Predator-prey spatiotemporal interactions in a multi-use landscape

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Abstract

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Apex predators can influence ecosystems by changing the density and behavior of herbivores and other predators. As an ecosystem superpredator, humans may also shape top-down effects in ecological communities by altering apex predator abundance and behavior. In many parts of the world, apex predators live in, or are returning to, landscapes that are human dominated. Thus, it is important to understand the ecological role of apex predators in anthropogenic, multi-use landscapes. I used motion-activated camera traps set in a multi-use landscape in northeastern Washington to compare the effects of: 1) wolves (*Canis lupus*) on spatiotemporal activity patterns of mesopredators and sympatric apex predators; and 2) the effects of hunting and apex predators on the spatiotemporal activity of herbivorous prey. In areas with wolves, other predators used temporal niche partitioning to avoid wolves. Cougars (*Puma concolor*) and coyotes (*Canis latrans*) became more active during the daytime, when wolves were least active, which significantly increased their activity overlap with humans. By contrast, bobcats (*Lynx rufus*) exposed to wolves changed their activity in patterns opposite to coyotes at nighttime and dusk. Although both mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) increased nocturnality significantly during hunting seasons, the deer species showed species-specific spatiotemporal responses to hunting that, in the case of mule deer, deviated from their typical anti-predator behavior. This pushed mule deer, but not white-tailed deer, into greater spatiotemporal overlap with wolves during hunting seasons, and thus may lead to additive mortality on mule deer from increased wolf predation. In conclusion, the top-down effects of wolves on the behavior of their intraguild competitors appear to be resilient to human disturbance in this system. However, effects on their herbivore prey may be overwhelmed by humans during hunting seasons, leading to greater spatiotemporal overlap with predators. More broadly, my findings highlight that temporal behavioral plasticity is an underappreciated aspect of animal behavior that helps animals manage risk and reduce the negative effects of competition. In addition, the top-down effects of apex predators appear to persist in human-dominated landscapes, particularly within the carnivore guild.

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DEDICATION

To Shane and Killian

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GENERAL INTRODUCTION

Predators can directly influence prey by inflicting mortality and changing prey behavior. Predator-induced trait changes, known collectively as non-consumptive effects (Wirsing et al. 2020), can indirectly influence lower trophic levels, for example when anti-predator responses by herbivorous prey alter plant species composition or abundance (Estes et al. 2011, Ripple et al. 2014). Furthermore, meta-analyses suggest that the indirect impacts of risk effects may equal or even surpass those of predation (Schmitz et al. 2004, Preisser et al. 2005). Thus, there is now wide appreciation that predators do not need to cause heavy prey mortality to have substantial effects on the structure and function of ecosystems (Laundré et al 2001, Ripple and Beschta 2004, Schmitz et al. 2004, Creel and Christianson 2008, Heithaus et al. 2008; Pringle et al. 2019). Most of the research underpinning this paradigm has been conducted using controlled experiments with small-bodied animals (Preisser, Orrock and Schmitz 2007) or in wilderness or protected areas where the effects of humans on wildlife are minimal (Laundre et al. 2001, Ripple and Beschta 2004, Fortin et al. 2005). Yet, many predators live in or are recolonizing landscapes where humans are an integral part of the ecosystem (Chapron et al. 2014). In these human dominated ecosystems where apex predators are returning, what is the ecological function of apex predators? There has been a call in the peer-reviewed literature to incorporate anthropogenic effects into trophic ecology (Dorresteijn et al. 2015), or in other words for research to examine the ecological function of apex predators while also accounting for the unique ecology of human 'superpredators' and of human-dominated landscapes. Are the top-down effects of apex predators overwhelmed by humans, reducing carnivores to "Paws without claws," (Kuijper et al 2016) or do predators retain their ecological effectiveness and continue to exert top-down effects on herbivores and other predators, despite the effects of human superpredators (Darimont et al. 2015)? Currently, we lack research that provides an empirical basis to predict the strength and nature of non-consumptive predator effects on prey in these anthropogenic landscapes (Guiden et al. 2019), particularly in multi-predator systems where prey face the added pressure of hunting from humans (Kuijper et al. 2016). Part of what makes human predators unique is their ability to influence all components of food webs, directly by altering animal densities or behavior, and indirectly by influencing food resources from the bottom up. Accordingly, humans and apex predators can simultaneously create differing perceptual "risk landscapes," often referred to as "landscapes of fear" that prey must navigate (Kuijper et al. 2016).

There has been growing recognition that temporal niche partitioning is an important driver of community structure, and that humans can alter species temporal niches (Lone et al. 2014; Gaynor et al. 2019, Frey et al. 2020). Sympatric species must partition space or time to coexist, and a species temporal activity pattern can be characterized by its use of different biologically meaningful time periods, like daytime, night or twilight. Although partially controlled by an internal clock, species also have plasticity in temporal activity in response to factors like human disturbance (Gaynor et al. 2019) and the presence of apex predators (Brook et al. 2012, Shores et al. 2019) and competitors (Gerber et al., 2012). A meta-analysis published last year in *Science* on the effects of human disturbance on the temporal activity patterns of wildlife found that human disturbance was associated with increased nocturnality in a wide range of species, both carnivores and herbivores (Gaynor et al. 2019). This change in temporal behavior may impact complex ecological processes like intraguild competition, top-down effects of predators, or introduce various sub-lethal or lethal effects such as reduced access to water or food (Gaynor et al. 2019). Although this research documented singular species' responses to human disturbance, few studies have assessed how humans may alter species' temporal niche partitioning and thus their ability to enable coexistence within ecological communities.

Figure 1 below shows photographs of humans, wolves, coyotes and deer from my study area from the same camera location at different photoperiods. The photo of the wolf is from 2015, 5 years after wolves recolonized our study area after an absence of close to a century. Wolf recolonization of our study site set up a natural experiment that enabled us to test for the top-down effects of wolves in a human-dominated landscape. Although historically gray wolves ranged across most of North America, they were extirpated from most of the contiguous United States by the latter half of the 19th century due to human persecution. In the 1990s and early 2000s wolves started coming back naturally to Washington from coastal gray wolf populations in British Columbia and "continental" gray wolf populations in Idaho and western Montana. Washington state's first pack in over 70 years, the Lookout Pack, was confirmed in the Methow valley in the mountains west of Twisp in 2008. Two years later, in 2010, wolves were documented in our study area on the Colville Reservation. This recent and still ongoing recolonization of wolves in eastern Washington state has created spatial heterogeneity in wolf distribution (WDFW, 2017) in a multi-use landscape where logging, hunting (of all our study species, including wolves) ranching and motorized recreation also occur. The variation in wolf distribution in our study area created a natural experiment that allowed us to compare ecosystem properties in areas with and without wolves to better understand the ecological function of apex predators in human-dominated landscapes.

Accordingly, the overarching goal for my dissertation was to investigate the behaviorally-mediated effects of apex predators in multi-use landscapes on the spatiotemporal activity of sympatric predators and prey. In particular, I investigated the effects of apex predators on the spatiotemporal activity of sympatric apex predators (cougars, *Puma concolor*) and mesopredators (coyotes, *Canis latrans* and bobcats, *Lynx rufus*). For these chapters, I hypothesized that humans would function as ecosystem “superpredators,” and that subdominant predators would prioritize temporal niche partitioning away from humans rather than wolves as intraguild carnivore dynamics are superseded by the danger posed from humans. In addition, for Chapter 2 I investigated how top-down predator effects on the main herbivorous prey of wolves in our study system (mule deer, *Odocoileus hemionus*, and white-tailed deer, *Odocoileus virginianus*), play out when prey must also contend with hunting from humans. For this chapter, I hypothesized that during hunting seasons, humans will act as superpredators and temporarily override the anti-predator behavior of prey towards large carnivores, and that the behavioral changes of deer will push them into greater spatiotemporal overlap with cougars and wolves.

1.1 Figures

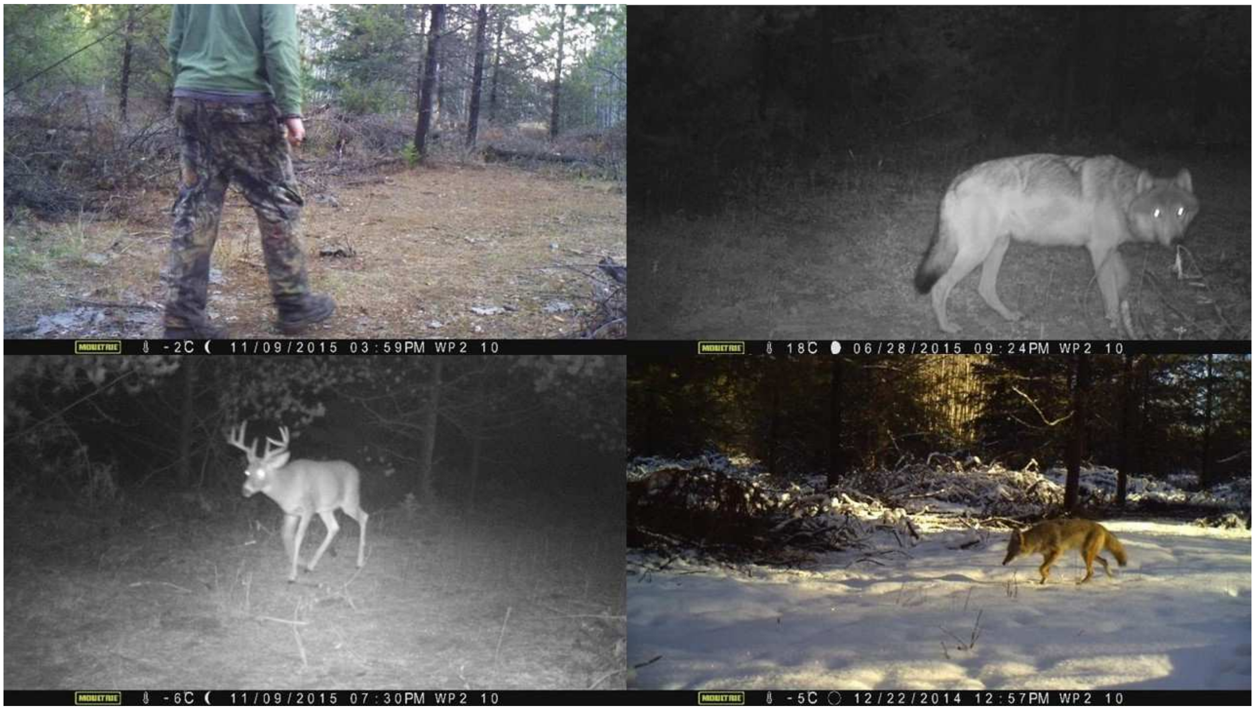

Figure 1. Camera trap photographs of a human, wolf, coyote and white-tailed deer, clockwise from the upper left, from my study sites in northeastern Washington.

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Chapter 1. MESOPREDATORS CHANGE TEMPORAL ACTIVITY IN RESPONSE TO A RECOLONIZING APEX PREDATOR

1.1 ABSTRACT

Apex predators can influence ecosystems through density and behaviorally mediated effects on herbivores and mesopredators. In many parts of the world, apex predators live in, or are returning to, landscapes that have been modified by people, so it is important to understand their ecological role in anthropogenic landscapes. We used motion-activated camera traps to compare the activity patterns of humans and two mesopredators, coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), in areas with and without an apex predator, the gray wolf (*Canis lupus*), in a multi-use landscape of the northwestern United States. In areas with wolves there was a significant increase in temporal niche overlap between the mesopredators owing to higher levels of coyote activity at all time periods of the day. Temporal overlap between mesopredators and humans also increased significantly in the presence of wolves. Coyotes exposed to wolves increased their activity during dawn, day, dusk, and nighttime. The increase in coyote activity was greatest during the day, when wolves were least active, and at dusk. The direction of change in bobcat activity in areas with wolves was opposite to coyotes at dusk and nighttime, suggesting a possible behaviorally-mediated cascade between wolves, coyotes, and bobcats, although these findings would need to be confirmed with further research. Our findings suggest that mesopredators in human-dominated systems may perceive humans as less dangerous than apex predators, that humans may be more likely to encounter mesopredators in areas occupied by top predators, and that behaviorally-mediated effects of apex predators on mesopredators persist in human-dominated landscapes.

Keywords:

Behaviorally-mediated effects, non-consumptive effects, carnivores, camera traps, wolves, coyotes

1.2 INTRODUCTION

Top predators can influence ecosystems through density-mediated pathways by decreasing prey abundance or via non-consumptive pathways by changing prey behavior (Oswald 2000, Terbough et al. 2001, Estes et al. 2011, Ripple et al. 2014). Importantly, these species also interact with populations of smaller carnivores, or mesopredators (Prugh et al. 2009). These interactions can take the form of intraguild predation (IGP), when the smaller predator is killed and sometimes consumed by its larger counterpart (Polis et al. 1989, Palomares and Caro 1999). IGP often occurs when there is niche overlap between predator species and the smaller predator is more efficient at exploiting a shared resource (Polis et al. 1989). Under these conditions, theory suggests there is selective pressure for the larger predator to suppress its smaller competitor, potentially leading to changes in the subordinate species' behavior, abundance, and distribution (Polis and Holt 1989; Ritchie and Johnson 2009). IGP is widespread across ecosystems and has been observed in diverse taxa including invertebrates, fishes, amphibians, and birds (Polis and Holt 1989, Holt and Polis 1997), as well as between disparate taxa (Potter, Greenville and Dickman 2018). Within mammalian carnivore guilds, IGP can account for over half of the mortalities experienced by smaller carnivores (Prugh and Sivy 2020) Palomares and Caro 1999). Consequently, changes to large predator populations have the potential to indirectly influence prey populations and patterns of biodiversity by modifying mesopredator abundance and behavior through IGP (Terbough et al. 2001, Prugh and Arthur 2015, Berger et al. 2008, Berger & Conner 2008, Prugh et al. 2009).

Most studies of top-down predator effects have occurred in wilderness and protected areas, leaving open the question of whether these effects persist in areas where human impacts are more pervasive (Kuijper et al. 2016). Humans can dampen the ecological effects of apex predators by reducing their densities below what would be supported by available prey (Liberg et al. 2012; Ripple et al. 2014) and by triggering avoidance behavior (Rogala et al. 2011; Dorresteijn et al. 2015). For example, Hebblewhite et al. (2005) found that the density-mediated indirect effects of gray wolves on plants attenuated in areas of high human use. By contrast, Kuijper et al. (2016) hypothesized that the strength of behaviorally-mediated top-down effects is more robust to human influence because predation risk can trigger defensive countermeasures even when predators are relatively scarce. This hypothesis likely applies to intraguild interactions among predators given that mesopredators invest in defensive countermeasures against apex predators even when the latter are at low densities (Laundré et al. 2001). To date, however, behavioral interactions between apex and mesopredators in human-dominated systems are not well understood. In the present study, we explored behavioral interactions between gray wolves and mesopredators in eastern Washington state, USA, where hunting, logging, motorized recreation and cattle grazing occur, to investigate whether behaviorally-mediated effects of apex predators on mesopredators are reduced in a landscape of pervasive human use.

Interactions between gray wolves and mesocarnivores are relatively well documented, but most of these investigations have taken place in national parks where human use is restricted to recreation rather than in multi-use landscapes where resource extraction, hunting, and livestock grazing also occur (Carbyn 1982, Crabtree and Sheldon 1989, Dekker 1989, Paquet

1992, Arjo and Pletscher 2002, Theuerkauf et al. 2003; Wilmers et al. 2003, Berger and Gese 2008, Berger et al. 2008, Merkle et al. 2009; Sivy et al. 2017). Collectively, these studies reveal that wolves both benefit (through scavenging opportunities) and suppress (by predation) coyote populations (Berger and Gese 2008, Berger et al. 2008; Wilmers 2003; Merkle et al. 2009). The few studies of wolf effects on mesopredators outside of national parks occurred in remote areas such as northern Canada (Fuller and Keith 1981) and Alaska (Thurber et al. 1992; Sivy et al. 2017). In the western portions of the contiguous United States being recolonized by wolves, however, only 6.8% of public lands are in national parks or wilderness areas, whereas the remaining 93.2% of public lands are in multi-use landscapes where resource extraction, cattle grazing and hunting occur (Vincent, 2014). Thus, in the interest of predicting the ecological consequences of apex predator recolonization, there remains a need for studies exploring wolf-mesopredator interactions in areas where humans are a major ecosystem player.

To date, most research on the ecological effects of wolves on mesopredators in North America has focused only on the relationship between wolves and coyotes (*Canis latrans*) while overlooking an abundant North American felid mesopredator, the bobcat (*Lynx rufus*). Coyote and bobcat spatial and dietary niches overlap extensively and coyotes are known to be intraguild predators of bobcats (Knick 1990; Gipson and Kamler 2002). Moreover, both coyotes and bobcats subsist primarily on lagomorphs, rodents and microtines. However, coyotes show signs of being opportunistic generalists, including more diverse items in their diet such as larger contributions from ungulates (some perhaps from carrion) and fruit, which is absent from bobcat diets (Witmer and deCalesta 1986; Neale and Sacks 2001; Riley et al. 2003; Smith et al. 2017). Given the extensive niche overlap and documented predation of bobcats by coyotes, coyotes may alter bobcat behavior or limit their populations through interference or exploitative competition.

However, wolves are not known to be intra-guild predators of bobcats, suggesting that any top-down effects of wolves on bobcats are likely to be transmitted indirectly by coyotes. With this possibility in mind, we investigated whether wolves modify spatial and temporal partitioning between bobcats and coyotes.

Temporal partitioning often allows mesopredators to coexist with apex predators by using the same space at different times and can play a crucial role in maintaining community structure in mammalian carnivore guilds (Durant 1998, Linnell and Strand 2000, Hayward and Slowtow 2009; Brook et al 2012). Moreover, generalist predators such as coyotes may be able to switch to different prey species or energy sources such as fruit more easily, and may thus have a greater capacity to change temporal activity patterns in comparison to bobcats, which mostly subsist on small mammals that are active at dawn or dusk. Indeed, prey switching by smaller invertebrate predators has been observed in response to the introduction of a larger predator (Siddon and Witman 2004). Coyotes, wolves, and bobcats are typically crepuscular (Murie 1940, Pringle 1960, Ozoga 1966; Witmer and deCalesta 1986; Arjo and Pletscher 1999; Tigas et al. 2002). To our knowledge, interactions between wolves and bobcats have yet to be studied, but one previous study found that coyotes became more diurnal in areas with wolves, presumably to increase activity when their intraguild predators are least active (Arjo and Pletscher 1999). By contrast, many predators (including bobcats and coyotes) become less diurnal in areas with increased human activity, presumably to avoid human contact (Tigas et al. 2002; Smith et al. 2017). Thus, spatiotemporal activity patterns of coyotes in areas with both wolves and humans could reflect the conflicting demands of avoiding both wolves and humans, whereas those of bobcats are more likely to reflect the influences of coyotes and humans.

