates/week) were on the low end of ratio estimates reported in similar wolf-elk systems (Banff NP: 1.47 – 2.38 kills/week, Hebblewhite et al. 2003; 2.03 - 3.57 elk/week, Kortello et al. 2007). Differences in winter rates between studies could relate to ecosystem variation in prey density or distribution, wolf population or pack dynamics (e.g. density, pack size, probability of attendance, time since recolonization start), environmental attributes that influence prey vulnerability to predation (e.g. severe winter, snow depth), or a combination of these factors. Elk density was higher, wolf density was lower, and snow depth was lower ($27.4 \pm 6.4\text{cm}$ vs. 50cm; Kortello et al. 2007) in this study (Fig. B5 & B6, Appendix B), and may account for any observed differences between our results and those reported for wolves in Banff NP.

To our knowledge, Metz et al. (2011, 2012) is the only other North American study to date to report estimates of summer wolf kill rates in elk dominated systems (but see Sand et al. 2008 for wolf-moose predation in Sweden). Adjusting for reporting differences, our estimates of

mean summer biomass intake (7.5 kg/wolf/day) were within the range reported for wolves in Yellowstone NP in the summer (4.1 - 9.5 kg/wolf/day), but winter biomass intake rates in our study were lower (6.2 kg/wolf/day) than reported elsewhere (6.7 - 8.5 kg/wolf/day; Metz et al. 2012). Variation in wolf probability of attendance (PA) at predation events can affect the accuracy of kill rate estimates (e.g. individual age or pack status, and season; Metz et al. 2011). Because only one GPS collared wolf in a pack with multiple collars was programmed for increased fix schedules in summer (30min intervals vs. 3hr intervals), our ability to detect and assign a second collared pack member to predation events was seasonally limited, and our summer PA results may underestimate attendance at carcasses. Additionally, our summer estimates come from a single pack that had multiple collars (3 GPS collared wolves) during summer monitoring. Therefore, our estimates of summer PA may also not be representative of all wolf packs in northeast Oregon. Probability of attendance for wolves in this study were higher than PA reported in YNP in summer ($PA_{YNP} = 0.59 \pm 0.04$ SE) and lower in winter ($PA_{YNP} = 0.95 \pm 0.01$ SE, Metz et al. 2011). Lower winter PA in our study may be due to both the number of yearling wolves in our sample of monitored individuals and our small sample size (i.e. yearling wolves have the lowest PA, see Metz et al. 2011). Our sample of packs with multiple collared individuals to estimate both summer and winter PAs was limited. Corrections fell within the confidence limits of our summer estimates ($KR_{corrected} = 4.36$ ungulates/wk; uncorrected 90%CI = 2.61, 4.30), but exceeded our winter confidence limit upper bound by 15% ($KR_{corrected} = 2.26$ ungulates/wk; uncorrected 90%CI = 1.11, 1.96). This could mean there is a PA threshold below which confidence in estimate accuracy becomes meaningful to inference, and emphasizes the importance of designing wolf predation studies that allow PA to be quantified, as variation across study systems should be expected. Our results add to those of Metz et al. (2011), recognizing the importance of accounting for dynamic aspects of group cohesiveness in the estimation of predation metrics for a social carnivore like the wolf.

We also observed that the higher summer wolf pack kill rates associated with shorter kill intervals coincided with the ungulate birth pulse and increased presence of ungulate neonates on the landscape (Jun – Aug). However, we found that seasonal differences in kill rates did not translate to seasonal differences in mean pack or per wolf biomass intake rates (kg ungulate/wk/w). Neither the per week number nor biomass of ungulates in our study varied across packs, but accounting for mean pack size revealed per wolf biomass intake rates differed

by pack. While it was unsurprising that the new pair we monitored had the highest per wolf biomass intake (fewer wolves sharing food), it was noteworthy that the collared wolf which formed this new pair split from the Wenaha pack, which had the highest pack size (of wolves monitored; 12 at the time of dispersal) and subsequent lowest per wolf biomass intake rate. Along with biological or density-dependent cues that can influence dispersal in wolves (age, survival rates, pack size, wolf and prey population densities, etc. Fuller et al. 2003), this could reflect a threshold in this system for individual vs. group fitness choices based on the tradeoffs an individual make between biomass intake versus the sociality of pack dynamics (probability of attendance, hunt effectiveness, breeding opportunities, intra-pack aggression; see Metz et al. 2011). The Oregon wolf population was expanding at the time of our study with highly variable pack sizes (range 2 – 15 wolves; ODFW Annual Wolf Reports), and mean pack sizes in our study area during predation monitoring were substantially lower than pack sizes reported in YNP (see Supporting Information available online). More work is likely needed to tease apart the strength of influence and role biological and behavioral mechanisms play in wolf dispersal.

Although our study provided a small sample size (3 packs with data for 4 reproductive pairs over 2 winters and 2 summers), we studied >20% of the annual number of wolf packs and pairs recorded in Oregon's population (ODFW Annual Wolf Reports 2014 - 2015). The wolf predation patterns we documented were similar to other elk dominant systems in North America. Therefore, in general, we believe our results are representative of the general patterns of predation occurring in northeastern Oregon for wolves feeding primarily on elk in areas where elk to deer (mule deer and white-tailed deer) ratios are relatively high and pack sizes are small to medium, as in this study.

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CHAPTER 3 – RESURRECTED COMPETITION? A COMPARISON OF
COUGAR PREDATION PATTERNS BEFORE AND AFTER
WOLF RECOLONIZATION IN NORTHEAST OREGON

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ABSTRACT

Expanding gray wolf (*Canis lupus*) populations and interspecific competition with sympatric cougars (*Puma concolor*) presents new challenges for management of carnivore and ungulate populations (e.g., elk, *Cervus canadensis nelsoni*; mule deer, *Odocoileus hemionus*) in these multi-carnivore systems. We compared predation patterns (diet composition, kill rate, search and handling time) of cougars (subordinate predator) before (2009–2012) and after (2014–2016) wolf (dominant competitor) recolonization of the Mt. Emily Wildlife Management Unit in northeast Oregon. We identified 542 predation events for cougars in the post-wolf period to compare with 1,213 cougar predation events documented before wolf recolonization. Cougar predation was different between study periods, with changes most evident in predation patterns of female cougars. Female cougars had lower proportions of mule deer in their summer diets (12%), lower summer kill rates (17% – 50%), lower biomass intake rates (14% – 61%), and longer search times (30% – 138%) than respective female cougar groups in the previous cougar study. Our study begins to quantify the costs of interspecific competition between cougars and wolves in northeast Oregon.

INTRODUCTION

Interspecific interactions, typified by direct and indirect effects from interference and exploitative competition, can weaken or strengthen top-down effects of multiple carnivores on prey populations (e.g. Sih et al. 1998, Palomares and Caro 1999, Vance-Chalcraft et al. 2007, Broekhuis et al. 2013). More than 50 years of research has provided a wealth of information about wolf (*Canis lupus*; Mech and Boitani 2003) and cougar (*Puma concolor*; Hornocker and Negri 2009) predatory behavior and their predation effects on prey populations, and wolf-cougar interactions have been studied in several systems (e.g., Schmidt and Gunson 1985, White and Boyd 1989, Boyd and Neal 1992, Kunkel et al. 1999, Jason S Husseman et al. 2003, Alexander et al. 2006, Atwood et al. 2007, 2009, Kortello et al. 2007, Jimenez et al. 2008, Bartnick et al. 2013, Elbroch et al. 2015). Collectively, these studies document the existence and asymmetry of agonistic interactions between wolves and cougars (e.g. direct killing, kleptoparasitism, avoidance behavior) and the subordinate nature of cougars relative to wolves (Elbroch and Kusler 2018). Individuals of competing species are expected to balance trade-offs in foraging efficiency with costs of competing (i.e. loss of food, threat of injury, or death). However,

linkages between species interactions and competition mechanisms to predation patterns and implications of these competitive effects remain unclear.

Dietary overlap between competing species is a fundamental aspect of competition for prey resources that can be indicative of the strength of interactions. Partitioning prey resources through spatial or temporal segregation of use may moderate potential competitive exclusionary effects for a subordinate competitor (Casula et al. 2006). Alterations or shifts in the age class of preferred shared prey or use of different species by a subordinate competitor could reduce dietary niche overlap, and limit costs of interacting with a dominant competitor. Vital rate and age class contribution to prey population growth rates are not equal, therefore selection or change in use of specific age classes of prey may or may not effect overall prey population size or sustainability under predation pressure. Understanding how interspecific competition may alter these aspects of prey use is important to understanding variability and overall effects of predation by multiple predators on prey populations.

Kill rates (i.e. number of prey killed per predator per unit time) are one basic element that structures the population biology of predation (Holling 1959, Taylor 1984), but has rarely been studied in the context of interspecific carnivore competition. Interference competition could negatively affect foraging efficiency (Carbone et al. 1997), limit subordinate competitor abundance (e.g. through loss of food resources), and alter predation effects to prey populations (Ives et al. 2005). Alternatively, loss of a carcass may decrease the time between predation events, potentially increasing subordinate predator effects to prey populations. How interference competition effects kill rates in terrestrial carnivores is understudied in general, and has not been studied between wolves and cougars using advancements in Global Positioning System technology (GPS). For management strategies of both carnivores and their prey to be effective, reliable estimates of kill rates and an understanding of the factors that cause these rates to vary, including effects from interspecies competition, is necessary to predict community-level effects.

Recent efforts to standardize methods and use unbiased estimators of kill rates has provided increasing evidence of generalizable patterns in factors influencing rates of both cougars and wolves. Cougar kill rates have been shown to vary based on cougar age (Knopff et al. 2010) and reproductive status (Knopff et al. 2010, Clark et al. 2014a, Blake and Gese 2016), while season and prey vulnerability have been shown to influence kill rates for both wolves (Peterson and Allen 1974, Metz et al. 2011, 2012) and cougars (Knopff et al. 2010, Clark et al.

2014a). However, some studies report no seasonal effects on cougar kill rates (Blake and Gese 2016), and contradictory results regarding the factors most strongly influencing wolf kill rates are well-documented and still being debated (Therberge 1990, Dale et al. 1994, Vucetich et al. 2002, 2005, 2011, Peterson et al. 2003, Vucetich and Peterson 2004, Jost et al. 2005, Zimmermann et al. 2015). Contradictory results could reflect the variability among systems or in methodology, and thus, the need for continued study. GPS advancements have aided efforts, providing a new platform to evaluate both predation patterns and carnivore interactions and we are beginning to gain insight into the causes of observed effects and consequences of large carnivore population expansion (Anderson and Lindzey 2003, Sand et al. 2008, Knopff et al. 2009, 2010, Metz et al. 2011, 2012, Clark et al. 2014a, Tallian et al. 2017).

The presence of two apex predators, coupled with previous research on cougar predation patterns in northeast Oregon, presented an ideal opportunity to investigate interspecific competition effects after a second predator (wolves) recolonized an area occupied for the past 60 years solely by cougars. We documented kill rates and prey use over 3 years for a sample of wolves and cougars in a re-established area of sympatry. Our primary objective was to examine the predation response of a subordinate predator (cougar) to the recolonization of a dominant predator (wolf). Using cougar predation patterns established for the area prior to wolf recolonization (Clark et al. 2014a), and those we documented for wolves (See Chapter 2), we investigated 1) whether the composition of ungulate prey in cougar diets change in the presence of wolves, 2) whether the dominant age class of ungulate prey in cougar diets change in the presence of wolves, and 3) whether cougars kill more frequently with wolves on the landscape? We predicted the ungulate composition of overall cougar diets would be unchanged between time periods with and without wolves (e.g. niche breadth established evolutionarily), but that cougars would shift seasonal use of specific ungulate age classes to avoid competition with classes of prey most frequently used by wolves. Alternatively, we considered the possibility cougars might switch to use of non-ungulate prey. If cougars did not shift the species or age class of prey in diets and used the same seasonal prey classes as wolves, we considered the possibility that cougars might compensate any competition effects by killing more frequently. Alternatively, we considered the possibility cougars might kill less frequently with wolves on the landscape. We posited this outcome could manifest if cougars spend more time avoiding wolf interactions while searching for, or handling, each prey carcass. Based on different food intake requirements

between cougar reproductive classes (Knopff et al. 2010, Clark et al. 2014a), we predicted the outcome of competition and any changes in cougar kill rates was likely to vary by cougar reproductive group.

METHODS

Study Area

The study area was located in the Blue Mountain Range of northeast Oregon (Fig. 3.1), and contained a mixture of private, public, and tribal lands (Confederated Tribes of the Umatilla Indian Reservation; CTUIR) covering 1,992 km². The U.S. Forest Service (USFS; Wallowa Whitman and Umatilla National Forests) and the State of Oregon manage public lands within the study area, and private land management was dominated by commercial agriculture and forest habitat, managed either as industrial forests or grazed rangelands. Elevation ranged from 360 – 1,850 m, with vegetation strongly influenced by topography, aspect, and elevation. On the west side of the study area low elevation sites were dominated by exposed upland slopes and riparian areas comprised of hawthorn (*Crataegus columbiana*), willow (*Salix* spp.), and blackberry (*Rubus armeniacus*) with scattered ponderosa pine (*Pinus ponderosa*), and black cottonwood (*Populus trichocarpa*). Mixed-conifer stands with exposed southern aspects characterized high elevation sites in the central and eastern part of the study area with common species including ponderosa pine, douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), and lodgepole pine (*P. contorta*).

Oregon Department of Fish and Wildlife (ODFW) manage wildlife populations using discretely bounded areas known as Wildlife Management Units (WMUs). Cougar predation was studied in the Mt. Emily WMU before wolves recolonized northeast Oregon (2009 – 2012; Clark et al. 2014a), and we studied wolf predation (Orning et al. in review) and re-examined cougar predation after 3 wolf packs were documented in the WMU (2014-2016). Some cougars (pre- and post-wolf recolonization) utilized areas outside Mt. Emily WMU in adjacent WMUs (Walla Walla, Wenaha, Catherine Creek, Ukiah, Starkey) over the course of predation monitoring, but

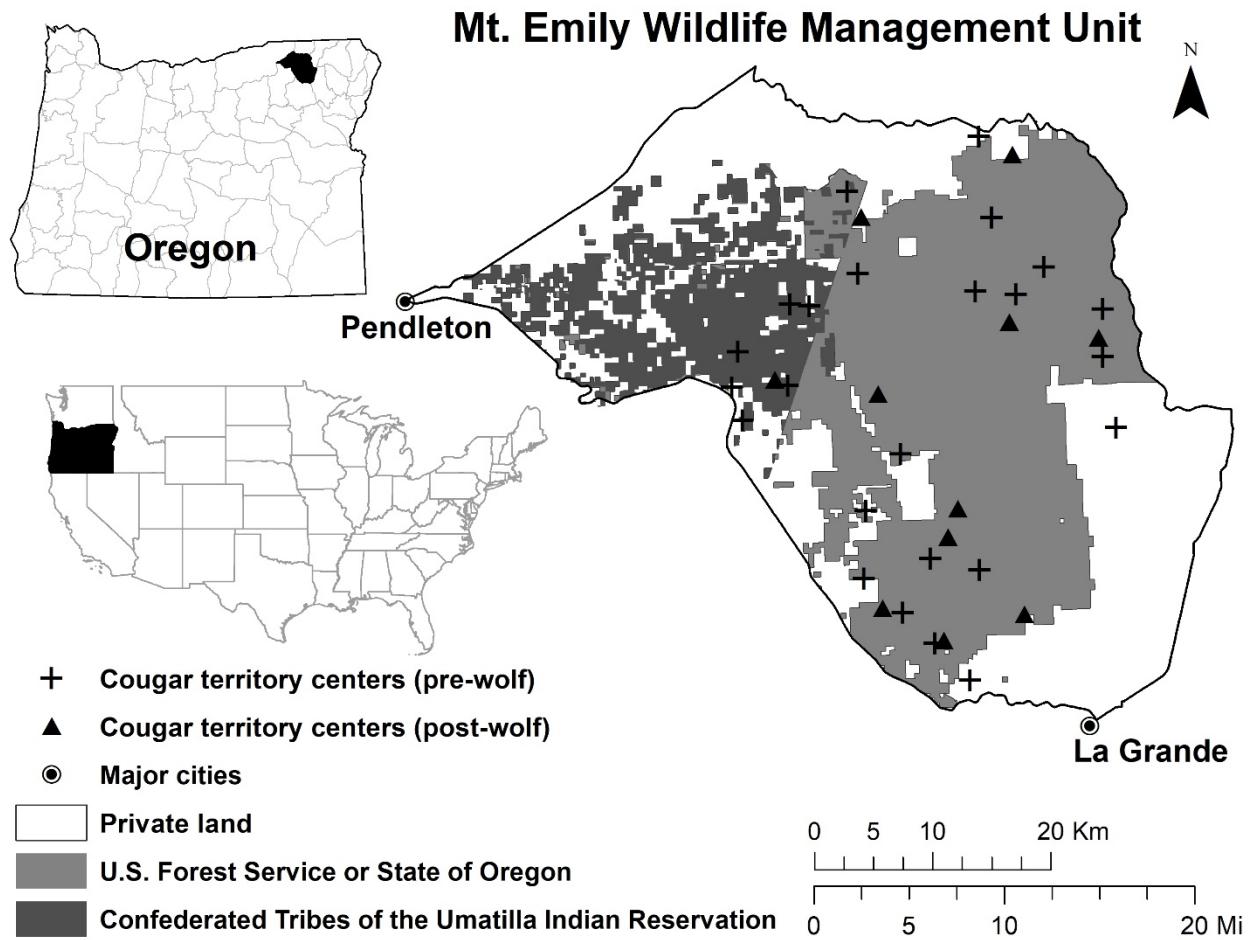


Figure 3.1. Location the Mt. Emily Wildlife Management Unit in northeast Oregon, USA, and approximate territory center points of cougars monitored with global positioning system (GPS) collars to determine changes in prey use and kill rates between time periods before (2009 – 2012) and after wolf recolonization (2014 – 2016).

activity centers were primarily focused in the Mt. Emily WMU. Wolf predation was monitored for two packs that primarily used the Mt. Emily WMU and two packs that primarily used the Wenaha WMU.

A number of potential large prey species inhabit the Blue Mountains, with the most abundant ungulates being elk (*Cervus canadensis nelsoni*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Moose, (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*) were present in small, localized populations. Feral horse (*Equus ferus caballus*) were also present on CTUIR lands and potentially available as prey

to large carnivores (C. Scheeler, CTUIR, pers. comm.). Additionally, livestock (e.g. cattle and sheep) were present throughout the year on private property and seasonally available as potential large prey on USFS and CTUIR managed grazing allotments and other privately owned lands. A myriad of smaller prey were also available in the study area (e.g. ground squirrel (*Spermophilus spp.*), snowshoe hare (*Lepus americanus*), badger (*Taxidea taxus*), beaver (*Castor canadensis*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*), but we primarily focused on large ungulates in our system as they were most likely to be accurately represented in diets of cougars (Knopff et al. 2010) and wolves (Sand et al. 2005). In addition to wolves and cougar, black bear (*Ursus americanus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and fox (*Vulpes vulpes*) were other predators that commonly occurred in the study area and may also be preyed on by cougars.

Cougar Capture and Monitoring

We captured cougars with the aid of trained pursuit dogs that chased animals up into a tree following the American Society of Mammalogists' guidelines for wild animal use in research (Sikes and Gannon 2011) and procedures approved by the Institutional Animal Care and Use Committees of Oregon State University and USDA Forest Service – Starkey Experimental Forest and Range. We chemically immobilized treed cougars with a mixture of Ketamine (200mg/mL; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine (20mg/mL; Rompun®; Bayer, Inc., Shawnee Mission, KS, USA). We determined the age, sex, and weight of immobilized cougars, attached radio-collars and reversed immobilization using yohimbine (0.125 mg/km; Yobine®; Lloyd Labortories, Shenandoah, IA). We determined cougar age by analyzing cementum annuli (Trainer and Matson 1988) after extracting the first premolar of adults, or by using field estimates from tooth wear (Ashman et al. 1983, Shaw 1986), gum-line recession (Laundré et al. 2000), and pelage spotting progression (Shaw 1986). We classified cougars as dependent kittens (< 1 year), subadults (independent females < 2 years and males < 3 years), and adults (females ≥ 2 years, and males ≥ 3 years). This classification system was developed to reflect differences in dispersal between subadult males and females to minimize the placement of GPS collars on non-resident cougars likely to disperse outside the study area (Clark et al. 2014a). Cougars that were likely to disperse or not large enough to carry a GPS collar were fit with a VHF collar. We equipped adult cougars with GPS collars (Lotek Iridium Plus or Track

M Basic, [Lotek Engineering, Newmarket, ON, Canada]). GPS collars used an Iridium platform and were scheduled to collect 8 locations per day (0100, 0400, 0700, 1000, 1300, 1600, 1900, 2200 hours).

Kill Site and Prey Remain Identification

We processed locations from GPS collars every 7-12 days and identified potential kill sites year round for cougars (2014-2016) using the PYTHON (Python Software Foundation, Hampton, NH) rule-based algorithm developed by Knopff et al. (2009) to generate clusters of GPS locations based on cougar-specific criteria (Anderson and Lindzey 2003, Knopff et al. 2009, 2010). Each cluster was defined as sets of ≥ 2 locations within 200 m over 6 days, with additional locations within 6 days of the last location adding to clusters. We also used seasonal predictive models (regression) developed for the previous cougar study (see Clark et al. 2014*a* for details) to aid prediction of cougar kill sites and maximize field investigative efforts at sites likely to contain prey remains.

We used ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA, USA) to map the algorithm-generated location clusters of potential cougar predation sites. We did not search potential predation sites when collared cougars were within 1 km of the area to be searched to minimize disturbance to cougar behavior. We navigated to the geometric cluster centers using handheld GPS units and systematically searched for prey remains following methods described in Clark et al. (2014*a*). Searches were conducted by walking a grid-like pattern of transect lines spaced 5-10 m apart (i.e. dependent on variability in terrain visibility) from the generated cluster center to the radius extent. Even after an initial carcass was detected we continued to search grids to the radius extent to identify multiple carcasses.

Once remains of prey were located, we used characteristics described by Ruth and Buotte (2007) to evaluate evidence at the site including signs of a struggle, drag marks, tufts of fur, broken branches, predator tracks or scat, cached or covered carcass remains, and chase trails to verify which carnivore likely made the kill or whether prey were scavenged. Scavenging behavior was determined using carcass characteristics (discarded harvest gut piles, remains with clear knife cut marks, severe trauma and proximity to roads or highways, age relative to cluster start dates), site evidence, and timing of other predators at the site. We determined prey species using skeletal, anatomical, and pelage characteristics (Moore et al. 1974, Verts and Carroway

1998, Jacobson 2003), and age of prey using body size, tooth eruption and wear patterns (Robinnette et al. 1957, Schroeder and Robb 2005), or skull size. When present, we also collected an incisor from ungulate individuals > 2.5 years old for aging prey via analysis of cementum annuli (Low and Cowan 1963; Matson's Laboratory, Milltown, MT). We used the presence of antler pedicels or pelvic characteristics (Edwards et al. 1982) to determine sex of non-juvenile deer and elk. Prey were classified into three age classes: juvenile (< 1 year), yearling (1 year), and adult (≥ 2 years). We examined prey remains for physical abnormalities and collected femur and/or mandible marrow, when present, for marrow fat analysis. Marrow fat can be used as an index of prey condition at time of death by providing a measure of pre-starvation absolute physical condition (Mech and Delgiudice 1985, Atwood and Gese 2007). Because marrow fat is a 1-way indicator of nutritional condition (i.e. can infer poor condition from low fat values, but high fat values do not necessarily equate to good condition), no minimum value can be set as a reliable cutoff for declaring poor vs. fit prey classifications. On a relative scale, any fat loss in marrow suggests poorer condition (see Mech and Delgiudice 1985), so we used a marrow fat content of $\leq 50\%$ as a conservative threshold to define the poorest condition ungulates preyed upon in our study. We removed and weighed a 5 – 7 cm marrow sample from the central portion of a bone (femur, humerus, or mandible if long bones were unavailable) from ungulate prey > 6 months of age. Samples were oven-dried at 60° C for 48 hours and reweighed to calculate the dry-to-wet mass of the fat (Neiland 1970, Atwood and Gese 2007). We adjusted mandible fat values to femur fat equivalents for elk (following Husseman et al. 2003) when only mandibles were available to sample. Marrow fat of prey were not normally distributed, therefore we used Mann-Whitney U-tests to compare relative condition of wolf and cougar killed prey across summer and winter seasons. We estimated carcass biomass for deer and elk as described by Clark et al. (2014a; see appendix 1 for list of age/weights) based on capture data from northeast Oregon (B. Johnson, ODFW, unpublished data).

Prey Composition

We calculated species and age composition of prey as, 1) the frequency of predation events where these prey characteristics were known for all cougar, and 2) a proportion of predation events for individual cougar. We then calculated mean proportions of the i^{th} ungulate prey species or age class for pre- and post-wolf cougars and compared diet composition between

the two study periods with a Student's *t* test. When *t*-statistics provided evidence of inequality (i.e. evidence of alternative hypothesis plausibility), we carried out permutation tests (5000 randomizations) to compare observed differences with the distribution of *t*-statistics calculated after randomly assigning study period to each cougar (Manly 2001, Good 2005). For example, if there were 16 pre- and 9 post-wolf predation events by cougars, 16 of the 25 events were randomly assigned to the pre-wolf time period and the remaining 9 were assigned to the post-wolf time period. We then used the randomized distributions to obtain p-values for the observed *t*-statistics by calculating the proportion of permuted statistics as far or further from zero than the one observed (Manly 2001). Thus, reported p-values (%P) refer to levels of significance based on positioning of our sample of cougars along a constructed *t*-distribution, and increased levels of significance correspond with increased strength of evidence against the null hypothesis of no difference between pre- and post-wolf cougar populations. Before making comparisons across study periods, we used ANOVA and Tukey's honest significance difference adjustment for multiple comparisons (Day and Quinn 1989) between groups known or suspected to influence cougar predation patterns to account for differences based on 1) cougar sex, 2) cougar age class, 3) cougar reproductive status, and 4) season. We defined female cougar reproductive status as solitary females with no kittens (Sol F), females with kittens < 6 months old (FG < 6 month), and females with kittens > 6 months old (FG > 6 month). We determined female cougar reproductive status based on nursery site visits, presence of kitten tracks at predation sites, or visual observation of kittens. Reproductive status was not monitored daily, therefore we may have misclassified female reproductive status over short time periods. For our assessment of seasonal differences we defined predation events that occurred from May – Oct as summer kills, and events from Nov – Apr as winter kills. For statistical tests, we considered $P \leq 0.10$ as evidence of effect and inclusion as a grouping factor for cross species and study period comparisons. All tests were carried out in R (R Core Team 2017).

Kill Rates and Inter-Kill Intervals

We estimated kill rates (KR) for cougar as both the number and live weight biomass of ungulate prey killed per cougar per unit time (week). We estimated seasonal kill rates of ungulates for the cougar reproductive classes outlined above. To facilitate comparison with the previous cougar study, we included individual cougars in our analysis that were monitored

continuously for ≥ 42 days in a given season and reproductive class. We estimated both frequency and biomass metrics to quantify ungulate kill and biomass intake rates using a ratio estimator with the total monitoring time as the denominator and both the number and kilograms of prey as numerators (no./wk or kg/wk). While ratio estimators require longer monitoring intervals to obtain reasonably precise estimates for cougar (Knopff et al. 2009, 2010), they are less biased and more conservative than other methods (Hebblewhite et al. 2003).

To test whether cougar kill rates increased after wolf recolonization we calculated intervals between first location fixes of consecutive ungulate predation events (intervals were assigned to the month in which they ended) for each cougar to investigate whether cougar inter-kill intervals (IKI) declined (i.e. cougars killed more often) after wolf recolonization. We used IKI to avoid problems estimating rates over very short monitoring periods (e.g. a few days), and because variation in interval length was a potential response of primary interest. It also allowed us to include a larger sub-sample of predation events from cougars with truncated monitoring periods due to capture or collar performance issues (e.g. missed transmissions, failures).

To isolate the source of variation in cougar IKI between time periods with and without wolves, we separated intervals into behavioral components of search (a function of the probability of encountering prey and the probability of killing prey given it was encountered) and handling time (amount of time spent consuming prey) similar to Knopff et al. (2010). We defined handling time (hr) as the number of GPS locations at a predation cluster divided by collar fix success over cluster duration, multiplied by the collar fix rate. We calculated search time (hr) by subtracting prey handling time at the beginning of an IKI from the total interval length. We assigned a search time of zero if a second prey was killed while the first prey was still being handled (simultaneous handling of multiple prey) where negative search times were calculated.

We used permutation procedures, as described above, to compare pre- and post-wolf cougar KR and IKI metrics. For our assessment of kill rates, we used individual cougar as the sample unit and tested differences in pre-and post-wolf cougar mean KR. For our assessment of intervals, we used each predation event as the unit of analysis and tested for differences in mean IKI, and mean search and handling times between study periods. We also controlled for season, sex, cougar age class, and reproductive status, as described above, to isolate variation from other factors and determine if these factors varied between study periods.

RESULTS

We captured and fit 11 cougar (8 female and 3 male) with GPS collars and monitored predation over a total of 3,864 cougar-days from July 24, 2014 to November 1, 2016. Each cougar was monitored a mean of 351 days (range 147 – 525 days). We investigated 1,557 GPS location clusters and identified the remains of 542 potential prey at 527 clusters. Mean fix success was 93.4% (range 76 – 98.2%) for collared cougars during predation monitoring. Median number of days between cluster generation and field investigation for sites with prey remains was 37 days ($\bar{x} = 65$ days, SD = 69).

Diet Composition, Prey Use, and Scavenging

Cougar Diet Composition. – Of the 481 cougar-killed prey, 92.3% were native ungulates (deer and elk) and 7.7% were other carnivores (coyote, badger, black bear), small mammals (beaver, ground squirrel, snowshoe hare), or birds (turkey (*Meleagris gallopavo*), ruffed grouse (*Bonasa umbellus*); for detailed diet breakdown see Appendix B). Over winter monitoring periods, mule deer were the primary ungulate prey found at sites with prey remains (56.5%). We determined genus and age class for 143 of 184 ungulates preyed on by cougar in winter. Across all cougars, deer fawns ($n = 48$; 33.6%) were the most frequent known age ungulate prey at winter predation sites. Over summer, elk (all ages) were the primary ungulate prey found at sites with prey remains (50.0%). We determined genus and age class for 231 of 260 ungulates preyed on by cougar in summer. Across all cougars, elk calves ($n = 104$; 40.0%) were the most frequent known age ungulate prey at summer predation sites, followed by deer fawns ($n = 58$; 22.3%). The mean marrow condition of cougar-killed ungulates was 1.21 times lower in winter ($\bar{x} = 67.4\%$, 90% CI = 61.2 – 73.6) than summer ($\bar{x} = 81.6\%$, 90% CI = 77.8 – 85.4; $W = 720$, $P = 0.002$), but consistent with winter marrow condition of road-killed ungulates over the same period ($W = 253$, $P = 0.65$). Of the cougar-killed ungulates for which we determined marrow condition to be $\leq 50\%$ ($n = 12$), the majority were mule deer ($n = 7$; 58.3%), followed by elk ($n = 4$; 33.3%), and white-tailed deer ($n = 1$; 8.3%), and most were adults ($n = 11$; 91.7%).

Cougar Scavenging. – Ten of 11 cougars we monitored engaged in scavenging behavior. We documented 54 cases of scavenging, which represented 10% of all prey remains. Most

scavenged carcasses were ungulates (47 of 54; 87.7%) killed by hunters or vehicles, but cougars also returned to their own kills from months earlier and cache sites of other cougar (kills confirmed to other GPS collared cougar). We also identified 2 cases in which ungulate remains visited and scavenged by cougars were confirmed wolf kill sites (GPS/field verified predation sites). Cougars also scavenged remains of discarded livestock ($n = 5$) and other cougar ($n = 2$).

Cougar Diet Comparison. – The previous study of cougar diets conducted prior to wolf colonization observed differences based on cougar sex, reproductive class, and season (Clark et al. 2014a), and other studies have observed differences in diet composition based on cougar age (Knopff et al. 2010). Our sample sizes of females with < 6 month and > 6 month old kittens were not large enough to make seasonal diet comparisons ($n = 3$ over summer, and 1 litter that transitioned from young to old kittens over winter), and while diet composition varied among reproductive classes in pre-wolf cougars (elk, $F_{41} = 2.84$, $P = 0.05$; mule deer, $F_{41} = 3.30$, $P = 0.03$), variation was explained by sex differences (elk, M-FG < 6 month, $P = 0.03$; mule deer, M-FG < 6 month, $P = 0.02$; all female group comparisons $P > 0.30$). We did not find any evidence of differences in ungulate diet composition of cougars after wolf colonization based on cougar age class (mule deer, $P = 0.53$; white-tail, $P = 0.11$; elk, $P = 0.35$), so we pooled subadult and adult females for our comparison across study periods. Therefore, we only made diet comparisons across study periods based on sex and season. Female cougar diets differed pre- and post-wolf colonization, where post-wolf female cougars had less mule deer in their summer diet than pre-wolf female cougars ($\%P = 8.8$; Fig. 3.2), but there was no difference in the proportion of elk in female summer diets ($\%P = 32.7$). Female cougars also differed in the seasonal proportion of specific age classes of deer in their diets between study periods, where post-wolf female cougar diets contained less fawn ($\%P = 6.0$; Fig. 3.3) and yearling ($\%P = 0.44$) age deer in their summer diets than pre-wolf female cougars, but no evidence of change in the age classes of deer in their winter diets ($P > 0.10$). Our sample of post-wolf period male cougars was small ($n = 3$), precluding population level inferences for that subgroup in this study, so we did not make comparisons of male diet composition across periods.

Kill Rates and Intervals

We used a subset of 340 ungulate predation events, representing 27 demographic and season-specific monitoring intervals ≥ 42 days, to calculate post-wolf cougar kill rates. We did

not calculate kill rates for 8 monitoring periods with durations < 42 days, which excluded the only female cougar monitored in our study with kittens > 6 months old from seasonal comparisons. Annually, cougars killed 0.82 ungulates/wk (90% CI = 0.75 – 0.88). Kill rates varied by season ($F_{1,25} = 13.74, P = 0.001$), where cougars had 1.58 times lower kill rates in winter ($\bar{x} = 0.65, SE = 0.07$) than summer ($\bar{x} = 1.03, SE = 0.08$), but there was no evidence rates varied based on cougar reproductive status (Table B5, Appendix B; $F_{2,24} = 0.07, P = 0.94$). Biomass intake rates did not vary by season (summer = 39 kg/wk, SE = 6; winter = 47 kg/wk, SE = 9; $F_{1,25} = 0.43, P = 0.52$), but varied by reproductive status ($F_{2,24} = 11.5, P = 0.0003$). Male cougars had mean biomass intake rates 2.4 times higher than solitary females and females with kittens < 6 months old, which had similar rates (M-FG < 6 months, $P = 0.01$; M-Sol F, $P = 0.0003$).

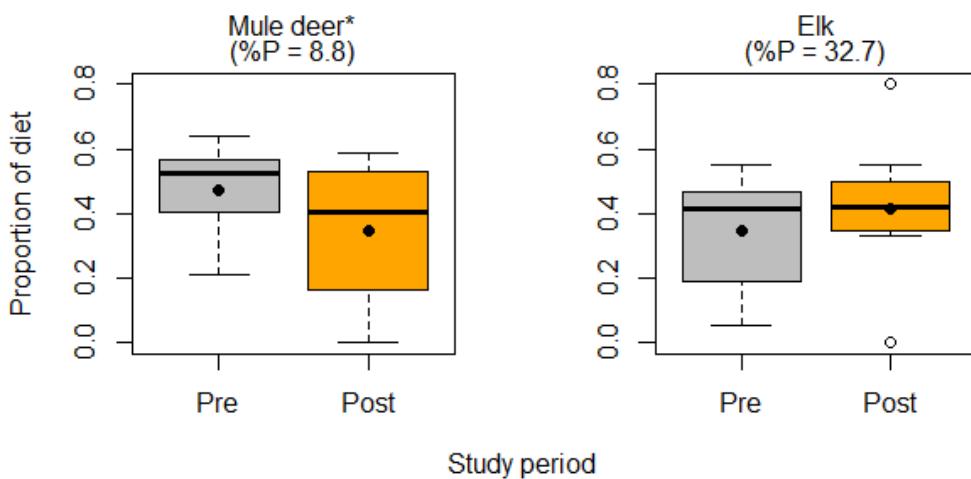


Figure 3.2. Comparison of ungulate species in summer (1 May – 31 Oct) diets of female cougars across pre- and post-wolf periods. Species composition of prey is expressed as the mean proportion of the i^{th} ungulate prey species at ungulate predation events of individual female cougars over pre- ($n = 13$) and post- ($n = 8$) wolf time periods. %P refer to levels of significance based on 5000 randomizations of cougar diets, and increased levels of significance correspond with increased strength of evidence against no difference in cougar diets. Mean values denoted by closed circles and strong evidence of difference denoted by *. Results were from 612 pre- and

190 post-wolf recolonization predation events for 21 cougars fit with GPS collars in the Mt. Emily WMU of northeast Oregon, USA, 2009 – 2012 (pre-wolf) and 2014 – 2016 (post-wolf).

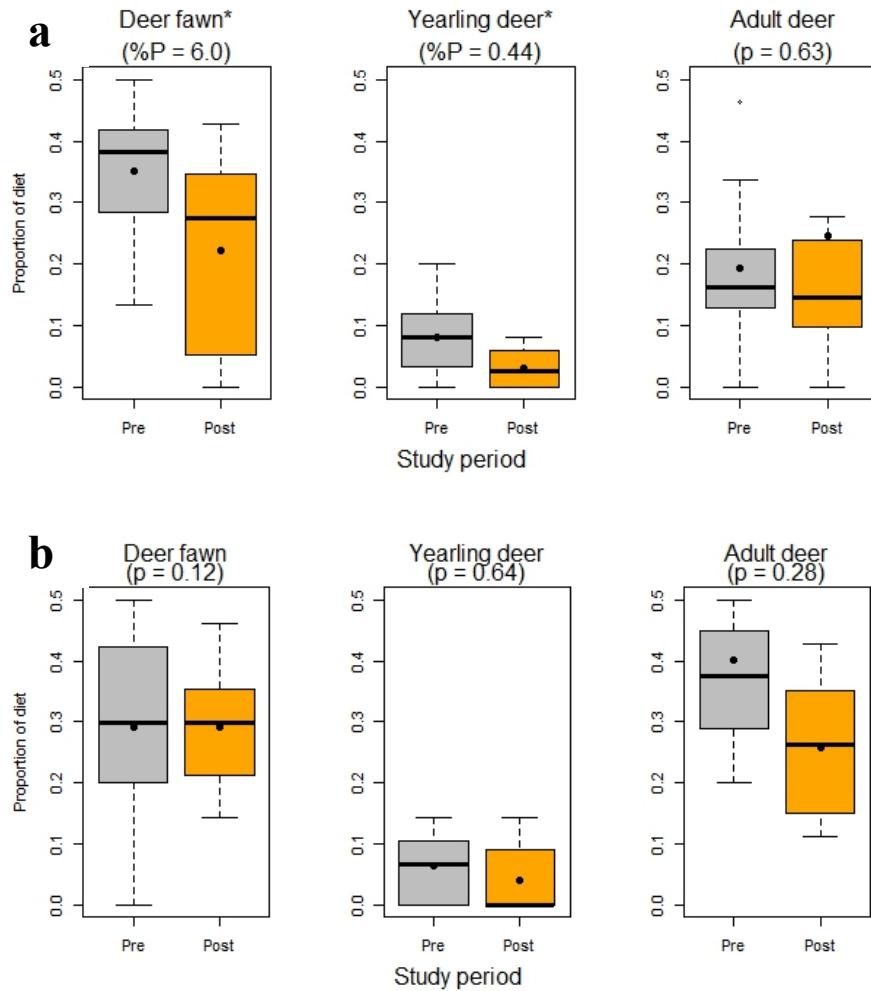


Figure 3.3. Comparison of deer age classes in diets of female cougars across pre- and post-wolf periods during (a) summer (1 May – 31 Oct), and (b) winter (1 Nov – 30 Apr). Species composition of prey is expressed as the mean proportion of the i^{th} ungulate known prey age class at predation events of individual female cougars over pre- ($n = 14$) and post- ($n = 8$) wolf time periods. %P refer to levels of significance based on 5000 randomizations of cougar diets, and increased levels of significance correspond with increased strength of evidence against no difference in cougar diets. Mean values denoted by closed circles and strong evidence of difference denoted by *. Results were from 892 pre- and 317 post-wolf recolonization predation events for 22 cougars fit with GPS collars in the Mt. Emily WMU of northeast Oregon, USA, 2009 – 2012 (pre-wolf) and 2014 – 2016 (post-wolf).

We used a subset of 443 ungulate predation events to calculate cougar IKI, search and handling times. Generally, the cougars we monitored killed at least once every two weeks ($\bar{x} = 8.61$, 90% CI = 8.1 – 9.13), and the longest interval we documented between ungulate predation events was 35 days. Cougars had 38% longer IKIs in winter ($\bar{x} = 10.32$, SE = 0.54) than summer ($\bar{x} = 7.49$, SE = 0.37; $F_{1,428} = 19.69$, $P < 0.0001$). We did not find any evidence of differences in IKI based on cougar sex (Table 1; $F_{1,428} = 0.95$, $P = 0.33$), or reproductive status ($F_{3,426} = 0.74$, $P = 0.53$). IKIs were 63% longer for subadult compared to adult cougars in summer ($\bar{x}_{\text{subadult}} = 11.83$, SE = 4.0; $\bar{x}_{\text{adults}} = 7.27$, SE = 0.36; $F_{1,256} = 3.59$, $P = 0.06$), and 79% longer in winter ($\bar{x}_{\text{subadult}} = 16.9$, SE = 2.18; $\bar{x}_{\text{adults}} = 9.44$, SE = 0.52; $F_{1,164} = 20.81$, $P < 0.0001$).

Mean handling time was 96% longer in winter ($\bar{x} = 98$ hrs, SE = 5) than summer ($\bar{x} = 50$ hrs, SE = 2; $F_{1,441} = 101.9$, $P < 0.0001$). We did not find evidence for differences in handling time based on cougar reproductive status (Table 3.1; $F_{3,439} = 1.48$, $P = 0.22$), but adult females spent 32% longer handling prey in winter than adult males ($\bar{x}_{\text{female}} = 100$ hrs, SE = 6; $\bar{x}_{\text{male}} = 76$ hrs, SE = 9; $F_{1,151} = 5.15$, $P = 0.03$). We found evidence handling times varied based on cougar age class ($F_{1,432} = 20.03$, $P < 0.0001$), but we did not find strong evidence handling times were different between subadult and adult female cougars in summer ($\bar{x}_{\text{subadult}} = 68$ hrs, SE = 27; $\bar{x}_{\text{adults}} = 48$ hrs, SE = 3; $F_{1,195} = 1.87$, $P = 0.17$), or winter ($\bar{x}_{\text{subadult}} = 122$ hrs, SE = 11; $F_{1,126} = 2.41$, $P = 0.12$), suggesting season and sex more strongly influence handling times than age class of cougar.

Mean time spent searching before making a kill was 33% longer in winter ($\bar{x} = 122$ hrs, SE = 12) than summer ($\bar{x} = 94$ hrs, SE = 8; $F_{1,428} = 3.76$, $P = 0.05$). We did not find any evidence of differences in search time based on cougar reproductive status ($F_{3,426} = 1.61$, $P = 0.19$), but adult males spent 44% longer searching for prey in summer than adult females ($\bar{x}_{\text{female}} = 114$ hrs, SE = 8; $\bar{x}_{\text{male}} = 164$ hrs, SE = 19; $F_{1,250} = 7.71$, $P = 0.01$). Subadult cougars spent 103% more time between predation events searching than adults (Table 3.1; $F_{1,422} = 23.8$, $P < 0.0001$). Seasonally, subadult females spent 82% more time searching in summer ($\bar{x}_{\text{subadult}} = 207$ hrs, SE = 83; $F_{1,194} = 3.76$, $P = 0.05$), and 97% more time searching in winter than adult females ($\bar{x}_{\text{subadult}} = 286$ hrs, SE = 47; $\bar{x}_{\text{adults}} = 145$ hrs, SE = 13; $F_{1,119} = 14.58$, $P = 0.0002$), suggesting some aspect of cougar age (e.g. inexperience locating and killing prey, or limited access to prey resources) contributes specifically to the amount of time searching for prey which lengthens the interval between ungulate predation events.

Table 3.1. Cougar age and reproductive group comparison of inter-kill interval (IKI; days between consecutive ungulate kills), and interval components of prey search and handling time (hrs). Results were from 443 consecutive cougar predation events from 11 cougars fit with GPS collars in northeast Oregon, USA, 2014 – 2016.

Cougar group	IKI		Search time		Handling time	
	(days)		(hr)		(hr)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Subadult ^a	16	1.92	268	41	110	11
Adult ^b	8	0.30	132	6	65	3
Male	9	0.62	151	14	60	5
Female ^c	8	0.34	125	7	67	3
Sol F ^d	8	0.36	118	8	68	4
FG < 6 month ^e	8	0.87	134	19	67	6
FG > 6 month ^f	11	2.98	216	61	39	10

^a All subadults were independent females < 2 years old at time of monitoring.

^b Females ≥ 2 years and males ≥ 3 years old at time of monitoring.

^c All female reproductive classes combined.

^d Solitary females with no dependent kittens at time of monitoring.

^e Adult females with dependent kittens < 6 months old at time of monitoring.

^f Adult females with dependent kittens > 6 months old at time of monitoring.

Cougar Study Period Comparisons. – Kill rates differed by study period, with annual kill rates 1.26 times lower for post-wolf cougars than rates reported for cougars prior to wolf recolonization (KR = 1.03 ungulates/wk, 90% CI = 0.94 – 1.12 from Clark et al. 2014a; %P = 0.02). When we accounted for seasonal variation in kill rates, study period differences were disparate across cougar reproductive groups. Female cougars with kittens < 6 months old had summer kill rates 1.53 times lower than respective female cougar family groups in the previous cougar study (Fig. 3.4a; %P = 0.16), and solitary female cougars had summer kill rates 1.18 times lower post-wolf (%P = 3.2). Our post-wolf sample of female cougars with kittens < 6 months ($n = 1$) and kittens > 6 months ($n = 0$) were not large enough to test for differences across study periods in winter. There was no evidence of study period difference in kill rates for male

cougars in either season (Fig. 3.4; summer: $P = 0.64$; winter: $P = 0.75$) or solitary female cougars in winter (Fig. 3.4b; $P = 0.71$).

Mean annual biomass intake rates for post-wolf cougars were also 32% lower than cougar intake rates prior to wolf recolonization ($\bar{x}_{\text{pre}} = 58 \text{ kg/wk}$, 90%CI = 53 – 63; $\bar{x}_{\text{post}} = 44 \text{ kg/wk}$, 90%CI = 38 – 50; % $P = 0.7$). We did not observe evidence for differences across all cougar reproductive groups, but there was strong evidence for decreased biomass intake rates for female cougars with < 6 month old kittens (% $P = 1.6$) and solitary female cougars (% $P = 3.4$). Reductions were seasonally evident across study periods as 61% lower biomass intake rates in summer (Fig. 3.4a; % $P = 1.4$), and 31% lower biomass intake rates in winter (Fig. 3.4b; % $P = 1.0$), for respective female groups.

The interval between consecutive ungulate cougar predation events differed by study period, where mean IKI was 30% longer for post-wolf cougars than pre-wolf cougars ($\bar{x}_{\text{pre}} = 6.61$, 90%CI = 6.16 – 7.06; % $P = 0$). Controlling for season or potential sex differences, there was evidence intervals were 29% longer for female cougars in summer (Fig. 3.5a; % $P = 0.04$) and 40% longer in winter (Fig. 3.5b; % $P = 0$) during the post-wolf period. There was weak to no evidence of differences in IKI for male cougars in either season (summer: % $P = 1.38$; winter: $P = 0.39$). When we controlled for effects of age class, there was weak evidence mean IKIs were 23% longer in summer for post-wolf solitary adult female cougars (Fig. 3.6a; % $P = 0.32$), but there was no evidence of differences in winter (Fig. 3.6b; $P = 0.73$). Effects were opposite for subadult solitary female cougars, with little evidence intervals were longer in summer (% $P = 18.4$), and weak evidence mean IKIs were 55% longer in winter (% $P = 0.2$).

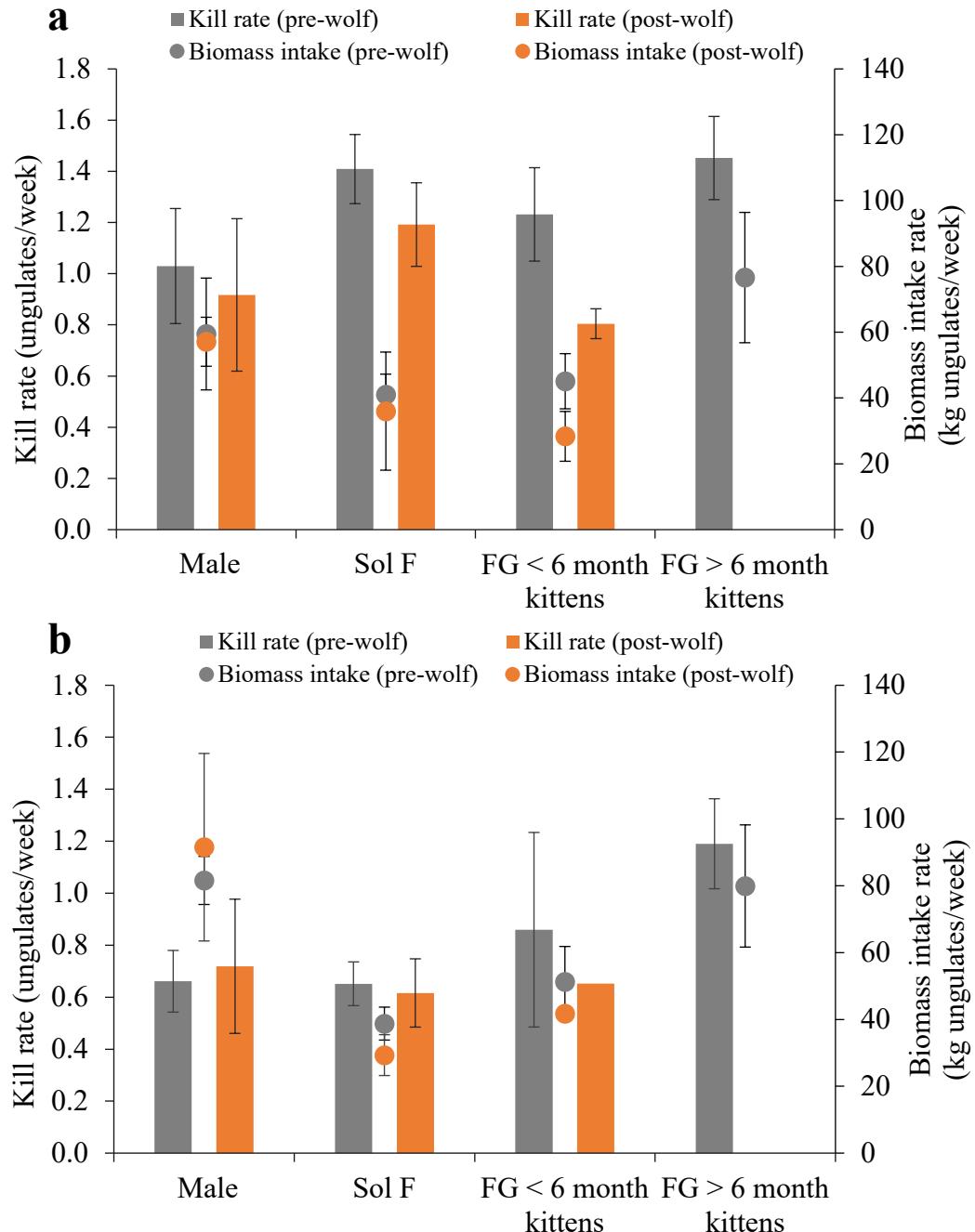


Figure 3.4. Estimate comparison of cougar kill rates (ungulates/week), biomass intake rates (kg ungulates/week), and associated 90% confidence intervals for cougar pre- ($n = 21$) and post- ($n = 11$) wolf recolonization over summer (a) and winter (b) seasons. Results were from 1,099 pre- and 340 post-wolf consecutive cougar predation events from 32 cougars fit with GPS collars in northeast Oregon, USA, 2009 – 2012 (pre-wolf) and 2014 – 2016 (post-wolf). We derived mean biomass intake rates from estimated weights of prey at cougar predation events.

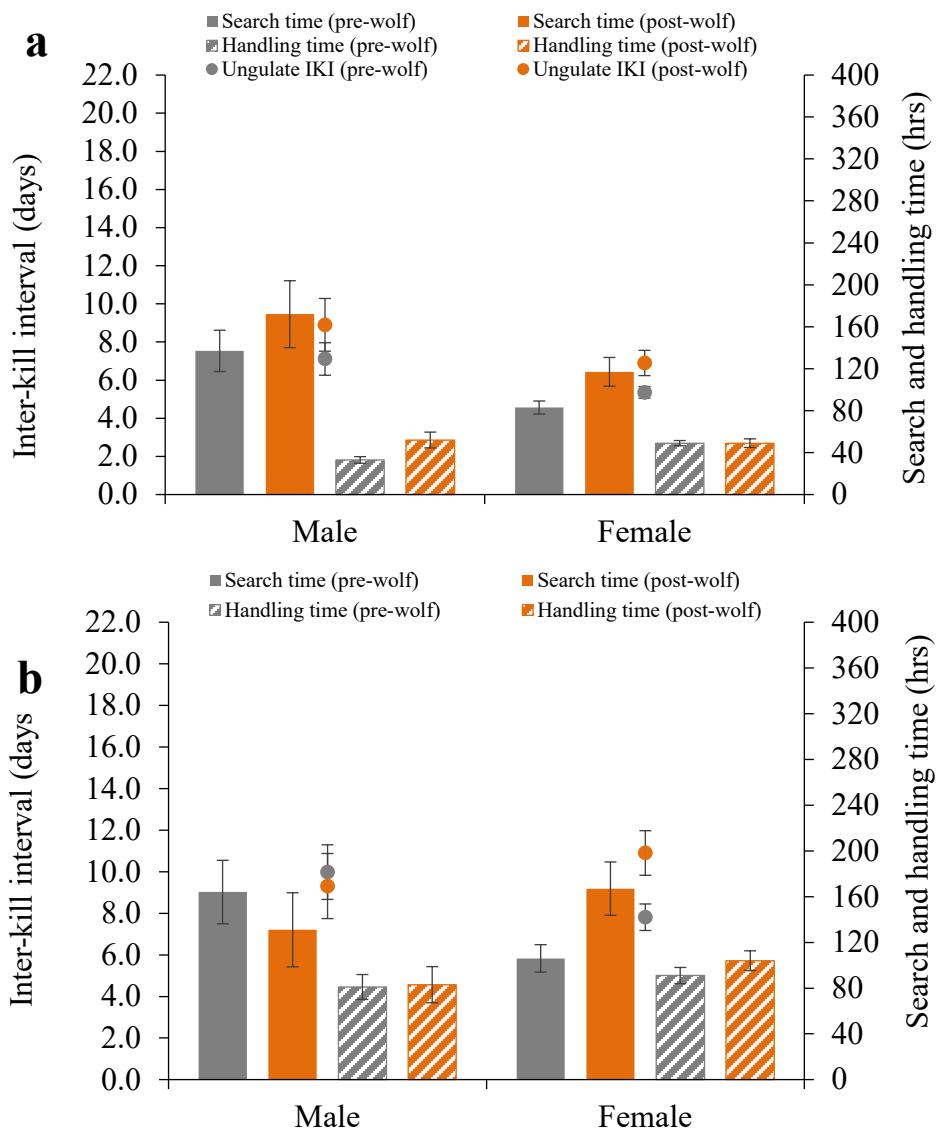


Figure 3.5. Seasonal estimate comparison of ungulate inter-kill interval (IKI; days), search and handling time (hrs), and associated 90% confidence intervals for cougar pre- ($n = 21$; 2009 – 2012) and post- ($n = 11$; 2014 – 2016) wolf recolonization by sex over summer (a) and winter (b). Results were from 1,085 pre- and 430 post-wolf consecutive cougar predation events from 32 cougars fit with GPS collars in northeast Oregon, USA. Search and handling time was derived from IKI using data from cougar predation events where the date of the previous kill was known.

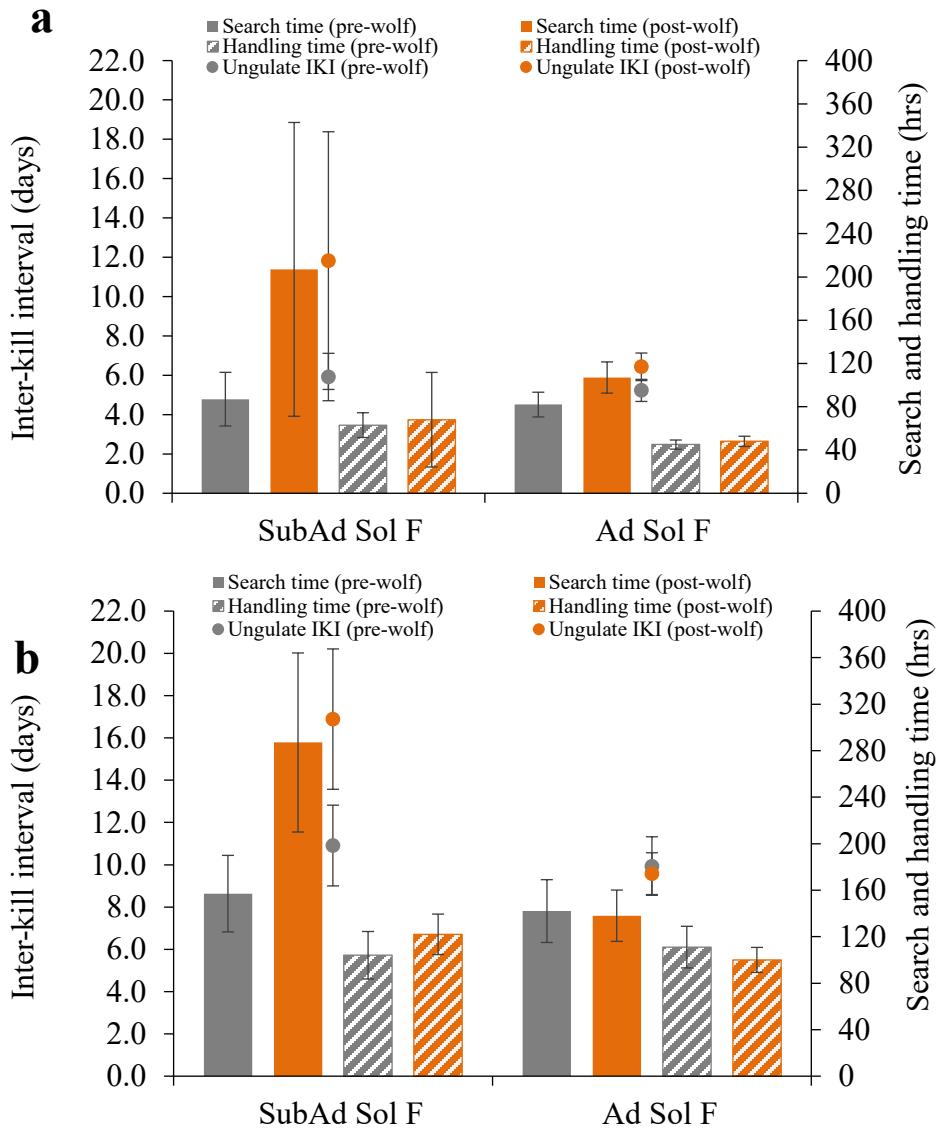


Figure 3.6. Seasonal estimate comparison of ungulate inter-kill interval (IKI; days), search and handling time (hrs), and associated 90% confidence intervals for cougars pre- ($n = 21$; 2009 – 2012) and post- ($n = 11$; 2014 – 2016) wolf recolonization by solitary female cougar age class in summer (a), and winter (b). Results were from 1,085 pre- and 430 post-wolf cougar predation events from 32 cougars fit with GPS collars in northeast Oregon, USA. Search and handling time was derived from IKI using data from cougar predation events where the date of the previous kill was known.

Mean handling times were 15% longer for cougars post-wolf recolonization ($\bar{x}_{\text{pre}} = 60$ hrs, 90%CI = 58 – 63; $\bar{x}_{\text{post}} = 69$ hrs, 90%CI = 65 – 74; %P = 0) and search times were 37% longer ($\bar{x}_{\text{pre}} = 103$ hrs, 90%CI = 97 – 110; $\bar{x}_{\text{post}} = 141$ hrs, 90%CI = 130 – 152; %P = 0.02). Post-wolf male cougars had 56% longer handling times in summer (Fig. 3.5a; %P = 0), while female cougars handling times were 14% longer in winter (%P = 1.4). Accounting for season, sex and age, differences in time spent searching for prey were most pronounced for solitary female cougars. In summer, adult solitary female cougars had 30% longer search times post-wolf recolonization (Fig. 3.5c; %P = 0.26), but there was no evidence of differences for subadult females (%P = 20.16). However, subadult solitary females had 83% longer search times in winter in the post-wolf period (Fig 3.5d; %P = 0.18).

DISCUSSION

Cougar Prey Use After Wolf Recolonization

Cougar preyed primarily on deer (mule deer and white-tailed deer combined) prior to wolf recolonization (Clark et al. 2014a). When we made comparisons across all cougars, annual predation patterns did not appear to have changed, with the overall proportion of deer and elk in diets similar for cougars across the annual cycle. However, when we investigated prey composition by season, we observed a switch in the most frequently used summer prey age class across all cougars from deer fawns (33.7%; Clark et al. 2014a), without wolves on the landscape, to elk calves (40%) after wolf recolonization of the study area. However, our evaluation of individual cougar diet compositions showed differences were more evident in female cougar diets, where post-wolf female cougars had less mule deer in their summer diets than respective pre-wolf female cougars, with no concurrent shift in the proportion of elk in female summer diets. We also observed a 6% increase in the frequency of scavenged prey remains, and a 3.2% increase in non-ungulate prey remains in cougar diets from pre- to post-wolf time periods. It is possible the decline we observed in the proportion of deer without an equivalent change in the proportion of elk in cougar diets was offset by food acquisition

from these other feeding behaviors. We believe the discrepancy between our comparison of proportional results for individual vs. all cougar diet count data highlight an important distinction understated in studies of cougar (and other carnivore) diet composition. The issue at hand equates to inappropriate sample unit designation and violation of statistical assumptions of independence and randomization when predation events/carcasses are treated as the sample unit as opposed to subsamples of events for individual cougar (Hurlbert 1984, Zarr 1999). Subsampling of predation events for individuals is often unequal (e.g. numerically, temporally), adding potential bias to population level inferences for individual level prey use and selection processes. Our use of permutation procedures accounts for any lack of randomization that might exist between our samples of cougars across study periods with regard to *t*-tests performed, but cross-study comparisons of overall cougar diet compositional changes should be considered cautiously.

Cougar Kill Rates After Wolf Recolonization

Contrary to our prediction that cougars would kill more often to meet energetic demands to offset interference competition, cougars killed less frequently, had lower numerical kill and biomass intake rates, and had longer search and handling times with wolves on the landscape. Our seasonal comparisons across study periods showed effects were unequal across cougar reproductive groups, largely effecting female cougar predation patterns. We observed summer kill rates of female cougars raising kittens < 6 months old to be 50% lower than rates for respective young cougar family groups before wolf recolonization. We found seasonal differences in the number of ungulates killed did not translate to differences in mean biomass intake rates (kg ungulates/wk/c) for post-wolf cougars regardless of reproductive status, consistent with seasonal kill rate correlation to mean prey size identified in other cougar studies (Knopff et al. 2010, Clark et al. 2014a). However, post-wolf female reproductive groups consistently had lower ungulate biomass intake rates than their respective pre-wolf cougar groups, on average 34% and 23% lower in summer and winter, respectively. Additionally, the longer search times we observed were most pronounced for solitary, subadult female cougars. This

could indicate spatial avoidance behavior tied to life stage traits, where inexperienced, non-territory-holding cougars mitigate intensity of interactions by reducing encounter rates with wolves. If increased search time also resulted in increased rates of movement (i.e. energy consumptive activity), less food intake would be an added cost with the greatest potential to affect cougar fitness and survival. This premise is consistent with other systems where wolves and cougars coexist, and necropsies of dead cougars revealed severe malnourishment (Ruth 2004a, Akenson et al. 2005, Kortello et al. 2007). The shifts in reproductive class biomass intake rates and search time we documented in this study could represent an important mechanism for how interspecific competition, and specifically interference competition, operates on the overall dynamics of cougar populations by affecting fitness and recruitment of young cougars into populations. The only female we monitored with > 6 month old kittens had the lowest biomass intake rate in our study (5 kg/wk over a 32-day period in summer), consistent with studies from the northern range in YNP after wolf recolonization, where orphaning, malnutrition, and wolf-caused mortality of cougar kittens occurred more frequently (Ruth et al. 2011). Wolf-caused mortality, competition-induced starvation, and slowed reproduction and recruitment in the absence of emigration from nearby source areas has the potential to produce cougar population declines (Kunkel et al. 1999, Ruth 2004b, Kortello et al. 2007) and our results are consistent with this paradigm.

Simultaneous predation monitoring with GPS based methods allowed us to document kleptoparasitism and scavenging events between wolves and cougars. Consistent with resource competition theory and results from other wolf-cougar studies (Kortello et al. 2007), these agonistic events appeared to be relatively rare. Although we aimed to identify direct interactions between wolves and cougars, our use of cluster methodology could have precluded our documentation of some kleptoparasitism events. For example, if a cougar was displaced less than 6 hours after making a kill, our collar fix rate and parameter definitions would not have identified a cluster for investigation.

Wolf-Cougar Competition

Interference competition is expected to have direct effects that result in the immediate exclusion of a competing individual (or population) from a resource (Krebs 1994, Ballard et al. 2003). Under this premise, the expectation is that interference competition with wolves would force cougars to prematurely abandon carcasses (e.g. kleptoparasitism), thereby shortening the intervals between predation events as a function of reduced handling times. We observed the opposite of this, with cougars exhibiting longer IKI, longer handling times, and longer search times in the presence of wolves. The relationship between mean monthly IKI and prey characteristics (size, age class) have been linked to seasonal variation in the proportion of juvenile ungulates (Knopff et al. 2010) and the mean weight of prey in cougar diets (Clark et al. 2014a). Under this premise, we would expect a larger mean prey weight to equate to higher proportions of larger age class deer or elk in summer cougar diets. While mean prey weight of summer carcasses was larger for cougars post-wolf ($\bar{x}_{\text{pre}} = 42 \text{ kg}$, SE = 1.68; $\bar{x}_{\text{post}} = 51 \text{ kg}$, SE = 3.62), our diet composition results did not show that cougars had increased the proportion of larger individuals in their diets. The decrease in several age classes of deer in female cougar diets and the increased amount of non-ungulate prey in all cougar diets would also create the effect of a larger mean prey size. Increased scavenging would also serve to lengthen intervals, and may partially account for the longer ungulate IKI observed in our study. Less than 10% of variation in IKI could be directly attributed to correlation with estimated prey weights for wolves ($R^2 = 0.09$, $P = 0.001$) or cougars ($R^2 = 0.04$, $P < 0.001$) in this study, and < 1 % of variation in cougar handling time was correlated with prey weight ($R^2 = 0.01$, $P = 0.04$). Combined these patterns suggest that the relationship between prey weight and IKI is complex and likely to reflect aspects of both the availability of different prey classes (i.e. density and distribution) and interspecific interactions (e.g. prey switching to non-ungulate prey and scavenging behavior).

Adequate niche differentiation (diet breadth/overlap or space use behavior) is expected to mitigate competitive exclusion effects and promote sympatric species coexistence (Krebs 1994). Dietary overlap in our study peaked in summer when elk calves were the primary prey identified in both wolf and cougar diets. Sufficient shared

resource density can mitigate competition effects. Thus, cougar use of elk calves may reflect use of an abundant prey resource limiting the severity of potential agonistic interactions with wolves. However, increased scavenging and use of non-ungulate prey coupled with lower summer kill rates and biomass intake rates relative to pre-wolf conditions provides reasonable evidence cougars in our study experienced interference competition with wolves. Of the two interval components, we observed stronger effects in the amount of time cougars spent searching for their next prey, which could mean cougars were spending more time actively avoiding wolves while they engaged in hunting.

MANAGEMENT IMPLICATIONS

The role interspecific interactions play in top-down effects from multiple carnivores and predator-prey dynamics is beginning to emerge for natural systems. Our estimates of cougar kill rates and our findings in relation to interspecific competition costs to cougar predation patterns can be applied to better anticipate and interpret wolf-cougar-ungulate dynamics. Whether patterns are generalizable across all wolf-cougar systems remains unclear and warrants further research. Beyond adding to the body of work characterizing the agonistic relationship between apex carnivores, our study begins to quantify the costs of interspecific competition (with wolves) for cougar populations in northeast Oregon. Importantly, expanding wolf populations do not obligate additive predation effects to ungulate prey populations with the addition of another carnivore to a system. Wolf recolonization simultaneously introduces elements of interspecific competition between wolves and other predators, including cougars. The strength of interspecific interactions, predator-specific sex and age class prey use, individual age class contributions to prey population growth, and the influence of abiotic (weather, disease, food limitation) factors determining species mortality will shape the implications of multiple predators for northeast Oregon and other systems with diverse carnivore communities. Our results parallel those of Tallian et al. (2017), demonstrating the capacity for interspecific interactions to counter-intuitively alter top-down effects by

reducing ungulate kill rates. Overlooking interspecific competition between predators could result in underestimating costs to subordinate competitor species and overestimating effects of multiple predators on prey populations.

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CHAPTER 4 – COUGAR HOME RANGE & PREDATION SITE
DISTRIBUTION FOLLOWING WOLF RECOLONIZATION
IN NORTHEAST OREGON

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ABSTRACT

Expanding populations of gray wolves (*Canis lupus*) could increase interspecific competition with populations of sympatric large carnivores, like cougar (*Puma concolor*), and alter predation effects on ungulate populations (e.g., elk, *Cervus elephas*; mule deer, *Odocoileus hemionus*). Interspecific competition can affect the spatial distribution, demography, and population dynamics of the subordinate predator, but the frequency and strength of agonistic interactions can be system specific. We used GPS collar data to evaluate spatial overlap and shifts in home range and predation site distribution based on kernel density estimates (KDE) generated for 1,213 cougar predation sites before (2009–2012) and 481 sites after (2014–2016) wolves recolonized northeast Oregon. We also compared cougar 50% and 95% and seasonal overlap of post-wolf cougar predation sites with density estimates from 107 wolf predation sites (2014 – 2015). Distribution of cougar predation sites differed between time periods with and without wolves and relative to areas wolves frequently made kills. Based on total predation site distributions, 19% of core summer range where cougars made kills overlapped core wolf prey use areas. Over annual periods, the amount of overlap between post-wolf cougars and wolves was down 9% at the 50% predation range scale and up 6% at the 95% predation range scale. Cougars were responding to the presence of wolves and our results suggest the spatial scale of that response occurs within a cougars' home range. Relative to pre-wolf cougar predation sites, post-wolf cougar predation sites were higher in elevation and closer to water. Coupled with little change in cougar diet composition, distributional shifts in areas cougar frequently kill prey could signal relatively unchanged effects to prey populations in this multi-predator system. Our study begins to quantify the costs of interspecific competition (with wolves) for cougar populations in northeast Oregon.

INTRODUCTION

Large carnivores have been expanding across portions of their historical range in North America, and populations of wolves (*Canis lupus*) and cougars (*Puma concolor*) are once again sharing habitat, home ranges, and prey resources (Kunkel et al. 1999,

Husseman et al. 2003, Ruth 2004), suggesting these coexisting apex predators are subject to the effects of interspecific competition (Ruth and Murphy 2010). Demonstrating competition effects through quantified measures or experiments has remained difficult for highly mobile terrestrial mammals like wolves and cougars that occur at relatively low densities. However, interspecific competition among carnivores can affect the spatial distribution, demography, and population dynamics of the weaker competitor (Fedriani et al. 2000, Terborgh and Estes 2010, Elbroch et al. 2015, Terborgh 2015), structure the dynamics of entire communities, and therefore warrants continued efforts to understand.

Strength of competition effects are often determined by the level of spatial overlap between sympatric competing species (Kitchen et al. 1999). The scale at which inter-species relationships manifest can be important because population level processes are often strongly influenced by individual-level mechanisms (e.g. movement linked to survival, food acquisition, or breeding success). How wolves and cougars distribute their home ranges, and the behavioral mechanisms that promote species coexistence remain poorly understood (Fuller et al. 2003). Wolves and cougars both typically have large, temporally variable (seasonal, reproductive period, etc.) home ranges (wolf ~ 293 – 891 km² in elk systems, cougar ~ 55 to > 700 km²; Mech and Boitani 2003, Bangs and Fitts 1993, USFWS et al. 2002, Hornocker and Negri 2010). While carnivore home range size may largely be influenced by prey density and distribution, subordinate predators also likely have to balance use of available resources within their ranges to maximize prey encounter and hunt success, and access to refugia to reduce potential intraguild predation or competition effects (Lendrum et al. 2014, Elbroch et al. 2015a, Elbroch et al. 2015b, Kusler et al. 2017). While it is well documented that cougar home range size and degree of overlap among individuals vary by sex (M~ 150 – 700 km², F~ 55 – 300 km², overlap greater among females; Logan and Swenor 2010), other intraspecific social aspects can also influence spatial distribution in cougars, with less rigid territoriality observed in some systems (Logan and Swenor 2000, 2001, 2010, Elbroch et al. 2015). Efforts to describe fine (daily activity) and course (seasonal) temporal variation in space use for both wolves (Kohl et al. 2017) and cougars (Bartnick et al. 2013) have highlighted the importance of investigating species relationships at multiple temporal and spatial scales.

Cougars specialize in killing disproportionately large prey, and typically spend extended periods of time (3 – 6 days) consuming a carcass when a kill has been made, often concealing prey remains of their kills from scavengers in a “cache” (e.g. remains drug into brush, covered with debris, etc.) to minimize carcass detection. Therefore these sites can also serve as epicenters of carnivore interactions (Ruth and Murphy 2010). Previous studies of wolf-cougar interactions have compared characteristics of wolf and cougar kill sites (Jason S Husseman et al. 2003, Woodruff 2006, Atwood et al. 2007, Bartnick et al. 2013, Woodruff et al. 2018) and demonstrated disproportionate habitat use (Alexander et al. 2006, Atwood et al. 2009), most often attributed to differences in hunting styles (coursing wolves vs. stalk-and-ambush cougars) and niche separation from an adaptive evolution standpoint. However, the question remains as to whether coexisting carnivores alter their behavior in measurable ways with regard to kill site placement on the landscape, or more specifically for cougars, cache site distribution. Quantifying the spatial distribution of predation patterns is an important step to understanding apex carnivore competition and potential effects to prey populations in multi-predator systems.

The absence of wolves over the last half of the 20th century may have allowed cougars to make use of vacated areas previously dominated by wolf use. The re-establishment of gray wolves, the dominant competitor in wolf-cougar interactions, could alter cougar behavior and change the distribution or space used by this subordinate competitor on the landscape (Lendrum et al. 2014, L Mark Elbroch et al. 2015, Elbroch and Kusler 2018). Threat of aggressive behavior (direct killing or injury) could cause the exclusion of cougars from a resource (i.e. competitive exclusion; Krebs 1994, Ballard et al. 2003). As the subordinate competitor, cougars might actively avoid wolves in order to reduce risks of food loss or direct mortality (Mills and Gorman 1997, Creel et al. 2001). If wolves monopolize shared prey resources, indirect competition effects of spatial avoidance behavior could reduce prey availability for cougars, increase the energetic costs of hunting (Gorman et al. 1998), and reduce cougar population density via limited access to prey (Creel et al. 2001). Competitive exclusion depends on degree of niche overlap, degree of spatial overlap, and availability of limited food and space resources (Ballard et al. 2003), such that if two sympatric species have adequate niche

differentiation they may coexist in a stable environment (Krebs 1994). Therefore, quantifying landscape-scale changes in the distribution of cougar home range or predation sites, or macro-scale characteristics at cougar kill or cache sites could provide evidence of resource partitioning and niche differentiation, and provide information about the strength of interspecific competition between these top carnivores.

Cougar predation patterns were established before wolf recolonization occurred (Clark et al. 2014a). We conducted a 3-year study after 3 wolf packs re-established sympatric use of the area and documented predation patterns for a sample of wolves and cougars (Chapter 2 & 3). The goal of this study was to evaluate the spatial response in home range and predation site distribution for a subordinate predator (cougars) after the recolonization of a dominant predator (wolf). Specifically, we wanted to answer whether: 1) the size and distribution of cougar home ranges had changed, 2) the distribution of predation sites had changed, 3) if macro-scale features of cougar predation sites had changed, and 4) if partitioning of wolf and cougar predation sites was evident in Oregon. We expected the presence of wolves to affect cougar space use, where active avoidance behavior would alter the spatial distribution of cougar home ranges relative to pre-wolf recolonization patterns. Further, we expected cougars and wolves in northeastern Oregon to exhibit resource partitioning in foraging niche based on evidence about wolf-cougar interactions in other systems (Alexander et al. 2006, Kortello et al. 2007, Atwood et al. 2009). We also considered cougars might shift their foraging niche, whereby selection of macro-scale features at predation sites could change relative to pre-wolf cougar selection. We considered evidence representative of resource partitioning if cougar predation sites occurred in areas disparate from wolf predation sites. If the indirect presence of, or direct interaction with wolves results in competitive exclusion from shared resources, we also expected a niche shift to be evident in the spatial distribution of cougar home range and predation sites between pre- and post-wolf recolonization periods.

METHODS

Study Area

We studied wolf-cougar spatial relationships in a 1,992 km² area of the Blue Mountain Range of northeast Oregon (Fig. 1). The study area contained a mixture of private, public, and tribal lands (Confederated Tribes of the Umatilla Indian Reservation; CTUIR), where the U.S. Forest Service (USFS; Wallowa Whitman and Umatilla National Forests) and the State of Oregon managed public lands, and private land was dominated by commercial agriculture and forest habitat, managed either as industrial forests or grazed rangelands (Clark 2014). Elevation ranged from 337 – 1,850 m, with vegetation strongly influenced by topography, aspect, and elevation. On the west side of the study area low elevation sites were dominated by exposed upland slopes and riparian areas comprised of hawthorn (*Crataegus columbiana*), willow (*Salix* spp.), and blackberry (*Rubus armeniacus*), with scattered ponderosa pine (*Pinus ponderosa*) and black cottonwood (*Populus trichocarpa*). Mixed-conifer stands with exposed southern aspects characterized high elevation sites in the central and eastern part of the study area with common species including ponderosa pine, douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), and lodgepole pine (*P. contorta*).

Oregon Department of Fish and Wildlife (ODFW) manages wildlife populations using discretely bounded areas known as Wildlife Management Units (WMUs). Cougar predation was studied in the Mt. Emily WMU before wolves recolonized northeast Oregon (2009 – 2012; Clark et al. 2014a), and we studied wolf predation and re-examined cougar predation after 3 wolf packs were documented in the WMU (2014 – 2016; Chapter 2 & 3). Some cougars and wolf packs occupied small areas outside Mt. Emily WMU in adjacent WMUs (Walla Walla, Wenaha, Catherine Creek, Ukiah, Starkey) over the course of monitoring.

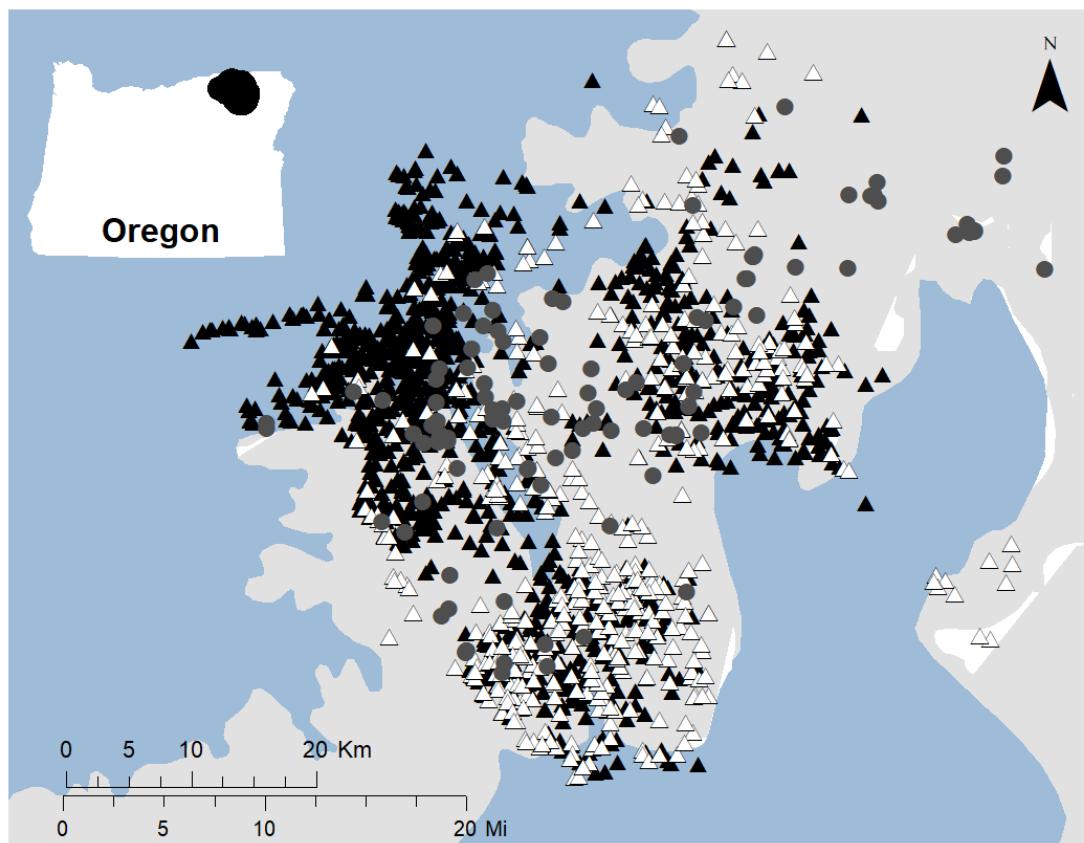


Figure 4.1. Study location in the Blue Mountain range of northeast Oregon, USA, where cougar distribution patterns were studied over time periods before (2009 – 2012) and after wolf recolonization (2014 – 2016). Black and white triangles represent predation sites obtained from 25 cougars before and 11 cougars after wolf recolonization, respectively. Gray circles represent predation sites obtained from 3 wolf packs from 2014 – 2016. Elk and mule deer range are shown in gray and blue, respectively.