In eastern Washington state, the recent and ongoing return of gray wolves after nearly 80 years of absence (Washington Department of Fish and Wildlife, 2016) has created spatial heterogeneity in their distribution that allows for natural experiments contrasting ecosystem properties in areas with and without resident wolf packs. Taking advantage of this opportunity in a region that experiences active logging, hunting (including of wolves, coyotes and bobcats), and cattle ranching we evaluated two hypotheses addressing spatiotemporal interactions between wolves and mesocarnivores. First, our 'human-dominant' hypothesis posits that humans reduce the top-down behavioral effects of wolves on mesopredators. Under this hypothesis, apex and mesopredator activity patterns should reflect avoidance of humans, leading us to predict: 1) no difference in the temporal niche overlap of coyotes and bobcats between wolf and non-wolf areas; 2) no difference in the temporal niche overlap of mesopredators and humans between wolf and non-wolf areas; 3) a negative effect of human activity on the activity of wolves, coyotes, and bobcats; and 4) no significant difference in the times of day when coyotes are active in areas with wolves vs. without wolves. Alternatively, wolves may retain their ecological effectiveness in anthropogenic landscapes, in which case coyotes should maintain temporal niche separation from wolves, and bobcats from coyotes, despite the presence of humans. Under this alternate 'wolf-dominant' hypothesis, we predicted: 5) an increase in temporal niche overlap between mesopredators in the presence of wolves; 6) an increase in temporal niche overlap between mesopredators and humans in the presence of wolves, because mesopredators will perceive humans as less dangerous than wolves; 7) no negative effect of human activity on wolf activity, because wolves will not avoid humans; 8) a difference in the times of day when coyotes are active in areas with wolves relative to areas without wolves to avoid time periods of peak wolf activity; and 9) a behaviourally-mediated cascade between wolves, coyotes and bobcats manifesting as a shift in the times of day when bobcats are active opposite to changes in coyote activity in areas with wolves.

1.3 METHODS

Study Area

We performed this study in the Okanogan Highland dry forest ecosystem of north-central Washington State, within the Northern Rockies ecoregion. We established four study areas, two in the Okanogan National Forest and two on the Colville Indian Reservation, which ranged in area from 550-680 km^2. Topography and vegetation were similar among all four study areas, as was human residential density, which ranged from 0 - 4 people per square kilometer within the census blocks comprising the study areas (‘WA Data and Research: Population Density by Census Block’, 2010). All four sites experienced logging, hunting, motorized recreation, and cattle grazing. Cattle grazing occurred from mid-June to mid-October in the study area, while logging and motorized recreation occurred year-round. Elevations within the region ranged from 300 to 2,065 m. The local topography was mostly gently rolling hills, interspersed with rugged, rocky cliffs in the Sanpoil River valley. This ecoregion is made up of diverse habitats that vary substantially based on elevation and aspect. On south-facing slopes at lower elevations, shrub-steppe habitat is dominated by big sage *(Artemisia tridentata*) and bitterbrush (*Purshia tridentata*). Low elevation forests are comprised of primarily ponderosa pine (*Pinus ponderosa*) and interior Douglas fir (*Pseudotsuga menziesii*). At higher elevations, subalpine fir (*Abies lasiocarpa*) and grand fir (*Abies grandis*) forests mixed with western larch (*Larix occidentalis*) predominate (Clausnitzer and Zamora 1987).

Over the course of the study, the two study sites on the Colville Indian Reservation were occupied by the Nc'icn and Strawberry wolf packs, for which the study sites are named (Fig. 1). Wolves recolonized the study sites from neighboring populations in 2010, or 5 years before this study took place. The Nc'icn pack had 5 wolves for the duration of the study and a home range size of 668 km^2, whereas the Strawberry pack had 7 members and a home range size of 807 km^2. Gray wolf average home range size, average pack size, and pack density in Washington state are similar to those of wolves in managed landscapes elsewhere in Washington (WA Dept. of Fish and Wildlife and in neighboring states ((WDFW et al. 2017; Jimenez and Becker 2016). However, pack size and pack density in Washington state and neighboring states are low relative to those in protected areas (Jimenez and Becker 2016). Wolf hunting was allowed on the Colville Indian Reservation but only by tribal members, and a Strawberry pack wolf was legally harvested under these guidelines during the Aug 1, 2016 - Feb 28, 2017 wolf hunting season (WDFW et al. 2017). There were no limits on the number of coyotes or bobcats that could be hunted within any of the study areas. Coyote hunting was allowed year-round across the study area. In the Okanogan National Forest, Bobcat hunting was allowed from Sept 1 – March 15, and trapping was allowed from Nov 1 – March 31. Bobcat hunting was open year-round on the Colville Indian Reservation, with a trapping season from November 1 – February 28 (wolf areas).

We determined that the two study areas in the Okanogan-Wenatchee National Forest were not occupied by wolf packs based on evidence from daily snow tracking surveys in winter and photographs from the camera traps (Figure 1). Four photos of wolves were captured in these areas over the three-year study period, however; three of these photos were of a wolf from the Strawberry pack, which indicated extra-territorial movement.

Cougars (*Puma concolor*), another apex predator in our study system, were never extirpated from the region and were present in both wolf and non-wolf areas. Cougars were not included in the analysis as their management was significantly different between the study areas. Cougars were hunted year-round with hounds and no bag limits in the wolf areas, whereas in the areas without wolves, cougar hunting with hounds was not allowed, was seasonally restricted, and had a bag limit. Due to these large differences in management, cougars were not included in the analysis. However, we analyzed overlap in cougar temporal activity patterns between areas and found that cougars had high temporal activity overlap between areas with and without wolves (Appendix 1); thus, this species was unlikely to be a confounding factor in observed differences in mesopredator activity between areas.

Camera placement

We established a camera trap grid in each study area in March 2013. Each grid was composed of 16 cells, and each cell had an area of 4 km^2 (Fig. 1). The cameras (Moultrie M80 Game Spy, EBSCO Industries Inc., Birmingham, AL) featured infrared triggering with a 50 degree-wide field of view, a 12.2 m detection range, and a flash range for night photographs of 18.3 m. We secured the cameras with cable locks and locked metal security boxes to prevent theft and damage. Within each cell, we deployed a camera trap in forested habitat along a dirt road or game trail to maximize image captures of carnivores and ungulates. All camera locations were within Okanogan highlands dry forest ecotype, and there was little variation in habitat between camera sites. Cameras were deployed year-round and operated 24 hours per day. We checked the cameras for functionality, battery life, and data recovery at all sites every 2-4 months.

Photo identification and data standardization

We defined the sampling interval used for this analysis as a biologically meaningful time period for wolves and coyotes; namely, the average start of the denning and pup-rearing season on May 1st to April 30th of the following year (Mech and Boitani 2010). The study spanned three years from 5/1/2013 to 4/30/2016. Photographs over thirty minutes apart of wolves, coyotes, bobcats, and humans were counted as independent observations (Burton et al. 2015). We catalogued photographs from all cameras into a Microsoft Access database using the program CPW Photo Warehouse, developed by Colorado Parks and Wildlife (Newkirk 2016). Volunteers then identified the species and number of individual animals in each photograph. Multiple animals in the same photograph were counted as a single detection. Volunteers were trained and tested on species identification before they began recording data to ensure they could discriminate similar species. To ensure data quality, each photograph was independently identified by two trained volunteers for the entire dataset. The identifications were subsequently compared and, if they did not match, reviewed by the lead author (CS) who made a final determination.

To account for seasonal variation in day length, we standardized our observations by calculating the clock time of sunrise and sunset for each day of the study, and then binning the detections into four time categories: day, night, dawn and dusk in accordance with previous studies of temporal activity patterns (Farris et al. 2012; Ikeda et al. 2016). We designated day as one hour after dawn to one hour before sunset, night as stretching between dusk and dawn, and dawn and dusk periods as starting and ending one hour before and after sunrise and sunset, respectively (Farris et al. 2015). Accounting for changes in day length is necessary to determine patterns of behavior and activity for studies over three months in duration and in areas above or below 30° or -30° latitude (Nouvellet et al. 2012).

Temporal niche overlap

To quantify the effect of wolf presence on temporal overlap among mesopredators and between coyotes and humans, we used kernel density analyses, a non-parametric method for estimating the probability density function of a random variable (Worton 1989, Ridout and Linkie 2009). We regarded detections of a species as a random sample from a distribution of its underlying continuous activity pattern (Meredith and Ridout 2014). In our analysis, kernel density estimators show the probability of a species being detected at any specific time of day. To estimate the overlap in temporal activity patterns between species, we used the R package "*overlap*" (Meredith and Ridout 2014) with a smoothing parameter of 1. Meredith and Ridout (2014) outlined three methods for choosing the overlap coefficient (symbolized by Δ) and recommend using Δ_4 for large sample sizes ($n > 75$), which we followed. A smoothing parameter of 1 is optimal for the Δ_4 overlap coefficient, as determined by simulations described by the authors Meredith and Ridout (2014). We calculated Δ_4 between species by measuring the overlapping area of the two density functions. We estimated 95% confidence intervals for Δ_4 to compare differences in the overlap coefficients between areas with and without wolves from a smoothed bootstrapping distribution ($N = 10,000$). We concluded that temporal niche partitioning between species differed between treatments if the 95% confidence intervals did not overlap. Separate confidence intervals are considered a stronger test for significance than $P < 0.05$ (Johnson 1999).

Generalized linear mixed models

Next, we used generalized linear mixed models (GLMMs) to test for differences in the specific times of day during which mesopredators were active in areas with and without wolves and an effect of wolf and human activity on mesopredator activity. We modeled the number of photo capture events y_{ijk} for each species on each sampling day *i*, for each time category *j* (dawn, day, dusk, night), at study site *k*, with a zero-inflated generalized linear mixed effect model with a Poisson error distribution and a random intercept for camera location. We also included an offset equal to the number of hours available in each time category. This model structure enabled us to test for significant differences in each mesopredator's use of different time periods between the wolf and non-wolf areas, indicated by 95% confidence intervals that do not overlap, and to evaluate the direct effect of one species' activity patterns on those of another, indicated by 95% confidence intervals that do not overlap zero. The random intercept for camera location controlled for random variation in camera sites that may have influenced the results. However, we also compared standardized habitat variables (distance to roads, slope, % forest cover and % shrub cover) for camera sites between the wolf and non-wolf areas to determine if habitat differences could contribute to differences in activity patterns observed between study sites. We evaluated a set of *a priori* models (Appendix 2) based on known information about human, wolf, coyote and bobcat interactions with the R package *glmmTMB* (Brooks et al. 2017). We used AIC to rank models and Akaike weights (w_i) to evaluate model likelihood (Akaike 1974).

We did not include a strictly spatial analysis of species' association such as co-occupancy modelling because this so called "static" measure of interaction ignores the dynamic nature of most interactive behaviour (Long et al. 2014, Cusack et al. 2017). Our chosen modelling approach accounts for the dynamic nature of species' interactions by indexing species' activity by both temporal (date, time of day) and spatial (camera location) factors. In addition, a comparison of spatiotemporal and strictly spatial methods to study carnivore interactions found that co-occupancy, a strictly spatial analysis method, failed to discern significant patterns, which was attributed to the need for a higher camera density (> 1 camera/2km^2; Cusack et al. 2017) than the camera density in this study (1 camera/4 km^2).

1.4 RESULTS

The cameras recorded a total of 10,169 independent detections of the four study species (Table 1). Humans were the most photographed species, with a total of 5,787 independent detections, whereas wolves were the least photographed species with 306 independent detections. The cameras also captured a gradient of human activity, with some locations recording >900 human independent detections and others <20 (Table 1). A comparison of habitat variables at the camera sites between wolf and non-wolf study areas found no significant differences (Appendix 3)

Temporal activity overlap

All species showed distinct temporal activity patterns (Fig. 2). Humans were diurnal with higher activity at dawn in the wolf areas (Fig 2a, 2b). Wolves were crepuscular with peaks in activity before dawn and after dusk and little activity during the day (Fig. 3). Coyotes exhibited different activity patterns in areas with and without wolves, with a noticeable diurnal shift in their activity peak in areas with wolves (Fig 2). Bobcats were crepuscular with high levels of nocturnal activity in both study areas ~~but had higher levels of activity at dawn and during the day in the wolf areas~~ (Fig 2c, 2d).

Temporal activity overlap (Δ_4) between bobcats and coyotes was 11% greater in areas where wolves were present: in areas without wolves, bobcat and coyote temporal activity overlapped by 77% (95% CI = 74 – 79%, Fig. 2c), compared to a temporal overlap of 88% (95% CI = 0.85 – 0.91, Fig. 2d) in the presence of wolves.

Coyotes and bobcats both had greater temporal overlap with humans in areas with wolves. Temporal overlap (Δ_4) between coyotes and humans was 19% greater in areas with wolves (Δ_4 = 77 %; 95% CI = 74 -79%, Fig. 2b) than in areas without wolves (Δ_4 = 58%; 95% CI = 55-60%; Fig. 2a). Activity peaks for humans and coyotes in the wolf areas occurred between 10:00 – 11:00 AM (Fig. 2b), whereas in non-wolf areas coyote activity peaked at 7:00 AM while the human activity peak remained at 11:00 (Fig. 2a). Bobcats and humans also exhibited 24.2% greater temporal overlap in areas with wolves (Δ_4 = 69%; 95% CI = 63-74%) than in areas without wolves (Δ_4 = 45%; 95% CI =37-50%), and the 95% confidence intervals for these estimates did not overlap.

In areas with wolf packs, coyotes showed similar degrees of overlap with wolves (Δ_4 = 78%; 95% CI = 74-83%; Fig. 3b) and humans (Δ_4 = 77%; 95% CI = 74-79%, Fig. 2b). Wolf overlap with humans was 57.9% (Fig. 3a, 95% CI = 53-62%). In the study areas with wolves, bobcats had greater temporal overlap with wolves (Δ_4 = 85% 95% CI = 79–92%) than with humans (Δ_4 = 69.0%; 95% CI = 63.0-74.2%). Coyote and bobcat activity between wolf and non-wolf areas had average temporal overlap values (Δ_4) of 92 (90-96%) and 83% (76-90%), respectively (Appendix 1).

Generalized linear mixed models

Our generalized linear mixed modelling results for species activity patterns further support our second hypothesis of behaviorally-mediated top down effects of wolves in human-dominated landscapes (see Table 2 for the top models and Appendix 2 for a complete list of every model evaluated). Namely, human spatiotemporal activity did not have a negative effect on wolf or coyote activity (prediction 7), coyotes significantly changed the times of day during which they were active in areas with wolves (prediction 8), and bobcat activity changed in the opposite direction to coyote activity in areas with wolves during dusk and night-time hours (prediction 9, Figs. 4, 5, Appendix 4), but increased activity at dawn and during the daytime. Incident risk ratios (IRR, Long 1997) for the rate of photographs of coyotes in the wolf areas, when holding other variables in the model constant, revealed that coyotes were 1.1, 2.0, 2.1, and 1.6 times more likely to be active during the dawn, day, dusk, and at night, respectively, relative to the non-wolf areas (Figs. 4, 5, Appendix 4). Day was the only time that wolves avoided, whereas humans were most active during daytime hours (Fig. 4). By contrast, in areas with wolves, bobcats were 0.6 times less likely to be photographed at night and dusk, although bobcats increased their activity at dawn and during the day, by 3.3 and 2.2 times, respectively (Fig. 4, 5).

Human activity did not have a negative effect on coyote or bobcat activity and was not included in the top models of each species' spatiotemporal activity patterns. Although human activity was included as a parameter in one of the top models (AIC <2) of wolf spatiotemporal activity, the parameter estimate was not statistically significant (β = -0.38, 95% CI = -1.21 to 0.46). Wolf activity was significantly positively correlated with coyote activity, as were bobcat and coyote activity (Figure 4, Appendix 4). See Appendix 4 for a complete list of the parameter coefficients and intercepts for each of the top species spatiotemporal activity models.

1.5 DISCUSSION

Our findings suggest that apex predators may influence the temporal activity patterns of mesopredators in human dominated landscapes. By contrast to the predictions under our 'human-dominant' hypothesis (predictions 1-4), human activity did not have a significant negative effect on the activity of either apex or mesopredators (prediction 3). Consistent with the 'wolf-dominant' hypothesis, on the other hand, we found evidence suggesting that mesopredators manifest different temporal activity patterns in the presence of an apex predator. Namely, we found that coyotes appeared to avoid wolves temporally rather than spatially. Coyotes in areas with wolves increased their levels of activity during daytime hours, when wolves were the least active, as well as at dusk (prediction 8). Temporal overlap between mesopredators, and between mesopredators and humans, also increased significantly in areas with wolves (predictions 5 and 6). The increase in temporal overlap between mesopredators may have been due in large part to the diurnal shift of both coyotes and bobcats in the wolf areas. The finding of reduced temporal niche partitioning has not been reported previously and indicates that temporal niche partitioning among smaller predators and between mesopredators and humans may be degraded in the presence of an apex predator. In addition, our results suggest a possible behavioral cascade among carnivores, evidenced by changes in bobcat temporal activity opposite to changes in coyote activity at dusk and night, prime bobcat foraging times, in areas with wolves (prediction 9). However, the evidence for a behavioral cascade is mixed, as the temporal response of bobcats in wolf areas are mixed (decreased activity at dusk and night, increased activity during dawn and day), so further research is needed to clarify this result. These results add to our knowledge of interactions within the carnivore guild, underscore the role of temporal partitioning in determining carnivore community structure, and offer new insights regarding the top-down effects of apex predators in human-impacted landscapes.

In the study areas with wolves, coyotes increased their daytime activity, when wolves were the least active, consistent with Prediction 8. Daytime may be a less productive time for coyote foraging because their primary prey (deer, small mammals) are crepuscular or nocturnal (Beier and McCullough 1990; Appendix 5). However, because coyotes are generalist predators they may be able to compensate by switching to foods sources that are more available during the day. The shift in coyote activity to a more diurnal niche also resulted in greater temporal overlap between coyotes and humans, another coyote predator. The use of suboptimal temporal niche space by mesopredators in order to avoid apex predators has also been found in leopards (*Panthera pardus*) responding to tigers (*Panthera tigris*) and feral cats (*Felis catus*) and red foxes (*Vulpes vulpes*) responding to dingoes (*Canis lupus dingo*) outside of protected areas (Azlan and Sharma 2006; Brook et al. 2012).

Coyotes also exhibited high spatiotemporal correlation with wolves. This positive correlation combined with the increase in activity of coyotes when wolves were least active suggests temporal avoidance and spatial overlap between wolves and coyotes. Coyotes may balance the risk of intraguild predation and the reward of scavenging from wolf kills by using the same areas as wolves when wolves are least active to minimize predation risk. It may also be explained by coincidental use of similar habitat by the two canids. However, habitat overlap is unlikely to be the primary factor behind the strong association given the marked differences in prey and home range sizes of the two predators (Witmer and deCalesta 1986; Koehler and Hornocker 1991; Haight et al. 1998, Newsome et al. 2016, WDFW 2017). Our results corroborate previous findings that coyotes are more active and vigilant in areas with wolves, likely to decrease predation risk (Arjo and Pletscher 1999; Switalski 2000). Importantly, those prior studies were conducted in areas where wolves were not hunted (Montana Fish Wildlife and Parks 2009). Hence, our findings are the first to suggest that wolves continue to trigger changes in coyote behavior in multi-use landscapes where wolves are hunted.

The increased activity of coyotes in the presence of wolves also affected temporal partitioning between coyotes and their close intraguild competitor, bobcats. Temporal overlap between coyotes and bobcats increased markedly (+11%) in the areas with wolves, suggesting that temporal niche partitioning between these mesopredators is diminished in the presence of an apex predator, consistent with Prediction 5. This process may have been partly driven by the encroachment of coyotes into the crepuscular and nocturnal niche space of bobcats, the subdominant mesopredator, as well as the increase in diurnal activity of both mesopredators. In the absence of apex predators, humans may also decrease mesopredator temporal niche partitioning (Wang et al. 2015; Smith et al. 2017). Thus, it is possible that humans partly drove the observed increase in mesopredator temporal overlap given that higher levels of human activity were recorded in the areas with wolves. However, coyotes and bobcats simultaneously increased temporal overlap with humans (+19% and +24%, respectively) in the areas with wolves, suggesting that the increased mesopredator temporal overlap was not the result of avoidance of humans.

Although wolf presence apparently reduced temporal niche partitioning between mesopredators, bobcats also appeared to shift their activity in response to the behavioral changes of coyotes in the wolf areas (Prediction 9). Bobcats are normally crepuscular and nocturnal, presumably to match the activity of their small mammal prey (Mech et al. 1966, Witmer and deCalesta 1986; Neale and Sacks 2001). However, in the presence of wolves, bobcats increased their activity at dawn and during the day, but also decreased their activity at night and dusk. This was opposite to some changes in coyote activity, which increased activity during dawn, day, dusk, and night. Given that coyotes are intraguild predators of bobcats (Knick 1990; Gipson and Kamler 2002), bobcats' shift away from optimal hunting periods (dusk and night) in areas with wolves may have minimized predation risk and exploitation competition by avoiding increased coyote activity. Our results differ from several previous studies that found no evidence of temporal avoidance between coyotes and bobcats (Witmer and deCalesta 1986; Neale and Sacks

2001, Smith et al. 2017). However, these studies relied on VHF telemetry and scat collection, both of which have limited capacity to discover patterns of fine-scale temporal partitioning (Witmer and deCalesta 1986; Neale and Sacks 2001, Smith et al. 2017). By contrast, camera traps capture animal activity throughout the 24-hour daily cycle and are thus an effective method for examining fine-scale temporal patterns (Frey et al. 2017). In addition, the previous studies exploring bobcat-coyote interactions were conducted in southern regions of the United States where small mammal prey densities are higher and no wolves are present. In the northern contiguous United States, lower levels of prey biomass may lead to stronger exploitation and interference competition between the two mesopredators (Witmer and deCalesta 1986; Neale and Sacks 2001) and consequently drive avoidance behavior in the subdominant mesopredator. However, the previously mentioned studies (Witmer and deCalesta 1986; Neale and Sacks 2001, Smith et al. 2017) found little evidence of avoidance behavior between coyotes and bobcats, so coyotes may not be dangerous to bobcats. Given the mixed temporal activity responses of bobcats in the wolf areas, it is possible that the changes in bobcat activity we observed were in response to wolves themselves, although there is no research on interactions between these two carnivores to suggest this idea. Moreover, low dietary overlap between wolves and bobcats, in comparison to high overlap in prey use between coyotes and bobcats, render it more likely that bobcats would avoid coyotes, a close intraguild competitor. Mesopredators may also prey switch to survive in different temporal niches, which would alter the predation pressure experienced by mesopredator prey species. This possibility may be important to consider in ecosystems with threatened small mammals or ungulates. Further research on factors influencing potential spatiotemporal niche partitioning between coyotes and bobcats would help to further understand intraguild competition dynamics between these two mesopredators.

Despite our study being set in a human-impacted landscape, we did not document an inverse relationship between human and predator activity, consistent with prediction 7. This result is surprising because humans were the most recorded species on the cameras and hunted all three predator species in the study areas. Yet, human activity had no significant correlation with coyote or wolf activity and was positively correlated with bobcat activity. Furthermore, both coyotes and bobcats exhibited significant increases in temporal overlap with humans in the areas with wolves (+19% and +24%, respectively; Prediction 6). This pattern is likely due to the previously discussed behaviorally mediated cascade between wolves and mesopredators, which caused increases in mesopredator activity during the day (coyotes) and dawn (bobcats) in the wolf areas, the two time periods with the most human activity. Increased temporal overlap between mesopredators and humans in the presence of an apex predator suggests that in some human-modified systems mesopredators may perceive humans as less dangerous than apex predators; and that humans may be more likely to encounter mesopredators in areas with apex predators. Similarly, after the successful recovery of tigers in India, leopards were pushed into areas of high human use, resulting in increased leopard depredations on livestock (Carter et al. 2015). This potential for increased human-mesopredator conflict emphasizes the need for consideration of behavioral interactions between carnivores when recovering an apex predator.

Our findings that suggest apex predators exert behaviorally mediated effects in human-dominated landscapes are correlational, not causative. Thus, it is possible that underlying differences between the study areas for which we did not account may have contributed to our results. However, we designed our study to strengthen inference and minimize confounding factors in several ways. First, we followed recommended approaches (Ford and Goheen 2011; Kuijper et al. 2016) by developing competing hypotheses based on previous research. Second, we took advantage of a natural experiment that leveraged spatial heterogeneity in wolf distribution across ecologically similar areas; the use of these quasi-experiments permits stronger inference than purely observational studies (Rosenbaum 2002). Third, we spatially replicated our sites in wolf present and wolf absent areas to account for confounding variables that may have otherwise influenced our results. Finally, the use of a random effect in our statistical models accounted for potential environmental variation between camera locations. In addition, a comparison of habitat variables at camera sites between the study areas with and without wolves found no significant differences (Appendix 2).

Although our study was designed to minimize confounding factors, its correlational nature necessitates examination of alternative explanations. The changes in bobcat and coyote activity patterns between areas with and without wolves could also have reflected changes in prey activity. Small mammals, including lagomorphs, are the primary prey for both mesopredators (Witmer and deCalesta 1986). Lagomorphs were predominantly nocturnal in both study areas, but in wolf areas they were significantly more nocturnal (Appendix 5). Furthermore, potential ungulate prey such as white-tailed deer (*Odocoileus virginianus*) showed no change in temporal activity, while mule deer (*Odocoileus hemionus*) showed increased nocturnal activity in areas with wolves (Shores et al. in prep). These changes in both lagomorph and ungulate activity between study areas do not match the changes we observed in mesopredator activity, supporting interspecific competition, not prey use, as the most plausible explanation for the observed changes to mesopredator temporal behavior. However, further research into changes in prey activity between areas with similar carnivore guilds would strengthen this conclusion.

In addition, it is possible that differences in black bear (*Ursus americanus*) activity between our study areas could have influenced our findings. However, coyotes did not show a significant difference in activity in relation to our designation of the onset of winter (Fig. 1.4; winter defined as Nov 16 – April 30), which aligns with the seven-month hibernation of black bears in neighboring western Idaho from mid-October to mid-April (Beecham et al. 1983). Bobcats increased activity during the winter (Fig. 1.4), but there are no documented interactions between black bears and bobcats of which we are aware, and dietary niche overlap between the two is likely to be low, as black bear are primarily herbivorous. In addition, previous research has found that black bears are primarily diurnal, with a vespertine peak in activity (Bridges et al. 2004, Elbroch and Rinehart 2011), and both mesopredators increased diurnality year-round in the areas with wolves, so this behavioral change is unlikely to be driven by avoidance of black bears.

Finally, it is possible that mesopredators adjust behavior at a habitat scale as well as a temporal scale, such as altering movement behavior away from common travel corridors and towards areas that are less ideal for movement but superior for predator avoidance. Our cameras sites were located along game trails or secondary roads, so our study design does not allow for a rigorous test of this hypothesis. However, if coyotes were altering their movement behavior away from travel corridors to avoid wolves, who select for trails and roads to increase travel efficiency (Dickie et al. 2016), one would expect fewer records of coyotes in the areas with wolves, as all cameras were located along movement corridors. Instead, more photographs of coyotes were recorded in the wolf areas (Table 1), which suggests coyotes may not be avoiding movement corridors in areas with wolves. However, we recommend further research into avoidance of movement corridors and other potential changes in habitat use by coyotes and bobcats in areas with and without wolves.

Other questions to address in future work include whether prey switching occurs when mesopredators shift their temporal activity to avoid apex predators, and if such switching has subsequent impacts on lower trophic levels. In addition, the high similarity of cougar temporal activity patterns between areas with and without wolves (Appendix 1) suggests a potential lack of effect of wolves on the temporal activity patterns of this apex felid predator. Further in-depth research into wolf and cougar interactions would be needed to confirm this finding. Finally, it is important to consider that the type of human activity may influence the strength of top-down predator effects. Humans primarily used our study areas for resource extraction such as logging and hunting. Logging trucks may be perceived as less dangerous by wildlife because they differ visually and acoustically from personal vehicles used by hunters. Further research is therefore needed to clarify if the type of human activity alters the strength of top-down behaviorally mediated effects of apex predators.

Data Accessibility

Analyses reported in this article can be reproduced using the data provided by Shores et al. (2019).

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1.7 TABLES AND FIGURES

Table 1. Summary of independent detections, or photographs separated by at least 30 minutes, of humans, wolves (*Canis lupus*), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) in the study areas with (n = 2) and without (n = 2) established wolf packs.

Species	Without wolf packs	With wolf packs	Total
Human	1796	3991	5787
Wolf	4	302	306
Coyote	1345	1746	3091
Bobcat	202	247	449

Table 2. The top zero-inflated Poisson generalized linear mixed models for the activity patterns of each species. For each model presented, ΔAIC is the absolute difference in AIC values relative to the model with the lowest AIC. Any model with a ΔAIC ≤ 2 is included. Numbers of parameters in the model are indicated by K; d.f. = degrees of freedom; LL = log likelihood; and w_i = AIC model weight. Camera locations were included as a random effect in every model.

Model parameters	ΔAIC	K	Residual d.f.	LL	Residual dev.	W_i
Human						
Location + time + season	0	7	280569	-17355.2	34710.4	1.00
Wolf						
Location + time + season	0	7	280569	-2018.7	4037.3	0.60
Human + location + time + season	0.8	8	280568	-2018.0	4036.1	0.40
Coyote						
Wolf + time*wolf presence + location + season	0	10	280564	-15681.7	31363.3	0.80
Bobcat						
Human + wolf + coyote + location + time*wolf presence + season	0	12	280561	-3092.9	6185.5	0.83

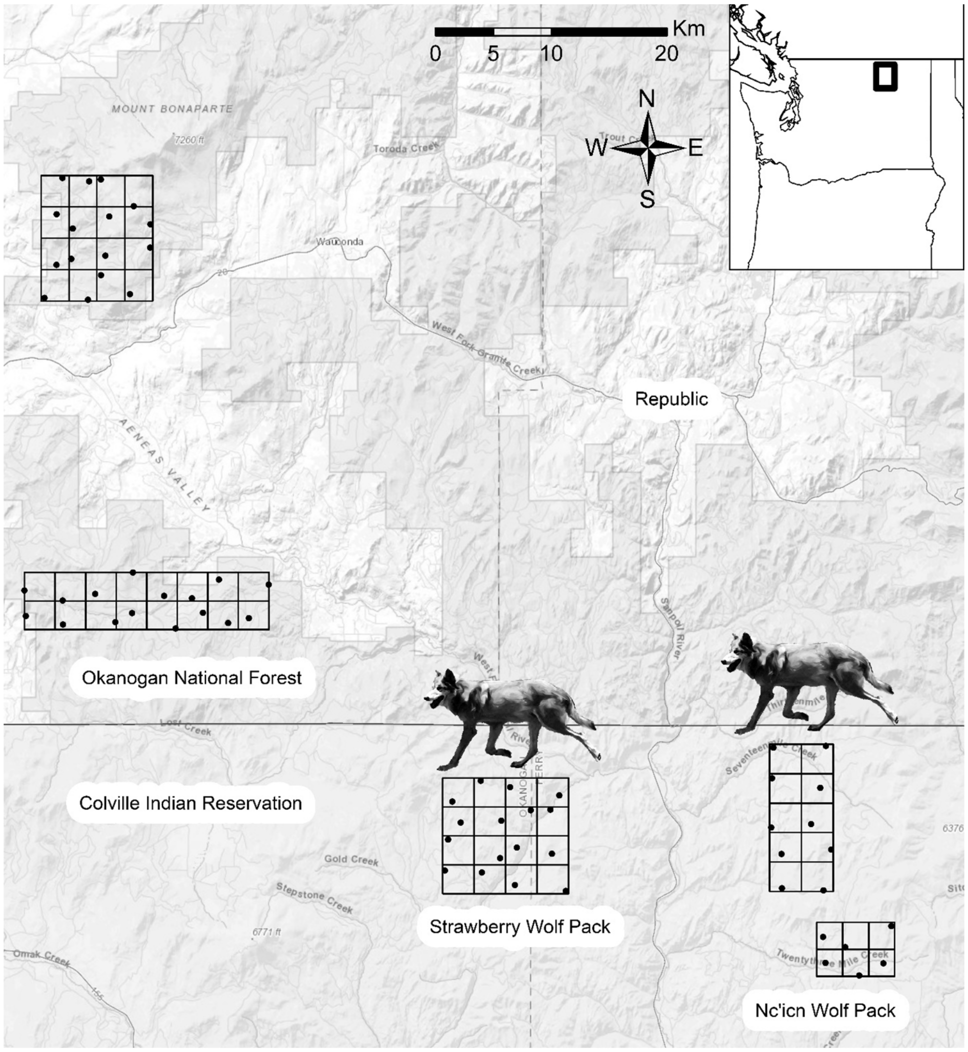


Figure 1. Grids of camera trap locations (black dots) in each of the four study areas. For each grid, single cameras were deployed inside a 2 x 2 km^2 grid cell along secondary dirt roads and trails. The two southern study areas on the Colville Indian Reservation are home to the Strawberry and Nc'icn wolf packs. The two northern study areas without wolves fall within the Okanogan-Wenatchee National Forest. The town of Republic is also marked, and the inset shows the location of the study area in north-central Washington state, USA.

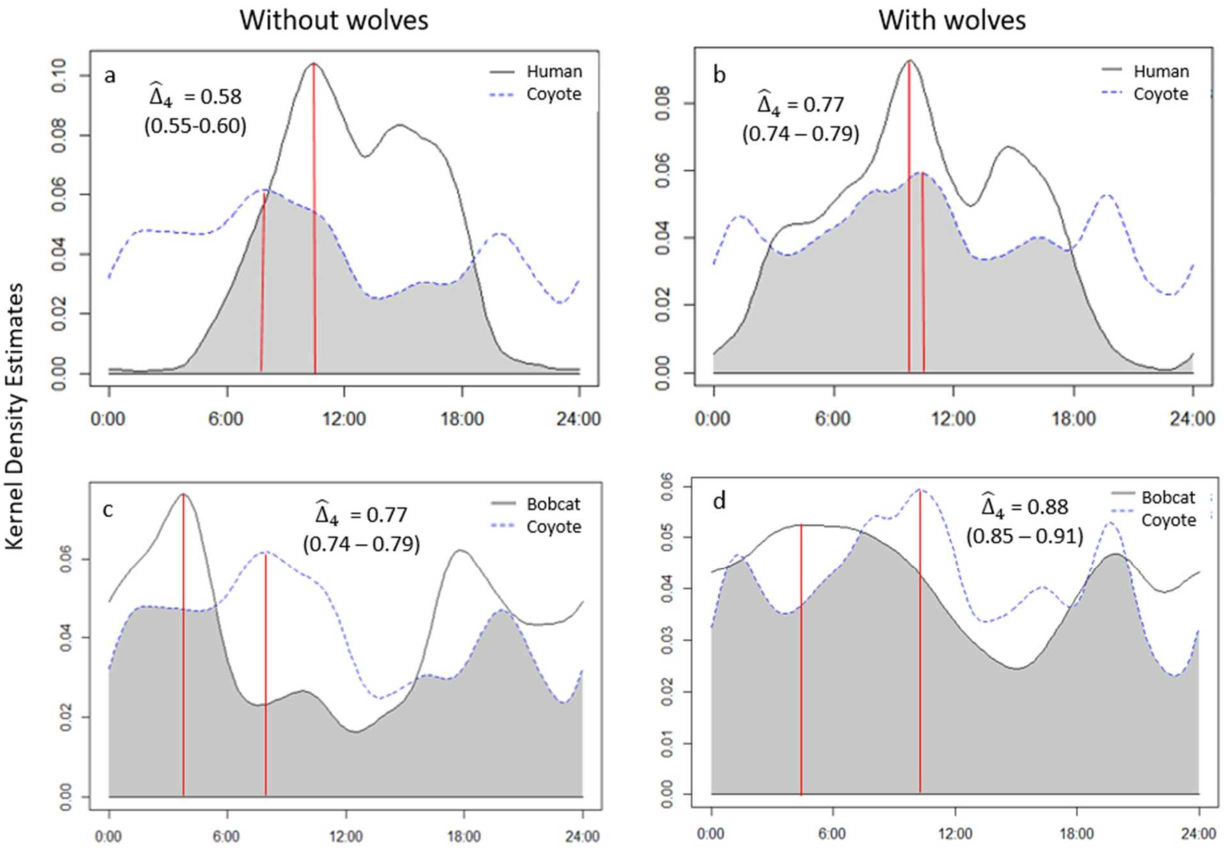


Figure 2. Kernel density estimators of bobcat, human and coyote temporal activity pattern overlap.(of humans and coyotes (panels a and b) and bobcats and coyotes (panels c and d) in areas with and without wolves. Higher density indicates increased activity. Red lines show the timing of peak activity. The x-axes represent time over a 24-hour period and the y-axes quantify the density of temporal activity, with higher values indicating increased activity. Overlap area between species is shown in grey. Overlap values (Δ_4) with 95% confidence intervals were estimated with 10,000 bootstrapped replicates.