Large prey species in the study area included primarily elk (*Cervus elephas*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*), with small, localized populations of moose, (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Feral horse (*Equus ferus caballus*) were also present on CTUIR lands (C. Scheeler, CTUIR, pers. comm.) and numerous smaller prey were available in the study area (e.g. ground squirrel (*Spermophilus spp.*), snowshoe hare (*Lepus americanus*), badger (*Taxidea taxus*), beaver (*Castor canadensis*), and raccoon

(*Procyon lotor*). Black bear (*Ursus americanus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and fox (*Vulpes vulpes*) also commonly occur in the study area.

Wolf and Cougar Data

Forty cougars and 17 wolves were captured between January 2009 and August 2018 (Clark et al. 2014a, Chapter 2 & 3). Cougars were captured with the aid of trained pursuit dogs following the American Society of Mammalogists' guidelines for wild animal use in research (Sikes and Gannon 2011) and procedures approved by the Institutional Animal Care and Use Committees of Oregon State University and USDA Forest Service – Starkey Experimental Forest and Range. Wolves were captured by Oregon Department of Fish and Wildlife (ODFW) as part of their wolf population monitoring program. We categorized the status of captured wolves as 1) single (alone), 2) part of a pair (two wolves), or 3) part of a pack (> 2 wolves). Wolf status was determined intermittently using GPS collar data (co-travel), trail cameras maintained by ODFW for wolf monitoring, or during annual aerial wolf count operations (conducted in January each year; R. Brown, personal comm.), so we may have misclassified status over short monitoring periods.

We fit captured animals with GPS radio collars (wolves: GPS PLUS II, $n = 13$, Vertex Survey, $n = 4$ [Vectronic Aerospace GmbH, Berlin, Germany]; cougars: Track M Basic, $n = 14$, GPS Plus, $n = 1$, 4400S or 7000SA, $n = 25$ [Lotek Engineering, Newmarket, ON, Canada]). Ultra-high frequency (UHF) and ARGOS platform GPS collars were used for cougars prior to wolf recolonization (see Clark et al. 2014) and we used Iridium platform GPS collars for cougars in the post-wolf colonization portion of the study (Chapter 3). Wolf GPS collars also used an Iridium platform and predation behavior was monitored for 3 wolf packs (Chapter 2). Collars used to monitor predation patterns were programmed to obtain fixes every 3 hrs for both species (2014 – 2016), but fix schedules were increased to every 30 min for wolves over summer predation monitoring periods (2014, 2015). During predation monitoring, mean fix success for collared wolves was 92.4% (range 77.8 – 97.2%), 72.0% (38.4 – 100%) for

UHF/ARGOS platform collared cougars and 93.4% (range 76.0 – 98.2%) for Iridium platform collared cougars. Outside of predation monitoring periods, fix schedules for wolf collars were highly variable depending on the number of collared wolves per pack and ODFW management goals; fixes ranged from 2 – 24 locations per day, with some irregular schedules (i.e. increased fix rates at crepuscular times), but the most common schedule were fixes every 3 hrs. Mean fix success for all GPS collared wolves was 85.4% (range 48.9 – 97.6%).

Thirty-five of the 40 GPS collared cougars were part of a predation behavior study (Chapter 3), with approximately 30 – 40 predation sites identified per cougar. We used 1,213 predation sites identified for 24 cougars before (2009 – 2012, Clark et al. 2014a) and 481 predation sites identified for 11 cougars after (2014 – 2016, Chapter 3) wolves recolonized the study area for spatial analyses. We identified 159 predation sites for wolves in the study area from 2014 – 2015 (Chapter 2), and used a subset of 107 wolf predation sites located within a 20-km buffer of the study area for spatial analyses (summer kills = 35, winter kills = 72). These kills included all age and sex classes of wolf- and cougar-killed prey. The majority of kills were native ungulate species (>90% of kills for both predators were elk, mule deer, or white-tailed deer). Non-ungulate prey were classified as “other” during field investigations and were typically small prey (< 15 kg) such as coyote, snowshoe hare, grouse spp., or turkey (Chapter 2 & 3, Appendix B). Distances between cougar cache and kill sites were not recorded during the initial pre-wolf cougar study, but we used a subset of 108 post-wolf cougar predation sites for which both cache and kill sites could be identified to determine drag distances and identify any potential bias with our use of cache vs. exact kill sites in our spatial analyses.

Spatial Analyses

Home Range Estimation. – We used a static measure of interaction based on home range overlap to evaluate distributional changes across study periods and between predator species. We used GPS locations to generate fixed kernel density estimates (KDE) of individual cougar, and population-level wolf utilization distributions (UD), and

built isopleth probability surfaces at the 50th and 95th percentiles (Millspaugh et al. 2004). We defined the 50th percentile as “core” use range, as this area contained 50% of locations for either wolves or cougars. We also estimated KDEs and overlap for individual wolves and packs (Appendix C), but made interspecific comparisons based on wolf population-level use. KDEs and isopleth home ranges were generated in Geospatial Modeling Environment (GME; Beyer 2012) using the PLUGIN bandwidth at a 30-m resolution.

We calculated spatial area overlap as the percent overlap in core and 95% KDE ranges following:

$$[(\text{area}_{\alpha\beta}/\text{home range}_\alpha)(\text{area}_{\alpha\beta}/\text{home range}_\beta)]^{0.5} \quad (1)$$

where $\text{area}_{\alpha\beta}$ is the overlapping zone common to α and β , and range_α and range_β are the 95% KDE ranges for individual cougar α and wolf population or pack β (Atwood and Weeks 2003). Index overlap calculations were carried out in ArcMap (version 10.3.1, Environmental Systems Research Institute, Redlands, CA, USA).

We then calculated mean percent overlap for individual pre- and post-wolf cougars and tested for differences between the two study periods with a Student’s t test. We considered the pre-wolf cougar overlap indices as a ‘prior’ distribution of cougar home ranges representative of naïve interspecies overlap for our comparison to post-wolf cougar home range overlap estimates. When t -statistics provided evidence of inequality (i.e. evidence of alternative hypothesis plausibility), we carried out permutation tests (5000 randomizations) to compare observed differences with distribution number of t -statistics calculated after randomly assigning study period to each overlap percentage (Manly 2001, Good 2005). For example, if there were 25 pre- and 15 post-wolf home range overlap indices for cougars, 25 of the 40 overlap indices were randomly assigned to the pre-wolf time period and the remaining 15 were assigned to the post-wolf time period. We then used the randomized distributions to obtain p-values for observed t -statistics by calculating the proportion of permuted statistics as far or further from zero than the one observed (Manly 2001). Therefore, reported p-values (%P) refer to levels of significance based on constructed t -distribution positioning of our sample of cougars, and increased levels of significance correspond with increased strength of evidence against

the null hypothesis of no difference between pre- and post-wolf cougar populations. Before making comparisons across study periods, we used ANOVA and Tukey's honest significance difference adjustment for multiple comparisons (Day and Quinn 1989) between groups known or suspected to influence cougar home range distribution patterns to account for differences based on: 1) cougar sex, or 2) season. For our assessment of seasonal differences we defined KDE range and overlap estimates from May – Oct as summer, and estimates from Nov – Apr as winter. For statistical analyses, we considered $P \leq 0.10$ as evidence of effect and inclusion as a grouping factor for cross species or study period comparisons. We carried out statistical analyses in R (R Core Team 2017). For our comparison of cougar distribution between study periods, we considered the lack of area overlap at the 95% and core home ranges as suggestive of strong and weak niche shift behavior, respectively. Similarly, for our evaluation of carnivore resource partitioning, we considered that lack of interspecific overlap at the 95% and core home ranges as suggestive of strong and weak avoidance of heterospecifics, respectively.

Predation Range Estimation. – As a secondary assessment of cougar niche shift, we evaluated cougar UD probability percentiles for changes in where cougars most frequently acquired prey across time periods with and without wolves. First, we used the cougar probability surface from the pre-wolf time period as a ‘prior’ distribution of predation sites and examined the proportion of post-wolf cougar predation sites in each contour. Second, to evaluate the distribution of prey use between predator species and across study periods we used a static measure of interaction based on the range overlap of areas where wolf and cougar predation occurred on the landscape. We generated population-level UDs for wolf and cougar predation sites to estimate the relative intensity of prey use across space for each species (Millspaugh et al. 2004). We calculated fixed KDEs and built isopleth probability surfaces at the 50th, 95th, and 99th percentiles (as described above for HR) to characterize the UD for wolf and cougar predation site ranges. For spatial comparisons, we defined the 50th percentile as described above, and further defined the 99th percentile as the “total” predation use range for each carnivore. We calculated spatial area overlap using Eqn. 1, where range_α and range_β were the core 50%, 95%, or total 99% KDE predation ranges for, 1) pre-wolf cougar α and post-wolf

cougar β , 2) pre-wolf cougar α and wolf β , and 3) post-wolf cougar α and wolf β . We made these comparisons at both the population level, using predation events from all wolf packs and cougars (pre- and post-wolf), and at the individual level for cougars (e.g. individual cougar ranges compared to population level wolf predation use range).

We also compared overlap of static predation site ranges based on 1) prey species, and 2) season, to evaluate if any seasonal or prey-species specific distributional effects were evident. We created prey species specific KDE for deer (mule deer and white-tailed deer combined), elk, and other prey species. We combined deer species to estimate deer-specific KDEs. Our sample size of wolf predation events precluded us from making seasonal prey-specific KDE comparisons for wolves and cougars. For our comparison of cougar prey use between study periods, we considered the lack of area overlap at the 95% and core ranges as suggestive of strong and weak niche shift behavior, respectively. Similarly, for our comparison of prey use between wolves and cougars, we considered that lack of interspecific overlap at the 95% and core ranges as suggestive of strong and weak avoidance of heterospecifics, respectively.

Latent Selection Differences

We investigated site-level changes in characteristics of cougar predation sites using latent selection difference functions (LSDF; Mueller et al. 2004, Fischer and Gates 2005, Erickson et al. 2014). LSDFs use a logistic regression framework to provide estimates of selection behavior differences and allow direct comparison of characteristics of use between two groups of interest, quantifying a measurement of relationship strengths (Latham et al. 2011, Latham et al. 2013, Erickson et al. 2014, Lendrum et al. 2017). We carried out two LSDFs to compare characteristics between wolves and cougars and between study periods for cougars. Using predator species as the dependent variable the model takes the form,

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i) \quad (3)$$

where $w(x)$ represents the relative probability of a cougar predation site (coded as 1) occurring on the landscape compared to a wolf predation site (coded as 0). The selection coefficient β_i is represented for each predictor variable (x_i) from a vector of covariates (x)

and is interpreted as the relative difference in selection between wolves and cougar, not the selection or use of a given habitat (Czetwertynski et al. 2007). To evaluate any changes in habitat characteristics at cougar predation sites across time periods, our second LSDF quantified the relative probability of a cougar predation site with wolves on the landscape (coded as 1) compared to a cougar predation site with no wolves (coded as 0). We used R to carry out logistic regression and the *lme4* package (Bates et al. 2011) to estimate coefficients contrasting any differences between wolves and cougar, and between cougar before and after wolf recolonization, as it relates to predation site characteristics. We carried out regressions over both annual and seasonal (winter, summer) time frames. This allowed variation in the distribution of ungulate prey (elk and deer) on the landscape associated with seasonal foraging range fidelity (Mao et al. 2005, Sawyer et al. 2006, Kauffman et al. 2007) to account for and characterize season-specific effects as well as broad-scale annual influences.

Our goal was to observe any predation site-level changes in attributes, therefore we included continuous abiotic and biotic explanatory variables (Table 4.1) already documented as associated with wolf and cougar predation site characteristics (Husseman et al. 2003, Atwood et al. 2009, Atwood and Gese 2010, Barwick and Van Deelen 2013). We developed input layers for each variable as 30-m resolution Geographic Information System (GIS) coverages in ArcMap. All layers were projected into NAD83 UTM Zone 11N (prior to extraction in Arc), screened for non-linearity using smoothed scatterplots, and pairwise tested to ensure no variables were highly correlated ($|r| > 0.7$) prior to regression (Hosmer and Lemeshow 2000). We added quadratic terms to distance variables when appropriate. For our analyses, we fit a global model including all non-correlated variables for each LSDF (wolf-cougar, cougar-pre/post) and inferred relative change in selection during annual, summer, and winter periods. To allow comparison of the magnitude of effects for regression coefficients and to facilitate model convergence, we standardized continuous predictor variables by subtracting their means and dividing by their standard deviations (Zurr et al. 2006, Gelman and Hill 2006). We used methods adapted from Czetwertynski (2007) and Latham et al. (2011), where exponentiated coefficients from our LSDF analyses are interpreted to mean that with every unit increase

in the proportion of, or distance to, a given feature, the relative selection of that feature by post-wolf cougars compared with wolves (or pre-wolf cougars) increased or decreased by $x\%$. Relative selection was calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$. For example, if $\beta = -1.5$ for variable A , the effect was calculated as $[1 - \exp(-1.5)] \times 100 = 78$, and inferred to mean that with every unit increase in variable A , relative risk of the selection of that feature by cougars was 78% lower than risk of selection by wolves.

Wolf Variables. – We considered several measures of wolf presence to evaluate whether wolves influenced cougar predation site characteristics and at what spatial or temporal scale. Our first measure was distance to nearest wolf predation site. Our second measure was distance to nearest 50% contour edge based on wolf predation KDEs. As a third measure, we used wolf predation site KDEs to obtain relative intensity of use based directly on UDs. Finally, to contrast any differences related to wolf use outside predation, we used a measure of the relative intensity of use based on wolf GPS location KDEs. Wolves were not known to be present in the study area at densities we would expect cougars to respond to during the pre-wolf time period (2 wolves recolonized in 2012). Therefore, for our second LSDF analysis we considered the mean measures of wolf variables relative to pre-wolf cougar predation sites as a hypothetical representation of how a naïve cougar population would select features and distribute their predation on the landscape without wolves, in contrast to cougar selection and distribution in the presence of wolves. We calculated distance (m) metrics using the Euclidean Distance tool in ArcMap.

Landscape Variables. – We used the 1-arc-second digital elevation model (DEMs; USGS National Elevation Dataset 2011) to obtain elevation (m), and to derive slope (i.e. steepness, or average change in vertical elevation per unit horizontal distance), and aspect (maximum rate of change in downslope direction) layers (degrees). We used sine and cosine functions to transform aspect into linear distance measures from east and north bearings, respectively. We derived a terrain ruggedness index (TRI) from DEMs using the Arc toolbox for Surface Gradient and Geomorphometric Modeling (version

2.0.0, Evans et al. 2014). TRI is a vector ruggedness measure of terrain heterogeneity, computed as the sum of absolute value elevation differences between a central grid cell (of a raster) and a designated number of nearest neighbors (3×3 grid = 8 neighbors; Riley et al. 1999, Sappington et al. 2007). We used existing road layers from ODFW (2014), Oregon Department of Forestry (ODF, 2015), and Oregon Department of Transportation (ODOT, 2011) to derive a single road layer encompassing multiple road use levels (highway, gravel, 4×4 dirt two-track, and decommissioned road beds). As our only anthropogenic related variable, we considered proximity to roads as the important feature that might be related to wolf and cougar predation site distribution. We obtained vegetation and stream data from the U. S. Geological Survey LANDFIRE (EVC – percent live forest canopy cover; Wildland Fire Science, Earth Resources Observation and Science Center 2010) and National Hydrography Datasets (NHD Flowline, Waterbodies, 2009) to generate distance to water and forest edge feature variables. We generated a simple random sample of 10,000 points in ArcGIS to obtain an estimate of the distribution of canopy cover values. Significant discontinuity in tree canopy cover distribution and natural thresholds for categorizing forest and non-forest raster cells is well recognized (Alexander et al. 2006, Bartnick et al. 2013), and we similarly observed a clear break in canopy cover at 15% across our study area. Therefore, we used a cell value of $\geq 15\%$ to represent forested cover, and values $\leq 14\%$ canopy cover to represent non-forested (i.e. open) habitat, and the Spatial Analyst ArcMap extension to reclassify canopy cover as a binary raster layer of “forested” (coded as 1), and “non-forested” (coded as 0) habitat. We then used the majority filter to replace cells with ≤ 4 agreeing neighbors with the majority value to reduce the number of forest patches likely insufficient for cougars to hunt or use as a prey cache, or as prey cover. We considered proximity to forested habitat as the important feature related to cougar predation site distribution. Therefore, we then used the ‘extractedge’ call in GME to create a line that defined the edge around groups of forest and non-forest cells. We calculated distance (m) to roads, water features, and forest edge using the Euclidean Distance tool in ArcMap.

Table 4.1 Variables used in latent selection difference functions (LSDFs) of wolf (*canis lupus*) and cougar (*puma concolor*) predation site characteristics in northeastern Oregon, USA, 2009 – 2018.

Variable	Description	Min	Max	Mean	SD
elev	Altitude (km)	0.3	1.8	1.0	0.3
slope	Average change in vertical elevation per unit horizontal distance (degrees)	0	47.0	14.4	11.5
east	Linear distance from east bearing (sine[aspect])	-1	1.0	0.0	0.7
north	Linear distance from north bearing (cosine[aspect])	-1	1.0	0.0	0.7
tri	Terrain ruggedness as the difference in elevation within 90 m	0	5.1	2.4	1.2
cc	Percent (0 - 100) tree canopy enclosure	0	75.0	21.5	21.7
dist.edge	Euclidean distance (km) to nearest forest edge	0	5.1	0.3	0.7
dist.water	Euclidean distance (km) to nearest water	0	2.4	0.2	0.2
dist.rds	Euclidean distance (km) to nearest road	0	2.4	0.3	0.3
dist.wps	Euclidean distance (km) to nearest wolf predation site	0	19.9	5.9	4.3
dist.wps.s	Euclidean distance (km) to nearest summer wolf predation site	0	31.4	10.8	7.3
dist.wps.w	Euclidean distance (km) to nearest winter wolf predation site	0	19.9	5.9	4.3
dist.waedge	Euclidean distance (km) to nearest wolf predation 50% contour edge	0	27.5	6.6	6.3
dist.waedge.s	Euclidean distance (km) to nearest summer wolf predation 50% contour edge	0	40.2	11.6	9.1
dist.waedge.w	Euclidean distance (km) to nearest winter wolf predation 50% contour edge	0	29.2	9.6	7.5
wolf.ps.use	Based on kernel density estimate (KDE) of wolf predation sites	0	0.00191	0.00039	0.00045
wolf.ps.use.s	Based on kernel density estimate (KDE) of summer wolf predation sites	0	0.00350	0.00041	0.00082
wolf.ps.use.w	Based on kernel density estimate (KDE) of winter wolf predation sites	0	0.00285	0.00038	0.00057
wolf.use	Based on kernel density estimate (KDE) of wolf locations	0	0.02745	0.00044	0.00117
wolf.use.s	Based on kernel density estimate (KDE) of summer wolf locations	0	0.03972	0.00044	0.00150
wolf.use.w	Based on kernel density estimate (KDE) of winter wolf locations	0	0.01086	0.00044	0.00082

RESULTS

We did not generate individual summer HRs for 4 cougars that lacked a sufficient number of GPS locations to generate estimates in that season. We also did not generate individual predation ranges for 8 cougars that lacked a sufficient number of predation sites (< 25 kills) to generate estimates. Over the duration of our study, the pack status of the 17 wolves we monitored varied. We generated HR estimates for all 17 individual wolves (Appendix C), and for wolf groupings based on pack status using combined GPS location data. We then made comparisons across pack ($n = 6$), pair ($n = 3$), and single wolves ($n = 2$) at the wolf population level using range estimates generated from locations of all 17 wolves.

Mean drag distance between cougar kill and cache sites was 9.2 m (range: 0 – 40 m). Although some classification errors based on kill or cache placement within a given pixel would still be possible, our observed drag distances were well within the 30-m resolution of our spatial data layers. Therefore, we carried out spatial analyses using our complete dataset of cougar cache/kill sites across study periods.

Home Ranges

Wolf Home Range. – Wolf HR sizes varied depending on whether wolves were members of established packs, newly formed pairs, or were single wolves (i.e. pack status) at both 50% ($F_8 = 54.23, P < 0.001$) and 95% ($F_8 = 22.3, P = 0.001$) use scales, and were highly variable among established packs (range_{50%}: 13.5 – 82.3 km², range_{95%}: 114.5 – 814 km²; Appendix C). Therefore, here we report mean HR sizes for wolves based on pack status. Mean annual 95% HR size for wolf packs in the study area was 348.6 km² (90%CI 180.9 – 517.2). HR sizes (95%) for single wolves that used the study area were 356% larger than established pack HR sizes, while newly formed wolf pair HR sizes were similar to those of packs ($\bar{x}_{\text{pairs}} = 317.6 \text{ km}^2, 90\% \text{ CI } 80.6 – 554.6$; $\bar{x}_{\text{singles}} = 1,590.1 \text{ km}^2, 90\% \text{ CI } 1,420.4 – 1,759.7$). Excluding single wolves, 95% HR sizes varied

with season ($F_{14} = 5.12, P = 0.04$), where winter HR sizes ($\bar{x} = 442.4 \text{ km}^2$, 90%CI 255.2 – 629.7) were 172% larger than summer HR sizes ($\bar{x} = 162.4 \text{ km}^2$, 90%CI 86.1 – 238.6).

Cougar Home Range. – Annual cougar HR size varied by sex at both 50% ($F_{37} = 11.23, P = 0.00186$) and 95% ($F_{37} = 7.242, P = 0.0106$) scales, with male ranges 96% and 71% larger than female ranges at core and 95% annual HR scales, respectively ($\bar{x}_{\text{male}50\%} = 53.2 \text{ km}^2$, 90%CI 39.8 – 66.5; $\bar{x}_{\text{female}50\%} = 27.2 \text{ km}^2$, 90%CI 21.3 – 33.2; $\bar{x}_{\text{male}95\%} = 230.4 \text{ km}^2$, 90%CI 179.9 – 280.8; $\bar{x}_{\text{female}95\%} = 135.0 \text{ km}^2$, 90%CI 102.0 – 168.2). Accounting for the influence of sex, we found marginal evidence supporting seasonal differences in 50% HR size ($F_{71} = 2.15, P = 0.12$), where the majority of male and female cougars for which we had range estimates across both seasons (21 of 35) had core summer ranges 19% – 242% larger than their respective core winter ranges ($\bar{x}_{\text{summer}} = 32.6 \text{ km}^2$, 90%CI 25.0 – 40.3; $\bar{x}_{\text{winter}} = 25.1 \text{ km}^2$, 90%CI 20.6 – 29.5). There was no evidence of seasonal differences in 95% HR size ($F_{71} = 0.73, P = 0.39$; $\bar{x}_{\text{summer}} = 141.5 \text{ km}^2$, 90%CI 110.8 – 172.1; $\bar{x}_{\text{winter}} = 135.9 \text{ km}^2$, 90%CI 109.7 – 162.1). When we accounted for sex and season we did not find evidence of any differences in 50% HR size between pre- and post-wolf periods for either male or female cougars in summer (Table 4.2; Female: $t_{18} = -0.47, P = 0.64$; Male: $t_8 = 0.72, P = 0.49$) or winter (Female: $t_{18} = 0.22, P = 0.83$; Male: $t_9 = 1.04, P = 0.33$). Though 95% HR sizes for male cougars were 50% and 53% larger in the post-wolf period during summer ($t_5 = 1.56, P = 0.18$) and winter ($t_6 = 1.28, P = 0.25$), respectively, there was only marginal evidence in support of this effect for either season and we therefore did not carry out permutation testing. We also found no evidence of study period differences in 95% HR size for female cougars during summer ($t_{18} = -0.17, P = 0.87$) or winter ($t_{20} = 0.33, P = 0.75$)

Table 4.2 Mean home range (HR) estimates (km^2) and associated 90% confidence intervals for 40 cougars used to compare distribution patterns over time periods pre- (2009 – 2012) and post-wolf recolonization (2014 – 2018). HR sizes were derived from 50% and 95% probability contours of kernel density estimates (KDE) for male ($n = 13$) and female ($n = 27$) GPS collared cougars over annual, summer (May – Oct), and winter (Nov – Apr) seasons in northeast Oregon, USA.

Cougar sex	Annual				Summer				Winter			
	Pre-wolf		Post-wolf		Pre-wolf		Post-wolf		Pre-wolf		Post-wolf	
	\bar{x}	90%CI	\bar{x}	90%CI	\bar{x}	90%CI	\bar{x}	90%CI	\bar{x}	90%CI	\bar{x}	90%CI
Male												
50% HR	48.0	32.3, 63.7	62.5	37.2, 87.8	50.1	32.9, 67.3	61.5	42.0, 81.0	27.2	17.1, 37.2	37.7	24.4, 50.9
95% HR	200.3	162.9, 237.6	284.6	161.8, 407.3	191.2	140.1, 242.3	287.0	199.9, 374.2	134.6	96.5, 172.7	206.6	122.7, 290.4
Female												
50% HR	28.7	19.9, 37.4	25.1	17.8, 32.3	23.0	11.5, 34.4	19.3	14.0, 24.6	21.2	14.7, 27.7	22.7	14.0, 31.3
95% HR	140.7	91.6, 189.8	126.6	86.1, 167.1	101.1	51.6, 150.6	95.3	71.7, 119.0	116.6	71.2, 162.0	130.6	77.0, 184.3

Wolf-Cougar Range Overlap. – Overlap of individual cougar HR with population-level wolf 95% use range was constant across study periods, with no evidence of overlap difference observed between pre- and post-wolf cougar ranges at 50% ($\bar{x}_{\text{pre}} = 10.3\%$, 90%CI 8.6 – 12.0; $\bar{x}_{\text{post}} = 10.5\%$, 90%CI 8.0 – 12.9; $t_{27} = 0.34$, $P = 0.93$) and 95% ($\bar{x}_{\text{pre}} = 22.3\%$, 90%CI 19.3 – 25.4; $\bar{x}_{\text{post}} = 22.6\%$, 90%CI 17.9 – 27.4; $t_{25} = 0.09$, $P = 0.93$) annual HR scales. Overlap with core wolf 50% use range was also constant, with no evidence of difference in overlap between pre- and post-wolf cougars at 50% ($\bar{x}_{\text{pre}} = 1.6\%$, 90%CI 1.0 – 2.6; $\bar{x}_{\text{post}} = 2.2\%$, 90%CI 0.0 – 4.5; $t_{18} = 0.37$, $P = 0.72$) or 95% ($\bar{x}_{\text{pre}} = 6.9\%$, 90%CI 4.3 – 9.5; $\bar{x}_{\text{post}} = 5.7\%$, 90%CI 2.6 – 8.7; $t_{32} = -0.50$, $P = 0.62$) annual HR scales. When we accounted for any differences in cougar home range size or distribution based on sex or season influences, overlap with wolf use range at all HR scales were similar with no evidence of difference between pre- and post-wolf cougars (Table 4.3, all $P > 0.20$). Winter 95% HR overlap with 95% wolf use range was 1.2 times higher (up 5.3%) for male cougars after wolf recolonization ($t_{12} = 1.20$, $P = 0.25$), but there was only marginal evidence in support of this effect and we did not carry out permutation tests.

Table 4.3. Mean percent cougar home range overlap with core (50%) and 95% wolf use range. Annual and seasonal (summer: 1 May – 31 Oct, winter: 1 Nov – 30 Apr) home ranges were derived from kernel density estimates of 25 pre- (2009 – 2012) and 15 post-wolf (2014 – 2018) cougar GPS locations ($n = 98,557$) and 38,324 GPS locations from 17 wolves (2012 – 2018) in northeast Oregon, USA.

Home range	50 % wolf use range		95% wolf use range	
	Pre (90%CI)	Post (90%CI)	Pre (90%CI)	Post (90%CI)
Male 50%				
Annual	1.6 (0, 3.2)	5.2 (0, 12.0)	12.7 (9.7, 15.6)	14.9 (12.0, 17.8)
Summer	3.4 (0.8, 6.7)	8.0 (0.9, 15.1)	10.8 (6.4, 15.2)	13.9 (9.0, 18.9)
Winter	3.3 (0.2, 6.1)	3.7 (0, 8.5)	10.9 (8.0, 13.8)	12.7 (10.7, 14.7)
Male 95%				
Annual	8.8 (4.4, 13.3)	10.0 (2.3, 17.7)	27.5 (22.7, 32.3)	30.7 (25.2, 36.2)
Summer	7.4 (3.7, 11.2)	12.4 (5.2, 19.6)	21.8 (14.7, 28.9)	22.4 (113.7, 31.0)

Winter	9.6 (3.3, 15.9)	12.6 (4.5, 20.8)	23.6 (18.0, 29.2)	28.9 (24.3, 33.5)
Female 50%				
Annual	1.7 (0.5, 2.8)	1.0 (0.1, 1.3)	8.9 (7.0, 10.8)	8.2 (5.5, 10.9)
Summer	1.6 (0, 3.0)	0.8 (0, 2.1)	7.0 (5.1, 10.0)	9.0 (5.4, 12.6)
Winter	1.6 (0, 3.2)	0.8 (0, 2.1)	7.4 (5.7, 9.0)	7.9 (5.7, 10.0)
Female 95%				
Annual	5.8 (2.5, 9.0)	3.5 (1.5, 3.4)	19.2 (15.8, 22.6)	18.6 (13.0, 24.2)
Summer	4.3 (1.6, 7.0)	2.1 (0, 4.4)	17.0, (12.0, 21.9)	18.6 (11.5, 25.7)
Winter	5.7 (2.2, 9.1)	3.4 (0.6, 6.2)	16.4 (12.9, 20.0)	19.5 (14.8, 24.2)

In order to consider any potential differences between cougar response to wolf use based on wolf locations (general presence) vs. wolf predation (epicenter of potential agonistic interaction), we also compared overlap of individual cougar HR with population-level wolf predation use range. We observed that while the magnitude of overlap varied based on both temporal and spatial scale (Table 4.3 & 4.4, Appendix C), the overall patterns were similar within each scale of comparison, with overlap at 95% ranges higher than 50% ranges. We similarly observed that over annual periods, there was little evidence of any difference in overlap with wolf predation range at either HR scale between pre- and post-wolf female cougars ($P > 0.36$), or at the 50% HR scale between pre- and post-wolf male cougars ($t_6 = 0.67$, $P = 0.52$). However, there was evidence 95% HR overlap with 95% wolf predation range was 1.57 times higher (up 1.6%) for post-wolf male cougars than respective pre-wolf male cougars ($t_7 = 2.34$, $\%P = 0.44$).

Cougar Predation Site Overlap

The proportion of post-wolf cougar predation sites per pre-wolf cougar predation site probability contour was consistent at the largest scales (99%, 95%), but deviated from expected proportions at the 75th percentile and continued to be 2 – 6 times less than expected within core 50% and 25% use areas over which cougars had acquired prey without wolves on the landscape (Fig. 4.2). Overall, areas where cougars acquired their food resources during annual periods changed very little, with 74% of population-level 95% cougar predation range overlapping between study periods (Fig. 4.3a).

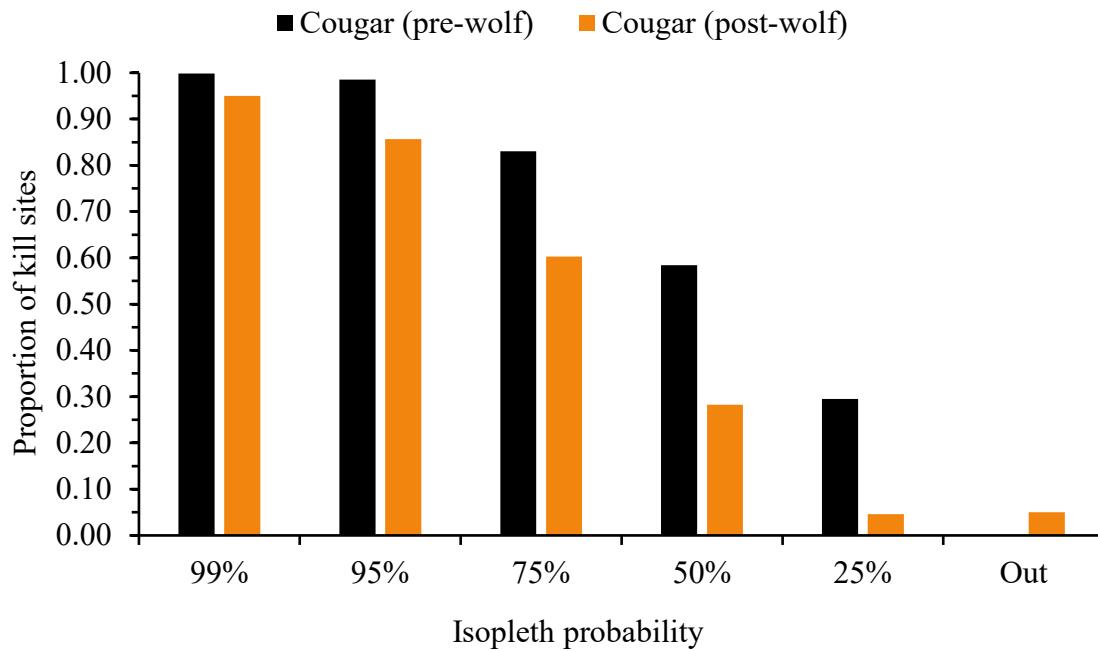


Figure 4.2. Proportion of post-wolf cougar predation sites ($n = 481$; 2014 – 2016) within each isopleth probability contour of pre-wolf cougar predation site distribution. Isopleth probability contours were derived from kernel density estimates of 1,214 pre-wolf use cougar predation sites in northeast Oregon, USA (2009 – 2012).

Table 4.4. Mean percent annual cougar home range overlap with core (50%), 95%, and total (99%) wolf predation range. Home ranges were derived from kernel density estimates of 98,557 GPS locations from 25 pre- (2009 – 2012) and 15 post-wolf (2014 – 2018) cougars and 107 wolf predation sites in northeast Oregon, USA.

Sex	50% wolf predation range		95% wolf predation range		99% wolf predation range	
	Pre (90%CI)	Post (90%CI)	Pre (90%CI)	Post (90%CI)	Pre (90%CI)	Post (90%CI)
Male						
50% HR	10.2 (4.2, 16.2)	8.6 (2.3, 15.0)	12.5 (9.1, 15.9)	15.9 (11.9, 19.9)	11.8 (9.1, 14.5)	14.9 (11.4, 18.4)
95% HR	1.7 (0.7, 2.6)	2.5 (0.7, 4.2)	2.8 (2.1, 3.4)	4.4 (3.4, 5.4)	2.8 (2.4, 3.1)	4.4 (3.4, 5.3)
Female						
50% HR	4.5 (2.5, 6.4)	2.8 (0.5, 5.0)	9.5 (7.9, 11.1)	8.2 (6.1, 10.3)	8.8 (7.4, 10.2)	7.8 (6.3, 9.3)
95% HR	1.8 (1.1, 2.6)	1.2 (0.2, 2.2)	3.1 (2.4, 3.8)	3.4 (1.9, 5.0)	3.0 (2.3, 3.6)	3.2 (1.9, 4.5)

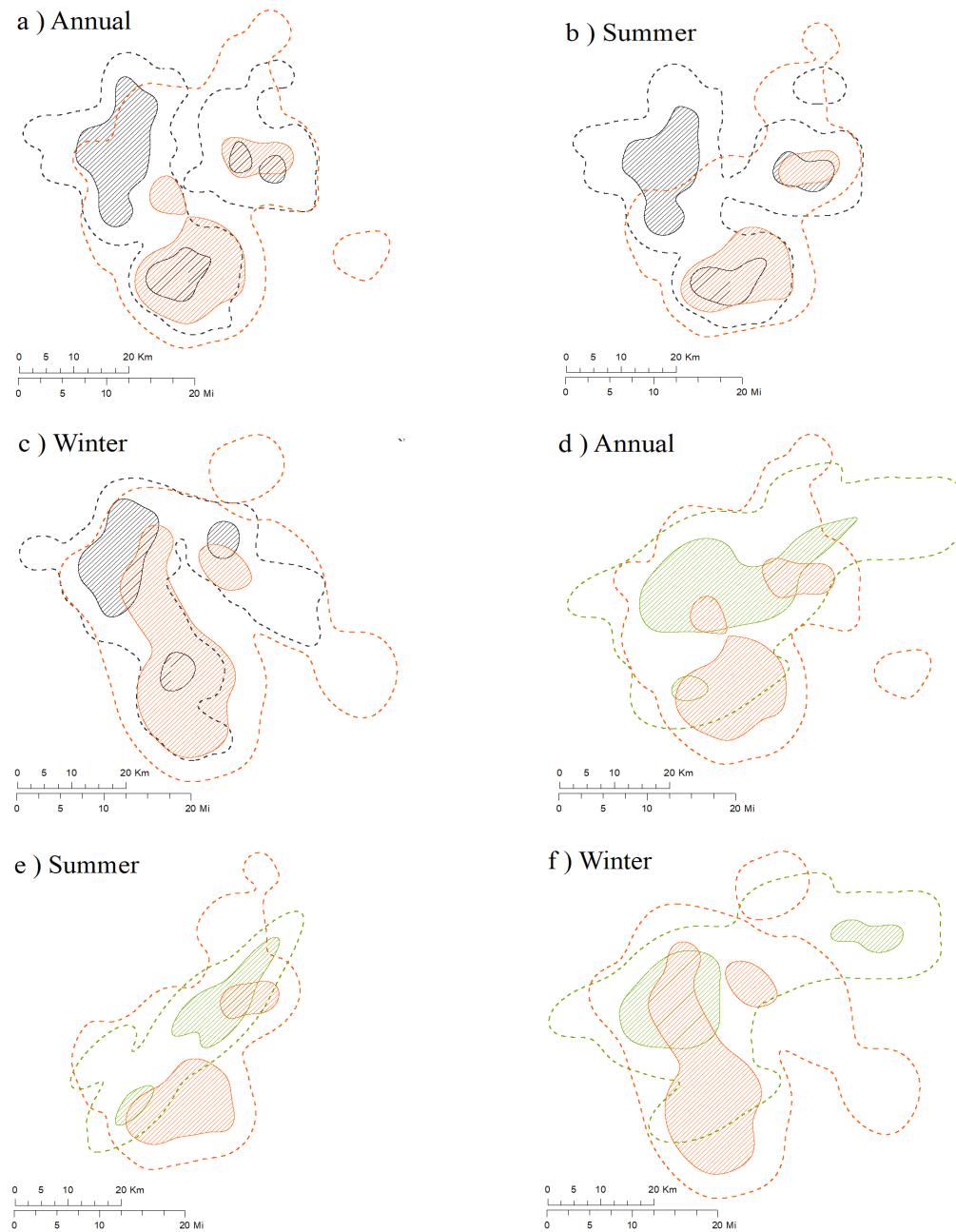


Figure 4.3 Predation range overlap for pre- and post-wolf cougars (a – c), and for wolves and cougars (d – f) over annual (a, d), summer (b, e), and winter (c, f) seasons. Ranges are 50% (diagonal slash) and 95% (dashed line) isopleth probability contours derived from population-level kernel density estimates of pre- (black, $n = 1,214$) and post-wolf

(orange, $n = 481$) use kills from 36 cougars and 3 wolf packs (green, $n = 107$) in northeast Oregon, USA (2009 – 2016).

However, there was less overlap of areas cougars frequented most often for food, with only 30% of cougar population-level 50% core predation use areas overlapping between time periods with and without wolves. Seasonally, the areas cougars acquired most of their food resources were similar with more than half their 95% predation ranges overlapping (66% and 71% across summer and winter, respectively; Fig. 4.3b, c). However, less overlap of areas frequented most for food was evident in both seasons, with only 38% of summer core use predation areas overlapping between pre- and post-wolf cougars. We observed further reductions in overlap between summer and winter, with only 22% of core use predation areas overlapping between pre- and post-wolf cougar populations in winter.

We observed differences in prey-species specific distributions of cougar predation across study periods (Fig. 4.4a – c, f). Areas where cougars acquired most of their deer prey (mule and white-tailed deer combined) were similar with more than half their 95% deer predation site ranges overlapping (66%), but only 12% of core 50% deer predation range overlapped between pre- and post-wolf cougar populations. We observed less change in the areas cougars acquired most of their elk prey, where 80% of their 95% elk predation use range overlapped, and 48% of core 50% elk predation range overlapped between pre- and post-wolf cougar populations. Coyotes made up the majority of prey at non-ungulate cougar predation sites (40 of 91), and the areas cougars acquired most of their coyote prey were dissimilar. Only 36% of 95% coyote predation site range overlapped, and 2% of core 50% coyote prey use range overlapped between pre- and post-wolf cougar populations.