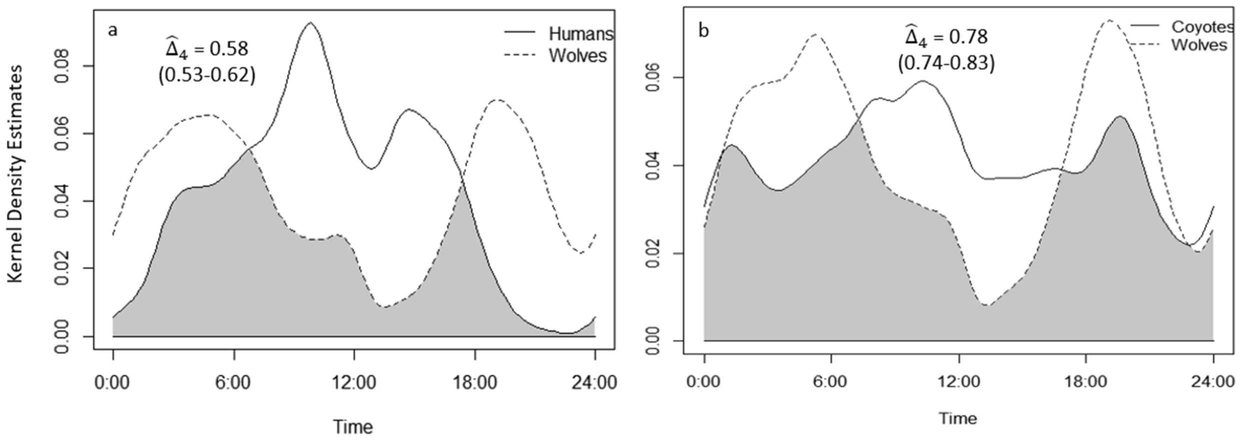


Figure 3. Kernel density estimators of wolf, coyote and human temporal activity pattern overlap where higher density represents increased activity of a) wolves and humans and b) coyotes and wolves in our two study sites with wolves. For each panel, the x-axis represents time over a 24-hour period and the y-axis is the density of temporal activity, with higher values indicating increased activity. The overlap of temporal activity between species is shown in grey. Overlap values (Δ4) with 95% confidence intervals were estimated with 10,000 bootstrapped replicates.

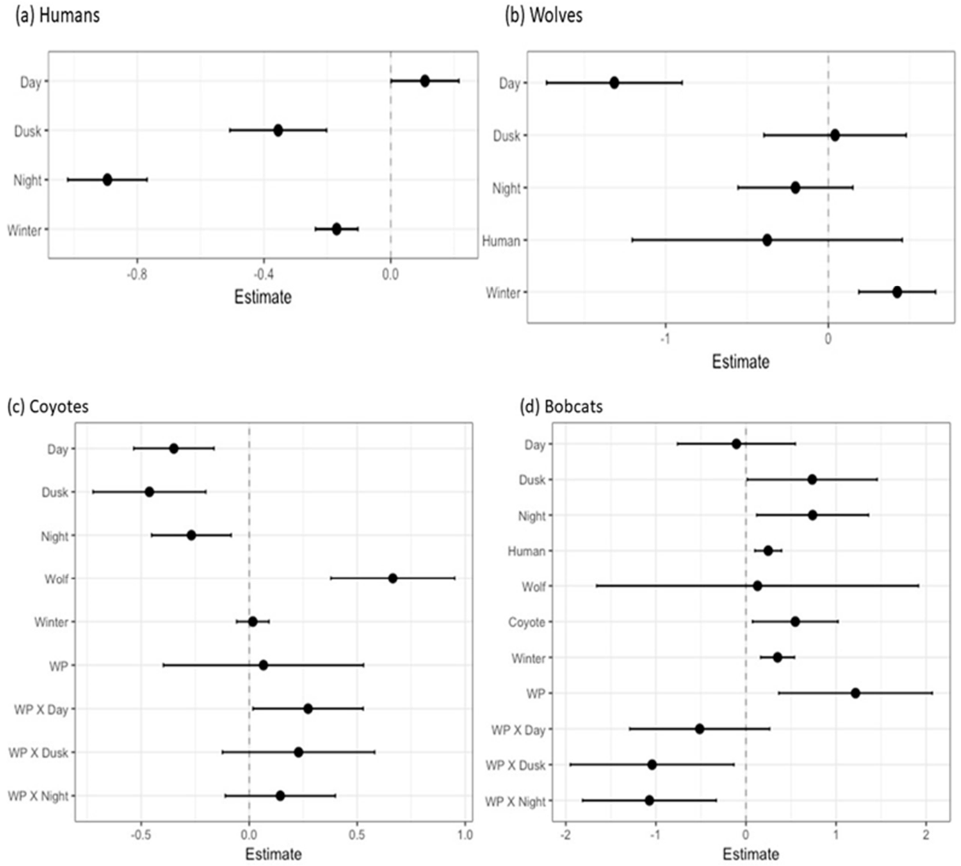


Figure 4. Coefficient estimates (black dots) with 95% confidence intervals for model parameters (listed on the y-axis) for the top zero-inflated Poisson generalized linear mixed models of species activity patterns for (a) humans (Intercept β = -0.9, 95% CI = -1.3 to -0.4), (b) wolves (Intercept β = -4.5, 95% CI = -5.6 to -3.4), (c) coyotes (Intercept β = -1.5, 95% CI = 1.9 to -1.2), and (d) bobcats (Intercept β = -4.4, 95% CI = -5.43 to -3.40). Wolf presence, a binary variable indicating whether the camera site was in an area where a wolf pack was present over the three year study period, is represented by WP. "Wolf" and "Human" parameters indicate the spatiotemporal activity patterns of these species as indexed by date, camera locations and time of day, which is a four level categorical variable (dawn, day, dusk or night), with dawn as the reference level. See Appendix 4 for a complete list of all coefficient values.

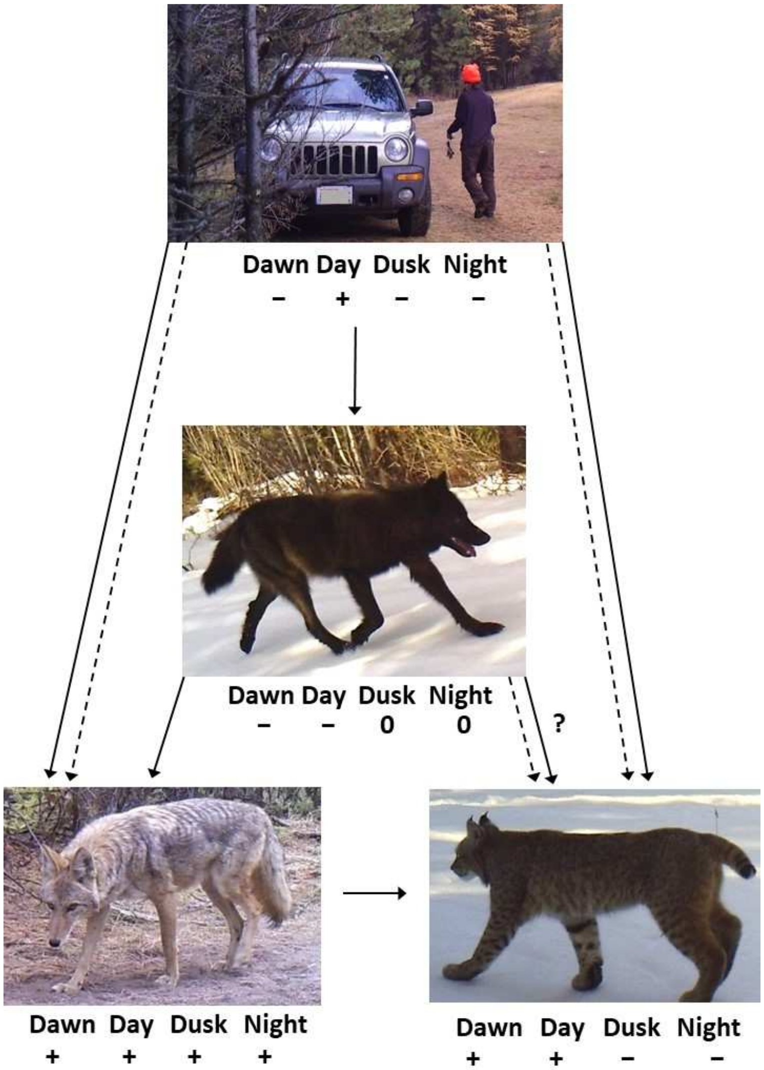
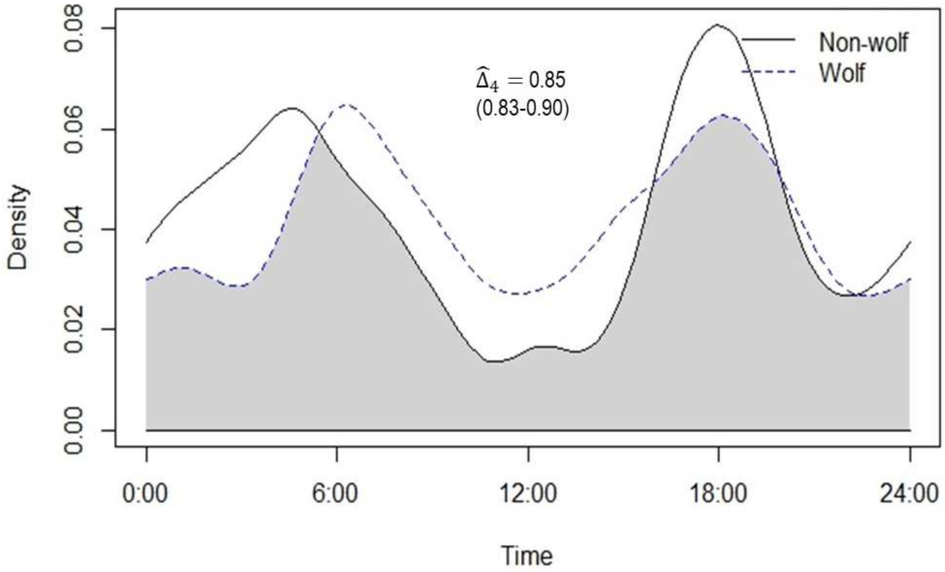


Figure 5. Diagram of temporal activity patterns of humans, wolves, bobcats and coyotes. Arrows indicate potential direct (solid arrows) and indirect (dashed arrows) temporal interactions between species. For example, humans might directly exclude all three carnivores from temporal niches, or indirectly open temporal niche space for coyotes by altering the behavior of wolves. Similarly, changes in wolf temporal activity could indirectly affect temporal niche space for bobcats by altering diel patterns of coyote activity. The +/- signs for humans and wolves indicate whether the species showed a significant ($P < 0.05$) positive or negative association with the corresponding time period (dawn, day, dusk, or night). A “0” indicates that the species showed no significant association with the time period. The +/- signs for coyote and bobcat indicate the direction of change in the species’ activity in the study areas with wolves. The question mark (?) between wolves and bobcats indicates uncertainty about the direct effect wolves may have on bobcat temporal activity.

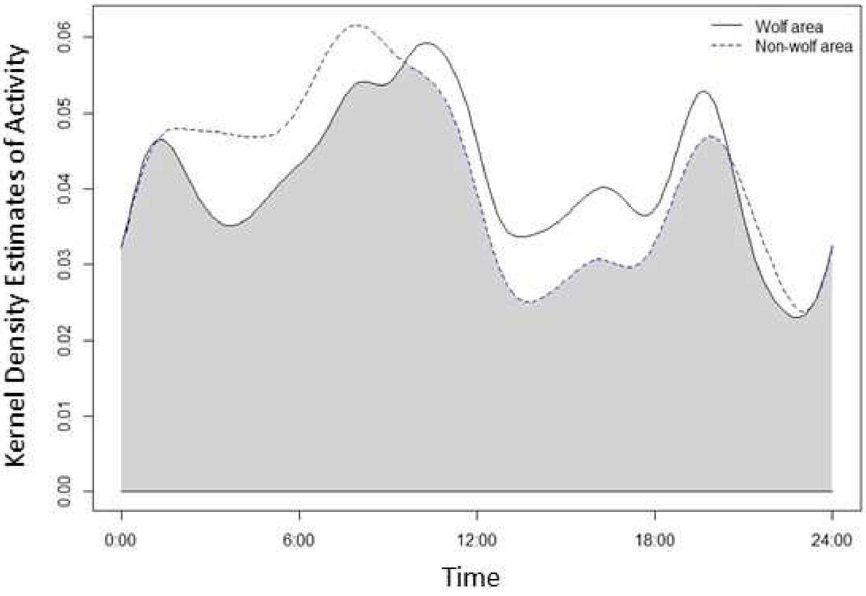
1.8 APPENDICES

Appendix 1: Intraspecies kernel density estimators of temporal activity overlap between wolf and non-wolf areas based on independent observations (> 30 min apart) from camera traps of (a) cougars (*Puma concolor*; N = 453) of cougars in areas with wolves (n=271) and without (n=182) wolves;(b) coyote and (c) bobcats. Temporal activity overlap values (Δ_4) for coyotes between wolf and non-wolf areas is 92% (95% CI = 90-96%), and for bobcats is 83% (95% CI = 76-90%).Higher density indicates increased activity. The x-axes represent time over a 24-hour period and the y-axes quantify the density of temporal activity, with higher values indicating increased activity. Overlap in temporal activity is shown in grey. Overlap values (Δ_4) with 95% confidence intervals between wolf and non-wolf areas were estimated with 10,000 bootstrapped replicates.

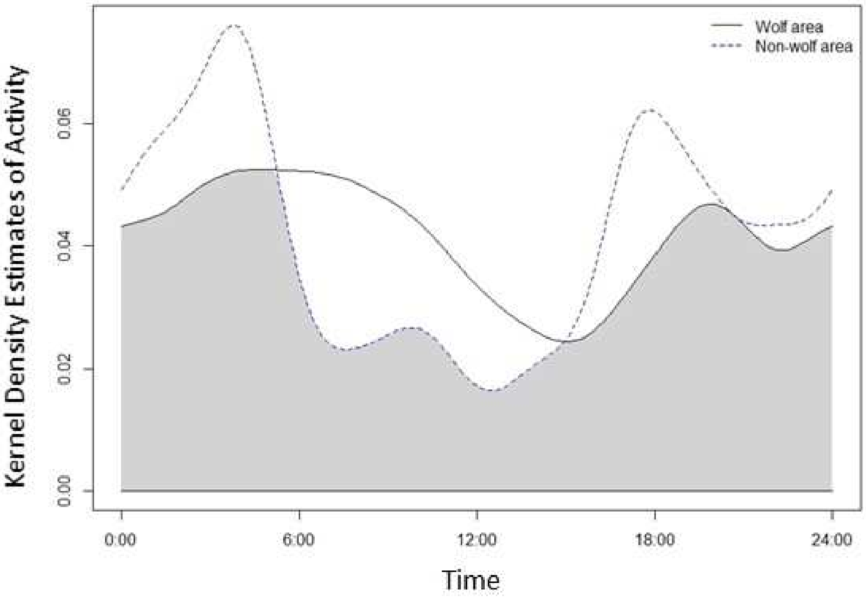
a) Cougar



b) Coyote



c) Bobcat

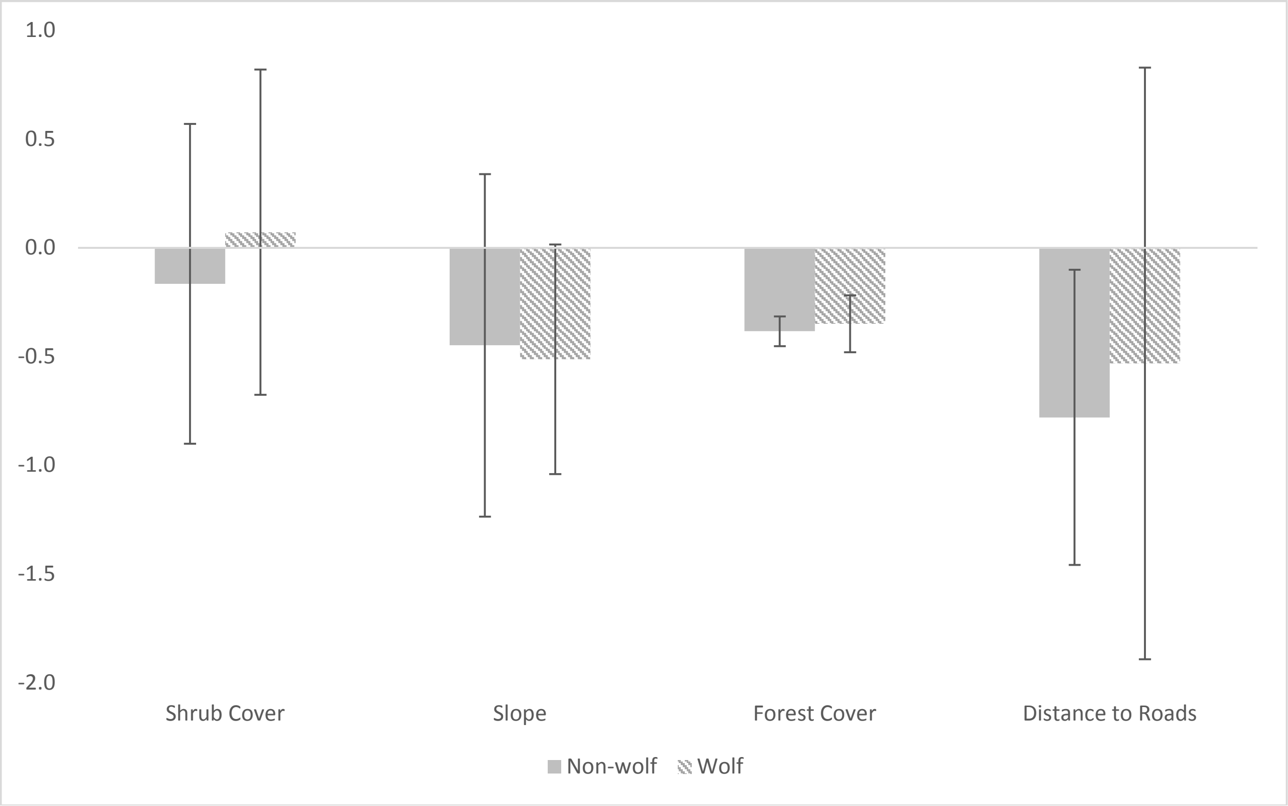


Appendix 2.