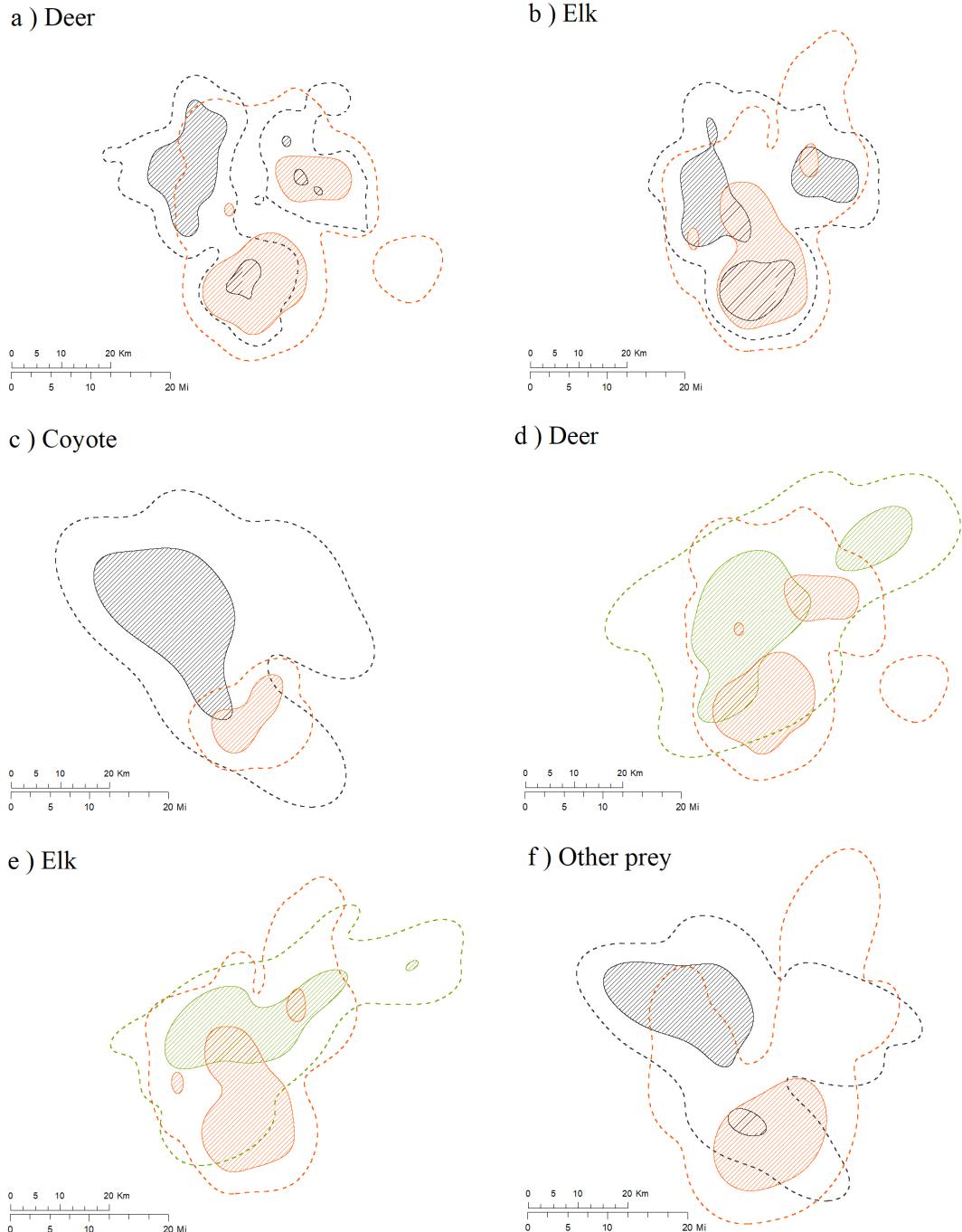


Figure 4.4 Prey-species specific predation range overlap for pre- and post-wolf cougars (a – c, f), and for wolves and cougars (d – e) for deer (a, d), elk (b, e), coyote (c), and other prey (f) over annual periods. Ranges are 50% (diagonal slash) and 95% (dashed line) isopleth probability contours derived from population-level kernel density estimates of

pre- (black, $n = 1,214$) and post-wolf (orange, $n = 481$) kill sites from 36 cougars and 3 wolf packs (green, $n = 107$) in northeast Oregon, USA (2009 – 2016).

Spatial Overlap in Wolf and Cougar Predation Sites

Overall, areas wolves and cougars acquired their food resources during annual periods were similar, with 72% of population-level 95% predation range overlapping between carnivore species (Fig. 4.3d). However, there was less overlap of areas frequented most often for food, with only 23% of population-level cougar 50% core predation use areas overlapping population-level wolf core predation use areas. Seasonally, the areas where wolves and cougars acquired most of their food resources were similar with more than half their 95% predation site ranges overlapping (66% and 61% across summer and winter, respectively; Fig. 4.3e, f). However, less overlap of areas frequented most for food was evident in both seasons, with only 33% of winter core use areas overlapping between species. We observed further reductions in overlap between winter and summer, with only 19% of core use areas overlapping between wolves and cougar in summer.

We observed differences in prey-species specific distributions of wolf and cougar predation in the study area (Fig. 4.4d – e). Areas wolves and cougars acquired most of their deer prey (mule and white-tailed deer combined) were similar with more than half their 95% deer predation site ranges overlapping (66%), but only 18% of core 50% deer predation range overlapped between wolf and cougar populations. We observed similar patterns in areas wolves and cougars acquired most of their elk prey, with 72% of their 95% elk predation range overlapped, and 21% of core 50% elk predation use range overlapped between species.

When we compared annual, seasonal, and prey-species specific wolf-cougar overlap with the theoretical overlap pre-wolf cougar populations would have “shared” with wolves, the amount and direction of change in overlap varied based on both temporal and spatial scale. Over annual periods, the amount of overlap between post-wolf cougars and wolves was down 9% at the 50% predation range scale and up 6% at the 95% predation range scale. However, overlap between post-wolf cougars and wolves was

consistently higher over seasonal periods, relative to pre-wolf cougar overlap with wolves; up 5% and 15.5% at the 50% and 95% summer predation range scales, respectively. Overlap in winter was 4% higher over both spatial range scales. Disparity in direction and amount of overlap was most pronounced in cougar-elk predation ranges. Relative to pre-wolf cougar overlap with wolf-elk predation range, post-wolf cougar overlap with wolf-elk predation range was down 19% and up 2% at 50% and 95% elk predation range scales, respectively. Less change was evident in cougar-deer predation ranges, where post-wolf cougar overlap with wolf-deer predation range was down 2% and up 2% at 50% and 95% deer predation range scales, respectively.

Carnivore Predation Latent Selection Differences

In general, over the annual period cougar predation sites were closer to water sources ($\beta = -0.34$, Appendix C) relative to wolf predation sites, where every 1 km increase in distance to water, reduced relative risk of selection by cougars compared with wolves by 29%. Relative to wolf predation sites, cougar predation sites were also more likely to occur in more rugged terrain ($\beta = 0.38$), with every unit increase in ruggedness increasing risk of selection by cougars by 1% compared with wolves. In summer, cougar predation sites were more likely to occur at lower elevations ($\beta = -0.64$, Table 4.5), and closer to water ($\beta = -0.30$), with every 1 km increase in elevation or distance to water reducing risk of selection by cougars relative to wolves by 47% and 26%, respectively. In winter, cougar predation sites were more likely to occur in rugged terrain ($\beta = 0.75$, Table 4.6) and farther interior from forest edges ($\beta = 0.48$), with every unit increase in ruggedness and 1 km distance from forest edge increasing risk of selection by cougars relative to wolves by 2% and 2%, respectively. Similar to summer, cougar predation sites in winter were also more likely to occur closer to water ($\beta = -0.38$), with every 1 km increase distance to water reducing risk of selection by cougars relative to wolves by 32%.

Table 4.5. Latent selection difference function (LSDF) model comparing relative predation site feature selection by wolves (*Canis lupus*; coded as 0) and cougars (*Puma concolor*; coded as 1) over summer periods in northeastern Oregon, USA, 2014 – 2016.

Variable	β	SE	P	Relative selection (%) ^a
Elevation	-0.6382	0.2339	0.0044	47
Eastness	0.0246	0.2873	0.9298	1
Northness	0.2970	0.2587	0.2717	1
Terrain ruggedness	0.1962	0.2677	0.4521	1
Distance to forest edge	-0.2580	0.1817	0.1153	23
Distance to water feature	-0.2994	0.1966	0.0967	26
Distance to road	-1.1131	0.6836	0.1580	67
Distance to road ²	1.1908	0.8794	0.2816	3

^a Relative selection calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$. Relative selection for variables with $\beta < 0$ should be interpreted as with every unit increase in the proportion of, or distance to, said feature, the relative selection of that feature by post-wolf cougars compared with wolves is reduced by $x\%$.

Table 4.6. Latent selection difference function (LSDF) model comparing relative predation site feature selection by wolves (*Canis lupus*; coded as 0) and cougars (*Puma concolor*; coded as 1) over winter periods in northeastern Oregon, USA, 2014 – 2016.

Variable	β	SE	P	Relative selection (%) ^a
Elevation	-0.2326	0.1732	0.1658	21
Eastness	-0.0540	0.2257	0.8032	5
Northness	0.0460	0.2116	0.8324	1
Terrain ruggedness	0.7529	0.1938	0.0003	2
Distance to forest edge	0.4798	0.2112	0.0077	2
Distance to water feature	-0.3809	0.1802	0.0275	32
Distance to road	-0.0811	0.4305	0.8746	8
Distance to road ²	0.2625	0.4457	0.6897	1

^a Relative selection calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$. Relative selection for variables with $\beta < 0$ should be interpreted as with every unit increase in the proportion of, or distance to, said feature, the relative selection of that feature by post-wolf cougars compared with wolves is reduced by $x\%$.

Cougar Predation Latent Selection Differences

Over the annual period post-wolf cougar predation sites were higher in elevation ($\beta = 0.98$, Appendix C) and closer to water ($\beta = -0.16$), with every 1 km increase in elevation increasing risk of selection by 3%, and every 1 km increase in distance to water reducing risk of selection by 15%, relative to pre-wolf cougars. Post-wolf cougar predation sites were also more likely to occur in areas of lower intensity wolf use ($\beta = -0.28$), with every unit increase in wolf use reducing risk of selection 24% by post-wolf cougars. In summer, post-wolf cougar predation sites were more likely to occur at higher elevations ($\beta = 1.14$, Table 4.7), with every 1 km increase in elevation increasing risk of selection by post-wolf cougars relative to pre-wolf cougars by 3%. Similar to annual periods, post-wolf cougar predation sites in summer were also more likely to occur in areas of lower intensity wolf use ($\beta = -0.28$), with every unit increase in wolf use reducing risk of selection by post-wolf cougars by 25%. In winter, post-wolf cougar predation sites were again more likely to occur at higher elevations ($\beta = 0.75$, Table 4.8), but also further from forest edges ($\beta = 0.48$), with every 1 km increase in elevation and distance from forest edge increasing risk of selection by post-wolf cougars relative to pre-wolf cougars by 2% and 1%, respectively.

Table 4.7. Latent selection difference function (LSDF) model comparing relative predation site feature selection by pre- (coded as 0) and post-wolf (coded as 1) cougars (*Puma concolor*) over summer periods in northeastern Oregon, USA, 2009 – 2016.

Variable	β	SE	P	Relative selection (%) ^a
Elevation	1.1416	0.1343	< 0.0001	3
Eastness	-0.1103	0.1079	0.3106	10
Northness	0.0368	0.1077	0.7265	1
Terrain ruggedness	0.0077	0.0990	0.9389	1
Distance to forest edge	-0.1073	0.0791	0.1645	10
Distance to water feature	-0.1546	0.0899	0.0707	14
Distance to road	-0.0524	0.2115	0.8146	5
Distance to road ²	0.3404	0.1800	0.0990	1
Distance to summer wolf predation 50% KDE contour edge	0.6737	0.3102	0.0325	2
Distance to summer wolf predation 50% KDE contour edge ²	-1.3990	0.4548	0.0021	75
Intensity of summer wolf use	-0.2821	0.1201	0.0314	25

^a Relative selection calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$. Relative selection for variables with $\beta < 0$ should be interpreted as with every unit increase in the proportion of, or distance to, said feature, the relative selection of that feature by post-wolf cougars compared with pre-wolf cougars is reduced by $x\%$.

Table 4.8. Latent selection difference function (LSDF) model comparing relative predation site feature selection by pre- (coded as 0) and post-wolf (coded as 1) cougars (*Puma concolor*) over winter periods in northeastern Oregon, USA, 2009 – 2016.

Variable	β	SE	P	Relative selection (%) ^a
Elevation	0.8508	0.1219	> 0.0001	2
Eastness	-0.0397	0.1408	0.7777	4
Northness	0.1341	0.1389	0.3302	1
Terrain ruggedness	0.1963	0.1411	0.1700	1
Distance to forest edge	0.2017	0.0968	0.0470	1
Distance to water feature	-0.0294	0.0975	0.7792	3
Distance to road	-0.0732	0.2720	0.7921	7
Distance to road ²	0.1932	0.2331	0.4510	1
Distance to winter wolf predation 50% KDE contour edge	-0.8565	0.3234	0.0149	58
Distance to winter wolf predation 50% KDE contour edge ²	1.3023	0.3197	0.0002	4
Intensity of winter wolf use	-0.2162	0.1990	0.1850	19

^a Relative selection calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$. Relative selection for variables with $\beta < 0$ should be interpreted as with every unit increase in the proportion of, or distance to, said feature, the relative selection of that feature by post-wolf cougars compared with pre-wolf cougars is reduced by $x\%$.

DISCUSSION

Wolf home range sizes are heavily influenced by prey biomass (i.e. primary prey type, moose vs. elk vs. deer), density, and distribution, but also pack size, mean annual rate of population change (wolf population growth), season, and landscape scale habitat types (Fuller et al. 2003). Smaller summer and larger winter home ranges are consistent with limited mobility of young wolves over denning and pup rearing periods, and movement to maintain access to food in the form of migratory prey populations, respectively. Even though home range size was highly variable across individual wolves in our study, overall pack HR sizes were consistent with sizes reported for other wolf-elk systems and the expanding nature of Oregon's wolf population. Cougar home range sizes in northeast Oregon were also consistent with sizes reported for other cougar populations (Hornocker and Negri 2010). An increase or decrease in home range sizes might have indicated a response by cougars relative to competition with wolves (e.g. avoidance, or change in prey distribution/abundance = increase; restricted movement or exclusion from prey resources = decrease), but we did not observe those changes in this study. The consistency we observed in cougar home range sizes across time periods with and without wolves could be a reflection of evolutionary niche requirements unaffected by the time-scale of wolf absence, but also suggests stability in the system relative to the features incorporated by a cougar's home range (access to food, mates, refugia).

We believe this is the first study to conduct a comparison of home range and predation site range overlap between pre- and post-wolf cougar populations. The size and distribution of pre-wolf cougar home ranges should have no relation to wolf predation or intensity of use (i.e. random relative to knowledge of, or response to wolves), and we believe demonstrated a naïve 'prior' representation of static cougar space use of the landscape. If wolf presence and interaction affected cougar home range size and distribution on the landscape we would have expected overlap indices to change between pre- and post-wolf cougars. The lack of change we observed suggests cougar placement of their home ranges on the landscape was unchanged, relative to the presence of wolves. We did observe some evidence male cougars might be spatially responding to the presence of wolves based on increased 95% male cougar home range overlap with 95%

wolf predation range during the post-wolf time period, but the 1.6% increase we observed may not be biologically meaningful.

There were small-scale shifts in the distribution of cougar predation on the landscape, but the change we observed could have resulted from mechanisms other than competition with wolves. If prey population density (deer abundance) or distribution changed, the distribution of cougar predation would likely also change. However, the general agreement in individual cougar home range distributions does not support the idea of a large-scale change in prey distribution. Like many western states in the U.S. (Wallmo 1981, Unsworth et al. 1999), Oregon has observed fluctuations in mule deer population trends (ODFW Mule Deer Herd Reports 2009 – 2017, Peek et al. 2002). As mule deer are the primary ungulate prey of cougar in northeast Oregon (Chapter 3), fluctuations in mule deer abundance could affect cougar populations and the distribution of predation locations (i.e., sites where they are capturing prey). However, it's difficult to determine if the magnitude of deer population declines are representative of a prey decline that would result in a behavioral response from cougars (i.e. indirect effect of functional response, see Chapter 3). Alternatively, the changes we observed could be an indirect effect of wolf presence through a prey behavioral response resulting in altered activity or space use patterns by ungulate prey (i.e. behavioral trophic cascade, landscape of fear concepts; Beckerman et al. 1997, Laundré et al. 2001, Kauffman et al. 2010, Laundré 2010).

Wolf-Cougar Interactions and Community Effects

Results from our latent selection analyses suggest that while broad scale patterns of cougar predation were similar, cougars were responding to the presence of wolves. Our results also suggest the spatial scale of that response is likely a result of individual-level movement that occurs within a cougars' home range (i.e. patch-level 4th order selection; Johnson 1980). Inarguably, we observed a change in the distribution of cougar predation sites, evident as shifts observed in the core areas cougars used to acquire most of their food resources related to expected proportions across study periods. This is consistent with local scale shifts in space use that might come about from competitive

interactions. The high overall range overlap at the largest spatial scales and our uncertainty with regard to mechanisms mean our findings are inconclusive, but our results do provide weak evidence of a shift in the realized niche of cougars in the study area after wolf recolonization.

Although our results clearly demonstrate a shift in cougar predation site distribution from time periods without wolves, the mechanisms causing that shift are not as clear. We carried out our spatial analysis using the predation site as the sample unit. Agreement based on overlap of paired individual cougar home and predation range estimates was fairly high (75%, range: 48 – 87%) at larger (95% HR) spatial scales, but less consistent (55%, range: 18 – 78%) at the 50% core use spatial scale (see Appendix C for details). This could have introduced bias to our results for a territorial carnivore like cougars, where individual traits like reproductive status (e.g. females with kittens vs. males) or hunt success (age related) could influence an individual's access to prey through changes in abundance or availability. These factors could have influenced where and how cougars moved around their ranges, thereby affecting encounter rates with wolves and the intensity of competitive interactions; which was not accounted for in our measures of static range overlap. Changes in prey base could also be indirectly influenced by wolves through ungulate response to risk of predation by a coursing vs. ambush predator, which could alter ungulate distribution, in turn altering cougar distribution.

Interference competition is expected to have direct effects that result in the immediate exclusion of a competing individual (or population) from a resource (Krebs 1994, Ballard et al. 2003). Under this premise, the expectation is that interference competition with wolves would force cougars to shift their distribution to use of unoccupied or potentially lower quality habitat. However, we observed considerably more overlap between wolf and cougar predation ranges at larger spatial scales than we would expect if there were strong competitive effects and complete exclusion of cougar from shared prey resources. The amount of overlap we observed was consistent with our predictions of wolves competing with cougars, but suggested weak competitive avoidance by cougars. Adequate niche differentiation (diet breadth/overlap or space use behavior) is expected to balance exclusion effects and promote sympatric species

coexistence (Krebs 1994). Our results demonstrated that at a smaller spatial and temporal scale (summer), when wolves and cougars have the greatest dietary overlap, some spatial partitioning was evident in space use. The least amount of overlap in space use between wolves and cougars coincides with the period both were making use of the same prey resource, i.e., elk calves (Chapter 2 & 3). Expanding wolf populations simultaneously introduce elements of interspecific competition, which can alter the realized niche other predators, including cougars, and how the members of carnivore communities distribute themselves on the landscape. Overlooking interspecific competition between predators could result in underestimating costs to subordinate competitor species and overestimating effects of multiple predators on prey populations. As wolf populations continue to expand, additional research is needed to clarify the effect of wolves and cougars on prey behavioral response and ungulate population dynamics.

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CHAPTER 5 – SPATIAL CONSEQUENCES IN COUGAR DIEL
ACTIVITY AND HABITAT SELECTION FOLLOWING WOLF
RECOLONIZATION

Elizabeth K. Orning, Katie M. Dugger, and Darren A. Clark

ABSTRACT

After a 40-year absence from Oregon's landscape, expanding gray wolf (*Canis lupus*) populations are reestablishing elements of interspecific competition with sympatric large carnivores, like cougars (*Puma concolor*). We evaluated activity patterns (distance traveled, rates of travel, time of day) for cougars before (2009-2012) and for wolves and cougars after (2014-2018) wolves recolonized northeastern Oregon. We compared movement rates (km/hr) based on 42,892 and 48,723 GPS relocations of cougars from pre- and post-wolf periods, respectively. We also compared diel patterns of cougars with patterns generated from 79,437 GPS relocations of northeast Oregon wolves. Cougar movement and diel activity differed between time periods. Cougars moved shorter distances per 3-hr time step with wolves on the landscape ($\bar{x}_{\text{pre}} = 0.60 \text{ km}$, 90%CI 0.49 – 0.70; $\bar{x}_{\text{post}} = 0.43 \text{ km}$ 90%CI 0.38 – 0.47, %P = 0.34). We observed a change in the pattern of cougar activity over the diel cycle from peak movement rates in the evening followed by night > day > morning, peak rates of activity in the evening > morning > night > day. We used step-selection functions (SSFs) and a two-stage approach to incorporate movement and evaluate individual and population level selection for three variables associated with spatial risk of wolf interaction (openness, wolf kill density, wolf intensity of use). We found that female cougars were selecting for less open habitats in winter after wolf recolonization (%P = 0). By examining individual selection we were able to demonstrate different competition mitigation strategies between male and female cougars. Our results demonstrated cougars changed aspects of their activity that may exemplify an optimal foraging strategy to balance fitness costs of competition.

INTRODUCTION

Recolonizing wolf populations in western North America have provided a platform to observe dynamic processes that can improve our understanding of predator-prey and predator-predator dynamics. As a foundational ecological concept, it is well-accepted that interspecific competition can affect the feeding patterns, spatial distribution, and population dynamics of a subordinate competitor (Holt and Polis 1997, Linnell and Strand 2000, Creel et al. 2001). However, because the fitness or population costs of

exploitative (e.g. consumption of a shared resource to the point of population limitation) and interference (e.g. direct contests, injury, or killing) competition have remained difficult to quantify in free-living carnivores, there is a paucity of evidence linking the mechanisms of competition between apex predators, like wolves (*Canis lupus*) and cougars (*Puma concolor*), with the theoretical dynamics of competition.

In addition, sympatric predators that compete for shared prey resources could involve intraguild predation (Polis and Holt 1992, Sih et al. 1998, Sitvarin and Rypstra 2014). This suggests subordinate predators may also engage in balancing risk of intraguild predator encounters with procurement of food through hunting. Risk of predation is recognized as a factor strongly influencing species' distribution and animal behavior, but is often studied from the standpoint of prey species in predator-prey dynamics (Gervasi et al. 2013, Latombe et al. 2013, Middleton et al. 2013, Kohl et al. 2017), or across carnivore guild members largely disparate in body size (Palomares and Caro 1999, Donadio and Buskirk 2006, Levi and Wilmers 2012). While predator density is generally thought to be the main predictor of predation risk for classic predator-prey interactions, fine-scale landscape structure can induce large variation in predation risk independent of density effects (Mark Hebblewhite et al. 2005, Atwood et al. 2009, Gervasi et al. 2013). The importance of landscape structure and associated space use on both predator encounter rate of prey and success at killing prey may be more important than the influence of prey density (Forester et al. 2007, Kauffman et al. 2007, 2010, DeCesare 2012b, Middleton et al. 2013).

How predators involved in intraguild dynamics perceive risk of predation by other predators, and at what scale a subordinate predator responds to risk could have important implications on predation processes for ungulate populations as well as cascading trophic effects to entire communities. Aggressive interspecific interactions from interference competition (killing, exclusion from areas) are the most likely to be detected, as they are also the most likely to produce large scale patterns in carnivore spatial distributions. When a competing predator is relegated to a subordinate position in a system, whether a classic “prey” response can be expected is not clear, though some evidence has been emerging for cougars (Lendrum et al. 2014, L. Mark Elbroch et al. 2015, L. Mark Elbroch

et al. 2015a, Kusler et al. 2017). Persistence of prey populations is theorized to depend on heterogeneity in predation rates resulting from spatial or temporal refugia (i.e. predator-prey shell games; Kittle et al. 2008, Laundré 2010, Kohl et al. 2017). While access and use of spatial refugia are common outcomes associated with avoidance behavior evident through spatial partitioning of resource use or selection, use of spatio-temporal refugia (same space, different times) is equally capable of shaping community dynamics (Lendrum et al. 2014, L Mark Elbroch et al. 2015, Elbroch et al. 2017).

Time allocation is inarguably involved in how animals manage predation risk (i.e. vigilance, optimal foraging relative to patch use), but time is often subsumed to a static assumption of fixed risk relative to predator presence. Technological advancement in Global Positioning Systems (GPS) has improved our ability to collect high quality spatial and temporal data, allowing us to investigate and quantify how subordinate predators balance acquisition of necessary resources (food in the form of prey) and the risk of competition or predation from intraguild members of re-established carnivore communities. How animals respond to risk in space and time has been gaining momentum as an important feature of predator-prey interactions and intraguild interactions (Dröge et al. 2017, Kohl et al. 2017, Gaynor et al. 2019), and therefore warrants efforts to understand these relationships between carnivores as predator guilds are re-established through population recolonizations.

We conducted a 9-year study (2009 – 2018) of wolf and cougar populations before and after wolf recolonization in northeast Oregon (Clark 2014, Chapter 2, 3, & 4). Our goal for this study was to investigate habitat selection, movement, and spatial time allocation for a subordinate predator (cougar) in response to recolonization of a dominant predator (wolf). Specifically, we wanted to answer whether: 1) the distance and rate at which cougars move had changed, 2) if the distribution of cougar activity across the diel cycle changed, and 3) whether any variation across cougar diel cycles was related to wolf daily activity patterns. We expected the presence of wolves to affect cougar space use, where active avoidance behavior would alter the spatio-temporal distribution of cougar activity relative to pre-wolf recolonization patterns. Based on evidence about wolf-cougar interactions in other systems (Alexander et al. 2006, Kortello et al. 2007, Atwood et al.

2009), when spatial overlap is high (e.g. seasonal elk calf diet overlap in summer, Chapter 3 & 4), we expected cougars and wolves in northeastern Oregon to exhibit temporal resource partitioning over the diel period in foraging niche.

METHODS

Study Area

Our study of wolf-cougar spatial relationships occurred in a 1,992 km² area of the Blue Mountain Range of northeast Oregon (45°32' 17.65" N, 118°13'21.90" W). Climate across the study area varied with topography and elevation where mean maximum temperature recorded at nearest stations (National Oceanic and Atmospheric Administration; elevations 1,093m and 1,543 m) ranged from 3.8 to 1.7° C during winter (Nov – Apr), and 19.1 to 16.8° C during summer (May – Oct), for low to high elevation portions of the study area (Western Regional Climate Center, data from 1968 – 2016). Mean total precipitation ranged from 9.8 to 18.0 cm during winter, and 4.1 to 4.7 cm during summer and mean total snowfall during winter ranged from 58.7 to 133.6 cm (Western Regional Climate Center). Vegetation was strongly influenced by topography, aspect, and elevation (range 337 – 1,850 m). Low elevation sites on the south and west side of the study area were dominated by exposed upland slopes and riparian areas comprised of hawthorn (*Crataegus columbiana*), willow (*Salix* spp.), and blackberry (*Rubus armeniacus*), with scattered ponderosa pine (*Pinus ponderosa*) and black cottonwood (*Populus trichocarpa*). High elevation sites in the central and eastern part of the study area were characterized by mixed-conifer stands with exposed southern aspects and common species including ponderosa pine, douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), and lodgepole pine (*P. contorta*).

Study Populations

We analyzed movement and habitat selection for 39 cougars and 34 wolves caught between January 2009 and August 2018 (Clark et al. 2014a, Chapter 2 & 3, ODFW Annual Wolf Report 2018). This study occurred during a period when wolf populations were expanding in northeast Oregon and wolf numbers in the study area

ranged from 2 – 20 individuals in one to six packs (ODFW Annual Wolf Reports, R. Brown, person. comm.). Wolves were captured by Oregon Department of Fish and Wildlife (ODFW) as part of their wolf population monitoring program. Wolves were fit with GPS radio collars (GPS PLUS II, $n = 29$, Vertex Survey, $n = 5$ [Vectronic Aerospace GmbH, Berlin, Germany]) that used an Iridium platform.

Cougars were captured with the aid of trained pursuit dogs following the American Society of Mammalogists' guidelines for wild animal use in research (Sikes and Gannon 2011) and procedures approved by the Institutional Animal Care and Use Committees of Oregon State University and USDA Forest Service – Starkey Experimental Forest and Range. Cougars were also fit with GPS radio collars (Track M Basic, $n = 14$, GPS Plus, $n = 1$, 4400S or 7000SA, $n = 25$ [Lotek Engineering, Newmarket, ON, Canada]). Prior to wolf recolonization (2009 - 2012; see Clark et al. 2014), GPS collars fit to cougars used ultra-high frequency (UHF) and ARGOS platforms and had variable fix intervals based on time of day and sex (1.5, 3 or 3hr collection schedules, see Clark 2014), and the later portion of the study (2014 – 2018; see Chapter 3) GPS collars fit to cougars used an Iridium platform with 3hr fix schedules.

Fix schedules for wolf collars were highly variable depending on the number of collared wolves per pack, ODFW management goals, or other research objectives (Chapter 2), with fix schedules from 2 – 96 locations per day and some irregular schedules (i.e. increased fix rates at crepuscular times). However, the most common schedule across the two species and collar platforms were fixes every 3 hours and mean fix success for GPS collared wolves was 87.2% (range 37.9 – 97.6%). Mean fix success for GPS collared cougars was 72.0% (38.4 – 100%) and 92.2% (range 70.0 – 98.2%) for UHF/ARGOS and Iridium platforms, respectively.

Diel Activity Patterns

Locomotion is a valid proxy for patterns of diel activity in large mammals (Ensing et al. 2014), and we used movement rate to index diel activity patterns for wolves and cougars in our study. We generated movement metrics (step length, turn angle, interval) using Geospatial Modeling Environment (GME; Beyer 2012) with movement

rate equal to the Euclidean distance of the preceding 3-hr time step (i.e. step length), similar to Kohl et al. (2017). We used step lengths and intervals to extrapolate hourly movement rates (km/hr) and describe diel patterns of activity for wolves and cougars, and 3-hr movement rates (km/3-hr) to test how cougar habitat selection and movement responded to diel wolf activity. We used 3-hr movement rate in our habitat selection analysis to match the most consistent time interval across carnivores, between cougar studies (pre- and post), and between consecutive cougar locations. We subset \leq 1-hr wolf data to 3-hr data by retaining locations of the 3-hr collection time beginning with the first scheduled 3-hr fix available. We filtered all GPS location data sets based on intervals and used only consecutive locations to calculate movement rates. To verify 3-hr data extrapolated hourly movement rates, we used a subset of 4,710 hourly fixes obtained from 9 GPS collared wolves (6 packs, 2 pairs, 1 single) recorded during summer and winter seasons. We also subset \leq 30-min wolf data to 1-hr data by retaining hourly locations to increase the number of 1-hr fix wolf data available for verification of extrapolated hourly rates (see Appendix D).

We estimated population-level patterns in wolf and cougar diel movement rate using generalized linear mixed-effects models fit to 3-hr locations and the lme4 package in R (version 3.4.1, R Core Team 2017). We included random intercepts for individual wolf or cougar to account for repeated measures of individuals across the study (Table D.1 – D.4, Appendix D). Prior to modeling, we evaluated diel activity patterns for the influence of longer temporal scale effects based on monthly, seasonal (6-month designations), or inter-annual variation and observed evidence in support of seasonal effects (Appendix D). We also evaluated diel activity patterns for evidence of species specific factors that might influence diel behavior (pack for wolves, or sex, age class, reproductive status, and study period for cougars), and observed evidence in support of study period and sex effects for cougars (Appendix D). Therefore, for our evaluation of wolf and cougar diel activity we calculated separate summer and winter population-level estimates as a univariate function of time of day within a given season, and report separate estimates for male and female cougars. We defined activity from May – Oct as summer, and estimates from Nov – Apr as winter. Our seasonal averages subsume the

approximate 3-hr timing shift of dusk and dawn that occurs between November and April, which may add variation to our hourly measurements of activity.

To assess change in rates between pre- and post-wolf time periods, we used mean movement rates for individual cougars and tested for differences with a Student's *t* test and permutation (5000 randomizations). We carried out permutation to compare observed differences with distribution number of *t*-statistics calculated after randomly assigning study period to each overlap percentage (Manly 2001, Good 2005). For example, if there were 25 pre- and 15 post-wolf movement rates for cougars, 25 of the 40 rates were randomly assigned to the pre-wolf time period and the remaining 15 were assigned to the post-wolf time period, an a new *t*-statistic was calculated. This process was repeated 5000 times and the proportion of statistics that were as large or larger than the original represented the p-value for the test (Manly 2001). Before making comparisons across study periods, we evaluated cougar movement patterns for variation based on: 1) cougar sex, or 2) season (periods defined above). We considered $P \leq 0.10$ as evidence of effect and inclusion as a grouping factor for pre- and post-wolf period comparisons (see Appendix D for details).

Spatial Risk of Wolf Interaction

We considered several indices of spatial variation in risk of wolf interaction for cougars because it is unclear how carnivores perceive risk. We calculated three indices to represent spatial risk of interaction with wolves: density of wolf-killed elk and deer, openness, and intensity of wolf use. Kill sites are a well-established measure of ungulate predation risk (Gervasi et al. 2013, DeCesare et al. 2014, Kohl et al. 2017) that can also serve as epicenters of carnivore interactions (Ruth and Murphy 2010, Ruth et al. 2011). Openness is well-linked to wolf ungulate kill occurrence (Kunkel and Pletcher 2002, Kauffman et al. 2007, Gervasi et al. 2013, Courbin et al. 2013), but could also be linked to increased likelihood of wolf encounter and interaction (or perceived risk of interaction) based on increased wolf use of open terrain for hunting and travel (Gervasi et al. 2013, Dickie et al. 2013). Perceived risk may not be strictly tied to prey resources, therefore, to contrast any differences related to wolf use outside predation, relative intensity of use

could be an important cue cougars respond to and we based our measure of intensity on the density of GPS collared wolf locations. We developed all spatial indices of risk using GME or ArcMap (version 10.3.1, Environmental Systems Research Institute, Redlands, CA, USA) at a 30-m resolution projected into NAD83 UTM Zone 11N.

Wolf Kill Density. – We used kernel density estimates (KDE) to characterize the spatial distribution of wolf-killed elk and deer in northeast Oregon from 2014 – 2015 winter (Jan – Mar) and summer (14 days in June, July, or August) seasons of our study (Fig. 5.1a, b; Chapter 2 & 4). A total of 70 wolf-killed elk and 31 wolf-killed deer (mule deer and white-tailed deer combined) were identified across 2 winter and 2 summer periods each (Chapter 2, Appendix B). These kills included all age and sex classes of wolf-killed deer and elk. KDEs were generated using the PLUGIN bandwidth and standardized to scale from 0 to 1.

Openness. – We calculated openness (Fig. 5.1c) as the sum of non-forested cells within a 250-m moving circular window centered on each grid cell (range 0 [dense forest] – 197 [open grassland]) similar to Boyce et al. (2003). We obtained vegetation data from the U. S. Geological Survey LANDFIRE (EVC – percent live forest canopy cover; Wildland Fire Science, Earth Resources Observation and Science Center 2010) dataset to generate a measure of openness based on a clear break in canopy cover distribution and reclassification into forest and non-forest habitat (Chapter 4). We used the Spatial Analyst extension in ArcMap and the binary raster from Chapter 4 to reclassify “forested” habitat as 0, and “non-forested” habitat as 1, and used this layer to calculate openness. We verified that our map of openness was representative through visual match with aerial photos (Google Earth, 07/15/2017).

Intensity of Wolf Use. – We used population-level wolf utilization distributions (UD) based on fixed KDEs of wolf GPS locations (Chapter 4) as a measure of relative intensity of wolf use. We used a subset of 38,324 wolf GPS locations from 17 wolves that fell within a 10-km buffer of the boundary used for cougar predation studies (Mt. Emily Wildlife Management Unit, see Clark et al. 2014a & Chapter 3). We included individual wolves with ≥ 25 locations inside the study area buffer using a PLUGIN bandwidth to generate estimates. We standardized intensity of wolf use KDEs to scale from 0 to 1.

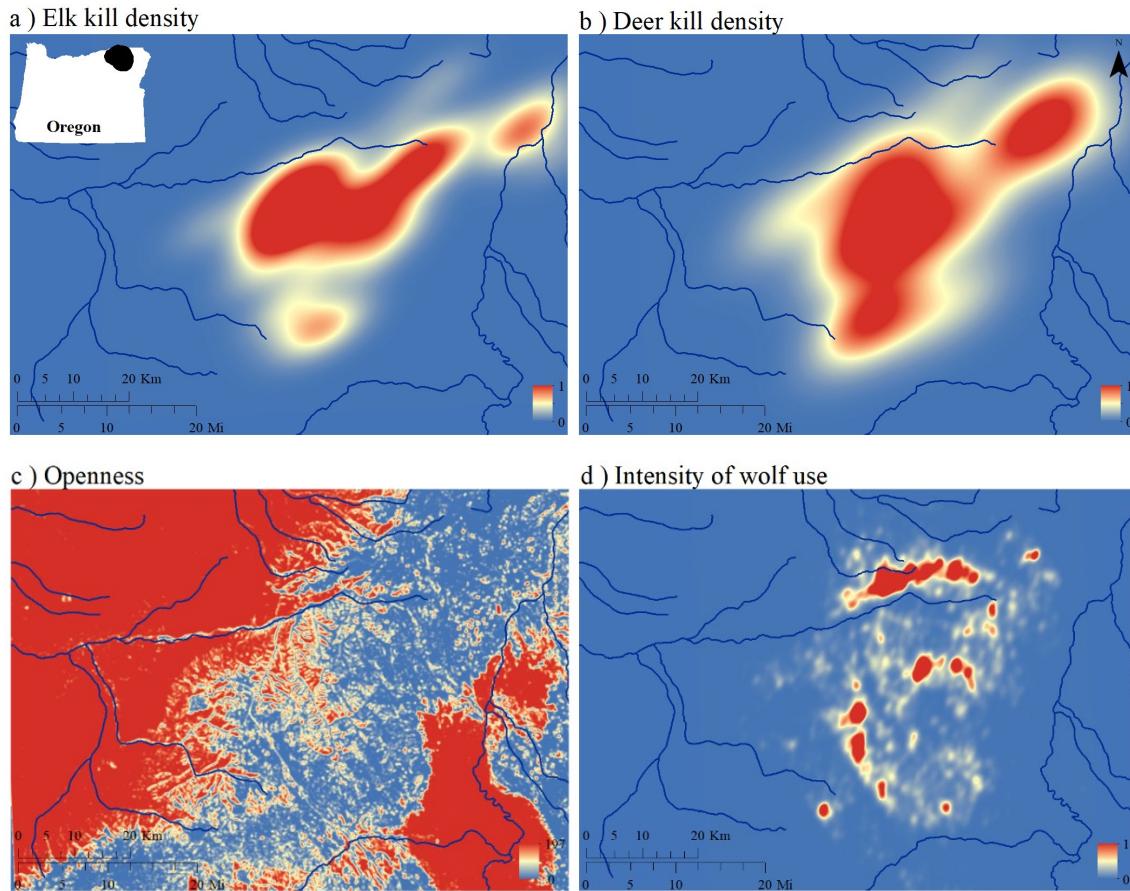


Figure 5.1. Spatial variation in potential wolf interaction and predation risk in northeast Oregon indexed as density of wolf-killed elk (a) and deer (b), openness (c), and wolf intensity of use (d). Panels a and b represent conditions in the first two years of the post-wolf recolonization period of study (2014 – 2015), and panels c and d represent wolf recolonization conditions over the duration of the study (2012 – 2018). Openness was consistent over the study duration. Blue lines denote major rivers.

Cougar Habitat Selection

We quantified cougar movement and resource selection using step-selection functions (SSFs; Fortin et al. 2005, Thurfjell et al. 2014). SSFs allow information from consecutive animal locations (defined as steps) to link the domain of availability to the movement characteristics of the animal. Related to the use-availability design of a customary resource selection function (RSF, Manly et al. 2002), an SSF contrasts used

steps with a limited domain of random steps based on the movement of the animal, enabling association of parameters that influence animal movement through the landscape. We used a matched case-control logistic regression (CCLR) framework (Thurfjell et al. 2014) with a 1:3 empirical sampling design that paired the end location of each observed step (at time t) with a set of 3 available locations (sampled with replacement) based on each individual's respective step-length and turn angle distributions. We fit mixed-effect conditional logistic regression models using the *TwoStepCLogit* package in R (Fieberg et al. 2010, but see Duchesne et al. 2010, Thurfjell et al. 2014). We used the two-stage modeling approach (Fieberg et al. 2010, for examples see Squires et al. 2013, Northrup et al. 2016), and fit selection models to individual cougars (stage 1). This allowed us to accommodate variable habitat selection responses among individual cougars to make inferences within and between groups (e.g. male and female cougars and pre- and post-wolf studies). We used the estimated individual coefficients to test responses in habitat selection relative to cougar sex, season, and wolf variables. We used permutation procedures, as described above to evaluate variation in coefficients (i.e., beta values) which would reflect differences in selection between cougar groups of interest (e.g. M/F, pre/post), using individual cougars as the sample unit. We considered regression coefficients of pre-wolf cougars as a 'prior' distribution of selection representative of naïve selection to risk of wolf interaction for our comparison to post-wolf cougar selection. To make inference on overall cougar habitat selection (stage 2), we averaged regression coefficients across individuals to produce seasonal population-level selection estimates.

RESULTS

Across seasons, most GPS-collared wolves were crepuscular with the highest hourly movement rates observed in morning followed by evening > night > day (see Fig. D.1 in Appendix D). There was less individual variation in activity over the diel cycle during summer than winter, and we found reasonable agreement in diel patterns between hourly extrapolated wolf movement rates (km/hr) and predicted population level mean wolf movement estimated from our GLMM built on 1-hr wolf data (Fig D.2 in Appendix

D). Wolves moved 38% further in winter than summer (per 3 hr step; $\bar{x}_{\text{summer}} = 1.3 \text{ km}$, 90%CI 1.2 – 1.5; $\bar{x}_{\text{winter}} = 1.8 \text{ km}$ 90%CI 1.5 – 2.0, $F_{36} = 7.09$, $P = 0.01$).

In general, cougars moved shorter distances per 3-hr time step with wolves on the landscape ($\bar{x}_{\text{pre}} = 0.60 \text{ km}$, 90%CI 0.49 – 0.70; $\bar{x}_{\text{post}} = 0.43 \text{ km}$ 90%CI 0.38 – 0.47, %P = 0.34). When we accounted for sex and seasonal variation in movement rates (see Appendix D for details), study period differences were disparate for male and female cougars. The mean distance male cougars traveled was 50% shorter in summer with wolves on the landscape (Fig. 5.2, $t_7 = 2.03$, %P = 2.2), but there was no evidence of differences in distances traveled for female cougars in either season (summer: $t_{21} = 1.00$, $P = 0.33$; winter: $t_{19} = 0.70$, $P = 0.49$). Consistent across seasons and time periods with and without wolves, most cougars had reduced activity levels over the diel cycle during daylight hours, and were somewhat crepuscular (Fig. 5.3). However, we observed a change in the pattern of cougar activity over the diel cycle where pre-wolf cougar hourly movement rates peaked in the evening followed by night > day > morning, and post-wolf cougar hourly rates shifted to a more crepuscular pattern of activity (evening > morning > night > day). Accounting for sex-based differences in movement rates, we observed a decrease in male cougar movement shifted to later in the morning and earlier in the evening after wolf recolonization (Fig. 5.4a). Male movement was also offset to wolf activity in summer. In winter, male cougar movement was also lower and similarly shifted, but not offset with wolf activity (Fig. 5.4b). Female cougar movement was similarly offset to wolf activity in summer, but had increased rates of movement after wolf recolonization (Fig. 5.5a). Further, mid-day periods of lower activity were 8 times higher after wolf recolonization. In winter, female cougar movement was similarly shifted to later in the morning and earlier in the evening, but rates were only increased in the morning (Fig. 5.5b).

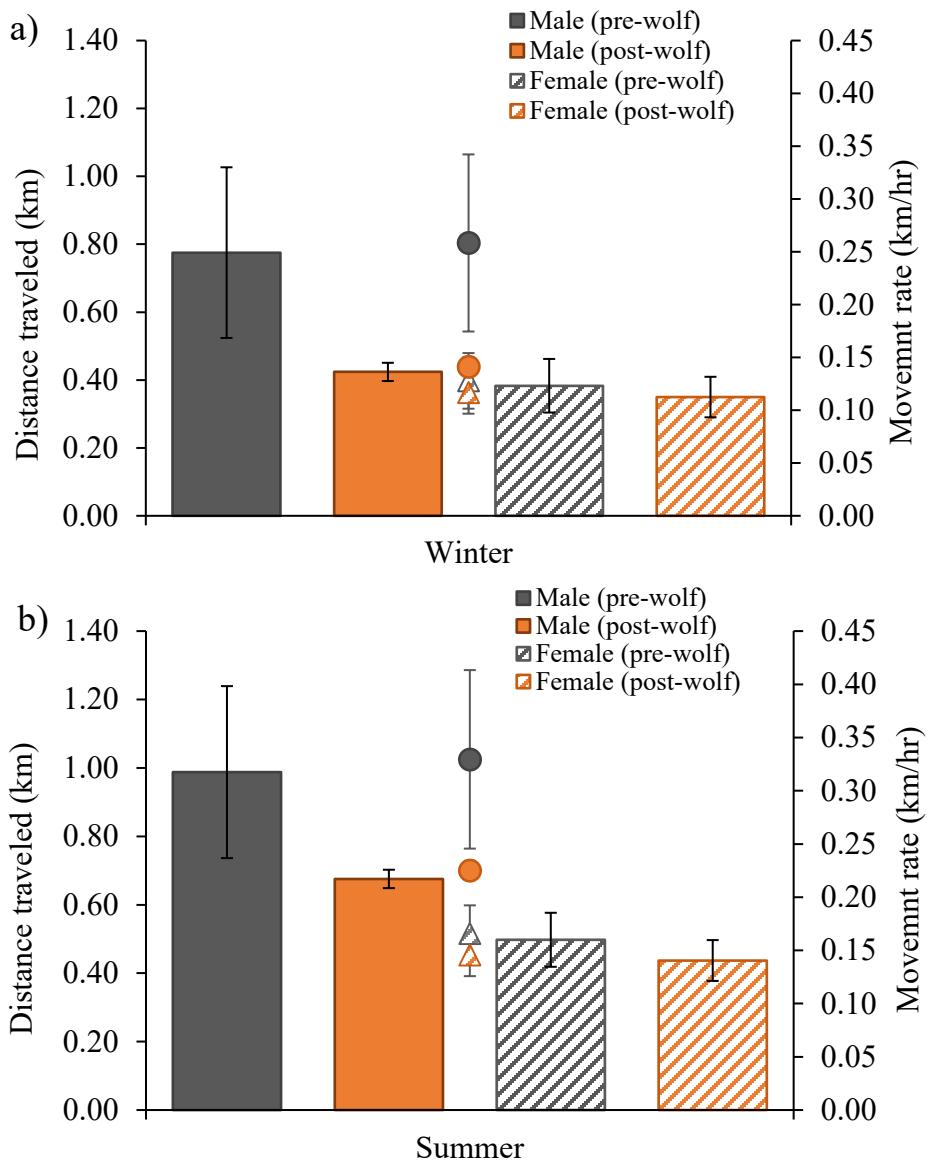


Figure 5.2. Seasonal distances (km) traveled (left axis), movement rates (km/hr; right axis), and associated 90% confidence intervals for 13 male (solid color fill) and 25 female (slashed line fill) GPS-collared cougars across pre- (gray, 2009 – 2012) and post-wolf (orange, 2014 – 2018) periods in northeast Oregon. Distances and movement from Nov – Apr defined as winter (a), and from May – Oct as summer (b). (*) Denotes evidence in support of differences for male cougars in summer across time periods with and without wolves based on Student's *t*-test and permutation (%P = 2.2).

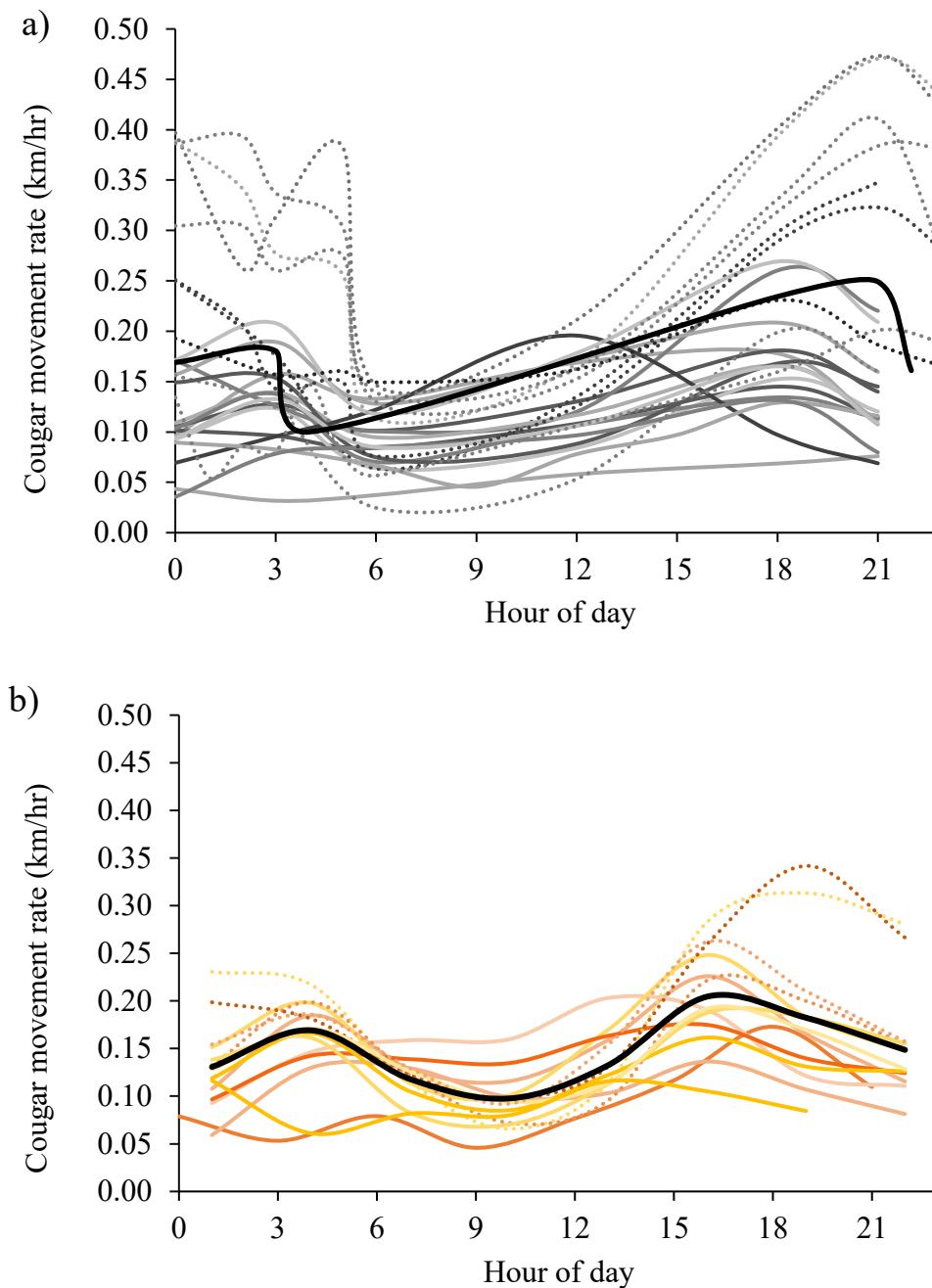


Figure 5.3. Diel activity patterns for cougars and wolves in northeast Oregon. Mean hourly movement rates (km/hr) for 35 GPS-collared male (broken lines) and female (solid lines) cougars with predicted population mean (solid black line) from generalized mixed models over pre- (a) and post-wolf (b) time periods.

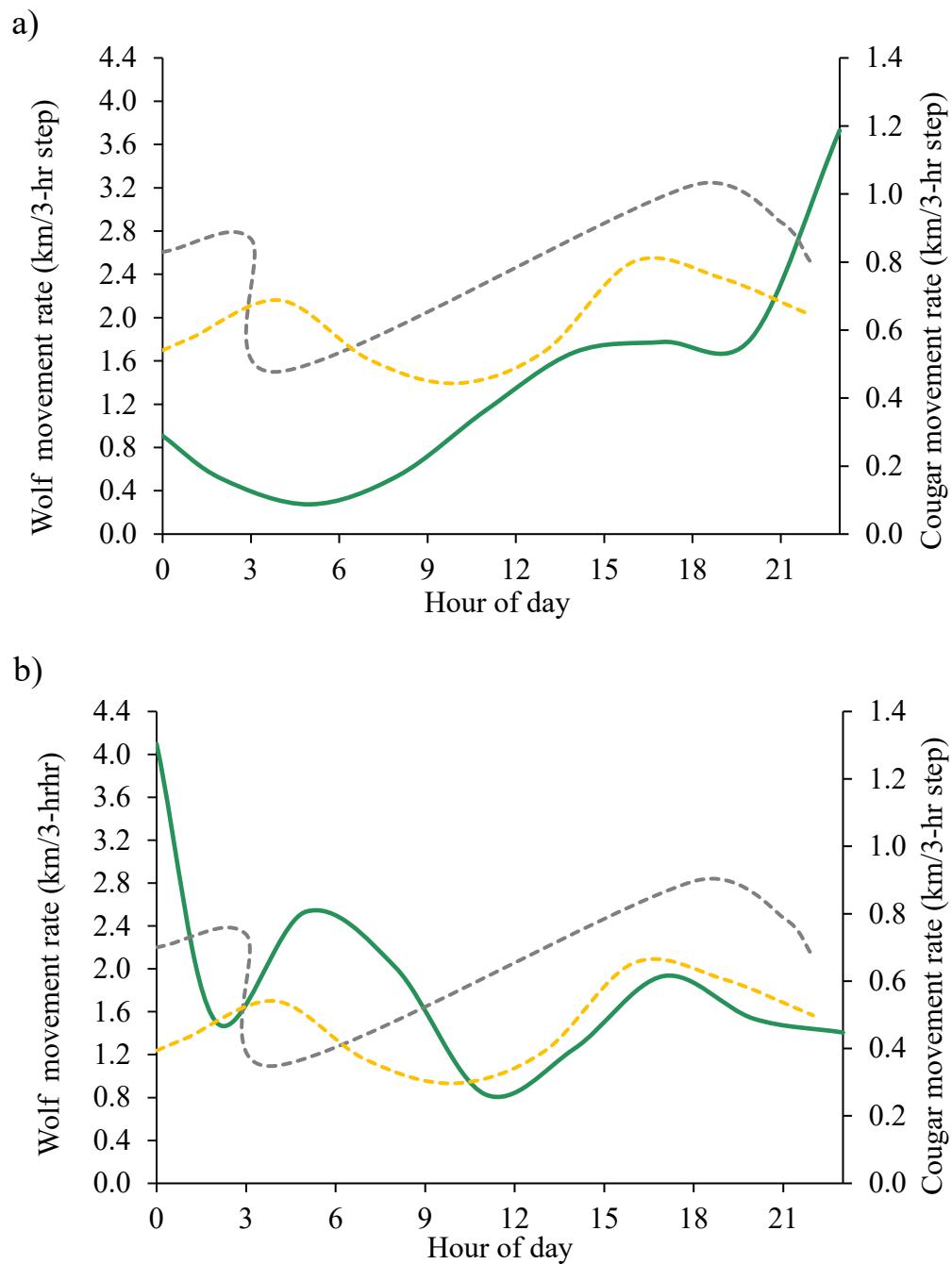


Figure 5.4. Predicted 3-hr movement rates during summer (a) and winter (b) seasons for 13 GPS-collared male cougars and 17 GPS-collared wolves (green) in northeast Oregon over pre- (grey) and post-wolf (orange) periods. Population mean movement predictions were from generalized mixed effect models.

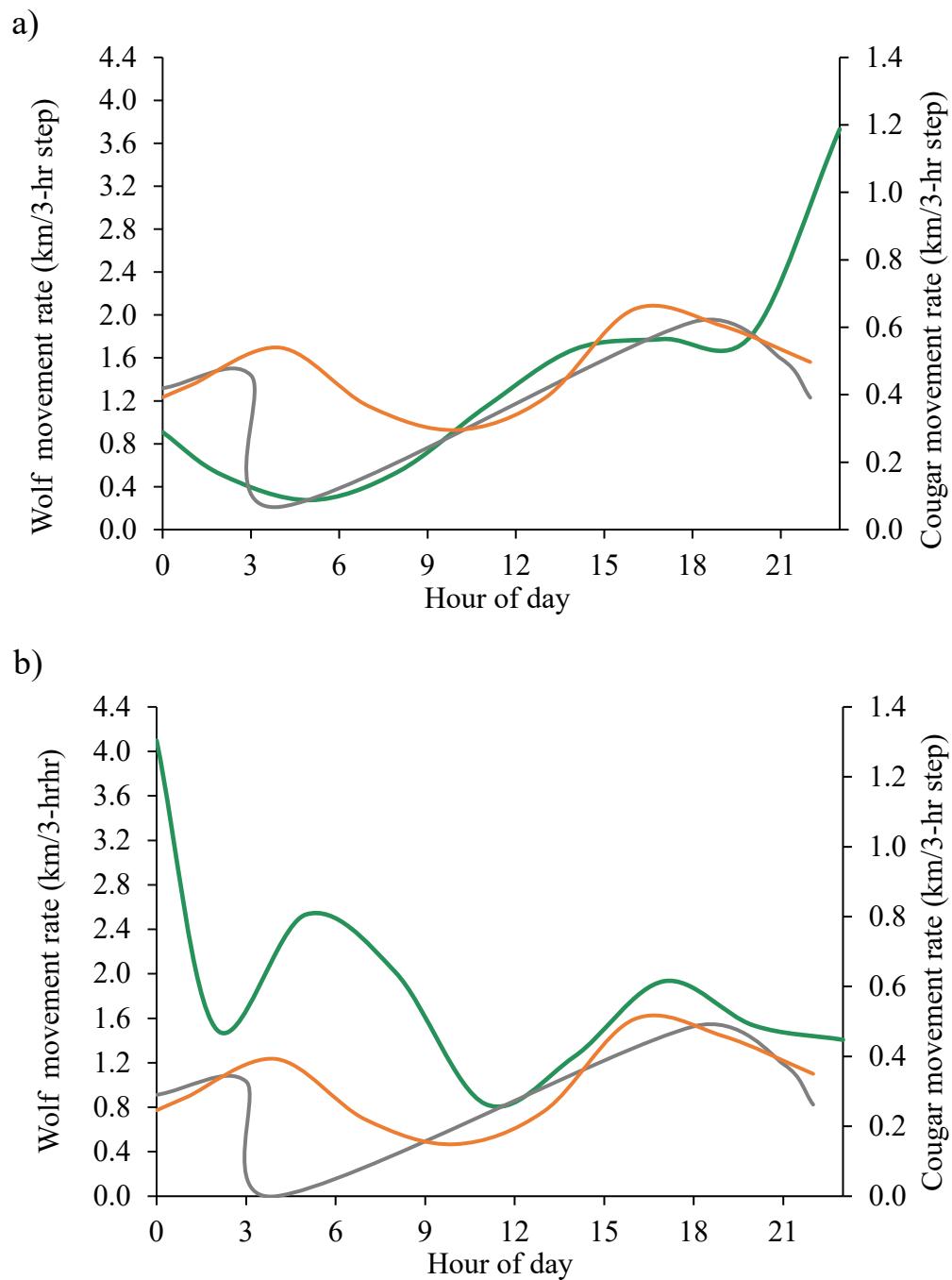
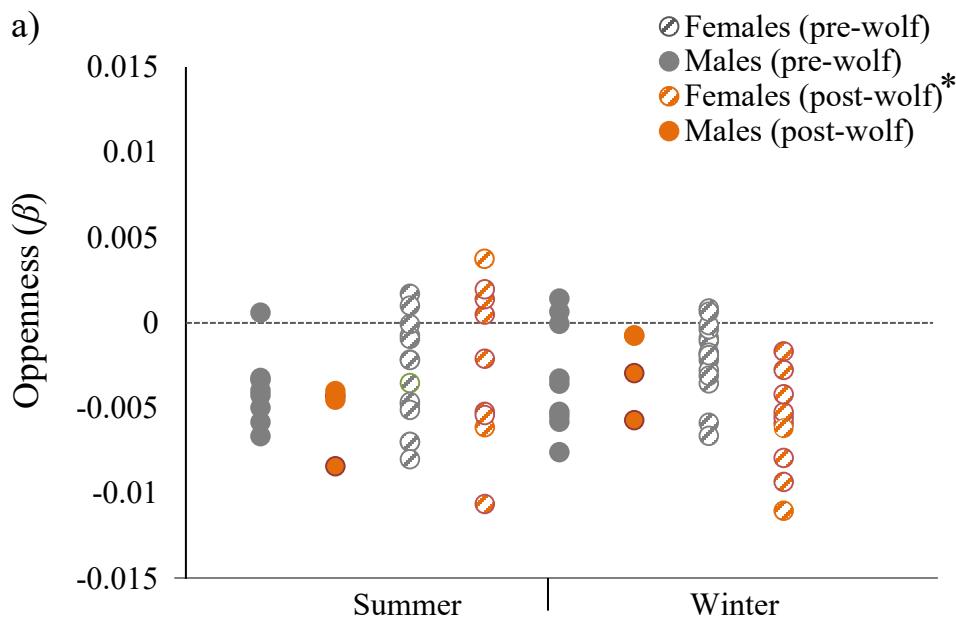
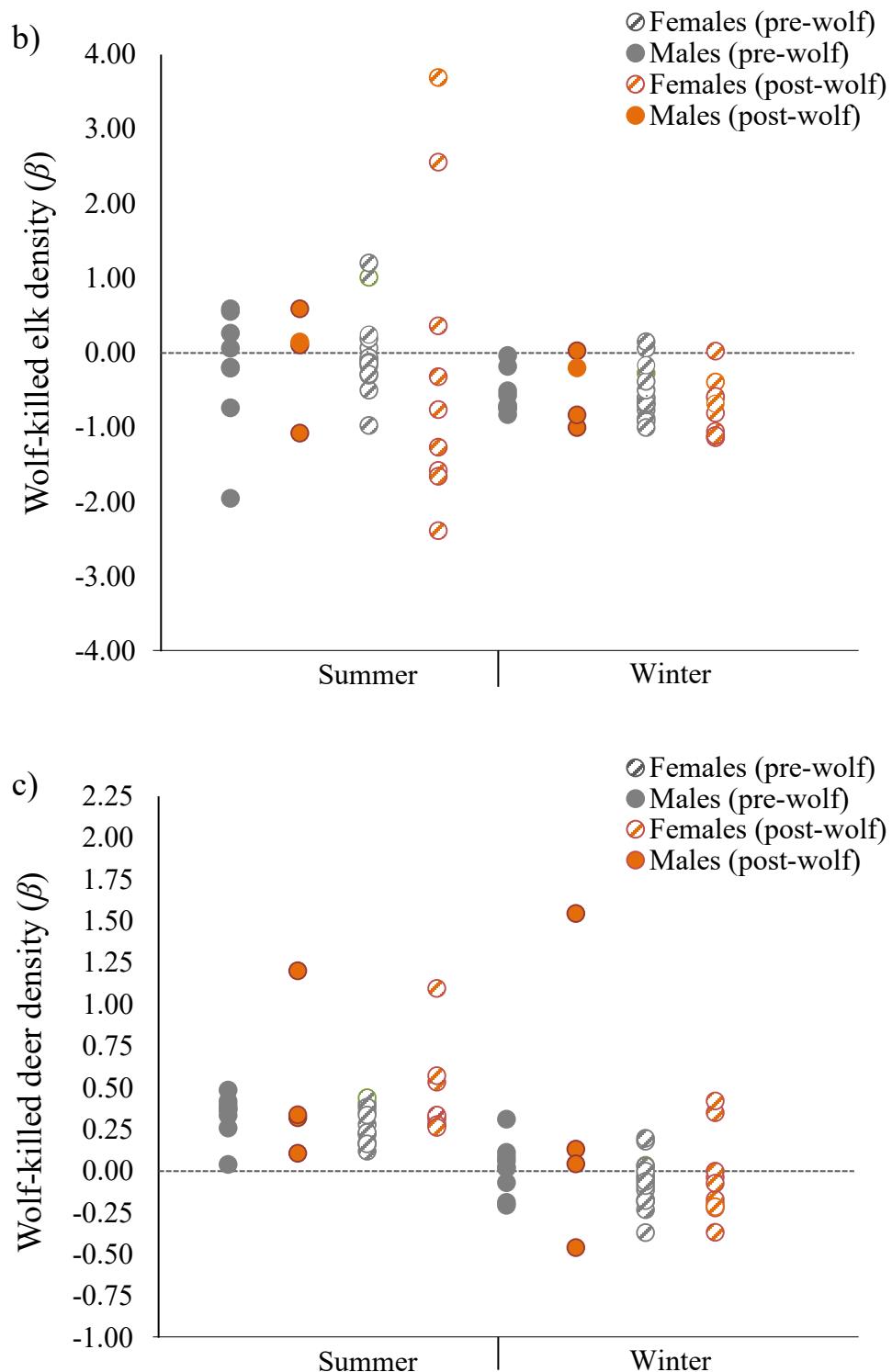


Figure 5.5. Predicted 3-hr movement rates during summer (a) and winter (b) seasons for 25 GPS-collared female cougars and 17 GPS-collared wolves (green) in northeast Oregon over pre- (grey) and post-wolf (orange) periods. Population mean movement predictions were from generalized mixed effect models.

For our most general SSF model, we did not account for season or sex, and we did not find strong evidence in support of regression coefficients being different between time periods with and without wolves (openness: $t_{42} = -1.54, P = 0.13$; elk kill density: $t_{32} = -0.38, P = 0.71$; deer kill density: $t_{32} = 1.37, P = 0.18$; wolf use: $t_{44} = -0.45, P = 0.65$). At the population-level openness did not appear to influence cougar movement in either summer or winter ($P > 0.10$). In general, cougars selected for areas of less wolf-killed elk density ($\beta = -0.087, P < 0.001$), but with increased wolf-killed deer density ($\beta = 0.351, P = 0.033$), and higher wolf use ($\beta = 0.351, P = 0.033$) in summer, and these patterns were consistent across seasons (Table D.14 Appendix D). However, when we incorporated the sex and season differences observed in cougar movement and looked at individual patterns of selection, we found stronger evidence suggesting that female cougars selected for less open habitats in winter after wolf recolonization (Fig. 5.6a; %P = 0). We did not find any evidence of differences in how cougars were selecting areas relative to any of the wolf density-based variables we examined (Fig. 5.6b-d, all t -test $P > 0.10$). However, regression coefficients for individual male and female post-wolf cougars showed a lot more variation within each sex than their respective male and female pre-wolf cougars.





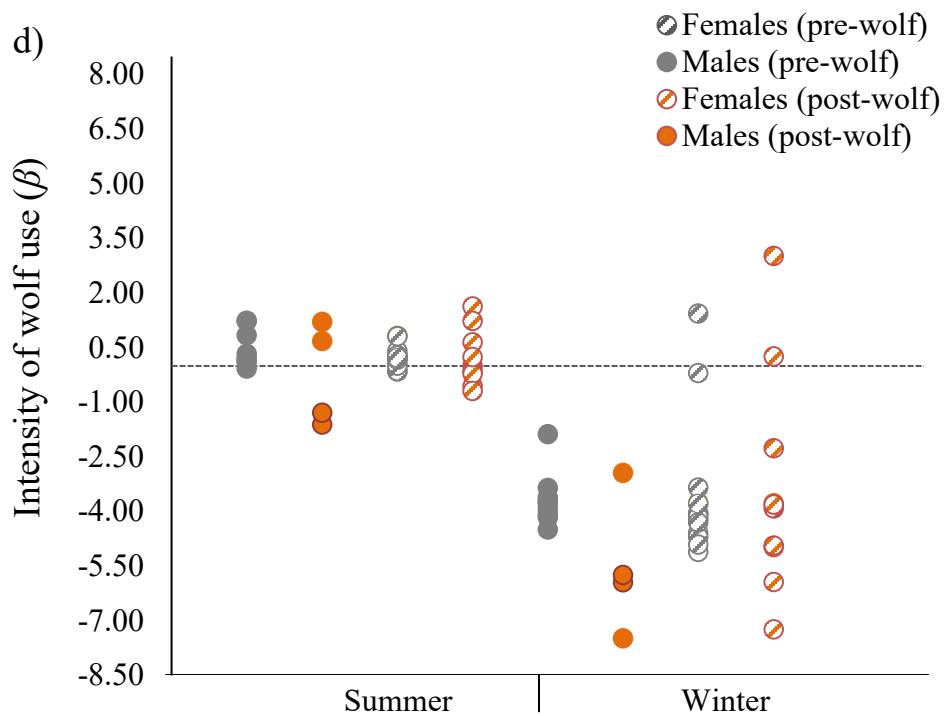


Figure 5.6. Individual selection coefficients (β) for 13 male (solid color fill) and 25 female (slashed line fill) GPS-collared cougars across pre- (gray, 2009 – 2012) and post-wolf (orange, 2014 – 2018) periods in northeast Oregon. Regression coefficients were estimated with step-selection functions (SSF) for (a) openness, (b) wolf-killed elk density, (c), wolf-killed deer density (mule deer and white-tailed deer), and (c) intensity of wolf use over summer and winter seasons. One female cougar (c167; red triangle) was part of both pre- and post-wolf studies. (*) Denotes evidence in support of differences across time periods with and without wolves based on Student's *t*-test and permutation.

DISCUSSION

We found that mean wolf movement varied over the course of a day and the winter rates we observed in northeast Oregon were similar to those reported in YNP (Kohl et al. 2017). While we observed a crepuscular pattern to winter wolf movement over the diel cycle, we did not observe as clear a bimodal pattern in summer daily movement. This could be due to seasonal changes in prey population behavior (increased availability of neonatal ungulates) or a response to anthropogenic factors experienced by

wolf populations that occur outside protected areas (e.g. development, use of roads, agriculture, etc.). We observed a clear shift in the timing of cougar daily movements to later in the morning and earlier in the evening. This shift resulted in a pattern that was offset to wolf daily activity patterns, particularly for male cougars in winter, resulting in activity far later in the morning during a time period when activity patterns of pre-wolf male cougars was low. In addition, male cougars also had generally reduced overall movement rates. Alternatively, while female cougars showed a similar shift in the timing of their activity over the course of a day, demonstrating they were active for longer periods in summer and at elevated rates in both seasons. Of note with relation to increased duration and overall movement rates for female cougars was the elevated level of their “low activity” periods in summer. This could have important consequences relative to cougar fitness.

Cougars were taking in less ungulate biomass and had longer intervals between ungulate kills after wolf recolonization of the study area (Chapter 2 & 3). Energetically, this has the greatest potential for becoming a fitness cost for cougars when longer search intervals (Chapter 3) are also associated with increased rates or duration of movement, as our results suggest may be the case for female cougars. This was not an equitable case between male and female cougars, and may suggest that the sexes engage in different strategies to offset competition effects relative to wolves. Male cougars appear to limit their potential for interaction with wolves by moving at different times of the day and at lower rates, while females also move at different times of the day, but appear to extend their activity during lulls in wolf activity, especially during summer when both predators make use of elk calves (i.e. greatest likelihood for conflict over a shared resource). With cougars overall moving at different rates and at different time periods over the course of a day, our results highlight the competition tradeoffs cougar’s balance in the presence of wolves.

The results of our habitat analysis lend further support to cougars using a sex-specific competition mitigation strategy in the presence of wolves. We were not attempting to predict cougar habitat selection *per se* in northeast Oregon, but to compare several variables that we might detect change in relative to wolf recolonization. We used

an unusual approach that made it possible to compare wolf-related variables between pre- and post-wolf cougar populations. We expected the habitat selection of pre-wolf cougars to reflect their movement through the landscape with no relationship to wolf predation or intensity of use (i.e. random relative to knowledge of, or response to wolves), and we believe our pre-wolf sample of cougars demonstrated a naïve ‘prior’ pattern of cougar selection and use of the landscape. If wolf presence affected cougar habitat selection and movement we expected evidence of differences to be present between individual selection coefficients of pre- and post-wolf cougars. The selection of areas less dense in wolf-killed elk from pre- to post-wolf periods suggests a general avoidance strategy by cougar (i.e. avoid potential interactions with wolves by avoiding encounter). Additionally, if there were strong direct competition effects we expected post-wolf cougars to have decreased individual selection coefficients compared to respective naïve pre-wolf cougars. So, while we expected cougars would select for less open areas to increase hunting opportunities or to maintain access to refugia regardless of wolf presence, the increased female selection for less open areas in winter we observed across pre- and post-wolf periods provides evidence post-wolf female cougars had altered their behavior to avoid areas associated with their dominant competitor. Further, the increased variation in β s we observed supports the idea of different sex-specific strategies for competition mitigation in cougars.

A major insight from our movement work demonstrated that, contrary to primarily expected nocturnal behavior, cougars were also active throughout the day. The ability for animals to allocate habitat use across periods of high and low predator activity within the diel cycle is an underappreciated aspect of animal behavior that helps explain why strong antipredator responses may trigger weak ecological effects. Alternatively, changes in prey base could also be indirectly influenced by wolves through perceived risk of predation and different antipredator responses to a coursing vs. ambush predator (Kunkel et al. 1999, Jason S Husseman et al. 2003, McPhee et al. 2012), or other factors like response to forage quality (Cook et al. 2004), or anthropogenic activities (Fortin et al. 2015, Klaczek et al. 2016). Any of which could alter ungulate distribution, in turn altering cougar movement and activity patterns. Species interactions are a function of

encounter rates, which are in turn, a function of predator activity levels. Our results demonstrate the capacity for interspecific interactions to alter movement rates, daily activity patterns, and selection of the habitat cougars move through on the landscape. Our work has highlighted that wolf recolonization simultaneously introduces elements of interspecific competition between wolves and cougars. Overlooking competition between predators could result in underestimating costs to subordinate competitor species and overestimating effects of multiple predators on prey populations.

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CHAPTER 6 – SUMMARY & IMPLICATIONS

Elizabeth K. Orning

Summary

Increasing attention is being paid to understanding the nature of intraguild carnivore dynamics (Levi and Wilmers 2012, Bartnick et al. 2013), but the nature of predator-predator interactions is crucial to understanding and predicting changes in community structure and any potentially cascading trophic effects (Ripple and Beschta 2004, Terborgh and Estes 2010, Newsome and Ripple 2014). In order to disentangle the complexities and evaluate the mechanisms of multiple predator-multiple prey systems, an understanding of baseline information on predator types and interactions, predation risk, and criteria for defining effects are necessary (Sih et al. 1998). My dissertation provided insight on the competitive dynamics involved in wolf and cougar ecology in Oregon through estimation of wolf diet composition and predation rates (Chapters 2), and the effects of wolf recolonization on cougar predation patterns (Chapter 3), home range and predation distribution (Chapter 4), movement and habitat selection patterns (Chapter 5). My results provided additional insight into the effects interspecific competition on the predation patterns, distribution, and movement of cougars, and contributed to the understanding of wolf and cougar ecology that will help guide carnivore management in Oregon. Below, I provide a review of each chapter of my dissertation and highlight important findings that will help manage carnivores and their prey populations.

Wolves in northeast Oregon preyed primarily on elk, and secondarily on deer, similar to other elk dominant systems with multiple ungulate prey species available to wolves (Husseman et al. 2003, Smith et al. 2004, Atwood et al. 2007, Kortello et al. Metz et al. 2012). My results were consistent with other studies of wolf predation, in that wolves tended to prey on seasonally available classes of vulnerable prey species (Husseman et al. 2003, Smith et al. 2004, Atwood et al. 2007, Kortello et al. 2007 Metz et al. 2012). Winter kill rates for wolf packs documented in my study were on the low end of estimates reported in similar wolf-elk systems (Hebblewhite et al. 2003, Kortello et al. 2007). My estimates of mean summer biomass intake for wolves were similar to those reported in Yellowstone NP in the summer, but lower in winter (Metz et al. 2012). To date, Metz et al. (2011, 2012) is the only other North American study to report estimates of summer wolf kill rates in elk dominated systems. I found that the higher summer wolf

pack kill rates associated with shorter kill intervals coincided with the ungulate birth pulse and increased presence of ungulate neonates on the landscape (Jun – Aug), but that seasonal differences in rates did not translate to seasonal differences in mean pack or per wolf biomass intake.

Cougars preyed primarily on deer (mule deer and white-tailed deer combined) prior to wolf recolonization (Clark et al. 2014a). My evaluation of individual cougar diet compositions showed differences were more evident in female cougar diets, where post-wolf female cougars had a lower proportion of mule deer in their summer diets than respective pre-wolf female cougars, with no concurrent shift in the proportion of elk in female summer diets. I also found cougars had increased frequency of scavenged prey remains in their diets, and an increased frequency of non-ungulate prey in their diets from pre- to post-wolf time periods. I found that cougars killed less frequently, had lower numerical kill and biomass intake rates, and had longer search and handling times with wolves on the landscape. My seasonal comparisons across study periods showed that effects were unequal across cougar reproductive groups, largely effecting female cougar predation patterns. I documented that summer kill rates of female cougars raising kittens < 6 months old were 50% lower than rates for respective young cougar family groups before wolf recolonization. I found seasonal differences in the number of ungulates killed did not translate to differences in mean biomass intake rates for post-wolf cougars regardless of reproductive status, consistent with seasonal kill rate correlation to mean prey size identified in other cougar studies (Knopff et al. 2010, Clark et al. 2014a). I found post-wolf female cougar reproductive groups consistently had lower ungulate biomass intake rates than their respective pre-wolf cougar groups, and that longer search times were most pronounced for solitary, subadult female cougars. The shifts in reproductive class biomass intake rates and search time I documented in this study could represent an important mechanism for how interspecific competition, and specifically interference competition, operate on the overall dynamics of cougar populations by affecting fitness and recruitment of young cougars into populations.

Although I found overall pack HR sizes in my study were consistent with sizes reported for other wolf-elk systems, home range size was highly variable across

individual wolves, and variation likely reflected the expanding nature of Oregon's wolf population. Cougar home range sizes in northeast Oregon were also consistent with sizes reported for other cougar populations (Hornocker and Negri 2010). The consistency I observed in mean cougar home range sizes across time periods with and without wolves could be a reflection of evolutionary niche requirements unaffected by the time-scale of wolf absence, but also suggests stability in the system relative to features incorporated within a cougar's home range (access to food, mates, refugia). Because I had a naïve 'prior' representation of cougar space use on the landscape, I used an unusual approach to compare home range and predation site range overlap between pre- and post-wolf cougar populations based on the idea pre-wolf cougars had no relationship or interaction with wolves. I found no change in cougar placement of their home ranges on the landscape. I did find some evidence male cougars might be spatially responding to wolves that could increase their encounter rates or chances of direct wolf-interaction, and possibly affect their visibility and accessibility for human harvest. Results from my latent selection analyses suggest that while broad scale patterns of cougar predation were similar, cougars were responding to the presence of wolves. My results also suggested the spatial scale of that response was likely a result of individual-level movement that occurred within a cougars' home range (i.e. patch-level 4th order selection; Johnson 1980). My results provided weak evidence of a shift to the realized niche of cougars in the study area after wolf recolonization. I found considerably more overlap between wolf and cougar predation ranges at larger spatial scales than I would expect if there were strong competition effects and complete exclusion of cougars from shared prey resources. But the amount of overlap I observed was still consistent with my predictions of wolves competing with cougars and suggested weak avoidance by cougars.

I found that mean wolf movement varied over the course of a day and that winter rates in northeast Oregon were similar to those reported in Yellowstone NP (Kohl et al. 2017). While I observed a crepuscular pattern to winter wolf movement over the diel cycle, I did not observe as clear a bimodal pattern in summer daily movement. I documented a clear shift in the timing of cougar daily movements to later in the morning and earlier in the evening. This shift was offset to wolf daily activity patterns and

appeared to particularly influence male cougars in winter, resulting in activity far later in the morning over a period during which pre-wolf male cougars had low activity. Male cougars also had overall reduced movement rates post-wolf recolonization. I found that female cougars showed a similar shift in the timing of their activity over the course of a day, but that they were active for longer periods in summer and at elevated rates in both seasons. I found that male and female cougars engaged in different strategies to mitigate competition effects relative to wolves. Male cougars appear to limit their potential for interaction with wolves by moving at different times of the day and at lower rates, while females also moved at different times of the day, but appeared to extend their activity during lulls in wolf activity, especially during summer periods when both predators make use of elk calves (i.e. greatest likelihood for conflict over a shared resource). At a population level I found cougars selected areas where wolf-killed elk locations were lower, suggesting a general avoidance strategy by cougars (i.e. avoid potential interactions with wolves by avoiding encounters). Through my individual level selection analysis I found that female cougars selected for less open areas in winter after wolf recolonization, potentially reflecting a behavioral shift to avoid areas frequently traveled in by their dominant competitor. A major insight from my movement work demonstrated that cougars are more diurnally active than has been previously documented. Species interactions are a function of encounter rates, which are in turn, a function of predator activity levels. My results demonstrated the capacity for interspecific interactions to alter movement rates, daily activity patterns, and selection of the habitat cougars move through on the landscape.