We designed the zero-inflated Poisson generalized linear mixed models for all species to test how much variability in activity the parameters of location, time of day, season, and the activity of other species explained in comparison to the null model, and to identify time periods during which each species was most and least active (Table A1 below). For every species, we tested a null model, a location-only model, and a location, time and season model. For humans, we only tested these basic models because we did not expect human activity to be influenced by the activity of any of the predator species. The candidate model set for wolves also included a model with the human activity parameter to test our third prediction that human and wolf activity would be negatively associated. The models for coyotes were designed to test our predictions that humans would have a negative effect on coyote spatiotemporal activity, that coyotes would change their temporal activity patterns in areas with wolves, and that there would be a correlation between wolf and coyote spatiotemporal activity. We tested whether the presence of wolves affected the temporal activity of coyotes with the interaction term *time*wolf presence*, where wolf presence was expressed as a binary variable indicating whether or not the camera location was in an area where a wolf pack was present during the study period. We tested if wolf and human activity affected the spatiotemporal activity of coyotes by adding human and wolf activity parameters, which were an index of activity by camera location, calendar date, and time period. In order to determine if models with human or wolf activity were a better fit to the coyote activity data, we tested models with a combination of these parameters. Finally, we built the bobcat models to test our prediction that humans would exert a negative effect on wolf, coyote and bobcat activity, evidenced by the inclusion of the human activity parameter. We examined the prediction under our alternate hypothesis, namely that a behaviorally mediated cascade exists between wolves, coyotes and bobcats, via the inclusion of the interaction parameter *time*wolf presence* that tested whether bobcat temporal activity changed significantly in the study areas with wolves. In order to determine if models with human, wolf, or coyote activity better explained the bobcat activity data, we evaluated models with a combination of these parameters.

Appendix 2 Table A1. A priori candidate set of zero-inflated Poisson generalized linear mixed effects models of activity for each of four focal species (humans, wolves, coyotes, bobcats). A random intercept effect for location was included in every model. ΔAIC is the absolute difference between the AIC value for a given model and the model with the lowest AIC; K represents the number of model parameters; d.f. is degrees of freedom; LL is the log likelihood; and w_i is the AIC model weight.

Model parameters	ΔAIC	K	LL	w_i
Human				
Location+time+season	0	7	-17355.2	1
Location	2036.1	3	-18377.3	0
Null	7265.6	1	-20993.0	0
Wolf				
Location+time+season	0	7	-2018.7	0.60
Human+location+time+season	0.8	8	-2018.0	0.40
Location	116.4	3	-2080.9	0
Null	641.8	1	-2344.6	0
Coyote				
Wolf+time*wolf presence+location+season	0	11	-15681.1	0.80
Wolf+human+location+time*wolf presence+season	2.8	12	-15681.7	0.20
Location+time+season	10.9	7	-15692.2	0
Human+location+time+season	11.9	8	-15691.0	0
Location	1356.1	3	-16368.7	0
Null	2347.7	1	-16865.0	0
Bobcat				
Wolf+coyote+human+location+time*wolf presence+season	0	12	-3092.9	0.95
Wolf+location+time*wolf presence+season	7.6	11	-3092.7	0.01
Wolf+coyote+location+time*wolf presence+season	7.6	11	-3096.4	0.02
Human+coyote+location+time+season	7.6	11	-3100.4	0.02
Human+location+time+season	7.9	8	-3102.6	<0.01
Coyote+location+time+season	11.3	8	-3104.3	0
Location+time+season	13.6	7	-3106.4	0
Location	221.4	3	-3214.4	0
Null	471.9	1	-3330.0	0



Appendix 3. Average standardized values for habitat parameters of % shrub cover, slope (degrees), % forest cover and distance to roads (km) with 95% confidence intervals at camera sites in study areas with (n= 32) and without wolves (n= 32).

Appendix 4. Parameter estimates with associated 95% confidence intervals from the top zero-inflated Poisson generalized linear mixed species activity models for each focal species. A hyphen indicates that the parameter was not included in the top model for that species. Wolf activity indicates the effect of the number of photographs of wolves taken at a specific site, date, and time. Wolf presence indicates the effect of the presence of a documented wolf pack in the study area.

	Human		Wolf		Coyote		Bobcat	
Fixed effects	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Intercept	-0.85*	-1.25 to -0.44	-4.52*†	-5.63 to -3.41	-1.53*	-1.88 to -1.17	-4.413*	-5.43 to -3.40
Day	0.11*	0 to 0.22	-1.32*†	-1.74 to -0.91	-0.35*	-0.54 to -0.16	-0.106	-0.76 to 0.55
Dusk	-0.36*	-0.51 to -0.20	0.04†	-0.40 to 0.48	-0.46*	-0.72 to -0.20	0.735*	0.014 to 1.46
Night	-0.90*	-1.02 to -0.77	-0.20†	-0.55 to 0.15	-0.27*	-0.45 to -0.08	0.740*	0.12 to 1.36
Season:winter	-0.17*	-0.24 to -0.10	0.42*†	0.19 to 0.66	0.02	-0.06 to 0.09	0.351*	0.16 to 0.54
Human activity	-	-	-0.38†	-1.21 to 0.46	-	-	0.246*	0.10 to 0.40
Wolf activity	-	-	-		0.67*	0.38 to 0.95	0.289	-1.57 to 2.15
Coyote activity	-	-	-		-	-	0.556*	0.08 to 1.03
Wolf presence X dawn (reference)	-	-	-		0.07	-0.40 to 0.53	1.220*	0.38 to 2.06
Wolf presence X day	-	-	-		0.27*	0.02 to 0.53	-0.514	-1.29 to 0.26
Wolf presence X dusk	-	-	-		0.23	-0.12 to 0.58	-1.042*	-1.95 to -0.14
Wolf presence X night	-	-	-		0.14	-0.11 to 0.40	-1.072*	-1.81 to -0.33
	Intercept	SE	Intercept	SE	Intercept	SE	Intercept	SE
Zero-inflation model	2.54*	0.03	2.85*	0.23	1.51*	0.09	1.71*	0.44

†Coefficients averaged between models with ΔAIC < 2s

* Significant at $P < 0.05$

Appendix 5.

Lagomorph Activity

The cameras were positioned to capture larger mammals, so it is probable that many small mammals such as lagomorphs, which are major components of both coyote and bobcat diets (Witmer and deCalesta 1986; Arjo et al. 2002), passed by the cameras undetected and therefore that photographic detections underrepresent the presence of these species. For this reason, we did not include lagomorphs in the activity models or temporal overlap estimation. However, here we present the spatiotemporal pattern of our lagomorph detections as an approximation of their activity in our study area, and the results of a chi-squared test comparing recorded activity during darkness, daylight, and crepuscular hours.

Over the course of the investigation, we detected two lagomorph species: snowshoe hares (*Lepus americanus*) and mountain cottontails (*Sylvilagus nuttallii*). Collectively, these species exhibited strongly nocturnal activity patterns (>85% of detections occurred during darkness) in both the wolf and non-wolf areas. Fewer lagomorphs were photographed in the wolf (N = 192) than non-wolf (N = 344) areas. However, lagomorph activity was significantly less variable (i.e., more nocturnal) in the wolf areas ($P < 0.001$, $X^2 = 16.51$). In the areas occupied by wolves, 96.9% (n = 186) of lagomorph detections were recorded at night, 2.6% (n = 5) during the day, and 0.5% (n = 1) at dawn/dusk. This pattern characterized the non-wolf areas as well, though we recorded more diurnal and crepuscular detections. Specifically, 86.0% of lagomorph photos were recorded at night (n = 296), 8.1% were recorded during the day (n = 28), and 5.8% were recorded during dawn/dusk time periods (n = 20). However, the higher variability in the non-wolf area may have been strongly affected by one camera location where a snowshoe hare was particularly active during the day.

Chapter 2. DIVERGENT SPATIOTEMPORAL RESPONSES OF SYMPATRIC PREY SPECIES TO CONFLICTING RISKS OF HUMAN HUNTERS AND LARGE CARNIVORES

2.1 ABSTRACT

1. There is growing recognition that humans can modify the ecological impacts of predators, but how humans shape predator risk effects in complex predator-prey communities remains largely unexplored. In many places, large carnivores occupy human-modified ecosystems where their prey are also hunted by people. In these ecosystems, prey may prioritize minimizing risk from human hunters rather than large carnivores, thereby modifying the risk effects of large carnivores on prey.

2. We investigated this possibility by deploying remote cameras in northeastern Washington, USA, over the course of three years to compare spatiotemporal activity of mule deer (*Odocoileus hemionus)* and white-tailed deer (*Odocoileus virginianus*) during hunting and non-hunting seasons in an ecosystem where deer are also prey for two large carnivores: wolves (*Canis lupus*) and cougars (*Puma concolor*).

3. We found that hunting superseded some of the risk effects of carnivores on the behavior of prey species, and that the risk effects of hunting differed markedly between the deer species despite their close ecological and evolutionary relationships. Outside of hunting seasons, both deer species used areas suiting their means of escaping large carnivores, with mule deer and white-tailed deer exploiting steeper and flatter terrain, respectively. During hunting seasons, mule deer increased their risk of predation from large carnivores by shifting to flatter terrain closer to forest cover. By contrast, white-tailed deer did not change any of their habitat associations in response to hunting. Mule deer also exhibited significant increases in nocturnal activity and decreases in diurnal activity. White-tailed deer only increased nocturnality. These

spatiotemporal behavioral changes during the hunting seasons pushed mule deer, but not white-tailed deer, into greater spatiotemporal overlap with large carnivores, particularly wolves.

4. Our results also suggest that human hunting of prey may temporarily dampen risk effects of large carnivores, and for the first time demonstrate that these responses are prey- and predator-specific. Finally, our results find that human hunting pushes some prey species into greater overlap with large carnivores, which may become a conservation concern if this results in additive prey mortality. Further research is needed to investigate if divergent responses of sympatric prey to the conflicting risks of human hunters and large carnivores lead to variable risk effects and patterns of direct predation on prey populations.

Keywords: predation risk, predator-prey interactions, game camera, risk effects, temporal niche partitioning

2.2 INTRODUCTION

Predators can directly influence prey populations by inflicting mortality and eliciting trait modifications. Predator-induced trait changes, known collectively as risk effects (Creel and Christianson, 2008), can indirectly influence lower trophic levels, for example when anti-predator responses by herbivorous prey alter plant species composition or abundance (Estes et al. 2011, Ripple et al. 2014). Furthermore, meta-analyses suggest that the indirect impacts of risk effects may equal or even surpass those of predation (Schmitz et al. 2004, Preisser et al. 2005). Thus, there is now wide appreciation that predators do not need to cause heavy prey mortality to have substantial effects on the structure and function of ecosystems (Laundré et al 2001, Ripple and Beschta 2004, Schmitz et al. 2004, Creel and Christianson 2008, Heithaus et al. 2008; Pringle et al. 2019). Most of the research underpinning this paradigm has been conducted using controlled experiments with small-bodied taxa (Preisser, Orrock and Schmitz 2007) or in wilderness or protected areas where the effects of humans on wildlife are minimal (Laundre et al. 2001, Ripple and Beschta 2004, Fortin et al. 2005). Yet, many predators live in or are recolonizing landscapes where humans are an integral part of the ecosystem (Chapron et al. 2014), and may function as a perceived predator by both large carnivores and prey (Frid and Dill, 2002). Currently, we lack research that provides an empirical basis to predict the strength and nature of predator risk effects on prey in these anthropogenic landscapes (Guiden et al. 2019), particularly in multi-predator systems where prey face the added pressure of hunting from humans (Kuijper et al. 2016, Prugh et al. 2019).

Prey can optimize their defenses by avoiding dangerous locations only at times when predators are most active (Lima and Bednekoff 1999, Kohl et al. 2018). In systems where human hunters are among the predator guild, however, prey may be squeezed between the different spatiotemporal risks posed by large carnivores and people and thereby forced to choose between behaviors that minimize danger from one or the other (Lone et al. 2014, Kuijper et al. 2016). Under these circumstances, prey responses to one predator may facilitate the other (Soluk and Collins 1988; Losey and Denno 1998). Most studies have focused on how prey negotiate this danger trade-off spatially (Thaker et al. 2011, Lone et al. 2014). For example, roe deer (*Capreolus capreolus*) reduced their mortality risk from human hunters but faced higher predation risk from Eurasian lynx (*Lynx lynx*) when seeking cover in dense understory vegetation (Lone et al. 2014). Yet, predation risk often also has a strong temporal component. For example, human hunters tend to be primarily diurnal whereas large carnivores are mostly crepuscular or nocturnal (Lone et al. 2014, Shores et al. 2019). Hunting may have a strong and predictable seasonal pulse of increased risk where it is regulated (Profitt et al. 2009, Cromsigt et al. 2013). Thus, prey in these hunted systems might be forced to choose between the conflicting "timescapes" of fear imposed by carnivores and people. Human hunting success is also spatially variable, tending to be higher near roads and in areas with steep terrain and low vegetative cover that offer clear lines of sight (Lone et al. 2014). Given the spatiotemporal predictability of human hunting, we might expect ungulates to prioritize minimizing hunting risk over the threat posed by large carnivores (Proffitt et al. 2009, Lone et al. 2014). To date, the spatial and temporal aspect of trade-offs in risk effects between human hunters and large carnivores has not been explored in multi-predator, multi-prey systems.

Within an anthropogenic landscape in eastern Washington, USA as our focal system, we investigated the spatiotemporal responses of two sympatric ungulates, mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*), to hunters and two large carnivores, wolves (*Canis lupus*) and cougars (*Puma concolor*). Mule and white-tailed deer have different running gaits with terrain-specific efficacy against cursorial predators like wolves. Mule deer stot, or leap forward with all four legs touching the ground at the same time, when fleeing danger (Lingle 1993). This bounding gait is most effective on uneven, rugged terrain because it helps with avoiding obstacles (Geist 1981). Conversely, white-tailed deer escape chasing predators with a galloping gait (Lingle 1993) which is most effective on gentle terrain (Lingle and Pellis 2002). By implication, mule deer are likely safest from wolves in areas with steep terrain, whereas white-tailed deer should be safer when using gentler, flat terrain. Against cougars, both deer species are likely to be safest away from structural complexity (e.g., forest cover), where cougar predation success is generally higher as it provides stalking cover (Atwood et al. 2007).

Under the hypothesis that changes to deer spatiotemporal activity in response to human predation risk supersede those induced by large carnivores, we made five predictions. Because risk from human hunters is higher in the daytime during hunting seasons, we predicted that 1) both deer species would be less diurnal and more nocturnal during hunting seasons. By contrast, we expected that outside of hunting seasons deer would prioritize temporal avoidance of large carnivores. Thus, during non-hunting seasons, we predicted that (2) both deer species would be less nocturnal and more diurnal to avoid large carnivores. During hunting seasons, we also predicted that 3) deer would be more likely to be associated with landscape features that may reduce mortality from humans, such as flat terrain, forest cover, and areas farther from roads. When human hunters were not present, on the other hand, we predicted that (4) deer would exhibit species-specific habitat associations that facilitate their escape from large carnivores, with white-tailed deer using flat slopes and mule deer steep slopes. Finally, we predicted that (5) changes in deer activity during the hunting season would result in greater spatiotemporal overlap with large carnivores.

2.3 METHODS

Study Area

We performed this study in the Okanogan Highlands ecosystem of north-central Washington, USA. Working with the Confederated Tribes of the Colville Reservation, we established two study areas that ranged in area from 550-680 km^2. Topography and vegetation were similar among the study areas, as was human residential density, ranging from 0 - 4 people per km^2 within the census blocks comprising the study areas (WA Data and Research: Population Density by Census Block, 2010). Both sites experienced logging, hunting, motorized recreation, and cattle grazing. Cattle grazing occurred from mid-June to mid-October, while logging and motorized recreation occurred year-round. Elevations within the region ranged from 300 to 2,065 m. The local topography was mostly gently rolling hills, interspersed with rugged, rocky cliffs. For a detailed description of the study site, see Shores et al. 2019.

Over the course of the investigation, the study sites were occupied by the Nc'icn and Strawberry wolf packs, for which the sites are named (Fig. 1). Wolves recolonized the study sites from neighboring populations in 2010, 3 years before this study took place. The Nc'icn pack, which was first documented in 2010, had 5 wolves for the duration of the study and a home range size of 668 km^2. The Strawberry pack, first documented in 2011, had 7 members and a home range size of 807 km^2. Wolf hunting was allowed on the Colville Reservation, and a wolf was harvested during the Aug 1, 2016 – Feb. 28, 2017 season (WDFW et al. 2017). A shorter trapping season for wolves ran from Nov 1 – Feb. 28th, although no wolves were trapped during our study. Six wolves could be harvested in the study areas per season inclusive of both hunting and trapping. Cougar hunting with hounds was allowed year-round with no season limit. Mule deer and white-tailed deer hunting began during early buck season (June 1 - September 30), when any male deer could be hunted. General deer season, when any male or female deer could be hunted, was between October 1 – Dec 31. Both hunting seasons had a daily bag limit of two deer per day. Deer hunting was not allowed at night. Hunting or trapping of any wildlife on the reservation is allowed only by Colville tribal members and not by the general public.

Camera placement

We established a camera trap grid in each study area in March 2013. Each grid was composed of 16 cells, each cell with an area of 4 km^2 (Fig. 1). The cameras (Moultrie M80 Game Spy, EBSCO Industries Inc., Birmingham, AL) featured infrared triggering with a 50 degree-wide field of view, a 12.2 m detection range, and a flash range for night photographs of 18.3 m. Within each cell, we deployed cameras in forested habitat along dirt roads or game trails to maximize detections of carnivores and ungulates. All camera locations were within Okanogan highlands dry forest ecotype, and the camera grids were placed within the wolf pack utilization distributions (Worton 1989), as determined from GPS collar data. Cameras were deployed year-round, 24 hours per day, and checked every 2-4 months.