Potential Effects To Elk And Deer Populations

The effects of predation on prey populations are tied to the complexities of intraguild dynamics, as the predation risk for shared prey can vary relative to the nature of predator-predator interactions as well as the behavioral responses of prey to predators (Atwood et al. 2009). Long-term downward trends in ungulate populations, including Rocky Mountain elk (hereafter elk; Schomer and Johnson 2003, Johnson et al. 2013), coupled with the return of apex predators to many ecosystems across western North

America generated management concern and intensified research by agencies charged with maintaining wildlife populations. Elk are considered a valuable resource in the state of Oregon, providing hunting and viewing opportunities that generate approximately \$40 million/year for the economy of the state (Bolon 1994). Complex direct and indirect interactions can influence elk and other ungulate population dynamics and no single factor has been linked to elk population declines, as a multitude of top-down, bottom-up, and abiotic factors, all of which are variable in space and time, can affect elk populations (Johnson et al. 2013). Wolf-cougar interactions may be important because cougar predation on juvenile elk was identified as a primary factor limiting survival and recruitment of juvenile elk in northeast Oregon (Rearden 2005, Johnson et al. 2013) and high cougar densities contributed to the reduced juvenile survival and population growth rates of elk (Clark 2014). The concern for Oregon was that the addition of a second predator to this system could increase predation on juvenile elk, or, alternatively, change cougar behavior that would shift predation to another elk age class or ungulate species (i.e. intensify predation on mule deer). Thus, understanding the underlying mechanisms driving predation risk is a critical component to effective elk and mule deer management in Oregon and other states in the Western US.

The first breeding pair of wolves documented in the study area (2012; ODFW Annual Wolf Report, R. Morgan, per. comm.) coincided with peak calf:cow ratios (number of calves per 100 cows) reported for the area over the past 8 years (36; ODFW Rocky Mountain Elk Herd Reports 2010 - 2017). Strong selective predation on elk calves coupled with high density cougar populations explained the low recruitment and reduced population growth rates of elk in Oregon prior to this study (Johnson et al. 2013, Clark 2014, Clark et al. 2014a, Davidson et al. 2014). Wolves showed continued use of juvenile age classes of elk from summer into winter, possibly reflecting higher availability of young, inexperienced, prey across seasons in my study area. The continued use of elk calves, at previously measured cougar densities, coupled with additional pressures of wolf predation, could intensify the top-down effects of carnivores on elk populations. Lagged response in prey use relative to availability has been reported in patterns of wolf predation for other systems (Kortello et al. 2007), where use of a specific prey resource

continued after availability decreased. This suggests the proportion of elk calves I observed in wolf and cougar diets was likely a reflection of the increased availability of calves on the landscape both seasonally (i.e. birth pulse), and relative to the 2012 peak in numbers of elk calves. Since that time, calf:cow ratios reported at the conclusion of my study (i.e., 5 years post-wolf recolonization) were similar to those reported before the peak (2017 = 12 vs. 2010 = 10). Combined with my finding of reduced cougar kill rates and longer intervals between predation events, this suggests the net effect on elk calf recruitment may be compensatory. If wolves simultaneously reduce cougar populations through exploitative and interference competition effects, as my results suggest might be the case, net effects to elk populations may be negligible.

A study of neonatal elk mortality across 12 populations found evidence for compensatory mortality by all predators (except ursids, bear predation was found to be additive), and that the effect of neonatal predation on overall population dynamics might be weaker than expected if predation was all additive (Griffin et al. 2011). The form of mortality varied between predator species, and interacted with climate, signifying the role of other abiotic factors as critical considerations in the evaluation of top-down effects to prey populations. Interspecific competition between cougar and black bear was an important factor contributing to observed effects, demonstrating how the presence and interaction with conspecific species can influence the form mortality (additive, compensatory, or partial combinations) takes within and among systems (Griffin et al. 2011).

However, even if cougar densities are unchanged relative to expanding wolf populations, subadult cougars have lower kill rates than adults, and females without kittens have lower kill rates than those with kittens (Stoner et al. 2006, Knopff et al. 2010, Clark et al. 2014a, this study). Therefore reductions in the proportion of female cougars raising kittens or shifts toward a younger age structured cougar population could diminish effects to prey populations (Stoner et al. 2006, Robinson et al. 2008). My comparative cougar predation results from northeast Oregon align with this conceptualized paradigm. Wolf density was consistent in the study area over my study duration, but on the low end of wolf densities reported across the Greater Yellowstone

Ecosystem and established wolf-elk systems in North America (see table 6.2 in Fuller et al. 2003), likely reflecting the expanding nature of Oregon's wolf population (see Appendix B). Thus, my study may have captured the process of a system equilibrating, with wolf and cougar population dynamics in flux and effects to prey populations not fully realized.

Wolf Competition Effects On Cougar Populations

Interference competition is expected to have direct effects that result in the immediate exclusion of a competing individual (or population) from a resource (Krebs 1994, Ballard et al. 2003). Under this premise, interference competition with wolves would force cougars to prematurely abandon carcasses (e.g. kleptoparasitism), thereby shortening the intervals between predation events as a function of reduced handling times. My predation results demonstrate the opposite of this, with cougars exhibiting longer intervals between kills, longer handling times, and longer search times in the presence of wolves.

Adequate niche differentiation (diet breadth/overlap or space use behavior) is expected to mitigate competitive exclusion effects and promote sympatric species coexistence (Krebs 1994). Dietary overlap in my study peaked in summer when elk calves were the primary prey identified in both wolf and cougar diets. Sufficient shared resource density can mitigate competition effects. Thus, cougar use of elk calves may reflect use of an abundant prey resource and a system with limited potential for severe agonistic interactions with wolves. However, increased scavenging and use of non-ungulate prey coupled with lower summer kill rates and biomass intake rates relative to pre-wolf conditions provides reasonable evidence cougars in my study experienced interference competition with wolves. Of the two inter-kill interval components (search and handling), I observed stronger effects to the amount of time cougars spent searching for their next prey, which could mean cougars were spending more time actively avoiding wolves while they engaged in hunting. My movement results lent further support to this idea and provide evidence for sex-specific differences in competition mitigation strategies. I simultaneously found decreased biomass intake rates of large prey by

cougars. Coupled with behavioral changes this could inhibit cougar survival or recruitment and could result in cougar population declines.

Management Implications

Our understanding of interspecific interactions and the role they play in predator-prey dynamics and top-down effects from multiple carnivores is improving for natural systems. My estimates of cougar kill rates and my findings in relation to interspecific competition costs to cougar predation and space use patterns can be applied to better anticipate and interpret wolf-cougar-ungulate dynamics. Whether patterns are generalizable across all wolf-cougar systems remains unclear and warrants further research. Beyond adding to the body of work characterizing the agonistic relationship between apex carnivores, my research begins to quantify the costs of interspecific competition (with wolves) for cougar populations in northeast Oregon. Importantly, expanding wolf populations do not obligate additive predation effects to ungulate prey populations with the addition of another carnivore to a system. Wolf recolonization simultaneously introduces elements of interspecific competition between wolves and other predators, including cougars. The strength of interspecific interactions, predator-specific sex and age class of prey use, individual age class contributions to prey population growth, and the influence of abiotic (weather, disease, food limitation) factors determining species mortality will shape the implications of multiple predators for northeast Oregon and other systems with diverse carnivore communities. My results parallel those of Tallian et al. (2017), demonstrating the capacity for interspecific interactions to counter-intuitively alter top-down effects by reducing ungulate kill rates. Overlooking interspecific competition between predators could result in underestimating costs to subordinate competitor species and overestimating effects of multiple predators on prey.

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APPENDICES

APPENDIX A – Cougar Predation Monitoring.

Table A.1. Months predation behavior was monitored for individual cougars post-wolf recolonization in the Mt. Emily WMU of northeast Oregon, USA from July 2014 to October 2016. Data are sorted by month and year, and blank cells indicate predation was not monitored during the month.

Cougar ID	Sex	2014						2015						2016														
		J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
C216	F	N ^a	N	Y ^b	Y	Y	Y	Y	Y	Y	O ^c	O	O	N	N	Y	Y	Y	N	N								
C219	F			S ^d	S	S	S	S	S	S																		
C220	F				N	N	N	N	N	N	N	N	N	N	Y ^e	N	N	N	N	N	N	N	N	N	N	N	N	N
C222	F				S	S	S	S	N	N	N	Y ^e	N	N	N	N	N	N	N	N	N	N	N	Y	Y	Y	Y	
C223	M				N	N	N	N	N	N					N	N	N	N	N	N	N	N	N	N	N	N	N	
C224	F					N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
C229	M														S	S	S	S	S	S	S	S	N	N	N	N	N	N
C230	F														N	N	N	N	N	N	N	N	N	N	N	N	N	N
C231	M														N	N	N	N	N	N	N	N	N	N	N	N	N	N
C232	F														S	S	S	S	S	S	S	S	S	S	S	S	S	S
C233	F														N	N	N	N	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y

^a N: adult cougar with no dependent kittens present at time of monitoring.

^b Y: female cougar with < 6 month old dependent kittens present at the time of monitoring.

^c O: female cougar with > 6 month old dependent kittens present at the time of monitoring.

^d S: subadult cougar with no dependent kittens present at time of monitoring.

^e Evidence of abandoned < 4 week old dependent kittens at time of monitoring.

APPENDIX B – WOLF & COUGAR PREDATION

Cluster identification and field verification

I used the PYTHON (Python Software Foundation, Hampton, NH) rule-based algorithm developed by Knopff et al. (2009) to generate clusters of GPS locations based on carnivore-specific criteria (Anderson and Lindzey 2003, Knopff et al. 2009, Sand et al. 2008, Decesare 2012). For wolves, each cluster was defined as sets of ≥ 2 locations within 300 m and 4 days of each other. For cougar, each cluster was defined as sets of ≥ 2 locations within 200 m over 6 days, with additional locations within 4 or 6 days of the last location adding to wolf and cougar clusters, respectively. I also used seasonal predictive models (regression) developed by Clark et al. (2014) to aid prediction of cougar kill sites and maximize field investigative efforts.

I investigated potential predation sites year-round for cougar (2014 – 2016) and over two seasons from 2014 – 2015 for wolves: 1) summer (1 – 15 of June and 1 – 15 July) and 2) winter (1 Jan – 31 Mar). I monitored predation for 6 wolves from 3 packs and one newly-formed pair over 489 winter wolf-days and for 4 wolves from 2 packs over 64 summer wolf-days ($n = 553$ total wolf-days) from July 10, 2014 to Jan 8, 2016. I investigated 656 wolf GPS location clusters and identified the remains of 159 potential prey at 152 wolf clusters. I investigated 1,557 cougar GPS location clusters and identified the remains of 542 potential prey at 527 cougar clusters. Median number of days between cluster generation and field investigation for sites with prey remains was 37 days ($\bar{x} = 65$ days, SD = 69) for monitored cougars and 6 days ($\bar{x} = 6$ days, SD = 3) in summer and 70 days ($\bar{x} = 92$ days, SD = 66) in winter for monitored wolves. While most edible biomass was consumed before kills were located, I identified species, sex, and age of prey from skeletal remains for both wolves and cougars throughout the year.

Wolf diet composition

Of the 132 wolf-killed prey identified at predation sites, 94.7% were native ungulates and 5.3% were other small mammals (ground squirrel, flying squirrel, snowshoe hare, feral horse Table B1). I located the remains of domestic livestock at 3.1% of all prey remains for wolves during our study, but 60% (3 of 5 cases) were classified as probable/positive scavenging events. The most common ungulate in wolf diets was elk (60.6%), followed by mule deer (21.2). Calves (56.3%) were the most frequent age class of elk observed at predation sites followed by adult

(31.2%), unknown age (7.5%), and yearling (5.0%) elk. Of the adult elk remains for which I could determine sex ($n = 26$), 77% were cows and 23% were bulls. Mule deer were the most common deer species in wolf diets (80%) for remains where I could distinguish between deer species ($n = 35$). Of the deer I documented at wolf predation sites, the most frequent age classes in wolf diets were adults (37.8%) and unknown age (37.8%) deer, followed by fawns (15.6%), and yearling (8.8%) deer. For the adult deer remains where I could determine sex ($n = 12$), 50% were bucks and 50% were does.

Seasonal wolf use of prey age class and sex. – I determined genus and age class for 72 of 94 ungulates at wolf predation sites over winter monitoring periods. For all packs, elk calves ($n = 26$; 36.1%) were the most frequent ungulate prey age class I documented at winter wolf predation sites, with adult elk only slightly less frequent ($n = 22$, 30.6%). I determined genus and age classes for 30 of 31 ungulates document at wolf predation sites over summer monitoring periods. For all packs, elk calves ($n = 19$; 63.3%) continued to be the most frequent age class of prey in summer wolf diets, followed by adult deer ($n = 4$; 13.3%), adult elk ($n = 3$; 10.0%), and yearling deer ($n = 2$; 6.7%). Yearling elk and fawns made up $\leq 5\%$ of the ungulates I identified in summer ($n = 1$ for both). I determined sex for 32 of 39 adult deer and elk identified at wolf predation sites over winter monitoring periods. Of adult deer for which I identified sex ($n = 9$), 55.6% were bucks and 44.4% were does. Of adult elk for which I determined sex ($n = 23$), 26.1% were bulls and 73.9% were cows. I determined sex for 6 of 7 adult deer and elk identified at wolf predation sites over summer monitoring periods. Of adult deer for which I identified sex ($n = 3$), 33.3% were bucks and 66.7% were does. Of adult elk for which I determined sex ($n = 3$), all were cows.

Age of wolf prey. – I obtained known prey age for ungulates less than 2.5 years of age ($n = 83$) based on field estimates of tooth eruption and wear (Robbinette et al. 1957, Schroeder and Robb 2005), and for ungulates greater than 2.5 years old from cementum annuli analysis (Low and Cowan 1963; Matson's Laboratory, Milltown, MT) for prey remains from which incisor teeth were recovered ($n = 34$). The median age of ungulate prey I identified at wolf predation sites across all packs and seasons was < 1 year (min = 0.05 years (< 1 week old), max = 22 years). Median prey age of wolf-killed ungulates was also < 1 year in both summer (0.05 years) and winter (0.83 years) seasons (Figure B1). Median age of adult ungulates at wolf predation sites was 8 years.

Table B1. Seasonal comparison of wolf diets for 3 packs over winter (Jan – Mar) and summer (14 days each in Jun, Jul, Aug) time periods. Results are from 132 predation events for 6 collared wolves from 3 packs in northeast Oregon, USA from 2014 – 2016.

	Meacham				Mt. Emily				Wenaha ^a	
	Summer ^b		Winter		Summer ^c		Winter		Winter ^d	
	%	n	%	n	%	n	%	n	%	n
Individual species										
Mule deer	25.0	3	13.0	3	13.0	3	32.3	10	21.4	9
White-tailed deer	8.3	1	4.3	1	0.0	0	3.2	1	9.5	4
Unknown deer spp. ^e	0.0	0	0.0	0	4.3	1	3.2	1	19.0	8
Elk	50.0	6	78.3	18	69.6	16	58.1	18	50.0	21
Other ^f	16.7	2	4.3	1	13.0	3	3.2	1	0.0	0
Condensed ungulate groups										
Deer	40.0	4	18.2	4	20.0	4	40.0	12	50.0	21
Elk	60.0	6	81.8	18	80.0	16	60.0	18	50.0	21
Ungulates by age class										
Fawn	0.0	0	13.6	3	5.0	1	6.7	2	2.4	1
Yearling deer	10.0	1	0.0	0	5.0	1	0.0	0	4.8	2
Adult deer	20.0	2	0.0	0	10.0	2	16.7	5	19.0	8
Unknown age deer ^g	10.0	1	4.5	1	0.0	0	16.7	5	23.8	10
Calf	40.0	4	50.0	11	70.0	14	30.0	9	14.3	6
Yearling elk	10.0	1	4.5	1	0.0	0	0.0	0	4.8	2
Adult elk	10.0	1	22.7	5	10.0	2	20.0	6	26.2	11
Unknown age elk ^g	0.0	0	4.5	1	0.0	0	10.0	3	4.8	2

^a No summer data available for this pack.

^b One summer period (August 2014).

^c Three summer periods (June 2014, June 2015, July 2015).

^d Two winters (2014, 2015).

^e Insufficient evidence to identify to species level.

^f Other prey items included ground squirrel, flying squirrel, snowshoe hare, feral horse, and domestic sheep; most livestock (60%) were classified as probable/positive scavenging events.

^g Insufficient evidence present to assign age class.

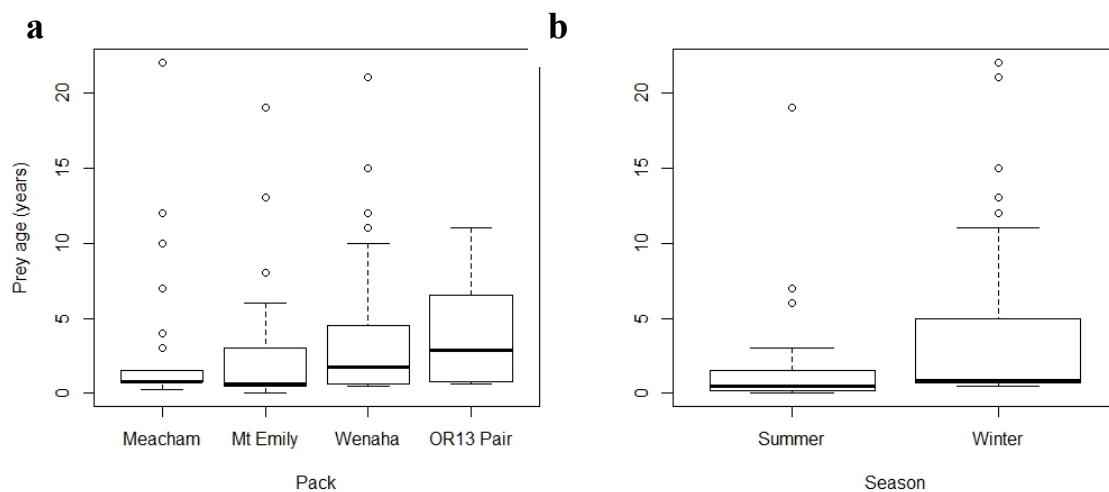


Figure B1. Cementum annuli (> 2 yrs) and field estimated (< 2 yrs) age of ungulate prey remains located at wolf predation sites by wolf pack (a) and season (b). Results are from 117 of 132 predation events for 6 collared wolves from 3 packs and 1 pair in northeast Oregon, USA from 2014 – 2015.

Condition of wolf prey. – Marrow fat content of prey remains located at wolf predation sites from which I was able to obtain marrow samples ($n = 53$) ranged from 16.1 – 100%, with a mean across all packs and seasons of 77.3% ($SD = 24.18$). There were no seasonal differences in the marrow condition between winter ($\bar{x} = 78.1\%$, 95% CI = 71.0 – 85.2) and summer ($\bar{x} = 72.7\%$, 95% CI = 55.5 – 89.9), but marrow fat content of winter wolf-killed ungulate prey was higher than the marrow condition of a road-killed sample of ungulates collected over similar winter conditions ($n = 10$, $\bar{x} = 62.7\%$, 95% CI = 45.7 – 79.8).

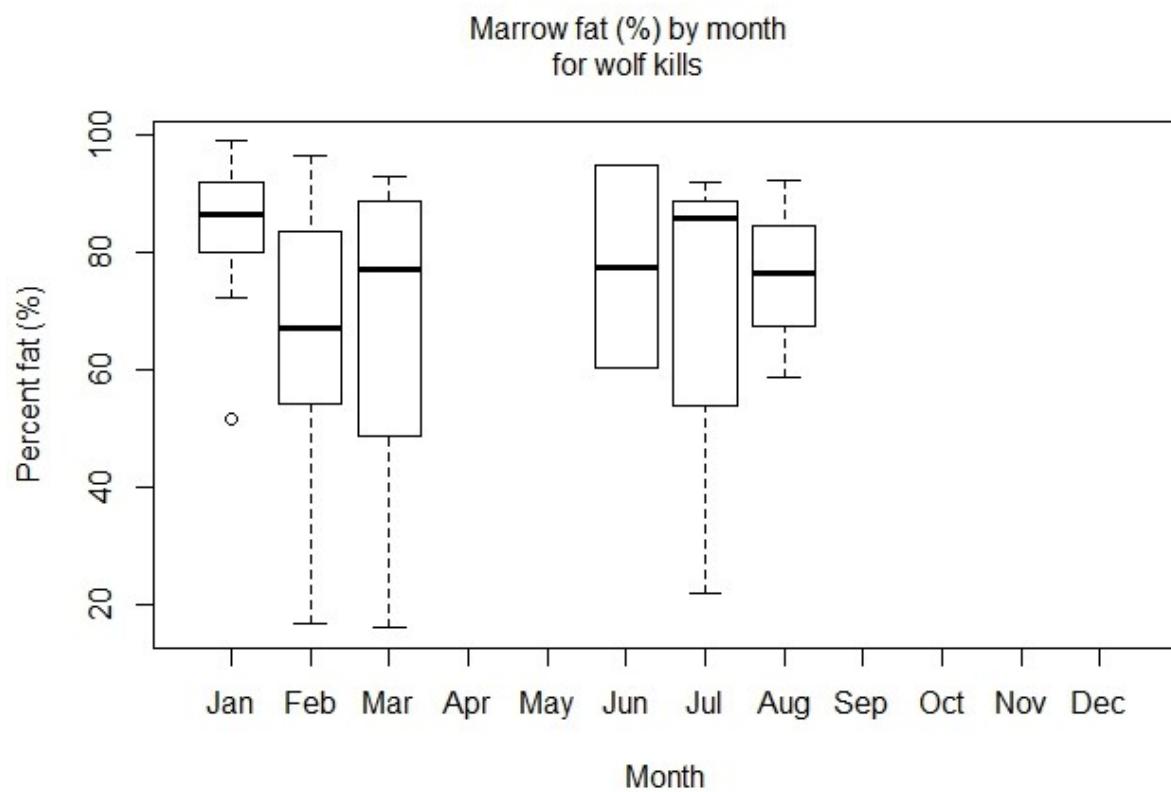


Figure B2. Median monthly marrow fat content (%) of ungulate prey remains located at wolf predation sites. Results are from 132 predation events for 6 collared wolves from 3 packs in northeast Oregon, USA from 2014 – 2016.

Table B2. Pack estimate comparison of wolf kill rates expressed as a numerical frequency (ungulates/week), mean biomass intake (kg ungulates/week), individual wolf biomass intake (kg ungulates/week/wolf), and inter-kill interval (IKI; days between consecutive ungulate kills). I derived mean biomass intake rates for wolf packs from estimated weights of prey at 134 consecutive wolf predation events in northeast Oregon, USA from 2014 – 2016. Wolf biomass intake rates were derived by dividing mean pack biomass intake by each packs' average group size. I estimated kill rates using data from 6 wolves (3 packs and one pair) with ≥ 14 day monitoring intervals over winter (Jan – Mar) and summer (Jun – Aug) seasons.

Wolf pack	Pack size	Prey age (years)	Kill rate (ungulates/week)		Biomass intake (kg ungulates/week)		Per wolf biomass (kg ungulates/week/wolf)		IKI (days)	
	\bar{x}	Median	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Meacham	5	<1	2.53	1.26	246	90	49	18	3	0.60
Mt. Emily	7.5	<1	2.28	0.48	183	14	24	2	3	0.38
Wenaha	11.5	2	2.08	0.35	195	23	17	1	3	0.56
OR13 pair	2	3	1.40	-	202	-	101	-	4	0.82

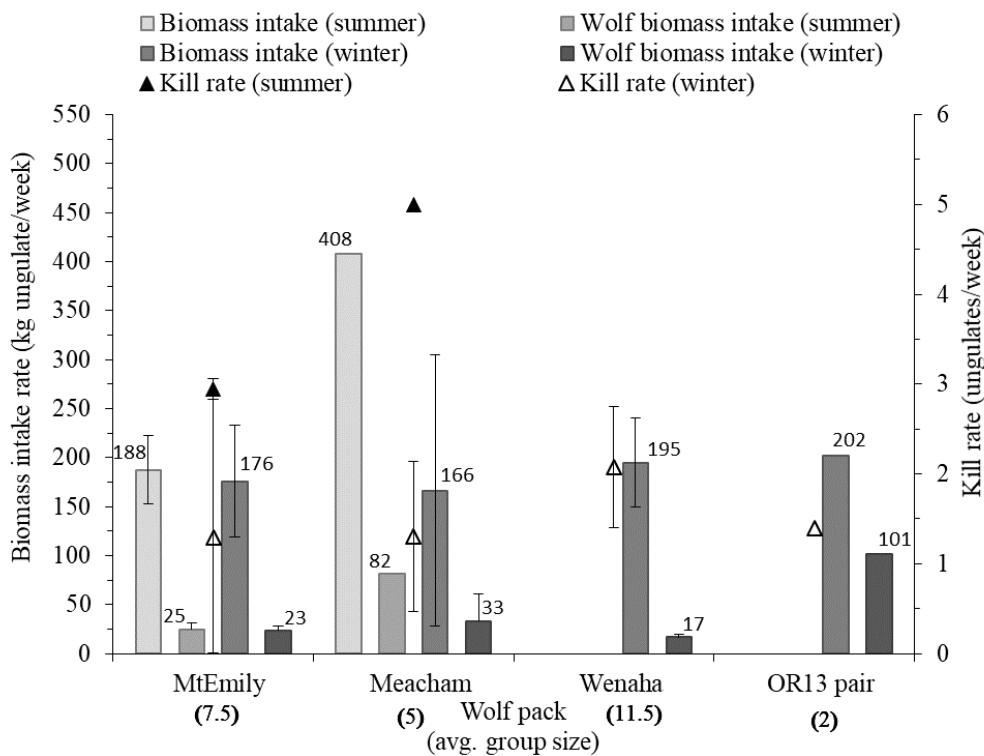


Figure B3. Estimate comparison of mean numerical wolf kill rate (ungulates/week/pack), biomass intake (kg ungulate/week/pack), individual wolf biomass intake (kg ungulate/week/wolf), and associated 95% confidence intervals by pack and season. I derived mean biomass intake rates for wolf packs from estimated weights of prey at 134 consecutive wolf predation events in northeast Oregon, USA from 2014 – 2016. Wolf biomass intake rates (kg ungulate prey/week/wolf) were derived by dividing mean pack biomass intake by each packs' average group size. I estimated kill rates using data from 6 wolves (3 packs and one pair) with ≥ 14 day monitoring intervals over winter (Jan – Mar) and summer (Jun – Aug) seasons.

Cougar diet composition

Of the 481 cougar-killed prey identified at predation sites, 92.3% were native ungulates (deer and elk) and 7.7% were other carnivores (coyote, badger, black bear), small mammals (beaver, ground squirrel, snowshoe hare), or birds (turkey, ruffed grouse; Table B3). During our study, domestic livestock (sheep, cattle, goat) were infrequently killed or scavenged by cougar (< 1.1% all prey remains). The most common ungulate I documented in cougar diets were deer (58.3%, mule deer and white-tailed combined), followed by elk (41.7%). Mule deer were the most common species in cougar diets (93.3%) for remains where I could distinguish between

deer species ($n = 223$). Of the 259 deer I documented at cougar predation sites, most were fawns (40.9%), followed by adult (27.8%), unknown age (21.6%), and yearling (9.7%) deer. For the adult deer remains where I could determine sex ($n = 42$), 76.2% were does and 23.8% were bucks. Calves (69.8%) were the most frequent prey age class of elk I documented at cougar predation sites, followed by adult (15.8%), yearling (7.0%), and unknown age (5.4%) elk. Of the adult elk remains for which I could determine sex ($n = 27$), 81.5% were cows and 18.5% were bulls.

Seasonal cougar use of prey age class and sex. – Of the 184 ungulates I documented at cougar predation sites in winter, I determined genus and age class for 143 individuals. Across all cougars, fawns ($n = 48$; 33.6%) were the most frequent ungulate prey at winter cougar predation sites, followed by adult deer ($n = 34$; 23.8%), and elk calves ($n = 25$; 17.5%). Yearling deer and elk made up < 10% of ungulates documented at winter predation sites ($n = 13$ and $n = 6$, respectively). Of the 260 ungulates I documented at summer cougar predation sites, I determined genus and age class for 231. Across all cougars, elk calves ($n = 104$; 40.0%) were the most frequent ungulate prey at summer predation sites, followed by fawns ($n = 58$; 22.3%), and adult deer ($n = 38$, 14.6%). Yearling deer and elk made up $\leq 5\%$ of the ungulates documented at summer cougar predation sites ($n = 12$ and $n = 7$, respectively). I determined sex for 29 of 56 adult deer and elk documented at cougar predation sites over winter monitoring periods. Of adult deer for which I identified sex ($n = 13$), 30.8% were bucks and 69.2% were does. Of adult elk for which I determined sex ($n = 16$), 18.8% were bulls and 81.2% were cows. I determined sex for 40 of 54 adult deer and elk documented at summer cougar predation sites. Of adult deer for which I identified sex ($n = 29$), 20.7% were bucks and 79.3% were does. Of adult elk for which I determined sex ($n = 11$), 18.2% were bulls and 81.8% were cows. Across seasons, adult elk were more frequently preyed on by male cougars (70% adult elk kills) than by female cougars, and 80% of bulls killed (4 of 5) were preyed on by male cougar.

Table B3. Comparison of cougar diets for adult males (AM, $n = 3$), independent subadult females (SF, $n = 3$), solitary adult females with no kittens (Sol F, $n = 8$), adult females with < 6 month old kittens (FG < 6 mo. old, $n = 3$), and adult females with > 6 month old kittens (FG > 6 mo. old, $n = 1$) over winter (1 Nov – 30 Apr) and summer (1 May – 31 Oct) seasons. Results were from 481 post-wolf recolonization predation events for 11 cougars in the Mt. Emily WMU, in northeast Oregon, USA from 2014 – 2016. One subadult female transitioned to adult during monitoring.

	AM				SF				Sol F				FG (< 6 mo. old)				FG (> 6 mo. old)			
	S		W		S		W		S		W		S		W		S		W	
	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n
Individual species																				
Mule deer	14.5	10	25.9	14	0.0	0	40.0	12	44.5	69	71.7	66	61.5	24	52.4	11	11.1	1	33.3	1
White-tailed deer	1.4	1	9.3	5	0.0	0	13.3	4	0.0	0	4.3	4	0.0	0	4.8	1	0.0	0	0.0	0
Unknown deer spp.	7.2	5	3.7	2	22.2	2	10.0	3	8.4	13	6.5	6	12.8	5	0.0	0	0.0	0	0.0	0
Elk	62.3	43	61.1	33	44.4	4	10.0	3	43.9	68	10.9	10	23.1	9	33.3	7	66.7	6	66.7	2
Other	14.5	10	0.0	0	33.3	3	26.7	8	3.2	5	6.5	6	2.6	1	9.5	2	22.2	2	0.0	0
Condensed ungulate groups																				
Deer	27.1	16	38.9	21	33.3	2	86.4	19	54.7	82	88.4	76	76.3	29	63.2	12	14.3	1	33.3	1
Elk	72.9	43	61.1	33	66.7	4	13.6	3	45.3	68	11.6	10	23.7	9	36.8	7	85.7	6	66.7	2
Age class of ungulate																				
Fawn	6.9	4	12.7	7	0.0	0	27.3	6	28.0	42	34.9	30	28.9	11	21.1	4	33.3	1	33.3	1
Yearling deer	5.2	3	5.5	3	0.0	0	9.1	2	4.0	6	9.3	8	7.9	3	0.0	0	0.0	0	0.0	0
Adult deer	6.9	4	9.1	5	16.7	1	18.2	4	16.0	24	25.6	22	23.7	9	15.8	3	0.0	0	0.0	0
Unknown age deer	6.9	4	12.7	7	16.7	1	31.8	7	6.7	10	18.6	16	15.8	6	26.3	5	0.0	0	0.0	0

Calf	48.3	28	21.8	12	66.7	4	0.0	0	41.3	62	5.8	5	23.7	9	36.8	7	33.3	1	33.3	1
Yearling elk	8.6	5	7.3	4	0.0	0	4.5	1	1.3	2	1.2	1	0.0	0	0.0	0	0.0	0	0.0	0
Adult elk	17.2	10	25.5	14	0.0	0	4.5	1	0.7	1	1.2	1	0.0	0	0.0	0	33.3	1	33.3	1
Unknown age elk	0.0	0	5.5	3	0.0	0	4.5	1	2.0	3	3.5	3	0.0	0	0.0	0	0.0	0	0.0	0

^a Insufficient evidence to identify to species level.

^b Other prey items included badger, beaver, black bear, coyote, ground squirrel, snowshoe hare, turkey, grouse spp., and domestic sheep, and cattle.

^c Insufficient evidence present to assign age class.

Table B4. Reproductive social class, monitoring duration, location fix success, and summary of scavenge events, non-ungulate, and ungulate prey located at predation sites with carcass detections for GPS collared cougars in the Mt. Emily WMU, in northeast Oregon, USA from 2014 – 2016. Adult males (AM), subadult females (SF), solitary adult females with no kittens (Sol F), adult females with < 6 month old kittens (FG < 6 mo. old), and adult females with > 6 month old kittens (FG > 6 mo. old) were monitored over winter (1 Nov – 30 Apr) and summer (1 May – 31 Oct) seasons. One subadult female transitioned into the solitary adult female class during predation monitoring. Three adult females had litters of kittens during predation monitoring, and one of those litters transitioned to the adult female with > 6 month old kitten class during the study.

	Reproductive	No.	No.	No.	No.	No.		
Cougar	social	Days	GPS	Fix success	carcass	scavenge	non-ungulate	ungulate
ID	class	monitored	locations	(%)	detections	events	prey	kills
C216	Sol F/FG<6/FG>6	540	4333	94.7	87	5	8	72
C219	SF	227	1582	98.2	26	5	6	14
C220	Sol F	516	3371	94.5	78	11	1	65
C222	SF/Sol F/FG<6	557	3933	97.6	78	6	8	63
C223	AM	490	3926	96.9	59	3	0	55
C224	Sol F	195	2056	76.0	39	0	0	39
C229	AM	256	2749	91.7	40	9	5	26
C230	Sol F	243	2700	90.5	37	2	1	34
C231	AM	306	2453	97.3	45	3	5	37
C232	SF	140	1179	95.0	12	4	0	8
C233	Sol F/FG<6	243	1950	95.9	40	6	3	31

Table B5. Cougar age and reproductive group comparison of mean annual kill rate estimates expressed as a numerical frequency (ungulates/week) and mean biomass intake (kg ungulates/week). Results were from 389 consecutive cougar predation events from 11 cougars fit with GPS collars in northeast Oregon, USA, 2014 – 2016. Estimates were calculated using data from individual cougars continuously monitored for ≥ 42 days. I derived mean biomass intake rates from estimated weights of prey at cougar predation events.

Cougar group	Kill rate		Biomass intake	
		(ungulates/week)		(kg ungulates/week)
	\bar{x}	95%CI	\bar{x}	95%CI
Subadult ^a	0.39	0.33, 0.44	16	9, 23
Adult ^b	0.86	0.80, 0.93	47	32, 62
Male	0.71	0.52, 0.89	68	50, 87
Female ^c	0.82	0.62, 1.01	32	6, 21
Sol F ^d	0.90	0.65, 1.15	37	22, 51
FG < 6 month ^e	0.74	0.60, 0.88	26	16, 35
FG > 6 month ^f	0.32 ^g	-	6	-

^a All subadults were independent females < 2 years old at time of monitoring.

^b Females ≥ 2 years and males ≥ 3 years old at time of monitoring.

^c All female reproductive classes combined.

^d Solitary females with no dependent kittens at time of monitoring.

^e Adult females with dependent kittens < 6 months old at time of monitoring.

^f Adult females with dependent kittens > 6 months old at time of monitoring.

^g Only one female with > 6 month old kittens met monitoring criteria for rate calculation.

Condition of cougar prey. – Marrow fat content of prey remains located at cougar predation sites from which I was able to obtain marrow samples ($n = 96$) ranged from 13.9 – 100%, with a mean across all cougars and seasons of 75.4% ($SD = 21.67$). The mean marrow condition of cougar-killed ungulate prey was lower in winter ($\bar{x} = 67.4\%$, 95% CI = 60.0 – 74.8) than summer ($\bar{x} = 81.6\%$, 95% CI = 77.1 – 86.1), but consistent with winter marrow condition of road-killed ungulates over the same period.

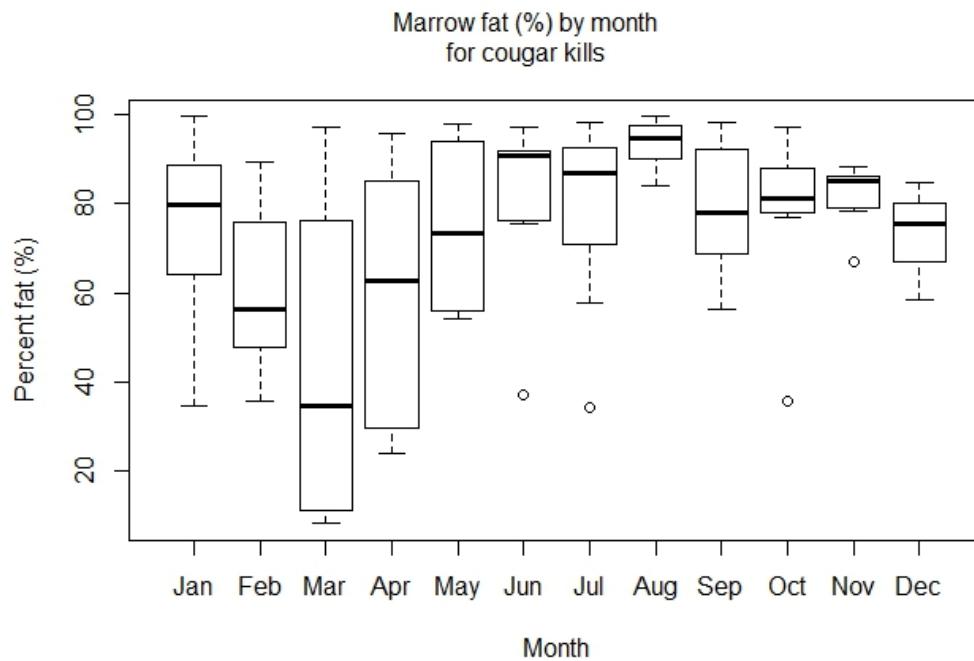


Figure B4. Mean monthly marrow fat content (%) of prey remains located at cougar predation sites. Results were from 481 post-wolf recolonization predation events for 11 cougars in the Mt. Emily WMU, in northeast Oregon, USA from 2014 – 2016.

Comparison of wolf and cougar prey condition

There was no difference between mean marrow fat of ungulates preyed on by wolves and cougars ($W = 2786, P = 0.40$). There was evidence the mean marrow condition of winter wolf-killed ungulates was 1.16 times higher (better condition) than winter cougar-killed ungulates ($W = 1225, P = 0.02$), but there was no evidence of differences in the marrow fat content of wolf- and cougar-killed ungulates in summer ($W = 171, P = 0.31$). I observed no seasonal differences in timing of predation by wolves or cougar ($n = 18; W = 31, P = 0.83$) on the poorest condition

ungulates ($\leq 50\%$ fat content), but most were preyed on by cougar ($n = 11$; 61.1%), including the lowest marrow fat content recorded for the study (13.9% from an adult white-tailed deer preyed on in March).

Study area wolf population summary

Wolf recolonization of northeast Oregon was first documented in 2009, but the onset of wolf activity and pack use in the study area (Mt. Emily WMU) began in 2011 (2011 – 2017 Annual Wolf Reports, Oregon Department of Fish and Wildlife, and 2009 – 2010 Rocky Mountain Wolf Recovery Interagency Annual Reports, US Fish and Wildlife Service). I compiled minimum estimates of wolf numbers for packs in the study area to produce study-area-specific estimates of wolf density (number of wolves per 1000km^2), which are relative to the Mt. Emily WMU and should not be used to make inferences about wolf density across the broader Oregon wolf population (Figure B5). Wolf density steadily increased over the first 3 years in Mt. Emily, but remained relatively constant after reaching 10 wolves/ 1000km^2 in 2014 (beginning this study). The 7-year mean wolf density for the study area was $6.2 (\pm 1.4 \text{ SE})$ wolves/ 1000km^2 . Mean pack size in the study area was $4.9 (\pm 0.64 \text{ SE})$ wolves (range: 2 – 8 wolves). Wolf density was consistent in the study area over our study duration (range: 7 – 10 wolves/ 1000km^2), but lower than wolf density reported in a similar Banff NP wolf predation study ($26.5 \pm 7 \text{ SE}$ wolves/ 1000km^2 ; Kortello et al. 2007) and on the low end of wolf densities reported across the Greater Yellowstone Ecosystem (range: 2 – 99 wolves/ 1000 km^2 ; Cubaynes et al. 2014) and established wolf-elk systems in North America (range: 8 – 26 wolves/ 1000km^2 ; from table 6.2 in Fuller et al. 2003). Study area size differences and associated variability in prey density between Mt. Emily WMU ($1,992\text{km}^2$) in Oregon, Bow Valley (340km^2) in Banff NP, as well as the Interior (7991km^2) and Northern Range (995km^2) of YNP (Cubaynes et al. 2014) may account for any observed differences between this study and those reported for wolf studies in other systems. Importantly, lower wolf density in our study is likely due to the expanding nature of Oregon's wolf population.