Photo Identification and data standardization

We defined the sampling interval used for this analysis as a biologically meaningful time period for deer beginning at the average start of fawning on May 1st. Accordingly, the study spanned three years from 5/1/2013 to 4/30/2016. Photographs over thirty minutes apart of humans, wolves, cougars, mule deer and white-tailed deer were counted as independent observations (Burton et al. 2015). We catalogued photographs from all cameras into a Microsoft Access database using the program Colorado Parks and Wildlife (CPW) Photo Warehouse (Newkirk

2016). Volunteers identified species and number of individual animals in each photograph. Multiple animals of the same species in a photograph were counted as a single detection. Volunteers were trained and tested on species identification before they began recording data to ensure they could discriminate similar species. To ensure data quality, each photograph was independently identified by two trained volunteers. The identifications were subsequently compared and, if they did not match, were reviewed by the lead author (CS).

To account for seasonal variation in day length, we standardized our observations by calculating the clock time of sunrise and sunset for each day of the study, and then binned the detections into four time categories: day, night, dawn, and dusk in accordance with previous studies of temporal activity patterns in mammals (Farris et al. 2015; Shores et al. 2019). Day lasted from one hour after dawn to one hour before sunset, night stretched between dusk and dawn, and dawn and dusk were defined by the two hours before and after sunrise and sunset (Farris et al. 2015). Accounting for changes in day length is necessary to study animal activity in studies over three months in duration and in areas above or below 30° or -30° latitude (Nouvellet et al. 2012).

Generalized linear mixed models

We evaluated predictions 1-4 with a generalized linear mixed effects model (GLMM) modeling the number of photo capture events y_{ijk} for white-tailed and mule deer on each sampling day i, for each time category j (dawn, day, dusk, night), and at study site k with a zero-inflated Poisson error distribution (ZIP). A random intercept for camera location helped control for unaccounted environmental variation among camera sites. We also included an offset equal to the number of hours available in each time category. This model structure enabled us to test for significant differences in species' use of habitat and different time periods between hunting and non-hunting seasons via the inclusion of interaction effects between the *hunting* and *time* or *habitat* covariates. Dawn and no-hunting were the reference levels in the categorical variables *time* and *hunting*, respectively. For example, the interaction between *hunting* and *slope* indicate whether a species' use of slope steepness changed significantly during the hunting season. Significant differences between species' use of time or habitat between the hunting and non-hunting seasons were indicated by non-overlapping 95% confidence intervals. We modeled the effects of hunting with a three-level categorical variable based on the deer hunting seasons: no hunting (Jan 1 – May 30), early buck season (any male deer, June 1 – Sept 30), and general deer season (any deer, Oct 1 – Dec 31).

We also modeled the association of the deer species with habitat attributes known to influence predation risk from humans and carnivores. The environmental covariates used in the models were distance to roads (m), distance to forest cover (m), and slope (degrees). Forest cover is associated with higher predation risk from both wolves and cougars (Husseman et al. 2003, Oakleaf et al. 2006, Atwood et al. 2007), but lower predation risk from humans (Lone et al. 2014). Slope steepness is positively associated with predation risk from humans (Lone et al. 2014), and negatively associated with predation risk from wolves (Kauffman et al. 2007). Distance to roads is positively associated with predation risk from large carnivores (Oakleaf et al. 2006), and negatively with human predation risk (Lone et al. 2014). We obtained raw data for the environmental covariates from the Washington GAP (Geospatial Analysis Project) raster habitat layer (United States Geological Survey, 2011), and from the Washington State GIS data clearinghouse. (https://wagda.lib.washington.edu/data/geography/wa_state/; accessed

11/15/2016). For a complete description of the methods to derive the habitat covariates, see Dellinger et al. 2019.

We evaluated the fifth prediction (effects of hunting on deer-predator associations) with the ZIP GLMM model structure described above, except in this analysis we excluded time of day (i.e., we modeled numbers of deer photo capture events y_{ik} on each sampling day i, at study site k). We used an interaction term between the categorial variable *hunting* and *wolf* or *cougar activity* (also indexed by sampling day i, at study site k) to test if the effect of predator activity on deer activity changed during hunting seasons. A coarser temporal scale (sampling day only) was required to evaluate this prediction given the low number of predator photos (cougar = 277, wolf = 302). When time of day categories were included as covariates in the same model, the mule deer activity model failed to converge because there was only one instance of overlap between mule deer and wolves in the same smaller defined time period. Because our final prediction was on how hunting altered the relationship between predator and prey, and did not involve changes in diel activity, we concluded that the simplified model structure was appropriate.

2.4 RESULTS

Our cameras recorded a total of 18,625 independent detections of the study species (Table 1). The cameras also captured a gradient of human activity, with some locations recording >900 human independent detections and others <20.

Changes to deer spatiotemporal associations

In support of our first and second predictions, both mule and white-tailed deer significantly increased nocturnal activity during hunting seasons (Figs. 2 and 3, Appendix 1). As an indicator of effect size, incidence risk ratios (IRRs) showed that mule deer and white-tailed deer were 12.6 and 8.3 times more likely to be photographed at night during the hunting seasons in comparison to the non-hunting seasons. In addition, mule deer were half as likely to be photographed during the day during the hunting season in comparison to the non-hunting season (Fig. 2, Appendix 1; IRR for *Hunt* = 0.5). In support of our third prediction, mule deer associated more with habitat features that may minimize human predation during hunting seasons. Namely, as indicated by patterns of activity, mule deer switched from steeper terrain outside of hunting seasons to significantly flatter terrain during hunting seasons (*slope x hunt* coefficient IRR = 0.3) and were also significantly closer to forest cover during hunting seasons (*forest x hunt* coefficient IRR = 0.6; Figs. 2 and 3, Appendix 1). By contrast, white-tailed deer did not change their habitat associations during hunting seasons, and there was no significant change for either deer species in their distance to roads during the hunting season (Figs. 2 and 3, Appendix 1). In support of our fourth prediction, the deer showed species-specific associations with slope steepness that were consistent with facilitation of their respective escape tactics during non-hunting seasons. Namely, outside of the hunting seasons, white-tailed deer were associated with flat slopes, where their galloping escape gait is more effective against cursorial predators, and mule deer with steep slopes (Figs. 2 and 3, Appendix 1) where stotting is believed to promote avoidance of obstacles.

Patterns of overlap between deer and large carnivores

In partial support of our final prediction, during the hunting seasons mule deer significantly increased spatiotemporal overlap with wolves (Fig. 4; non-hunting: β = -2.22, 95% CI = -4.20 to -0.24; hunting: β = 1.52, 95% CI = -0.34 to 3.38. Mule deer increased their overlap with cougars, although the increase was not significant (Fig. 4; non-hunting: β = -0.11, 95% CI = -0.76 to -

0.54; hunting: $\beta = 0.64$, 95% CI = -0.12 to 1.40). Mule deer were 4.6 and 1.9 times more likely to occur at the same camera location, on the same date as wolves and cougars, respectively, during the hunting seasons in comparison to the non-hunting seasons. Patterns of activity overlap between white-tailed deer and wolves (WTD-wolf overlap non-hunting seasons: $\beta = 0.25$, 95% CI = -0.01 to 0.49; WTD-wolf overlap hunting seasons: $\beta = 0.10$, 95% CI = -0.21 to 0.41) or cougars (WTD-cougar overlap non-hunting seasons: $\beta = 0.09$, 95% CI = -0.46 to 0.64; WTD-cougar overlap hunting seasons: $\beta = 0.15$, 95% CI = -0.58 to 0.88) did not differ significantly between during hunting seasons (Fig. 4).

Spatiotemporal patterns of human and carnivore activity

During the hunting season, humans moved toward more open and flatter terrain. In addition, humans increased activity throughout the day (Figure 5, Appendix 2), although they maintained a significant avoidance of nighttime throughout the year, and strongly selected for daytime activity during the hunting season (Fig. 5, Appendix 2). By contrast, during the hunting seasons both cougars and wolves significantly increased nocturnal activity. In addition, wolves in our study sites avoided daytime and used significantly more forested, flatter terrain during the hunting season (Fig. 5, Appendix 2). Cougars did not change their habitat associations.

2.5 DISCUSSION

There is growing recognition that humans can modify the ecological impacts of predators (Kuijper et al. 2016, Gaynor et al. 2019, Guiden et al. 2019, Prugh et al. 2019), but how humans shape predator effects in multi-predator, multi-prey communities remains largely unexplored. We addressed this knowledge gap by comparing diel and spatial activity patterns of mule and white-tailed deer between hunting and non-hunting seasons in an ecosystem where they are subject to risk from multiple large carnivores and human hunters. We found that hunting temporarily superseded some of the risk effects of carnivores on the behavior of prey species. However, the risk effects of hunting on our focal deer species differed markedly despite their close ecological and evolutionary relationships. Namely, during the hunting season mule deer exhibited a trend toward decreased daytime activity, increased nocturnality, and changes in habitat associations leading to increased spatiotemporal overlap with wolves. By contrast, white-tailed deer only showed an increase in nocturnality and did not change their habitat associations. Consequently, white-tailed deer spatiotemporal overlap with cougars and wolves did not change as a function of hunter presence. These results highlight the influential ecological role that humans can play as predators (Darimont et al. 2015), and the value of considering temporal as well as spatial responses of prey to both carnivores and humans. They also reveal that the non-consumptive impacts of humans can vary markedly among prey species, underscoring the importance of a community approach to studying predator-prey interactions.

Changes to prey temporal activity and habitat associations

Research on the effects of human hunting on prey diel activity patterns is scarce, particularly in areas with large carnivores (e.g., Kilgo et al. 1998, Bonnot et al. 2020). To the best of our knowledge, this study is the first to investigate prey temporal activity changes in a system where prey must also balance risks from multiple large carnivores and hunters. In agreement with our first and second predictions, both deer species increased their nocturnality during hunting seasons, when humans were least active and hunting was not allowed, and thus predation risk from humans was lowest. This observed increase in deer nocturnal activity to avoid hunting, which has not previously been reported, adds to the literature showing that ungulates are highly responsive to risk from hunters (Profitt et al. 2009, Cromsigt et al. 2013, Lone et al. 2014) and suggests that, as in other prey species (Kotler et al. 1993, Hayward and Slotow 2009), time is a dimension of niche-space that deer can exploit to manage predation risk. Yet, elevated nocturnality may also place deer at greater predation risk from large carnivores, because wolves and cougars are most active at night and dusk, respectively (Beier et al. 1995; Kohl et al. 2018). By contrast to our predictions, only mule deer trended toward a decrease in diurnal activity during hunting seasons. White-tailed deer may be able to maintain higher levels of daytime activity in the face of hunting by relying on cryptic behavior, such as hiding and retreating in dense cover (Grau and Grau 1988, Kilgo 1998). More research is needed to determine if mule deer forage less and experience increased nutritional stress due to reduced activity during the hunting seasons.

Hunting also affected prey habitat associations. Outside of the hunting seasons, mule deer used steeper slopes and white-tailed deer used relatively flat areas, where their respective escape gaits are most effective, in agreement with our fourth prediction. There is corroborative evidence to suggest that these habitat associations are at least partly due to predator avoidance. Namely, Dellinger et al. (2019) showed that the presence of wolves significantly enhanced the tendency of mule deer to exploit sloped terrain, and white-tailed deer to use gentle terrain. During hunting seasons, in accord with our third prediction, mule deer shifted toward landscape features – flatter terrain and forest cover – that likely increase their risk of predation by carnivores. Mule deer may suffer higher predation on flat ground, especially by wolves, where their stotting gait is slower than the galloping gait of white-tailed deer (Lingle 1993). Furthermore, both wolves and cougars make more ungulate kills in areas of higher cover (Husseman et al. 2003), and cougars prefer to hunt in structurally complex habitat (Atwood et al. 2007). Conversely, increased use of these landscape features may reduce human-caused mortality because they obscure lines of sight for hunters (Lone et al. 2014). By implication, mule deer appear to prioritize spatial avoidance of humans over carnivores during periods when humans are lethal. Similarly, Gehr et al. (2018) found that spatial avoidance of hunters by roe deer (*Capreolus capreolus*) led to increased predation from Eurasian lynx (*Lynx lynx*). Interestingly, mule deer maintained a positive association with roads throughout the year. This was an unexpected result as we predicted both deer species would move away from roads during the hunting seasons to minimize risk from humans. It is possible mule deer minimized increased risk from human hunters near roads during the hunting season by increasing their use of forest cover and flat terrain rather than the steeper, more open terrain that is easier to hunt with rifles (Lone et al. 2014. The areas near roads may also offer mule deer a halo of protection to deer from predators (Berger 2007). By contrast to the spatial shifts manifested by mule deer, white-tailed deer showed no change in their habitat use during hunting seasons. White-tailed deer in other ecosystems that lack large carnivores have also been found to maintain their core habitat use pattern during hunting seasons. Their ability to do so appears to hinge on a suite of behavioral tactics, such as decreased overall activity levels (Karns et al. 2012), increased nocturnality (Kilgo et al. 1998), and cryptic retreats (Grau and Grau 1980), which render them more difficult for humans to detect. Given the observed behavioral disparity between mule and white-tailed deer in relation to hunting, there is need for additional investigation of the habitat-, time-, and predator-specific risks posed to each deer species, and the associated costs and benefits of behavioral adjustments they make in response to the multifaceted tradeoffs they face.

To investigate the possibility that deer behavioral changes reflected seasonal changes rather than a response to human hunting, we analyzed changes in deer activity in relation to season (see Appendix 2). We detected seasonal variation in deer activity, but it did not explain the changes to deer behavior that coincided with hunting. Therefore, our results indicate that mule and white-tailed deer adjusted their spatiotemporal activity in response to both coarse- (hunting season) and fine- (diel) scale patterns of human predation risk. More broadly, they suggest that even in systems with multiple large carnivores, the danger posed by human hunters may temporarily override the risk from large carnivores perceived by ungulates, emphasizing the role of humans as "superpredators" (Darimont et al. 2015).

Patterns of overlap between deer and large carnivores

In agreement with our fifth prediction, we observed increased spatiotemporal overlap during the hunting seasons between mule deer and wolves. Thus, the changes in mule deer behavior triggered by the onset of hunting season increased not only their association with landscape features hampering their ability to flee from predators but also their likelihood of encountering wolves in these areas. Risk of predation to mule deer, especially from wolves, may be greatly enhanced in landscapes when human hunters are active. There were also significant differences in the spatiotemporal associations of the two deer species with wolves outside of hunting seasons. When human hunters were absent, mule deer were negatively associated, and white-tailed deer positively associated, with wolves, which agrees with an earlier study in our system (Dellinger et al. 2019). In conjunction with that study, our findings highlight the strong, but species-specific, effects that wolves can exert on prey behavior when they are not superseded by humans.

Relatively sedentary predators employing sit-and-wait or sit-and-pursue hunting modes, such as cougars, are predicted to elicit stronger antipredator responses than active predators like wolves because their movements and associated spatiotemporal risk signature is often more predictable (Preisser et al. 2007, Thaker et al. 2011). Yet, irrespective of the presence of human hunters, neither deer species avoided cougars. That mule deer did not exhibit strong avoidance of cougars is surprising, because recent studies show that cougar diet is heavily skewed toward mule deer when both deer species are available (Orning et al. 2019). Given that mule deer were negatively associated with wolves when human hunters were absent, this finding could indicate that mule deer perceive wolves as more dangerous than cougars. We acknowledge, however, that one or both deer species may have responded to cougars at scales, or in relation to habitat features, that we did not address. The guild context of predators may also play a role in the relationship between predators and their prey. For example, wolves may have a suppressive effect on cougars (Kortello et al. 2007), and humans on both predators, which may dampen or change the nature of risk these predators pose to prey.

Risk effects of human hunting on mule and white-tailed deer

Our findings suggest that sympatric ungulates may experience different risk effects (after Creel and Christianson 2008) as a result of human hunting. Although both deer species became more nocturnal during hunting seasons, mule deer manifested several additional behavioral changes including decreased diurnal activity, altered habitat use and increased spatiotemporal overlap with wolves. Collectively, these responses by mule deer to human hunters may entail costs from diminished foraging success (e.g., stemming from the abandonment of preferred foraging grounds and reduced activity) to lost opportunities for reproduction. Further work examining these costs and the possibility that they may impact mule deer populations is warranted. The greater response by mule deer to hunting also has management implications. For example, across much of Western North America where the two deer species are sympatric, hunting seasons limited to white-tailed deer may still elicit costly behavioral changes in mule deer even though they are not actively targeted by hunters.

Spatiotemporal patterns of carnivore activity

Similar to the two deer species, cougars significantly increased their nocturnal activity during the hunting season (Fig. 4). Wolves, by contrast, showed no significant change in their temporal behavior during the deer hunting season, but were significantly more active at night than during the day. The strong response of cougars to the hunting season may have owed in part to the high predation risk cougars experienced from humans in our study area, where year round hound hunting of cougars is permitted. While seasonal wolf hunting was also permitted, only one wolf was harvested during the three-year duration of our study. These results further emphasize the marked effect humans have on wildlife temporality (Gaynor et al. 2018) and reveal that, like their prey, sympatric large carnivores can exhibit divergent responses to humans. They also underscore the need to consider the impact of hunting seasons on the behavior of sympatric non-hunted species that are of conservation concern.

We did not include black bears (*Ursus americanus*) in the analysis as they are not primary predators of deer in our study system, unlike cougars and wolves. Black bears are primarily herbivorous and insectivorous, although at the start of summer for several weeks individual bears may become more carnivorous and prey upon deer neonates (Raine and Kansas, 1990, Elbroch and Rinehart 2011). Given the seasonal nature of bear activity due to their hibernation patterns, if deer were responding significantly to bear predation you would expect to see a significant difference in deer seasonal activity in relation to habitat types associated with black bear activity, such as forest cover. Black bears are strongly associated with forested habitats, which differentiates them from other North American bear species (Elbroch and Rinehart 2011). However, neither deer species showed a seasonal difference in relation to forest cover (Appendix 3).

Conclusions and future directions

A growing literature highlights the effects of temporally variable predation risk on prey habitat use (e.g., Tambling et al. 2012; Burkepile 2013; Kohl et al. 2018) and vigilance (Lima and Bednekoff 1999, Dröge et al. 2017). Most of these studies, however, have focused on predator-prey pairs or single prey species with multiple predators (Montgomery et al. 2019). To address this knowledge gap, we examined spatiotemporal responses of sympatric deer species to risk from human hunters and two large carnivores. Building on recent research demonstrating that human disturbance has increased wildlife nocturnality globally (Gaynor et al. 2018) and that hunting can increase diel overlap between ungulates and felid predators (Gehr et al. 2018, Bonnot et al. 2020), we found that both deer species increased their nocturnal activity in the face of hunting even though both cougars and wolves were most active during this part of the day, and that mule deer also trended toward decreased diurnal activity and altered their habitat associations in ways that may reduce human predation risk.

Previous research from terrestrial and marine systems has found that prey spatial responses to predators are contingent on a three way interaction between the escape tactic of the prey, hunting mode of the predator, and features of the physical environment (Heithaus et al.

2009; Wirsing et al. 2010, Wirsing et al. 2014). Our results build on this framework in three ways. First, along with Dellinger et al. (2019), they further underscore the general applicability of these three drivers of contingency in non-consumptive predator effects across aquatic and terrestrial ecological domains (Wirsing and Ripple 2011, Wirsing et al. 2020). Second, they reveal that non-consumptive predator effects effects are also contingent on temporally variable risk from different predators, including humans, in multi-predator systems, and that divergent prey behavior can play out in the temporal as well as the spatial dimension. Third, they show that divergent anti-predator responses of closely related prey species can hinge on how their escape modes interact with landscape features and these temporally variable levels of risk.

Our research reinforces the idea that humans can act as superpredators by overriding the typical antipredator responses of prey to other large carnivores (Darimont et al. 2015, Kuijper et al 2016). Spatial and overall activity overlap between white-tailed deer and carnivores was not affected by hunter presence, while mule deer spatiotemporal overlap with wolves increased significantly. Thus, for the first time, our findings also reveal that human mediation of predator risk effects can be prey species-specific. Further research is needed to investigate if divergent responses of sympatric prey to the conflicting risks of human hunters and large carnivores lead to variable risk effects and patterns of direct predation on prey populations, and to test the hypothesis that these behavioral changes may transmit cascading top-down impacts of humans through ecosystems via different pathways.

Data availability statement

All data associated with this will be deposited into the Dryad Digital Repository.

Author contributions

CS and AW were responsible for idea development. CS, AW and JD procured funding. CS, JD and SW collected data in the field. EN, SW and CS were responsible for data processing and formatting. CS performed the data analyses. CS and AW wrote the manuscript, and all co-authors contributed to editing.

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2.7 TABLES AND FIGURES

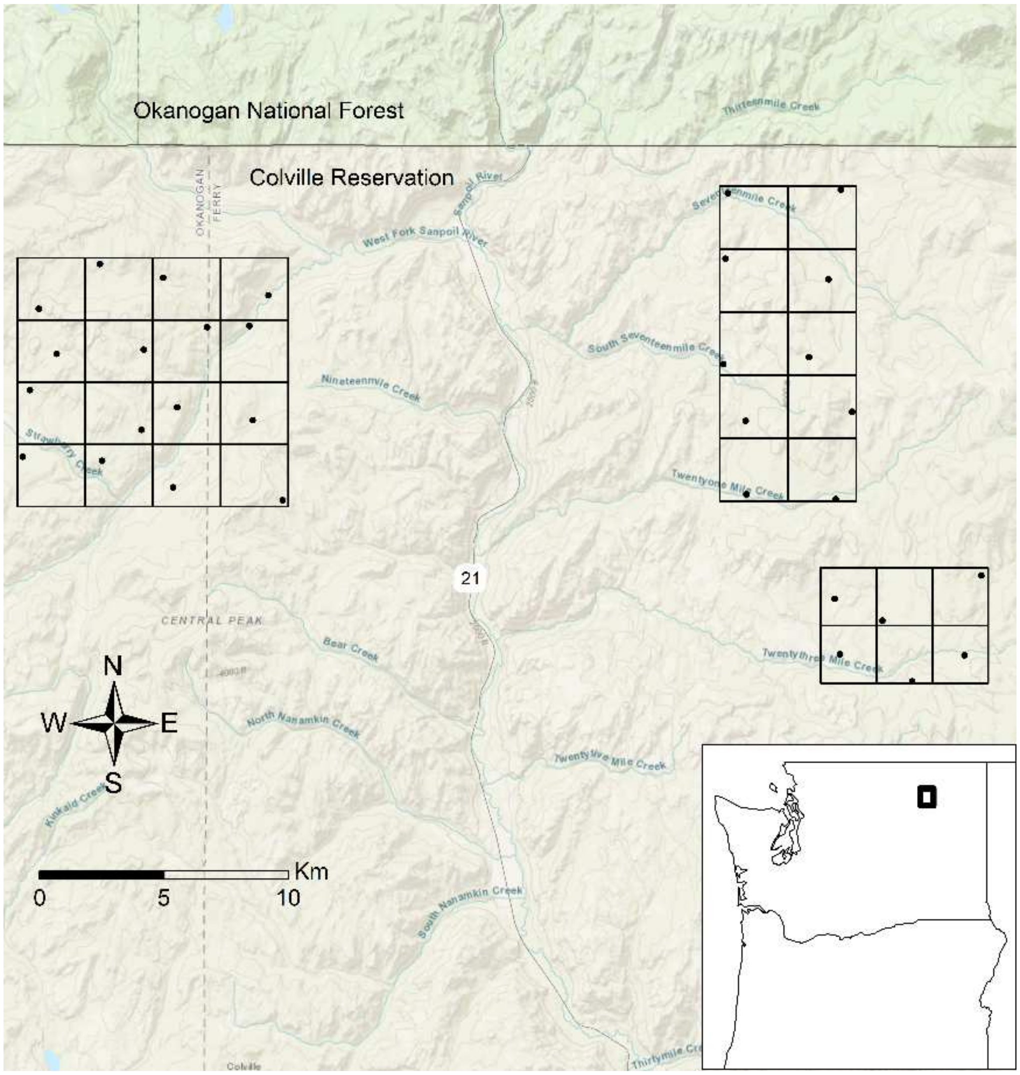
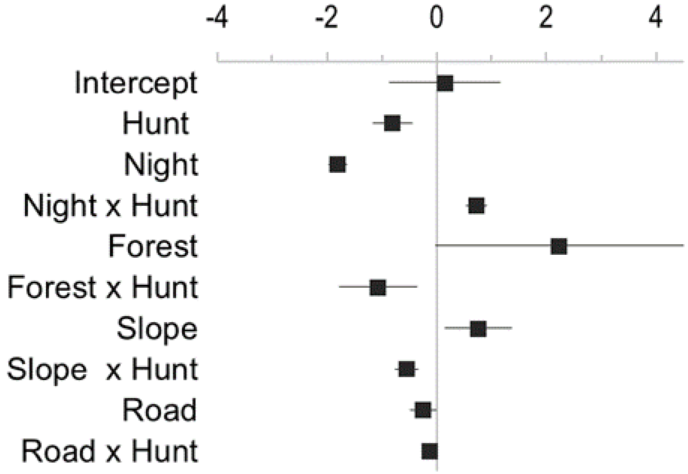


Figure. 1. Grids of camera trap locations (black dots). For each grid, single cameras were deployed inside a 2 x 2 grid cell along secondary dirt roads and trails. Both study areas are on the Colville Indian Reservation and are bordered by the Okanogan National Forest to the north. The inset shows the location of the study area in north-central Washington state, USA. The two eastern smaller grids make up on study area.

Table 1. Summary of independent detections, or photographs separated by at least 30 minutes, of humans (*Homo sapiens*), wolves (*Canis lupus*), cougars (*Puma concolor*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) over the course of three years (2013-2016) in north-central Washington, USA.

Species	Independent detections
Human	3,832
Wolf	302
Cougar	277
Mule Deer	6,786
White-tailed deer	7,422
Total	18,625

a) Mule deer



b) White-tailed deer

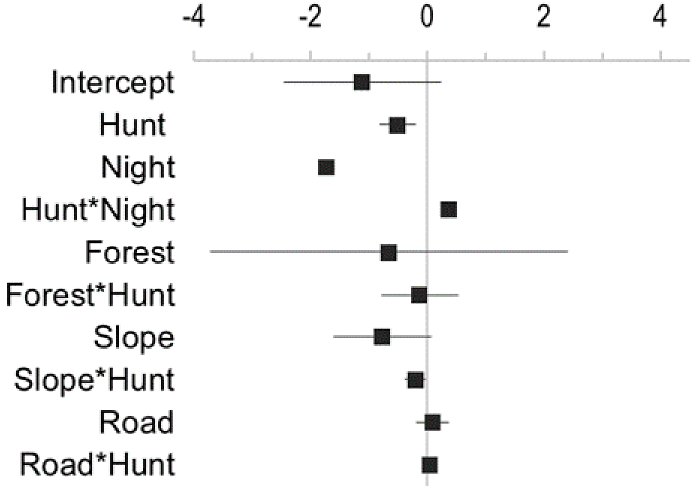


Figure 2. Coefficient estimatees with 95% confidence intervals (CIs) from zero-inflated Poisson (ZIP) generalized linear mixed models (GLMMs) of effects of hunting on mule deer (a) and white-tailed deer (b) activity (number of photo captures). Model interactions tested how deer use of different time periods (day or night; day is the model reference level) and habitats changed during the hunting season (no hunting is the reference level). A significant difference in deer activity during the hunting season is indicated by non-overlapping 95% CIs between deer use of that habitat or time during and outside of the hunting season (e.g., *Fores*t vs. *Forest x Hunt*). The intercept indicates deer daytime activity outside of hunting season and the *Hunt* parameter indicates deer daytime activity during the hunting season. The habitat variables are standardized (Dellinger et al. 2019), so a smaller value for distance to roads and forest means closer to roads or forest, whereas a larger value means farther away. For slope, a more positive value indicates steeper and a negative value indicates flatter.

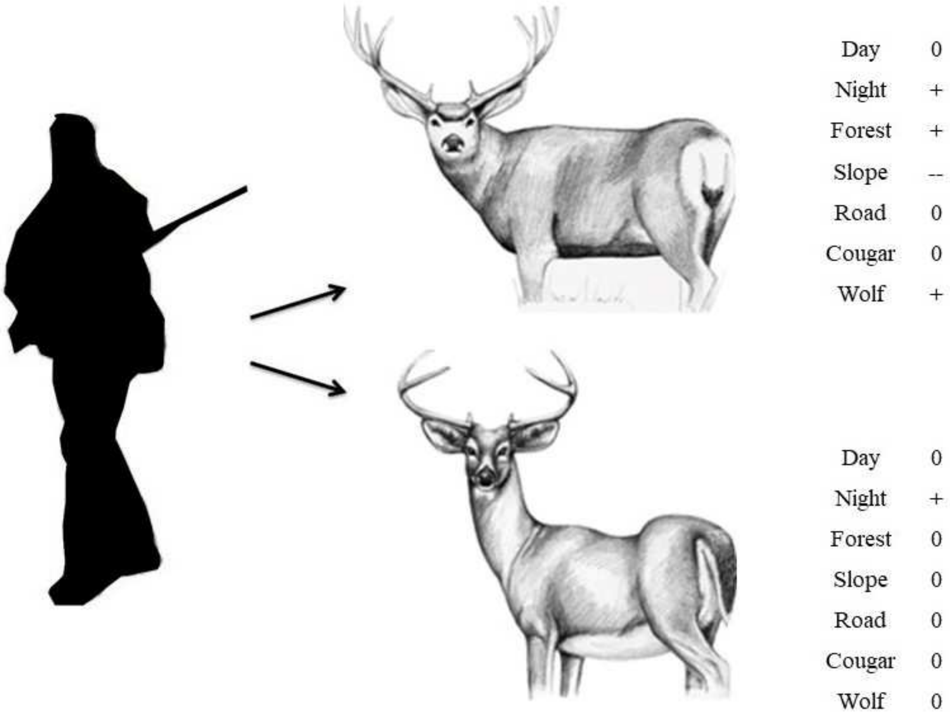
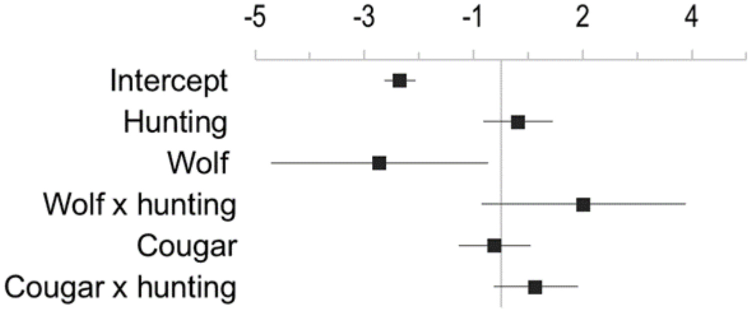


Figure 3. Diagram of mule deer (top) and white-tailed deer (bottom) changes in habitat associations and temporal activity during hunting seasons. The +/- signs indicate whether the deer species significantly changed their association with the habitat or time period variable during hunting season; as indicated by nonoverlapping 95% confidence intervals; ~~"ne"~~ "0" indicates no change during hunting season. Mule deer showed significant changes in 4 spatiotemporal categories during hunting season (Night, Forest, Slope, Wolf), while white-tailed deer only showed one significant change (Night).

a) Mule deer



b) White-tailed deer

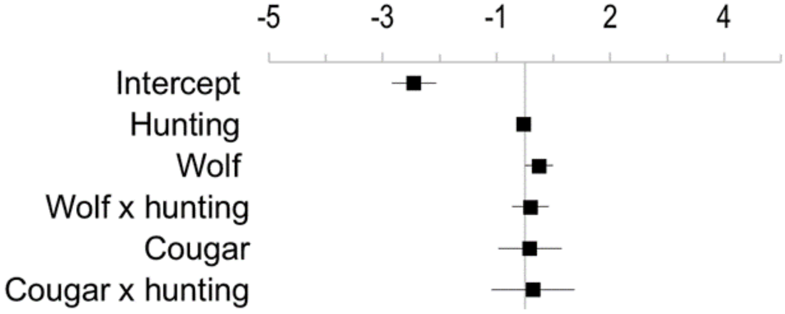


Figure 4. Results of zero-inflated Poisson (ZIP) generalized linear mixed models (GLMMs) testing for changes in (a) mule deer and (b) white-tailed deer association with predator activity during and outside of hunting seasons. The *predator*hunting* coefficient represents the association between predators and deer activity during the hunting seasons, the *predator* coefficient shows the association outside of the hunting season. Coefficient estimates are shown with ± 95% confidence intervals. Significant differences between the hunting and non-hunting seasons are indicated by non-overlapping confidence intervals.

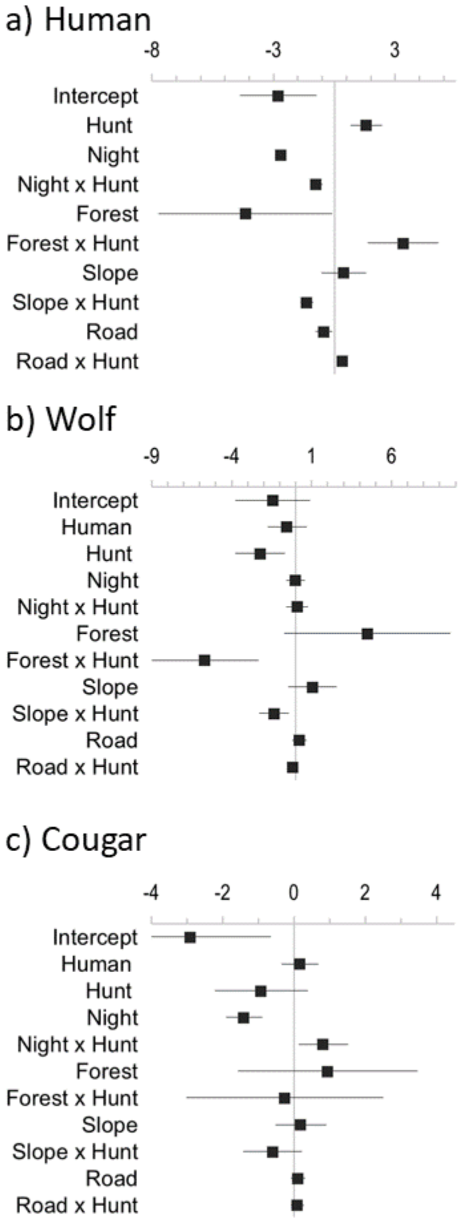


Figure 5. Results of zero-inflated Poisson GLMMs of species' activity patterns for humans, wolves, and cougars, and changes in these species' activity patterns and habitat associations during hunting seasons. Coefficient estimates are shown with ± 95% confidence intervals (see Appendix 2 for coefficients, standard errors, and zero-inflation model values). Hunting seasons are indicated by *Hunt*. A significant difference between the estimates for a parameter during hunting (e.g. *Forest x Hunt*) and non-hunting (e.g. *Forest*) is indicated by non-overlapping 95% confidence intervals. When testing for the main effect of hunting on activity (*Hunt* only), significance is indicated by a confidence interval that does not overlap zero. *Human* indicates a species association with human activity. The habitat variables are standardized (Dellinger et al. 2019), so a smaller value for distance to roads and forest means closer to roads or forest, whereas a larger value means farther away. For slope, a more positive value indicates steeper and a negative value indicates flatter.

2.8 APPENDICES

Appendix 1.

Results of zero-inflated Poisson generalized linear mixed models of changes in deer spatiotemporal activity patterns during hunting seasons. Hunting seasons are indicated by *Hunt*. Model interactions tested how deer use of different time periods (day or night; day is the model reference level) and habitats changed during the hunting season (no hunting is the reference level). The intercept indicates deer daytime activity outside of the hunting season and the *Hunt* parameter indicates deer daytime activity during the hunting season. The habitat variables are standardized (Dellinger et al. 2019), so a smaller value for distance to roads and forest means closer to roads or forest, whereas a larger value means farther away. For slope, a more positive value indicates steeper and a negative value indicates flatter.