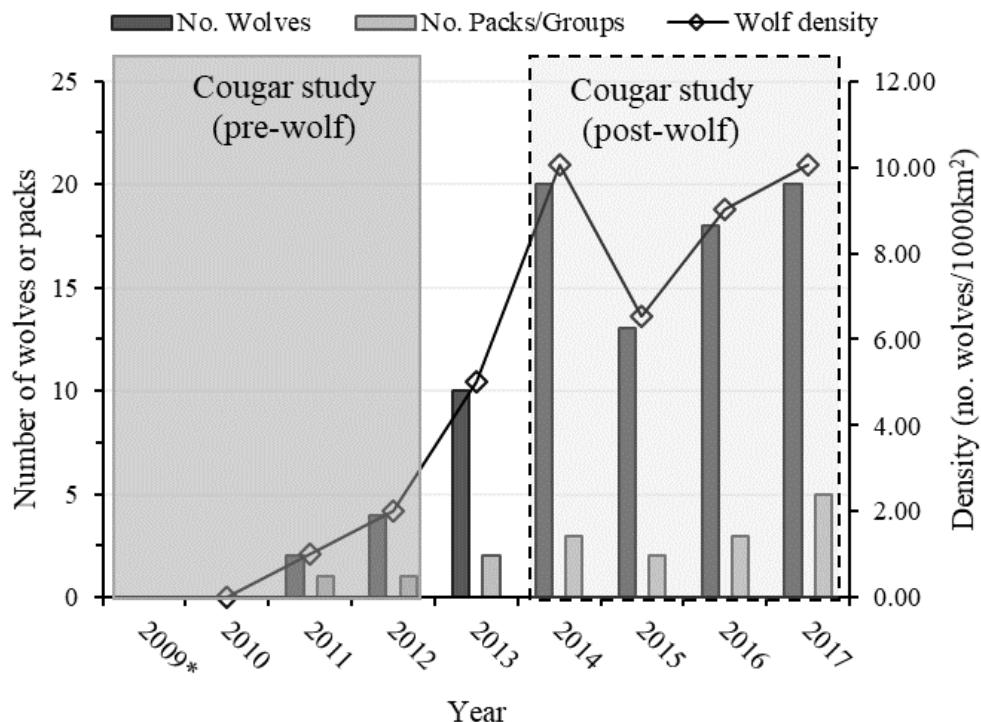


Figure B5. Number of individual wolves, wolf packs or groups, and estimated wolf density ($\text{wolves}/1000\text{km}^2$) from 2009 – 2017 in the Mt. Emily WMU ($1,992\text{km}^2$), in northeast Oregon, USA. A group of 2 – 3 wolves traveling together was defined as a wolf group/pair and a wolf pack was defined as 4 wolves traveling together in winter. Information on wolf numbers comes from Oregon Wolf Conservation and Management Annual Wolf Reports (2011 – 2017, Oregon Department of Fish and Wildlife) and Rocky Mountain Wolf Recovery Interagency Annual Reports (2009 – 2010, US Fish and Wildlife Service). Cougar studies were conducted prior to wolf recolonization (2009 – 2012) and after multiple wolf packs recolonized the management unit (this study, 2014 – 2016). Year recognized as Oregon wolf recolonization origination denoted by (*).

Study area elk and mule deer population summary

Information on ungulate numbers comes from Oregon Mule Deer and Rocky Mountain Elk Herd Reports (2009 – 2017, Oregon Department of Fish and Wildlife). I compiled minimum estimates of elk and mule deer numbers reported for the entire study area to produce study-area-specific estimates of elk and mule deer density (number of elk or deer per 100km^2), which are relative to Mt. Emily WMU and should not be used to make inferences about ungulate density

across Oregon elk or mule deer populations. Elk density was relatively constant with a slight increasing trend over the years spanning pre- and post-wolf cougar study periods, with a mean density of $152 (\pm 3 \text{ SE}) \text{ elk}/100\text{km}^2$. Mule deer density declined in the study area from 2009 – 2016, with a mean density of $212 (\pm 10.2 \text{ SE}) \text{ deer}/100\text{km}^2$. Mean elk density in this study was higher than mean elk density reported in a similar Banff NP predation study ($96 \pm 25 \text{ SE}$ elk/ 100km^2 ; Kortello et al. 2007). Higher elk density in our study could be due to study area size differences between Mt. Emily WMU and Bow Valley (outlined above). However, the reported elk density at the onset of wolf recolonization in Bow Valley ($176 \text{ elk}/100\text{km}^2$) was higher than elk density in our study area at the onset of wolf recolonization ($145 \text{ elk}/100\text{km}^2$), but coincided with a series of 156, 35, and 1 administrative management elk relocations out of Bow Valley over the first 3 years of that study. These extenuating circumstances related to human-induced changes in prey density at the onset of wolf recolonization may account for any observed differences between this study and those reported for Banff NP.

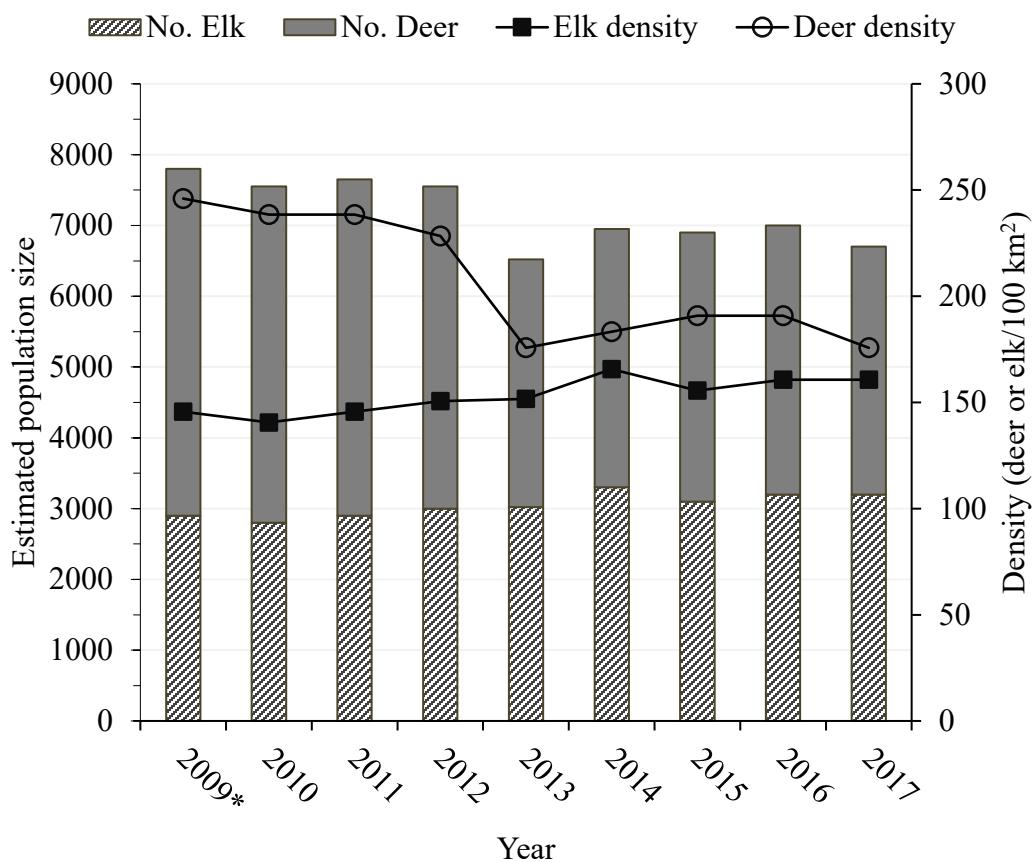


Figure B6. Number of mule deer and elk, and estimated density (number of deer or elk per 100km²) from 2009 – 2017 for the Mt. Emily WMU (1,992km²), in northeast Oregon, USA. Information on ungulate numbers comes from Oregon Mule Deer and Rocky Mountain Elk Herd Reports (2009 – 2017, Oregon Department of Fish and Wildlife). Year recognized as Oregon wolf recolonization origination denoted by (*).

APPENDIX C – WOLF & COUGAR HOME RANGE

Here I report additional information on wolf and cougar home range, predation distribution and latent selection (Chapter 4). I used GPS locations to generate fixed kernel density estimates (KDE) of individual cougar and wolf utilization distributions (UD), and built isopleth probability surfaces at the 50th and 95th percentiles (Millspaugh et al. 2004). I defined the 50th percentile as “core” use range, as this area contained 50% of locations for either wolves or cougars. I also estimated KDEs and overlap for individual wolves and their respective packs, for a subset of wolves with multiple collars per pack, to understand any bias in HR size (or overlap indices) that might have resulted based upon which individual pack member a GPS collar was deployed (e.g. a breeding vs. yearling wolf). KDEs and isopleth home ranges were generated in Geospatial Modeling Environment (GME; Beyer 2012) using the PLUGIN bandwidth at a 30-m resolution.

I calculated spatial area overlap as the percent overlap in core and 95% KDE ranges following:

$$[(\text{area}_{\alpha\beta}/\text{home range}_\alpha)(\text{area}_{\alpha\beta}/\text{home range}_\beta)]^{0.5} \quad (1)$$

where $\text{area}_{\alpha\beta}$ is the overlapping zone common to α and β , and range_α and range_β are the 95% KDE ranges for individual cougar α and wolf population or pack β (Atwood and Weeks 2003).

Table C.1. Individual wolf home range (HR) estimates (km^2) for 17 wolves from 6 packs used to compare distribution patterns with sympatric cougars in northeast Oregon, USA (2012 – 2018). HR sizes were derived from 50% and 95% probability contours of kernel density estimates (KDE) for wolves over annual, summer (May – Oct), and winter (Nov – Apr) time periods.

*Denotes wolf with locations for < 1 year.

Wolf ID	Home range size (km^2)					
	Summer		Winter		Annual	
	50%	95%	50%	95%	50%	95%
OR11	123.7	611.2	101.9	499.2	155.5	793.9
OR13	23.0	248.8	57.0	326.2	47.5	334.0
OR14	23.1	129.1	42.6	310.5	31.4	228.0
OR21	130.3	586.6	148.9	506.8	212.9	654.3
OR22	23.4	128.5	30.4	208.9	28.6	184.8
OR23	30.5	164.1	33.2	174.4	32.4	186.8
OR26	10.9	100.2	43.6	238.7	17.1	151.0

OR28	20.4	291.9	99.5	687.3	43.7	464.8
OR29	7.5	100.5	58.5	310.6	28.7	233.6
OR30	84.9	831.3	164.8	1330.5	185.6	1482.9
OR31	25.7	329.3	183.9	881.1	71.3	608.8
OR32	68.2	497.6	220.9	999.1	147.9	811.3
OR47	27.2	204.1	86.3	383.2	71.8	383.0
OR51	7.0	59.8	26.8	140.9	13.5	114.5
OR56	109.1	541.4	174.8	644.6	172.4	747.6
OR62	62.4	415.8	61.0	436.5	109.7	717.5
OR65*	5.0	84.0			5.0	84.0

Table C.2. Wolf pack home range (HR) estimates (km^2) for 6 packs from 17 wolves used to compare distribution patterns with sympatric cougars in northeast Oregon, USA (2012 – 2018). HR sizes were derived from 50% and 95% probability contours of kernel density estimates (KDE) for wolves over annual, summer (May – Oct), and winter (Nov – Apr) time periods. For packs with multiple GPS collars, HR were derived from density estimates of combined locations.

Pack	Home range size (km^2)					
	Summer		Winter		Annual	
	50%	95%	50%	95%	50%	95%
Meacham	12.7	136.9	57.7	345.3	26.0	238.0
Mt Emily	33.2	437.9	164.3	1074.0	82.0	814.1
North Emily	7.0	59.8	26.8	140.9	13.5	114.5
Ruckle Ridge	27.2	204.1	86.3	383.2	71.8	383.0
Umatilla River	20.1	118.3	31.0	214.1	25.6	180.0
Wenaha	15.8	95.5	95.0	367.9	82.3	361.7

Table C.3. Mean percent overlap and agreement between core (50%) and 95% individual wolf home range and pack use range. Annual and seasonal (summer: 1 May – 31 Oct, winter: 1 Nov – 30 Apr) home ranges were derived from kernel density estimates of GPS locations ($n = 38,324$) for 17 wolves from 6 packs with multiple collared wolves per pack in northeast Oregon, USA (2012 – 2018).

Table C.4. Individual cougar home range (HR) estimates (km^2) for 40 cougars used to compare distribution patterns over time periods pre- (2009 – 2012) and post-wolf recolonization (2014 – 2018). HR sizes were derived from 50% and 95% probability contours of kernel density estimates (KDE) for male ($n = 13$) and female ($n = 27$) GPS collared cougars over annual, summer (May – Oct), and winter (Nov – Apr) periods in northeast Oregon, USA.

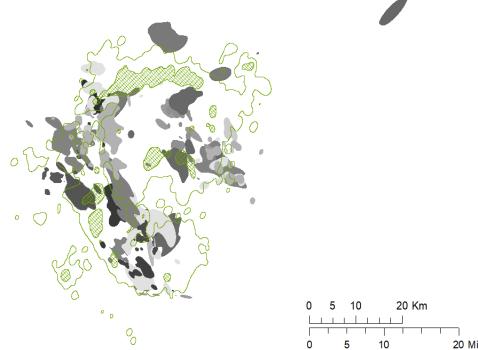
Cougar ID	Sex	Study period	Home range size (km^2)					
			Summer		Winter		Annual	
			50%	95%	50%	95%	50%	95%
c143	F	Pre-wolf	7.4	47.7	52.4	433.7	52.5	364.5
c145	F	Pre-wolf	0.1	0.6	5.2	25.2	3.0	22.3
c146	F	Pre-wolf	15.8	58.8	12.0	64.4	22.1	79.2
c147	F	Pre-wolf	46.1	139.9	32.0	114.9	42.5	137.4
c149	F	Pre-wolf	35.6	173.0	16.5	102.9	25.0	149.5
c150	F	Pre-wolf	15.8	71.3	38.6	158.5	38.1	145.1
c155	F	Pre-wolf	100.9	450.5	32.1	178.2	76.5	409.6
c156	M	Pre-wolf	34.4	130.2	18.1	73.3	35.5	133.6
c157	M	Pre-wolf	2.6	73.3	3.5	18.2	9.0	139.5
c158	F	Pre-wolf	36.4	162.8	43.4	238.3	56.8	260.4
c160	F	Pre-wolf	9.4	44.9	9.9	62.4	13.4	71.7
c161	F	Pre-wolf			29.1	137.4	29.1	137.4
c162	M	Pre-wolf	84.1	262.7	62.2	222.3	101.6	309.1
c163	F	Pre-wolf	9.7	48.3	16.1	65.4	17.2	75.6
c164	M	Pre-wolf	89.1	347.5	37.7	196.9	63.5	281.5
c166	M	Pre-wolf	55.3	191.8	26.1	180.9	41.4	195.8
c167	F	Pre-wolf	11.7	48.5	9.3	35.3	12.6	46.1
c176	F	Pre-wolf	16.2	80.4	5.6	39.9	19.5	86.7
c187	F	Pre-wolf	3.1	15.0	7.6	39.8	10.5	46.1
c192	M	Pre-wolf	41.2	157.9	18.7	126.9	58.3	242.1
c193	F	Pre-wolf	13.3	73.7	8.2	52.4	11.7	79.3
c194	M	Pre-wolf	67.8	237.5	44.1	178.1	72.7	225.3
c197	M	Pre-wolf	26.3	128.4	7.7	60.5	23.8	121.2
c201	M	Pre-wolf			26.1	154.3	26.1	154.3
c167	F	Post-wolf			4.7	33.8	4.7	33.8
c216	F	Post-wolf	18.0	88.3	29.6	113.1	31.2	125.2
c219	F	Post-wolf	22.9	91.2	19.3	92.8	24.8	104.2
c220	F	Post-wolf	41.1	174.2	47.8	300.8	49.6	257.1
c222	F	Post-wolf	11.9	92.5	50.8	303.3	37.1	233.8
c223	M	Post-wolf	54.9	216.4	40.3	204.7	50.8	223.5
c224	F	Post-wolf	16.2	59.8	11.8	55.2	16.8	66.9

c228	M	Post-wolf		13.4	56.9	13.4	56.9	
c229	M	Post-wolf	44.8	316.5	62.9	378.7	86.1	469.2
c230	F	Post-wolf	17.9	76.7	9.9	59.1	18.6	82.6
c231	M	Post-wolf	96.7	424.2	41.9	201.3	103.1	428.8
c232	F	Post-wolf	20.3	143.6	22.4	159.3	25.5	167.7
c233	F	Post-wolf	20.3	104.7	27.6	172.5	35.8	161.7
c244	M	Post-wolf	49.8	191.1	29.8	191.2	59.0	244.5
c245	F	Post-wolf	5.4	27.1	2.8	16.4	6.9	32.5

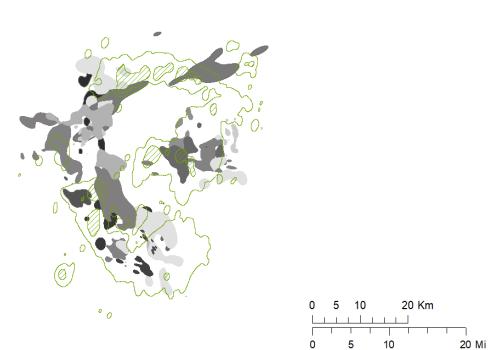
Table C.5. Magnitude and direction of change in overlap percentages for cougar home range (HR) and wolf use range (derived from GPS locations) vs. cougar HR and wolf predation range (derived from wolf predation sites).

Sex	50% wolf use vs. wolf predation		95% wolf use vs. wolf predation	
	Pre	Post	Pre	Post
Male				
50% HR	+8.6	+3.4	-0.2	+1.0
95% HR	-7.1	-7.5	-24.7	-26.3
Female				
50% HR	+2.8	+1.8	+0.6	0
95% HR	-4.0	-2.3	-16.1	-15.2

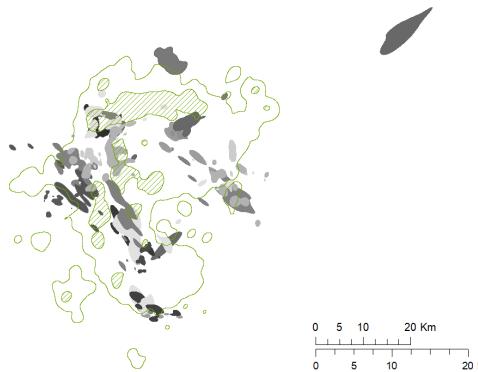
a) Annual



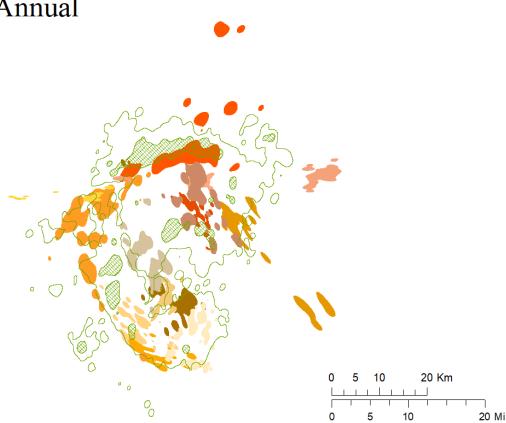
b) Summer



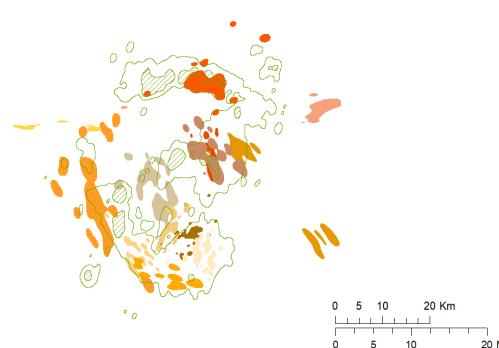
c) Winter



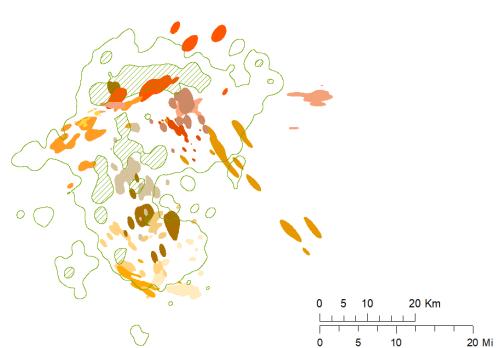
d) Annual



e) Summer



f) Winter



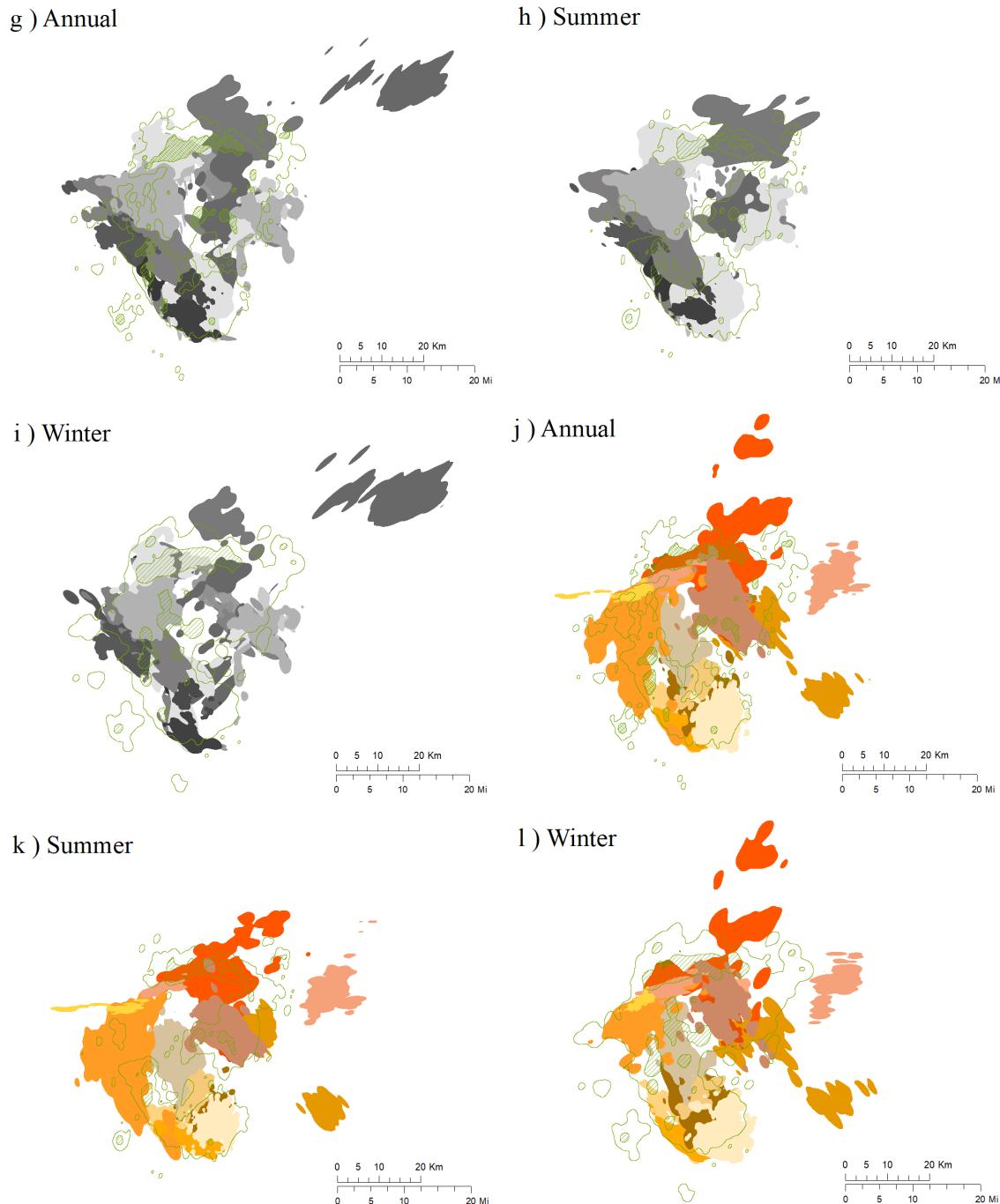


Figure C.1 Distribution of pre- (a – c, g – i) and post-wolf cougar (d – f, j – l) home range (HR) overlap with wolf range during annual (a, d, g, j), summer (b, e, h, k), and winter (c, f, i, l) seasons in northeast Oregon, USA (2009 – 2018). HR are 50% (a – f) and 95% (g – l) probability contours derived from the individual-level kernel density estimate (KDE) of pre- (gray scale, $n = 43,653$) and post-wolf (orange scale, $n = 54,904$) GPS locations from 40 cougars. Population-

level wolf range was derived from 17 wolves (green, $n = 38,324$), with 50% and 95% contours represented by diagonal slash and solid line polygons, respectively.

Latent selection difference functions (LSDFs) use a logistic regression framework to provide estimates of selection behavior differences and allow direct comparison of characteristics of use between two groups of interest, quantifying a measurement of relationship strengths (Latham et al. 2011, Latham et al. 2013, Erickson et al. 2014, Lendrum et al. 2017). I carried out two LSDFs to compare characteristics between wolves and cougars and between study periods for cougars. Using predator species as the dependent variable the model takes the form,

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i) \quad (3)$$

where $w(x)$ represents the relative probability of a cougar predation site (coded as 1) occurring on the landscape compared to a wolf predation site (coded as 0). The selection coefficient β_i is represented for each predictor variable (x_i) from a vector of covariates (x) and is interpreted as the relative difference in selection between wolves and cougar, not the selection or use of a given habitat (Czetwertynski et al. 2007). To evaluate any changes in habitat characteristics at cougar predation sites across time periods, our second LSDF quantified the relative probability of a cougar predation site with wolves on the landscape (coded as 1) compared to a cougar predation site with no wolves (coded as 0). I carried out regressions over both annual and seasonal (winter, summer) time frames. This allowed variation in the distribution of ungulate prey (elk and deer) on the landscape associated with seasonal foraging range fidelity (Mao et al. 2005, Sawyer et al. 2006, Kauffman et al. 2007) to account for and characterize season-specific effects as well as broad-scale annual influences.

Table C.6. Latent selection difference function (LSDF) model comparing relative predation site feature selection by wolves (*Canis lupus*; coded as 0) and cougars (*Puma concolor*; coded as 1) over annual periods in northeastern Oregon, USA, 2014 – 2016.

Variable	β	SE	P	Relative selection (%) ^a
Elevation	-0.0461	0.1318	0.7103	5
Eastness	-0.0860	0.1633	0.5878	8
Northness	0.0527	0.1522	0.7352	1
Terrain ruggedness	0.3800	0.1369	0.0100	1

Distance to forest edge	0.1074	0.1219	0.3369	1
Distance to water feature	-0.3465	0.1126	0.0015	29
Distance to road	-0.4748	0.3786	0.2501	38
Distance to road ²	0.6907	0.4228	0.2036	2

^a Relative selection calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$.

Relative selection for variables with $\beta < 0$ should be interpreted as with every unit increase in the proportion of, or distance to, said feature, the relative selection of that feature by post-wolf cougars compared with wolves is reduced by $x\%$.

Table C.7. Latent selection difference function (LSDF) model comparing relative predation site feature selection by pre- (coded as 0) and post-wolf (coded as 1) cougars (*Puma concolor*) over annual periods in northeastern Oregon, USA, 2009 – 2016.

Variable	β	SE	P	Relative selection (%) ^a
Elevation	0.9792	0.0760	< 0.0001	3
Eastness	-0.0747	0.0847	0.3781	7
Northness	0.0828	0.0832	0.3162	1
Terrain ruggedness	0.1286	0.0777	0.0992	1
Distance to forest edge	-0.0114	0.0606	0.8498	1
Distance to water feature	-0.1631	0.0677	0.0130	15
Distance to road	-0.1177	0.1589	0.4824	11
Distance to road ²	0.2778	0.1349	0.0725	1
Distance to wolf predation 50% KDE contour edge	-0.1718	0.1539	0.3058	16
Distance to wolf predation 50% KDE contour edge ²	0.6887	0.1890	0.0018	2
Intensity of wolf use	-0.2762	0.0976	0.0096	24

^a Relative selection calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$.

Relative selection for variables with $\beta < 0$ should be interpreted as with every unit increase in the proportion of, or distance to, said feature, the relative selection of that feature by post-wolf cougars compared with pre-wolf cougars is reduced by $x\%$.

APPENDIX D – WOLF & COUGAR MOVEMENT

Prior to modelling wolf and cougar movement over the diel cycle I explored variation in movement within species that might result from temporal and demographic aspects of wolf and cougar behavior. I used ANOVA and Tukey's honest significance difference adjustment for multiple comparisons (Day and Quinn 1989) between groups known or suspected to influence wolf or cougar movement patterns to evaluate evidence in support of differences based on: 1) wolf pack, or 2) cougar sex, 3) reproductive status, or 4) age class (adult or subadult), and temporal influences based on 5) time of day, 6) hour of day, 7), season, or 8) annual variation. At the time of capture, cougars were classified as dependent kittens (< 1 year), subadults (independent females < 2 years and males < 3 years), and adults (females ≥ 2 years, and males ≥ 3 years). I defined female cougar reproductive status as solitary females with no kittens (Sol F), females with kittens < 6 months old (FG < 6 month), and females with kittens > 6 months old (FG > 6 month). I determined female cougar reproductive status based on nursery site visits, presence of kitten tracks at predation sites, or visual observation of kittens. Reproductive status was not monitored daily, therefore I may have misclassified female reproductive status over short time periods. I also included reproductive status categories for male, dependent kitten, or unknown status. The unknown status category applied to post-predation monitored female cougars for which I did not have information on presence or absence of kittens. Based on local mean time (LMT), we classified movement over the diel cycle into morning (± 1 hr sunrise), day (daylight hrs), evening (± 1 hr sunset), and night (night time hours) categories in R using the ‘crepuscle’ function in the *maptools* package (Bivand et al. 2008). The function used algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) and allowed a classification that accounts for daylight savings at local mean times. This classification does not subsume the approximate 3-hr timing shift of dusk and dawn that occurs between November and April. I defined movement estimates from May – Oct as summer, and estimates from Nov – Apr as winter. For statistical tests, I considered $P \leq 0.10$ as evidence of effect and inclusion as a grouping factor for modeling diel patterns of activity.

Information on wolf movement comes from 29 GPS-collared wolves in northeast Oregon and GPS location data collected during 2010 – 2018 (Table D.1 & D.2). Information on cougar movement comes from 40 GPS-collared cougars in northeast Oregon and data collected during 2009 – 2018 (Table D.3 & D.4).

Table D.1 Sample size of movement steps (fix interval) used to calculate diel activity patterns for 20 GPS-collared wolves in northeast Oregon during 2010 – 2018. Values are number of steps calculated from consecutive 3-hr (outside parentheses) and 1-hr (inside parentheses) fix locations recorded over summer (May – October) periods. Bolded wolf IDs were part of the wolf-cougar interaction study in the Mt. Emily Wildlife Management Unit.

Wolf ID	Sex	Summer								
		2010	2011	2012	2013	2014	2015	2016	2017	2018
OR4	M	0 ^a	1139 (168)	675	1283	5				
OR9	M		965 (5)							
OR11	M									0 ^b
OR12	M			3						
OR13	F		592	1240	1212	619 (1)				
OR14	M		1015	1409	1400	1280				
OR18	M			1328	215					
OR20	F			1053	1126	108				
OR21	F			0 ^c	0 ^c	0 ^c				
OR22	M			0 ^c	0 ^c	0 ^c				
OR23^d	F		7 (23)	145 (505)	157 (530)	134 (464)				
OR26	M			1192 (331)	1352					
OR28	F			1086 (383)	1361 (325)	826 ^b				
OR29	M				1340	463				
OR30	M				1370	723	0 ^b	0 ^b		
OR31	M				1278 (351)					
OR32	F				833					
OR40	F					616				
OR42	F					423 ^b				
OR43	M					119				
OR47	M					674 ^b				

OR51	M						0 ^e	0 ^b
OR56	F						0 ^c	
OR58	F						0 ^b	
OR59	F						0 ^c	
OR62	M						0 ^b	
OR63	F						0 ^b	
OR64	M						0 ^b	
OR65	M						0 ^b	
Total 3-hr steps	0	2104	2285	6320	6381	9698	3304	674
Total 1-hr steps	0	173	0	23	1,219	1,207	464	0

^a 6-hr data collected

^b Variable fix data collected

^c 12-hr data collected

^d Collected hourly data one day a week; regularly collected 12-hr data

^e Poor fix success resulted in no useable scheduled fixes (irregular schedule)

Table D.2. Sample size of movement steps (fix interval) used to calculate diel activity patterns for 21 GPS-collared wolves in northeast Oregon during 2010 – 2018. Values are number of steps calculated from consecutive 3-hr (outside parentheses) and 1-hr (inside parentheses) fix locations recorded over winter (November – April) periods. Bolded wolf IDs were part of the wolf-cougar interaction study in the Mt. Emily Wildlife Management Unit.

Wolf ID	Sex	Winter								
		2010	2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	2017-18
OR4	M	0 ^a		635 (2)	1377	1079		0 ^b		
OR9	M		22 (9) ^{a,c}	0 ^b						
OR11	M								0 ^d	

OR12	M	0 ^a								
OR13	F		1328	1292	1275					
OR14	M		1378	1352	1391					
OR16	M		592							
OR18	M		362	1372						
OR20	F			1160	1087					
OR21	F			0 ^b	0 ^b					
OR22	M			0 ^b	0 ^b					
OR23^e	F		152 (536)	153 (531)	148 (530)					
OR26	M			1060 (1)	134					
OR28	F			1379	1411	0 ^d				
OR29	M			873	1383	108				
OR30	M			518	1385	0 ^d	0 ^d			
OR31	M			525	375					
OR32	F			208	415					
OR39	F				167					
OR40	F					0 ^d				
OR42	F						135 ^d			
OR43	M						549			
OR47	M						462 (10) ^d	297		
OR51	M							0 ^d		
OR56	F							0 ^b		
OR58	F							0 ^d		
OR59	F							43 (5) ^d		
OR62	M							0 ^d		
OR63	F							34 ^d		
OR64	M							0 ^d		
Total 3-hr steps		0	22	635	5037	6407	8469	5418	1254	374

Total 1-hr steps	0	9	2	0	536	532	530	10	5
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^a 6-hr data collected.

^b 12-hr data collected.

^c 4-hr data collected.

^d Variable fix data collected.

^e Collected hourly data one day a week; regularly collected 12-hr data.

Table D.3 Sample size of movement steps used to calculate diel activity patterns for 37 GPS-collared cougars in northeast Oregon during 2009 – 2018. Values are number of steps calculated from consecutive 3-hr fix locations recorded over summer (May – October) periods.

Cougar ID	Sex	Summer									
		2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
c143	F		342								
c145	F				78						
c146	F	487	297								
c147	F	417	381	563							
c149	F	538	424	179							
c150	F	353	158								
c155	F	461									
c156	M	98									
c157	M	138									
c158	F	495	273								
c160	F			315							
c161	F										
c162	M		215								
c163	F		351								
c164	M		145	91	11						
c166	M		123	8							

c167	F	616	614								
c176	F	247	115								
c187	F		206								
c192	M		135								
c193	F	629	14								
c194	M	164	109								
c197	M		60								
c201	M										
c216	F		679	1388							
c219	F			357							
c220	F			1334	560						
c222	F			1412	841						
c223	M			1416	1416						
c224	F			995							
c229	M				1072	563					
c230	F				1253	318					
c231	M				1399	953					
c232	F				275						
c233	F				1373	1377	229				
c244	M				93	1324					
c245	F					1424					
Total 3-hr steps		2987	3572	3157	134	0	679	6902	8282	5959	229

Table D.4 Sample size of movement steps used to calculate diel activity patterns for 37 GPS-collared cougars in northeast Oregon during 2009 – 2018. Values are number of steps calculated from consecutive 3-hr fix locations recorded over winter (November – April) periods.

Cougar ID	Sex	Winter									
		2008-09	2009-10	2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	2017-18

c143	F		132	57		
c145	F			128		
c146	F	345	384			
c147	F	286	377	468	224	
c149	F	167	392	488		
c150	F	194	288			
c155	F	113	315			
c156	M	93				
c157	M	45				
c158	F	17	366	283		
c160	F			18	238	
c161	F		147			
c162	M		147			
c163	F		189			
c164	M		92	80	145	
c166	M		65	79		
c167	F			588	268	713
c176	F			253		
c187	F			383		
c192	M			88	8	
c193	F			265	641	
c194	M				187	
c197	M				22	
c201	M			172		
c216	F				1282	604
c219	F				1170	
c220	F				1060	1112
c222	F				950	1376
c223	M				918	1360
c224	F				464	40
c229	M				663	1047

c230	F						983	1152			
c231	M						927	1266			
c232	F						849		12		
c233	F						432	1220	1301		
c244	M							1295	413		
c245	F						682		710		
Total steps		1260	2894	3178	1905	0	0	5844	8346	7983	2436

Wolf movement

There was evidence wolf movement varied over coarse and fine temporal scales, where movement was 33% further per 3-hr time step in winter than summer seasons ($F_{36} = 7.09, P = 0.01$). Wolf movement was greatest during morning hours (dawn > night > dusk > day; $F_{78} = 19.62, P < 0.001$), and variable over the course of a day ($F_{175} = 7.56, P < 0.0001$). While I did find evidence supporting year influenced wolf movement ($F_{51} = 8.89, P = 0.004$), 95% confidence intervals broadly overlapped across all years. Further, yearly variation was explained by the partial year of data included from 2018 (Jan – May), which included 3 months of high winter wolf activity and 3 months over the time of denning, a period of the lowest wolf activity (three 2018-other year comparisons $P < 0.10$; all other year comparisons $P > 0.20$). Because of the association of this period with the designated cut-point between summer and winter seasons, I believe any variation from 2018 was accounted for in the seasonal covariate included in modeling diel activity. I did not find any evidence wolf pack influenced movement (Table D.5; $F_{17} = 0.55, P = 0.88$). While there was marginal evidence in support of variation between movement of the subset of wolves used for wolf-cougar interaction analyses and other wolves in northeast Oregon ($F_{20} = 3.69, P = 0.06$), confidence intervals broadly overlap.

Table D.5. Comparison of pack movement rates from 29 GPS collared wolves in northeast Oregon. Wolf movement were calculated as extrapolated hourly (km/hr) or step interval (km / 3-hr) rates from 3-hr intervals ($n = 58,380$ locations).

Pack	<i>n</i>	Distance traveled (km / 3-hr step)	95% CI lower	95% CI upper	Rate (km / hr)	95% CI lower	95% CI upper
Chesnimnus	1	1.88	-	-	0.63	-	-
Imnaha	3	1.72	1.11	2.33	0.57	0.37	0.78
Meacham	2	1.28	1.24	1.33	0.43	0.41	0.44
Minam	1	0.99	-	-	0.33	-	-
Mt Emily	3	1.38	1.19	1.57	0.46	0.40	0.52
Noregaard	1	3.69	-	-	1.23	-	-
Pine Creek	1	1.50	-	-	0.50	-	-
Ruckle Ridge	1	1.65	-	-	0.55	-	-
Shamrock	1	1.46	-	-	0.49	-	-
Single wolves	7	2.75	1.27	4.24	0.92	0.42	1.41

Snake River	1	1.40	-	-	0.47	-	-
Starkey	1	2.10	-	-	0.70	-	-
Umatilla River	2	1.08	0.89	1.27	0.36	0.30	0.42
Walla Walla	2	1.63	0.95	2.32	0.54	0.32	0.77
Wenaha	2	0.87	-0.41	2.15	0.29	-0.14	0.72

Wolf movement modeling

I had a small number of wolves ($n = 9$) with hourly GPS data collection schedules to build mixed effects models for prediction of population level hourly wolf movement. Five of the 9 wolves had summer data, but only 2 wolves had consistent hourly data in winter (Fig. D1), and 2 wolves had irregular hourly collection times that I included in modeling (e.g. 1-2 hourly locations in morning or evening; not shown in graphs). In general, hourly movement rate estimates calculated directly from 1-hr wolf data were comparable to 3-hr data extrapolated to hourly rate estimates ($\text{km/hr} = \text{step distance} / \text{step interval}$), as well as all-fix data extrapolated to hourly rates (i.e. correction for irregular intervals calculated across missed fixes; see Table D.6 and Fig. D.2).

For prediction of population level wolf movement rates, I built season-specific models that included a random intercept for individual wolf and a fixed effect for hour of day for both 1-hr and 3-hr wolf data. Regression coefficients for seasonal 1-hr predicted movement rates are reported in Table D.7 and coefficients for predicted 3-hr movement rates are reported in Table D.8.

Table D.6. Comparison of wolf movement rates calculated as hourly (km/hr) or step interval (km / 1-hr or 3-hr) estimates derived from 1-hr, 3-hr, and all fix data from 22 northeast Oregon wolves and a subset of 17 wolves in the Mt Emily Wildlife Management unit included in the study of sympatric wolf-cougar interactions. All fix data included irregular intervals due to missed fixes extrapolated to an hourly rate (km / fix interval).

Data source	Movement rate			
	km/hr	95%CI	km/step	95%CI
NE Oregon wolf				
1-hr steps	0.48	0.32, 0.65	-	-

3-hr steps	0.53	0.44, 0.62	1.6	1.3, 1.9
All fix extrapolate	0.48	0.44, 0.52	-	-
Mt Emily wolf				
3-hr steps	0.44	0.41, 0.48	1.3	1.2, 1.4

Table D.7 Regression coefficients for hourly wolf movement rate (km/hr) from summer and winter generalized mixed effect models (GLMM) fit with hour of day fixed effect and a random intercept for individual wolf.

Hour of day	Summer			Winter		
	β	SE	P	β	SE	P
Intercept	0.735	0.106	0.00	0.571	0.142	0.00
01:00:00	0.002	0.126	0.99	-0.145	0.194	0.45
02:00:00	0.122	0.125	0.33	0.000	0.194	1.00
03:00:00	0.339	0.127	0.01	0.030	0.193	0.88
04:00:00	0.471	0.127	0.00	0.262	0.195	0.18
05:00:00	0.419	0.128	0.00	0.161	0.194	0.41
06:00:00	0.464	0.128	0.00	0.310	0.194	0.11
07:00:00	-0.147	0.126	0.24	0.251	0.195	0.20
08:00:00	-0.332	0.126	0.01	0.220	0.195	0.26
09:00:00	-0.376	0.127	0.00	-0.037	0.194	0.85
10:00:00	-0.546	0.128	0.00	-0.228	0.192	0.24
11:00:00	-0.612	0.127	0.00	-0.288	0.191	0.13
12:00:00	-0.629	0.126	0.00	-0.351	0.191	0.07
13:00:00	-0.642	0.126	0.00	-0.285	0.196	0.15
14:00:00	-0.621	0.126	0.00	-0.380	0.194	0.05
15:00:00	-0.581	0.127	0.00	-0.287	0.193	0.14
16:00:00	-0.558	0.127	0.00	0.012	0.191	0.95
17:00:00	-0.320	0.126	0.01	0.464	0.188	0.01
18:00:00	-0.156	0.126	0.22	0.465	0.189	0.01
19:00:00	0.118	0.127	0.35	0.204	0.189	0.28
20:00:00	0.227	0.126	0.07	0.034	0.184	0.85
21:00:00	0.216	0.126	0.09	0.144	0.189	0.45
22:00:00	0.056	0.126	0.66	0.067	0.190	0.72
23:00:00	-0.084	0.155	0.59	-0.415	0.644	0.52

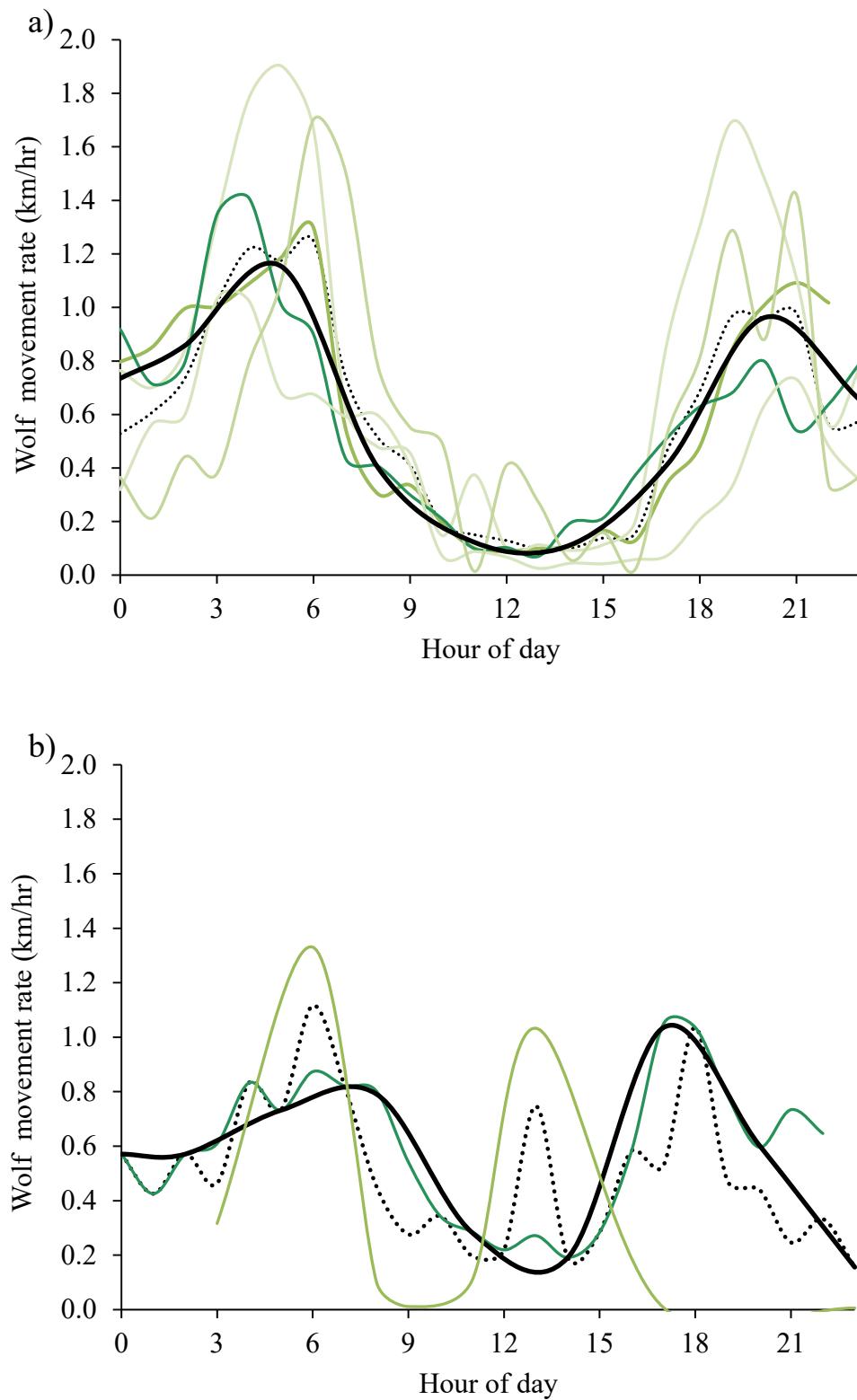


Figure D.1 Mean hourly movement rates (km/hr) for 9 GPS-collared wolves (green lines), mean movement across wolves with hourly collection periods (dotted blackline), and predicted population mean movement (solid black line) from generalized mixed model during (a) summer ($n = 5$ wolves) and, (b) winter ($n = 2$ wolves) in northeast Oregon. Two wolves had irregular hourly collection times not graphed (e.g. 1-2 hourly locations in morning or evening).

Table D.8. Regression coefficients for 3-hr wolf movement rate (km/3-hr) from summer and winter generalized mixed effect models (GLMM) fit with hour of day fixed effect and a random intercept for individual wolf.

Hour of day	Summer			Winter		
	β	SE	P	β	SE	P
Intercept	0.908	0.145	0.00	4.098	1.589	0.01
02:00:00	-0.396	0.682	0.56	-2.595	1.589	0.10
05:00:00	-0.633	0.620	0.31	-1.565	1.589	0.32
08:00:00	-0.368	0.594	0.54	-2.082	1.589	0.19
11:00:00	0.240	0.553	0.66	-3.266	1.589	0.04
14:00:00	1.404	0.594	0.02	-2.841	1.589	0.07
17:00:00	0.868	0.620	0.16	-2.164	1.589	0.17
20:00:00	0.902	0.682	0.19	-2.561	1.589	0.11
23:00:00	2.823	0.682	0.00	-2.691	1.589	0.09

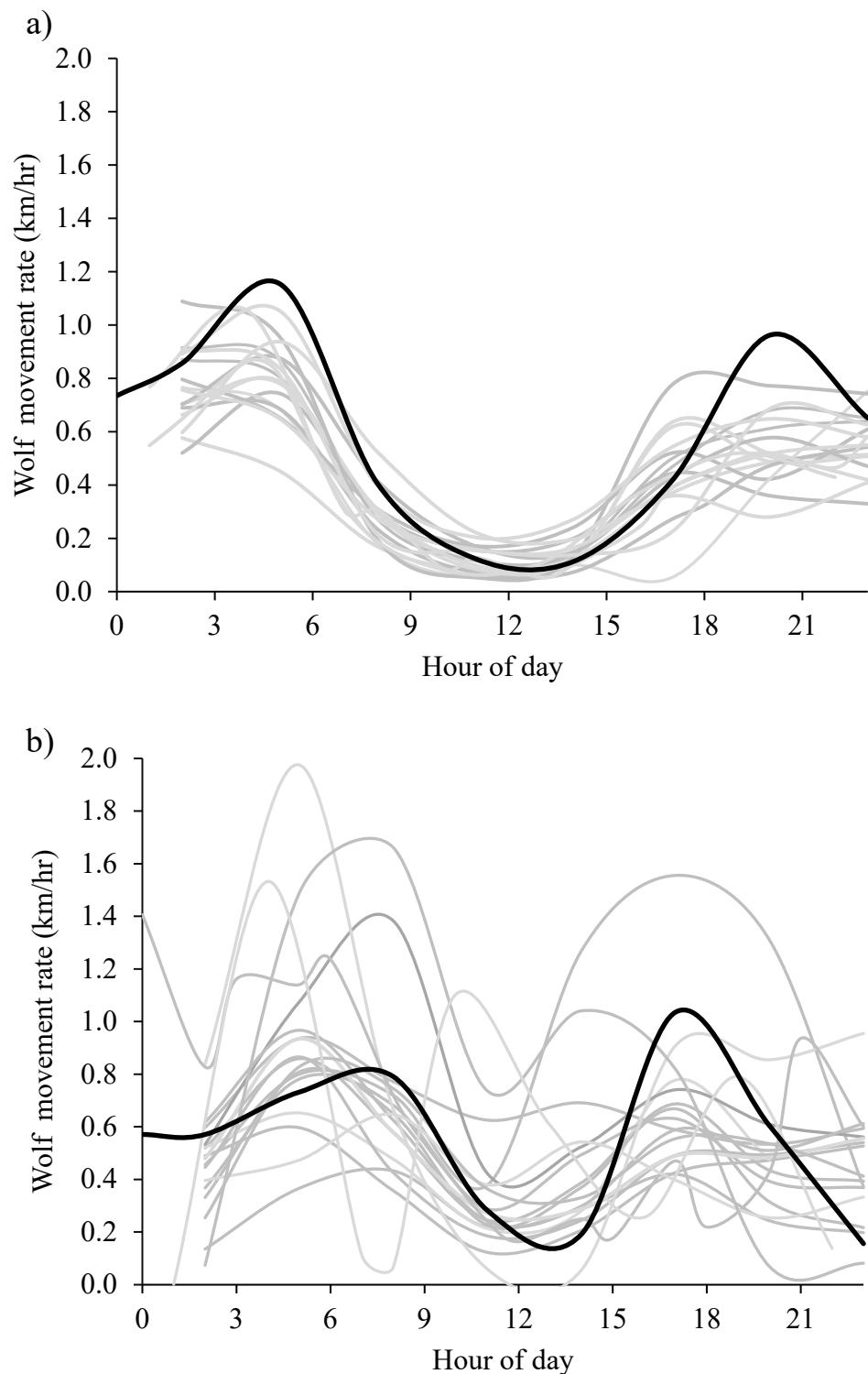


Figure D.2. Comparison of mean hourly movement rates (km/hr) extrapolated from 3hr-fix data for 20 GPS-collared wolves (gray lines) and predicted population mean

movement (solid black line) from a generalized mixed effect model built on 1-hr wolf data for (a) summer, and (b) winter periods in northeast Oregon.

Cougar movement

There was evidence cougar movement varied over coarse and fine temporal scales, where movement ranged from 1.3 to 1.4% further in summer than winter seasons ($F_{71} = 4.50, P = 0.04$) across pre- and post-wolf periods, respectively. Cougar movement varied over the course of a day ($F_{226} = 1.91, P = 0.01$), as well as by broader diel periods ($F_{143} = 3.41, P = 0.02$), where movement was greatest during daylight periods (day > dusk > dawn > night) for pre-wolf cougars, but shifted to greatest during evening periods for post-wolf cougars (dusk > dawn > day > night). I found little evidence in support of yearly variation in cougar movement rates ($F_{84} = 2.22, P = 0.14$). Nor did I find any evidence cougar age class influenced movement ($F_{42} = 0.31, P = 0.73$). While movement varied among cougar reproductive classes ($F_{64} = 10.91, P < 0.0001$), variation was explained by sex differences (all M-female group comparisons $P < 0.0001$; all female group comparisons $P > 0.20$). Consistent among seasons and time periods, male cougars moved 23 - 102% further per 3-hr step than female cougars, (Table D.9). I also found evidence in support of study period effects ($F_{36} = 3.80, P = 0.06$), where cougars moved 1.4 times shorter distances ($\bar{x}_{\text{pre}} = 597\text{m} (\pm 64 \text{ SE}), \bar{x}_{\text{post}} = 427\text{m} (\pm 28 \text{ SE})$), and subsequently at 1.4 times slower rates ($\bar{x}_{\text{pre}} = 0.60\text{km/step} (\pm 0.06 \text{ SE}), \bar{x}_{\text{post}} = 0.43\text{km/step} (\pm 0.03 \text{ SE})$ per 3-hr time step with wolves on the landscape.

Table D.9. Comparison of seasonal mean male and female cougar movement rates (km / 3-hr) from 35 cougars in northeast Oregon. Mean individual cougar movement was calculated as the distance traveled (km) per 3-hr location fix interval.

	Summer			Winter		
	n	km / 3-hr	95%CI	n	km / 3-hr	95%CI
Pre						
Male	8	0.987781	0.69, 1.29	9	0.775323	0.56, 0.99
Female	14	0.49765	0.40, 0.59	15	0.383165	0.30, 0.47
Post						
Male	4	0.675556	0.64, 0.70	4	0.423871	0.31, 0.53

Female	9	0.437095	0.37, 0.51	10	0.349813	0.31, 0.39
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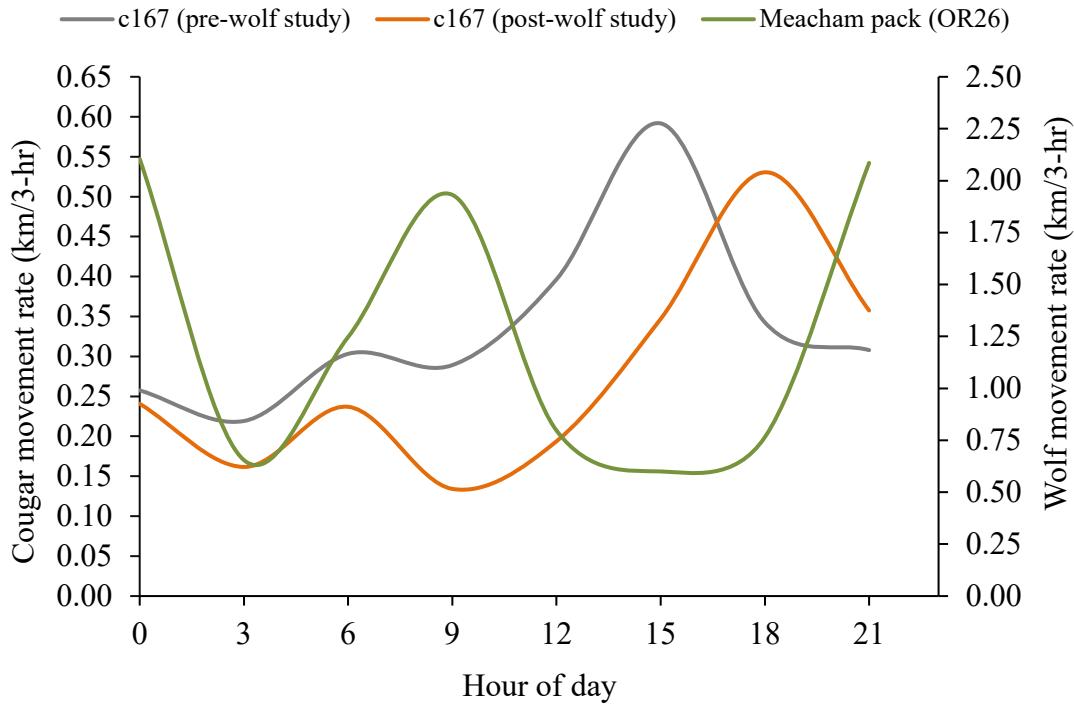


Figure D.3. Mean movement rate (km/3-hr) over the day for a female cougar that had GPS collar data over pre- (grey, 2010 – 2012) and post-wolf (orange, Dec 2016 – Apr 2017) winter periods and the associated wolf pack (green, Meacham) her home range overlapped in northeast Oregon.

Cougar movement modeling

For prediction of population level cougar movement rates and comparison with wolf movement, I built study period-specific models using 3-hr cougar data that included a random intercept for individual cougar and fixed effects for season, sex, and hour of day. GPS location collection schedules for cougars were different between study periods for all but one cougar and initial models with a study period variable produced biased diel patterns, where it was evident the large amount of post-wolf cougar data drove the overall pattern, obscured pre-wolf cougar diel patterns, and prevented identification of any changes between periods. Therefore I chose to model movement independently over each study period with sex, season, and hour of day covariates. For illustrative purposes, I also

built study period-specific predictive models for extrapolated hourly cougar movement rates without season and sex effects. Regression coefficients for predicted hourly movement rates are reported in Table D.10 and D.11, and coefficients for seasonal 3-hr predicted movement rates used in habitat analysis are reported in Table D.12 and D.13.

Table D.10 Regression coefficients for pre-wolf cougar hourly movement rate (extrapolated km/hr from 3-hr fix data) from generalized mixed effect model (GLMM) fit with hour of day fixed effect and a random intercept for individual cougar.

Hour of day	β	SE	P
Intercept ^a	0.169	0.021	< 0.001
01:00:00	-0.081	0.024	0.001
03:00:00	0.011	0.005	0.025
04:00:00	-0.069	0.239	0.773
18:00:00	0.065	0.005	0.000
21:00:00	0.029	0.005	0.000
22:00:00	-0.008	0.024	0.739

^a Intercept included 00:00:00 hour of day, male, winter

Table D.11 Regression coefficients for post-wolf cougar hourly movement rates (extrapolated km/hr from 3-hr fix data) from generalized mixed effect model (GLMM) fit with hour of day fixed effect and a random intercept for individual cougar.

Hour of day	β	SE	P
Intercept ^a	0.092	0.027	0.001
01:00:00	0.039	0.027	0.144
04:00:00	0.076	0.027	0.005
07:00:00	0.018	0.027	0.514
10:00:00	-0.006	0.027	0.825
13:00:00	0.026	0.027	0.338
16:00:00	0.113	0.027	< 0.000
19:00:00	0.097	0.027	< 0.000
22:00:00	0.062	0.027	0.021

^a Intercept included 00:00:00

Table D.12 Regression coefficients for pre-wolf cougar movement rate (km/3-hr step) from generalized mixed effect model (GLMM) fit with sex, season, and hour of day fixed effects and a random intercept for individual cougar.

Variable	β	SE	P
Intercept ^a	0.700	0.077	< 0.001
Sex ^b	-0.410	0.096	< 0.001
Season ^c	0.129	0.011	< 0.001
Hour of day ^d - 01:00:00	-0.251	0.072	0.001
Hour of day - 03:00:00	0.038	0.015	0.013
Hour of day - 04:00:00	-0.352	0.715	0.623
Hour of day - 18:00:00	0.197	0.015	< 0.001
Hour of day - 21:00:00	0.089	0.015	< 0.001
Hour of day - 22:00:00	-0.028	0.072	0.696

^a Intercept included male, winter

^b Male coded as 0

^c Winter coded as 0

^d Midnight 00:00:00 included in intercept

Table D.13 Regression coefficients for post-wolf cougar movement rates (km/3-hr step) from generalized mixed effect model (GLMM) fit with sex, season, and hour of day fixed effects and a random intercept for individual cougar.

	β	SE	P
Intercept ^a	0.394	0.084	< 0.001
Sex ^b	-0.148	0.039	0.003
Season ^c	0.147	0.007	< 0.001
Hour of day ^d - 01:00:00	0.037	0.078	0.633
Hour of day - 04:00:00	0.147	0.078	0.060
Hour of day - 07:00:00	-0.027	0.078	0.734
Hour of day - 10:00:00	-0.097	0.078	0.214
Hour of day - 13:00:00	-0.002	0.078	0.984
Hour of day - 16:00:00	0.260	0.078	< 0.001
Hour of day - 19:00:00	0.212	0.078	0.007
Hour of day - 22:00:00	0.104	0.078	0.182

^a Intercept included male, winter

^b Male coded as 0

^c Winter coded as 0

^d Midnight 00:00:00 included in intercept

Table D.14. Mean regression coefficients (population-level selection) estimated for cougars in northeast Oregon. Step-selection function (SSF) models for openness, wolf-killed elk density, wolf-killed deer density (mule deer and white-tailed deer), and intensity of wolf use covariates over summer and winter seasons were fit to individual cougars across pre- ($n = 25$; 2009 – 2016) and post-wolf ($n = 15$; 2014 – 2018) time periods. Estimates subsume sex and study period differences and represent a population level estimate of cougar selection in northeast Oregon.

Variable	Summer				Winter			
	β	SE	ρ	P	β	SE	ρ	P
Openness	-0.003	0.001	0.224	0.194	-0.003	0.001	0.240	0.146
Wolf-killed elk density	-0.087	0.329	0.727	< 0.001	-0.588	0.215	0.507	0.001
Wolf-killed deer density	0.351	0.173	0.363	0.033	-0.004	0.226	0.543	0.001
Intensity of wolf use	0.249	0.584	0.476	0.004	-3.738	1.375	0.388	0.016

Literature cited:

- Bivand, R. S., Pebesma, E. and Gómez-Rubio V. 2008. Package ‘maptools’ vignette. Applied Spatial Data Analysis with R, Springer-Verlag, New York.

APPENDIX E. General histories for individual cougars during post-wolf recolonization period of wolf-cougar study in northeast Oregon, USA from July 2014 to October 2016. Dependent kittens were monitored bi-weekly through relocation of VHF collars.

C167 – Iskuulpa Creek

UNKNOWN FATE

Adult female (5 yrs old) first captured 3/4/2010 on Gibbon Ridge and fit with a VHF collar (part of previous Mt. Emily cougar study). Recaptured 5/6/2010 in Iskuulpa Creek and fitted with a GPS collar. Territory use primarily in Iskuulpa Creek and along the breaks of the Umatilla River. Recaptured 5/7/2012 in Meacham Creek and fit with a VHF collar (end of 1st Mt. Emily cougar study). VHF signal detected in January 2015 but could no longer be detected by 2/15/2015 (suspect collar malfunction or end of battery life). Documented on Confederated Tribes of Umatilla Indian Reservation trail camera with two 3-6 month old kittens 7/26/2016. Recaptured 12/28/2016 and fit with a GPS collar with estimated age of 11 – 12 yrs old (based first capture cementum annuli estimates). Collar malfunction/failure in April 2017 with last location sent 4/6/2017; monitoring via VHF only. Last heard from flight 8 May 2017.

C193 – Meacham/Ukiah

DECEASED (legally harvested)

Subadult female (2 – 4 yrs old) first captured 2/16/2011 on Telephone Ridge and fitted with a GPS collar (part of Mt. Emily cougar study). Territory use primarily on Telephone ridge in Mt. Emily WMU and south across I-84 into Ukiah WMU. Recaptured 5/4/2012 in Iskuulpa Creek and fitted with a VHF collar (end of 1st Mt. Emily cougar study). Documented by ODFW wolf monitoring potentially breeding with an uncollared male in Mill Creek on 6/12/2016. Intermittent VHF monitoring only. Last heard from flight 24 August 2017. Harvested 12/22/2017 in McKay Creek (Ukiah WMU).

C216 – Pelican Creek

DECEASED (vehicle collision)

Adult female (estimated 3 – 4 yrs old) first captured 3/18/2014 in Pelican Creek and fitted with a VHF collar. Recaptured 7/24/2014 near Little John Day Creek and fitted

with a GPS collar. Territory use primarily in Pelican Creek and California Gulch but extends north to Meacham Creek and as far south as Five Points Creek. Died 1/23/16; hit by vehicle on Interstate 84.

- Produced 2 kittens (female C217, male C218) 9/20/2014 (estimated birth date based on cluster e489 start). Kittens were captured at a nursery site in Butcher Creek and fitted with VHF collars 10/23/2014 at 4 weeks of age. Male kitten C218's collar broke away 2/9/15 and was found at a cluster (e1543), and C217 appeared to have lost hers in early April 2015 (last heard 3/29/2015) on inaccessible private land; confirmation both kittens were alive and traveling with C216 on 5/13/2015 based on pictures from an ODFW wolf monitoring trail camera in Pelican Creek.
- Produced 3 kittens (male C225, male C226, female C227) 9/16/2015 (estimated birth date based on cluster e3330 start). Kittens were captured at a nursery site in California Gulch and fitted with VHF collars 10/23/2015 at 5-6 weeks of age. All three kittens died 11/7/2015 with strong evidence (necropsy & GPS points) they were killed by members of the Meacham wolf pack (OR26 and OR29 present).
- Was pregnant at time of death (two golf-ball sized fetuses).

Known kittens: C217 (female, 2014)
 C218 (male, 2014)
 C225 (male, 2015)
 C226 (male, 2015)
 C227 (female, 2015)

C217 – Pelican Creek

UNKNOWN FATE

Dependent female kitten (4 wks old) from C216 litter first captured 10/23/2014 at a nursery site in Butcher Creek and collared with a break-away VHF kitten collar. Lost contact with collar after 3/29/2015 and believe it broke away (4 mo old) on inaccessible private land on/near date of lost contact. Observed traveling with

C216 and C218 (sibling) on 5/13/2015 on a trail camera in Pelican Creek.

Presently uncollared and believed to have died given birthdate of next litter.

C218 – Pelican Creek

UNKNOWN FATE

Dependent male kitten (4 wks old) from C216 litter first captured 10/23/2014 at a nursery site in Butcher Creek and collared with a break-away VHF kitten collar. Collar broke away and was heard on mortality 2/9/2015 and was found at the base of a tree near a C216 kill site (e1543). Observed traveling with C216 and C217 (sibling) on 5/13/2015 on a trail camera in Pelican Creek. Presently uncollared and believed to have died given birthdate of next litter.

C225 – California Gulch

DECEASED (wolf killed)

Dependent male kitten (5 – 6 wks old) from C216 litter first captured 10/23/2015 at a nursery site in California Gulch and collared with a break-away VHF kitten collar. Found dead 11/10/2015; suspected wolf-killed 11/7/2015.

C226 – California Gulch

DECEASED (wolf killed)

Dependent male kitten (5 – 6 wks old) from C216 litter first captured 10/23/2015 at a nursery site in California Gulch and collared with a break-away VHF kitten collar. Found dead 11/10/2015; suspected wolf-killed 11/7/2015.

C227 – California Gulch

DECEASED (wolf killed)

Dependent female kitten (5 – 6 wks old) from C216 litter first captured 10/23/2015 at a nursery site in California Gulch and collared with a break-away VHF kitten collar. Found dead 11/10/2015; suspected wolf-killed 11/7/2015.

C219 – Rugg Cabin/Pelican Creek

DECEASED (unknown)

Subadult female (18 – 24 months old) first captured 11/30/2014 in Pelican Creek and fitted with GPS collar. Territory use primarily in Pelican and Five Points Creek area but

extended as far north as Butcher Creek and southeast to Robbs/Fox Hill areas. Found dead 6/24/2015 with estimated mortality 6/14/2015 of unknown causes; carcass too decomposed to send for necropsy. Not documented as having produced any kittens. Tentatively (based on range overlap and intraspecific proximity) think she could be offspring of C216; from a litter born prior to project start.

C220 – Phillips/Dry Creek

UNKNOWN FATE

Adult female (2 yrs old) first captured 12/1/2014 in Phillips Creek and fitted with a GPS collar. Territory use primarily in Phillips and Dry Creeks but has ranged as far west as North Fork Meacham Creek and Shimmiehorn Ridge/Creek, north to Buck Creek, and south to the breaks along Mt Emily (Smith's Ridge, Big Saddle). Think she might have produced and lost a litter in 5/10/2015; based on large number of locations without finding a kill or kittens off west side of Middle Ridge. Part of her home range burned (2,601 acres) in the Phillips Creek Fire (8/1/2015 – 8/20/2015 active firefighting period); 89% contained by 8/31/2015 but some areas by Indian point still burning as of 9/10/15. She started localizing like she might have a litter again 9/4/2015 across Hwy 204 on west side of Andies Ridge (in same place for past 6 days), but moved out of area after 8 days. Dispersed outside WMU to Wallowa range 1/26/16, using area in Indian and East Clark Creek. Collar end of life reached with last GPS location sent 11/30/2016.

Known kittens: None.

Possible failed litter 2014 (movement suggested den 5/10/2015 cluster g1356).

Failed litter 2014 (dead kitten found at cluster g2295 from 9/4/2015 start); suspected abandonment.

C221 – Thomas Creek

DECEASED (unknown)

Dependent female kitten (12 months old) first captured 12/13/2014 in Thomas Creek and collared with a VHF subadult collar. Tracks through winter indicate she is traveling with one other kitten and an adult female. Telemetry has territory use primarily in Thomas

Creek but signals heard on west side of Round Mtn in Spring Creek as well. As of winter 2015/2016 territory use primarily in North Fork Meacham Creek, Thimbleberry Mtn and Knob Creek area. Found dead 7/5/2016 with estimated mortality 7/3/2016 of unknown causes. Field necropsy showed smaller canine (coyote/dog) sized puncture wounds on rear quarter and abdominal wound with internal organ protrusion. Consultation with ODFW wolf personnel and investigation details do not suggest wolf. Classified as ‘unknown’ cause of death. Not documented as having produced any kittens.

C222 – Sugarloaf Mtn

DECEASED (legal harvest)

Subadult female (18 – 24 months old) first captured 12/26/2014 near Rugg Cabin and collared with a GPS collar. Territory use primarily around Sugarloaf and Green Mtns but extends almost to North Fork Meacham Creek, Wilbur Mtn, and Five Points Creek areas. Tentatively think she might be offspring of C224, but could also be from a litter by C216 based on early locations as far west as Pelican/Meacham Creeks. Location data had her potentially breeding with male C223 late winter (2/27/2016). May be related to C233; have shared kills (see clusters h4085/s633). Collar malfunction/failure in August 2016 with last location sent 8/14/16; VHF not working on collar, but kittens (C238, C239, C240) appear to be traveling with her. Legally harvested in April 2018 near Rugg Spring, turned in to ODFW 4/9/2018.

- Produced 3 kittens (female C238, male C239, male C240) 5/27/2016 (estimated birth date based on cluster h4164 start). Kittens were captured at the den site on Green Mtn and fitted with VHF collars 6/28/2016 at 4 weeks of age.

Known kittens: Failed litter 2014 (dead kitten(s) found 8/16/2015 at cluster h1887)
 C238 (female, 2016)
 C239 (male, 2016)
 C240 (male, 2016)

C238 – Green Mountain

UNKNOWN FATE

Dependent female kitten (4 wks old) from C222 litter first captured 6/28/2016 at den site on Green Mountain and collared with a break-away VHF kitten collar.

Collar broke away and was heard on mortality 10/9/2016 and was found 70m from a C222 kill site (no cluster ID; AD mule deer cache) at a bed site in a regen thicket. No evidence of kitten predation (elastic broken), though bear activity in area of cache.

C239 – Green Mountain

UNKNOWN FATE

Dependent male kitten (4 wks old) from C222 litter first captured 6/28/2016 at den site on Green Mountain and collared with a break-away VHF kitten collar.

Collar broke away and was heard on mortality 10/9/2016 and was found 20m from a C222 kill site (no cluster ID; AD mule deer cache) in a bed/romping area. No evidence of kitten predation (elastic expanded large enough to go over head), though bear activity in area.

C240 – Green Mountain

DECEASED (sylvatic plague)

Dependent male kitten (4 wks old) from C222 litter first captured 6/28/2016 at den site on Green Mountain and collared with a break-away VHF kitten collar.

Collar was heard on mortality 10/25/2016 and carcass was found 5m from a C222 kill site (no cluster ID; AD cow elk) at a base of bush. No evidence of predation or external damage so carcass was sent to lab for necropsy; died of sylvatic plague. Estimated actual mortality date 10/23/2016.

C223 – Meacham Creek

DECEASED (legally harvested)

Adult male (2 – 3 yrs old) first captured 12/27/2014 near Spring Mtn and collared with a GPS collar. Territory use centers around Black Mtn but extends north up Stumbough Ridge/Line Creek to Umatilla River, west to Iskuulpa Creek, east to Huckleberry Mtn, but not much farther south than Spring Mtn. Location data had him potentially breeding with female C224 in fall (9/21/2015) and female C222 in late winter (2/27/2016). Collar

end of life reached with last GPS location sent 1/17/2017. Harvested near Black Mtn
5/18/2018.

C224 – Spring Mtn

UNKNOWN FATE

Adult female (3 – 5 yrs old) first captured 2/22/2015 near Spring Mtn and collared with a GPS collar. Territory use centers around Drumhill Ridge/Wilbur Mtn primarily using Bear Creek, East Fork Meacham, and Spring Mtn areas. Location data had her potentially breeding with male C223 in fall (9/21/2015). Collar stopped transmitting locations 11/9/2015 and was monitored via VHF only. VHF tracking (ground/aerial) suggesting denning (June 2016). Last heard live VHF signal on flight in December 2016.

Known kittens: None.

C228 – Buck Mtn

UNKNOWN FATE

Subadult male (18 – 24 months old) first captured 11/16/2015 near Buck Mtn and collared with a GPS subadlt (vertex) collar. Territory use primarily along Buck Creek and the North Fork Umatilla River in the wilderness. Suspected to still be traveling with or using it's mother's territory (possibly C230). Collar stopped transmitting locations 4/15/2016 and no signal was heard for 3 flights.

C229 – Phillips Creek

UNKNOWN FATE

Subadult male (18 – 24 months old) first captured 11/23/2015 in Phillips Creek and collared with a GPS collar. Dispersed out of study area 12/4/2015, temporarily using areas along the WA/OR border in Mill Creek. Late spring territory use along Walla Walla River south of Blalock Mtn (Walla Walla WMU) extending into Umatilla Wilderness along Coyote/McDougal Ridge (Mt Emily WMU). Collar stopped transmitting locations 10/16/2017.

C230 – Thomas Creek

ALIVE (live as of 5/31/2018)

Adult female (3 yrs old) first captured 11/29/2015 in Thomas Creek and collared with a GPS collar. Initial territory use in Thomas Creek in and around Round Mtn but extending north to Buck Mtn, South into the upper parts of Dry Creek and as far west as Goodman Ridge. Recaptured 6/12/2017 and fitted with a new GPS collar. Collar still transmitting locations as of 7/22/2018. Collar stopped transmitting locations 1/19/2019.

C231 – Iskuulpa Creek

UNKNOWN FATE

Adult male (4 – 5 yrs old) first captured 12/30/2015 in Iskuulpa Creek and collared with a GPS collar. Territory use centers around Iskuulpa Creek extending north to Umatilla River, east along Meacham Creek and the north end of Stumbough Ridge, west to Buckaroo Creek and as far south as Little Iskuulpa Creek. Spring and summer location extend territory use as far south as California Gulch and south/west of I-84 in Kamela area. Collar stopped transmitting locations 10/7/2017.

C232 – Meacham Creek

UNKNOWN FATE

Subadult female (18 – 24 months old) first captured 1/8/2016 in Meacham Creek and collared with a GPS collar. Territory use primarily along the breaks of the Umatilla River between Iskuulpa and Bear Creek. May have still been traveling with her mother. Dispersed 6/3/2016 using areas along the Grande Ronde River between the town of Troy and Lookingglass in Wenaha and Sled Springs WMUs. Collar stopped transmitting locations 1/11/2018.

C233 – Mahogany Mtn

ALIVE (fate unknown as of Jun 2018)

Adult female (2 – 3 yrs old) first captured 3/2/16 on Mahogany Mtn and collared with a GPS collar. Initial space use in Five Points Creek, Three Cabin Ridge and Mahogany Mtn area. Private landowner trail camera documented her potentially breeding with an uncollared male late spring (4/19/2016). May be related to C222; have shared kills (see cluster h4085/s633). Collar stopped transmitting locations 5/31/2018.

- Produced 3 kittens (male C241, female C242, female C243) 7/11/2016 (estimated birth date based on cluster s1069 start). Kittens were captured at den site in Fiddlers Hell Creek and fitted with VHF collars 8/10/2016 at 4 weeks of age.

Known kittens: C241 (male, 2016)
 C242 (female, 2016)
 C243 (female, 2016)

C241 – Fiddlers Hell *UNKNOWN FATE*

Dependent male kitten (4 wks old) from C233 litter first captured 8/10/2016 at den site in Fiddlers Hell/Five Points Creek and collared with a break-away VHF kitten collar. Collar broke away and was heard on mortality 10/25/2016 and was found at C233 kill site (s1896; yearling mule deer cache) in the hair pile/cache in blowdown regen thicket. No evidence of kitten predation (elastic broken).

C242 – Fiddlers Hell *UNKNOWN FATE*

Dependent female kitten (4 wks old) from C233 litter first captured 8/10/2016 at den site in Fiddlers Hell/Five Points Creek and collared with a break-away VHF kitten collar. Collar broke away and was heard on mortality 12/13/2016 and was found 57m from a C233 ungulate kill site (cluster ID s2273 (E408966 N5033474); deer cache and latrine at site with evidence of cougar adult and dependent kittens) at a bed site in a regen thicket. No evidence of kitten predation (elastic broken), though investigation completed over 6 months post collar shed event (6/23/2017).

C243 – Fiddlers Hell *UNKNOWN FATE*

Dependent female kitten (4 wks old) from C233 litter first captured 8/10/2016 at den site in Fiddlers Hell/Five Points Creek and collared with a break-away VHF kitten collar. Collar broke away and was heard on mortality 11/8/2016 and was

found 5m from carcass at C233 kill site (s2001a; spike elk cache) in upper part cache drag along long down tree. No evidence of kitten predation (elastic broken).

C244 – Phillips Creek/Indian Point DECEASED (legal harvest)

Subadult male (2 – 3 yrs old) first captured 10/19/2016 in Phillips Creek and collared with a GPS collar. Territory use centers on Buck Mtn extending north to Umatilla River, west along Spring Creek/South Fork Umatilla, but as far as Black Mtn, east to Phillips Creek and as far south as lower reaches of Phillips/Dry creeks. Legally harvested 12/25/2017 in Phillips Creek.

C245 – Buckaroo Creek ALIVE (end of study collar removed)

Adult female (2 – 3 yrs old) first captured 1/30/2017 in Buckaroo Creek and collared with a GPS collar. Territory use centers on Umatilla River drainage with some lower reach use of Iskuulpa, Buckaroo, and Meacham Creeks. Recaptured 2/3/2018 in Iskuulpa Creek and GPS collar was removed (end of study).

APPENDIX F. Record of wolf-cougar interactions documented in the Mt. Emily WMU of northeast Oregon, USA from July 2014 to October 2018.

Interaction direction	Date	Wolf pack	Cougar	Identified from	Event description
wolf-cougar	8/14/2014	Meacham	Uncollared	cougar cluster investigation	Scavenged cache
wolf-cougar	9/23/2014	Unknown wolf or pack	C216	cougar cluster investigation	Scavenged cache; mule deer
wolf-cougar	12/15/2014	Meacham	C219	cougar cluster investigation	Cougar chased up a tree
wolf-cougar	3/7/2015	Meacham	Uncollared	wolf cluster investigation	Scavenged cache; cow elk
cougar-wolf	3/15/2015	OR29	Uncollared	wolf cluster investigation	Cougar visited wolf kill
wolf-cougar	6/3/2015	Meacham	C216	cougar cluster investigation	Revisited cache
wolf-cougar	7/1/2015	OR31	Uncollared	wolf cluster investigation	Visited cache; mule deer
wolf-cougar	7/20/2015	Mt Emily	C220	cougar cluster investigation	Scavenged cache; mule deer
wolf-cougar	8/16/2015	Meacham	C216	cougar cluster investigation	Scavenged cache; elk calf
wolf-cougar	8/30/2015	Meacham (OR26)	C216	cougar cluster investigation	Visited cache; mule deer
wolf-cougar	9/1/2015	Meacham (OR26 & OR29)	C216	cougar cluster investigation	Visited cache; elk calf
wolf-cougar	9/21/2015	Mt Emily (OR31 & OR32)	C220	cougar cluster investigation	Usurped kill; mule deer
wolf-cougar	10/4/2015	OR30 & OR28	C222	GPS date/time	Location overlap (day/time)
wolf-cougar	10/14/2015	Mt Emily	C224	cougar cluster investigation	Visited cache; elk calf
wolf-cougar	10/25/2015	Meacham	C216	cougar cluster investigation	Scavenged cache; elk calf
wolf-cougar	11/7/2015	Meacham	C216	cougar cluster investigation	Cougar chased up tree
wolf-cougar	11/7/2015	Meacham	C216	mortality signal(s)	Killed cougar kittens (C225,C226,C227)
cougar-wolf	11/21/2015	Unknown wolf or pack	C222	cougar cluster investigation	Cougar visited a wolf kill
wolf-cougar	6/3/2016	Mt Emily	C223	cougar cluster investigation	Usurped kill
wolf-cougar	6/8/2016	Mt Emily	C222	cougar cluster investigation	Usurped kill; mule deer