	Mule Deer		**White-tailed deer**	
Parameter	Estimate	SE	Estimate	SE
Intercept	0.15	0.51	-1.11	0.69
Hunt	-0.80	0.18	-0.51	0.16
Night	-1.80	0.08	-1.73	0.05
Night x Hunt	0.73	0.10	0.38	0.06
Forest	2.24	1.16	-0.66	1.56
Forest x Hunt	-1.07	0.36	-0.13	0.34
Slope	0.77	0.31	-0.77	0.43
Slope x Hunt	-0.55	0.11	-0.21	0.09
Road	-0.25	0.12	0.09	0.14
Road x Hunt	-0.12	0.06	0.04	0.02
Zero-inflation model	2.01	0.06	1.12	0.05

Appendix 2.

Results of zero-inflated Poisson generalized linear mixed models of species' spatiotemporal activity patterns for humans, wolves and cougars during hunting seasons. Hunting seasons are indicated by *Hunt*. Species association with human activity is indicated by *Human*. Model interactions tested how deer use of different time periods (day or night; day is the model reference level) and habitats changed during the hunting season (no hunting is the reference level). The intercept indicates deer daytime activity outside of hunting season and the *Hunt* parameter indicates deer daytime activity during the hunting season. The habitat variables are standardized (Dellinger et al. 2019), so a smaller value for distance to roads and forest means closer to roads or forest, whereas a larger value means farther away. For slope, a more positive value indicates steeper and a negative value indicates flatter.

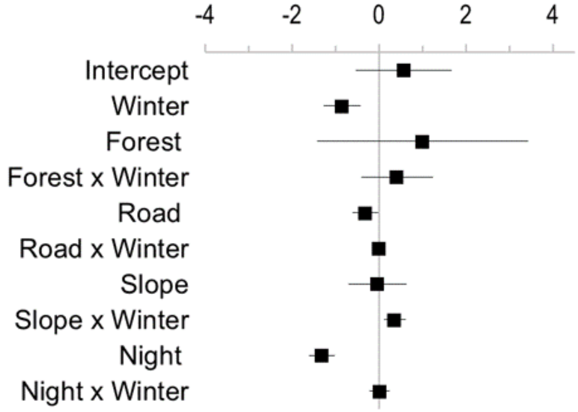
	Human		**Wolf**		**Cougar**	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-2.31	0.80	-1.43	1.18	-2.90	1.15
Human	na	na	-0.53	0.61	0.17	0.26
Hunt	1.32	0.32	-2.21	0.79	-0.92	0.66
Night	-2.20	0.10	0.00	0.28	-1.40	0.26
Night x Hunt	-0.75	0.13	0.10	0.34	0.83	0.35
Forest	-3.65	1.82	4.50	2.64	0.95	1.28
Forest x Hunt	2.84	0.74	-5.66	1.68	-0.26	1.40
Slope	0.40	0.47	1.05	0.76	0.20	0.36
Slope x Hunt	-1.13	0.13	-1.35	0.46	-0.60	0.42
Road	-0.42	0.18	0.24	0.23	0.12	0.10
Road x Hunt	0.35	0.08	-0.18	0.11	0.10	0.09
Zero-inflation model	2.42	0.05	3.21	0.22	1.91	1.14

Appendix 3. Disentangling the effects of season and hunting

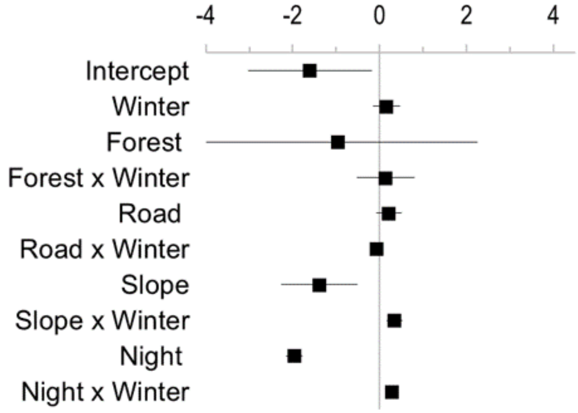
To investigate the possibility that observed changes in prey activity indicated a response to calendar season rather than hunting activity, we examined seasonal changes in activity patterns in both deer species. For this analysis, we defined May 1 – Nov 15 as summer/fall and Nov 16 – April 30 as winter/spring based on the start of spring migration and fawning and the fall breeding season (Garrot et al. 1987; Robinette and Gashwiler 1950), and controlled for changes to day length throughout the year as described in the Methods section. Both deer species exhibited significantly more night-time activity during the winter (Fig. A1). However, there is no apparent biological reason why deer would increase nocturnal activity during the winter; indeed, we might expect the opposite trend given the heightened thermal constraints imposed by nighttime activity during this season. Rather, given that an increase in white-tail nocturnal behavior in relation to hunting has been previously reported (Kilgo et al. 1998), we suspect that hunting during the winter drove the increase in nocturnal activity of white-tailed deer rather than a behavioral change due to the winter season itself, especially because this nocturnal shift coincided with the full duration of the hunting season rather than just the winter. White-tailed deer were also significantly more likely to be associated with steeper slopes during the winter, which may have been to avoid areas of deep snow (Gilbert and Gill 1970). This trend is opposite this species' observed association with flat terrain during and outside of the hunting seasons, however, strengthening our conclusion that white-tailed deer did not alter their use of slope steepness in response to the presence of human hunters. In addition, white-tailed deer were significantly more active during the winter, although this pattern did not match the lack of significant change in white-tailed deer activity in relation to hunting. Overall, seasonal changes in deer activity did not match the behavioral changes observed during the hunting seasons.

Figure A3. Zero-inflated Poisson generalized linear mixed model results for seasonal changes in spatiotemporal activity patterns in (a) mule deer and (b) white-tailed deer. Parameter estimates are shown with associated 95% confidence intervals (CI). Summer is defined as May 1 – Nov 15, and winter as Nov 16 – April 30. Summer is the reference level in the model. The intercept and standard error for the zero-inflation model for mule deer is $\beta = 1.78$ (0.06), and $\beta = 1.14$ (0.05) for white-tailed deer.

a) Mule deer



b) White-tailed deer



Chapter 3. COUGARS (*PUMA CONCOLOR*) PRIORITIZE TEMPORAL AVOIDANCE OF WOLVES (*CANIS LUPUS*) OVER HUMANS

3.1 ABSTRACT

Humans can shape top-down effects in communities by changing apex predator abundance and behavior. No prior study, however, has asked whether humans, as predators, affect intraguild behavioral relationships among apex carnivores. We deployed camera traps to evaluate changes in temporal activity of cougars (*Puma concolor*) in areas of northeastern Washington, USA, with and without resident wolves (*Canis lupus*) where both apex carnivores were also hunted by humans. Cougars were subject to year-round hound hunting in the wolf-occupied areas but only harvested opportunistically from September through March where wolves were absent. Nevertheless, in the areas with wolves, cougars significantly increased their activity during the daytime, when wolves were least active, leading to a significant increase (+25%) in temporal overlap between cougars and humans. These results challenge the paradigm of humans as 'superpredators', instead revealing that in some cases carnivores appear to be minimizing intraguild competition over avoiding humans and highlight the importance of the temporal dimension of large carnivore niche partitioning.

Keywords: apex predators, intraguild competition, carnivores, niche partitioning, anthropogenic disturbance, activity overlap, cameras

3.2 INTRODUCTION

Predators can influence ecosystems through their interactions with prey and mesopredators (Terborgh et al. 2001, Prugh et al. 2009, Estes et al. 2011, Ripple et al. 2014). Notably, they also interact with one another, primarily via intraguild predation, harassment, and kleptoparasitism of kills (Palomares and Caro 1999). These intraguild interactions may affect the abundance and/or behavior of competitors. Within mammalian carnivore guilds, for example, intraguild predation can account for over half of adult mortalities (Palomares and Caro 1999). Consequently, apex carnivore interactions have the potential to indirectly influence prey populations and biodiversity. To date, much of what we know about intraguild relationships among predators comes from studies of interactions between apex and smaller, or meso-, predators (~~Prugh et al. 2009,~~Prugh et al. 2020; Shores et al. 2019). Interactions among apex carnivores (*sensu* Sergio et al. 2014), by contrast, are less well understood.

Common challenges to studying apex predator interactions include their low density and elusive nature. In addition, apex predator distributions and populations have diminished globally due to human persecution (Estes et al. 2011; Ripple et al. 2014), meaning that these species are now absent from many ecosystems where they previously occurred. In the few remaining ecosystems where numerous apex predators overlap, they may suppress each other numerically or behaviorally. For example, on the Kamchatka peninsula in the Russian Far East, intraguild predation on gray wolves (*Canis lupus)* and kleptoparasitism of wolf kills by Amur tigers (*Panthera tigris altaica*) result in an inverse correlation between tiger and wolf numbers (Miquelle et al. 2005). The limitation of wolf populations by tigers cascades to lower trophic levels; roe deer (*Capreolus capreolus*), the primary prey for wolves, increased in areas where tigers returned (Miquelle et al. 2005). In the eastern Pacific Ocean, visits from killer whales

(*Orcinus orca*) displaced great white sharks (*Carcharodon carcharias*), reducing their predation on elephant seals (*Mirounga angustirostris*, Jorgenson et al. 2019).

Humans are increasingly being recognized as 'hyperkeystone' species, or ecosystem players that influence other keystone species (Worm and Paine 2016), because of their 'superpredator' role as highly lethal hunters of apex predators themselves (Darimont 2015; Kuijper et al. 2016). Apex predators may recognize and react to human-caused risk like that of prey responding to a predator (Ordiz et al. 2013), for example by altering their temporal activity to avoid periods of high human activity (Brook et al. 2012). By implication, avoidance of humans could override the effects of one apex predator on another (Clinchy et al. 2016). To date, no study to our knowledge has addressed apex predator interactions while also accounting for the influence of human predation risk, so this question remains open.

In the western United States, recolonizing gray wolves now overlap with another apex predator that was never extirpated from the region: the cougar (*Puma concolor*). Cougar population dynamics may not be affected by wolves (Ruth et al. 2011), but intraguild predation and kleptoparasitism do occur between these carnivores (White and Boyd, 1989; Ruth 2004; Jimenez 2008). Because wolves are often in packs, they are predicted to dominate encounters (Murphy et al. 1999). Accordingly, wolf kleptoparasitism of cougar kills has been frequently reported (Ruth and Hornocker 1996; Ruth 2004; Kortello et al. 2007), and cougars have altered their habitat and prey selection (Bartnick et al. 2013; Elbroch et al. 2015) in areas with wolves, possibly in response to exploitative competition. In Banff National Park, for example, cougars shifted to areas with higher levels of human activity to avoid wolves (Kortello 2007), and cougars in the Greater Yellowstone Ecosystem used more structurally complex habitats after wolves were re-introduced to the park (Ruth et al. 2011; 2015). However, most research on wolf-cougar interactions has focused on spatial ecology and excluded the temporal dimension of the predators' relationship. In addition, these studies have occurred primarily within protected areas rather than the multi-use landscapes that dominate western North America where carnivores must manage risk from human hunters. Thus, the extent to which humans shape interactions between cougars and wolves has yet to be explored.

Here, we explore apex predator interactions in the presence of humans by examining temporal partitioning between cougars and wolves in an anthropogenic landscape in northeastern Washington, USA. Our study took place where humans hunt both carnivores, thus allowing for a novel investigation of interactions between apex predators in the presence of human superpredators. Cougars are known to be sensitive to human disturbance. For example, Smith et al. (2017) showed that these felids abandon carcasses at the mere sound of a human voice. Thus, there is ample reason to expect cougars to avoid times when humans are most active, especially where they are targeted by disruptive and effective forms of harvest such as hound hunting (Cooley et al. 2009), as they are in our study area. Notably, however, niche overlap between cougars and wolves may be elevated in northeastern WA relative to other areas where prior research on interactions between these species has been conducted. Namely, our study areas are forested with gently rolling hills and little of the mountainous terrain and open habitat that cougars and wolves use to spatially segregate (Ruth et al. 2011; 2015; Bartnick et al. 2013; Elbroch et al. 2015). In addition, most previous research on cougar-wolf interactions has occurred in areas where cougars specialize on mule deer (*Odocoileus hemionus*) and wolves on larger ungulates such as elk (*Cervus elaphus*) or moose (*Alces alces*). By contrast, deer (*Odocoileus* sp.) are the main prey of both carnivores in our study area (Cooley 2010; Spence 2017). This higher niche overlap between wolves and cougars may create more pressure for temporal segregation between the two carnivores and, therefore, prompt cougars to prioritize wolf avoidance over that of humans.

In our study area, cougars in two of our four focal sites experienced low levels of human hunting and wolf exposure, whereas in two other sites they were targeted year-round by hound hunters and subject to intra-guild interactions with two resident wolf packs. Because humans (including hunters) in our system are largely diurnal whereas wolves are predominantly nocturnal (Shores et al. 2019) we were therefore able to determine whether cougars exposed to both risks prioritized temporal avoidance of one over the other. Under our first hypothesis that humans function as superpredators whose effects on large carnivore behavior overwhelm those of intra-guild competitors, we predicted that cougars would prioritize temporal niche segregation from humans, as evidenced by (1) low daytime activity in both study areas with and without wolves, and (2) no change in temporal niche overlap between cougars and humans in the presence of wolves. By contrast, under the alternate hypothesis that large carnivores respond more strongly to intraguild competitors than to humans, we predicted that cougars would prioritize temporal niche separation from wolves, as indicated by (3) increased diurnal activity in areas with wolves, the time period when wolves are least active, and (4) increased cougar-human temporal niche overlap in the presence of wolves.

3.3 METHODS

Study Area

We performed this study in the Okanogan Highland dry forest ecosystem of north-central Washington, within the Northern Rockies ecoregion. Working with the Confederated Tribes of the Colville Reservation, we established four study areas, two in the Okanogan National Forest and two on the Reservation, which ranged in area from 550-680 km^2. Topography and vegetation were similar among the study areas, as were human residential density and patterns of resource extractions and recreation (see Shores et al. 2019 for details).

Over the course of the investigation, the two Reservation study sites were occupied by the Nc'icn and Strawberry wolf packs. Wolves recolonized these sites from neighboring populations in 2010 and 2011, respectively, or 2-3 years before this study took place. The Nc'icn pack had 5 wolves for the duration of the study and a home range size of 668 km^2, whereas the Strawberry pack had 7 members and a home range size of 807 km^2. Gray wolf average home range size, pack size, and pack density in Washington are similar to those of wolves in managed landscapes elsewhere (Jimenez and Becker 2016, WDFW et al. 2017) but low relative to those in protected areas (Jimenez and Becker 2016). Wolf hunting was allowed on the Colville Reservation throughout the course of the study, and a Strawberry pack wolf was legally harvested during the Aug 1, 2016 – Feb. 28, 2017 wolf hunting season (WDFW et al. 2017). A shorter trapping season for wolves ran from Nov 1 – Feb. 28th, although no wolves were trapped during our study. Six wolves could be harvested in the Colville Reservation study areas per season inclusive of both hunting and trapping. We determined that the two study areas in the Okanogan-Wenatchee National Forest were not occupied by wolf packs based on evidence from daily snow tracking surveys in winter and photographs from the camera traps. Four photos of wolves were captured in these areas over the three-year study period, however; three of these photos were of a wolf from the Strawberry pack, which indicated extra-territorial movement.

Cougars (*Puma concolor*) were never extirpated from the region and were present in both wolf and non-wolf areas. Cougars were hunted year-round with hounds and no bag limits in the study areas with wolves. In the areas without wolves, cougar hunting with hounds was prohibited; opportunistic cougar hunting was seasonally restricted to Sept 1 – Mar 31 of the following year; a maximum of 17 cougars could be harvested from these areas with a bag limit of one per hunter.

Camera placement

We established a camera trap grid in each study area in March 2013. Each grid was composed of 16 cells, each with an area of 4 km^2 (Shores et al. 2019). Within each cell, we deployed a camera trap (Moultrie M80 Game Spy, EBSCO Industries Inc., Birmingham, AL) in forested habitat along a dirt road or game trail to maximize image captures of carnivores and ungulates. All camera locations were within Okanogan highlands dry forest ecotype, and a comparison of habitat variables at camera sites between wolf and non-wolf study areas found no significant differences (Shores et al. 2019). Cameras were deployed year-round, operated 24 hours per day, and checked for functionality, battery life, and data recovery every 2-4 months.

Photo Identification and data standardization

We defined the sampling periods used for this analysis as a biologically meaningful time period for wolves; namely, the average end of the denning season when pups emerge from the den (Fuller 1989) and wolf packs become more mobile, beginning on May 1st, through April 30th of the following year. Accordingly, the study spanned three years from 5/1/2013 to 4/30/2016. Photographs over thirty minutes apart of humans, wolves, and cougars were counted as independent observations (Burton et al. 2015). We catalogued photographs from all cameras into a Microsoft Access database using the program CPW Photo Warehouse, developed by Colorado

Parks and Wildlife (Newkirk 2016). Volunteers then identified the species and number of individual animals in each photograph. Multiple animals of the same species in a photograph were counted as a single detection. Volunteers were trained and tested on species identification before they began recording data. To ensure data quality, each photograph was independently identified by two trained volunteers. The identifications were subsequently compared and, if they did not match, reviewed by the lead author (CS) who made a final determination.

To account for seasonal variation in day length, we standardized our observations by determining the clock time of sunrise and sunset for each day of the study, and then binned the detections into two time categories: day and night. We designated day as lasting from one hour after dawn to one hour before sunset (Farris et al. 2015), and night included the rest of the 24-hour diel cycle.

Changes in cougar temporal activity

To test our predictions that, relative to conspecifics in the low-wolf sites, cougars in areas with wolves would either maintain (1) or increase (3) their activity during the daytime, when wolves are least active, we examined how cougar activity during day varied between areas with and without wolves using a generalized linear mixed model (GLMM). The activity of cougars was the response variable, represented by the number of photo capture events y_{ijk} for cougars on each sampling day i, for each time category j (crepuscular, day and night), and at study site k with a zero-inflated Poisson error distribution (ZIP) GLMM and a random intercept for camera location in the conditional model. Night was the reference level in the 2-level *time* categorical variable. Wolf absence was the reference level in the two-level categorical variable *Wolf* indicating wolf presence or absence. The random effect for camera location helped to control for unaccounted environmental variation among camera sites. We also included an offset equal to the number of hours available in each time category. This model structure enabled us to test for significant differences in cougar use of daytime periods between areas with and without wolves via the inclusion of interaction effects between the *wolf_presence* and *time* covariates. Significant differences between cougars' daytime activity between the wolf and non-wolf areas were indicated by a Wald test on the difference estimate between the coefficients *Day* and *Day x Wolf.*

Cougar-human temporal niche overlap

To test the prediction that cougar-human temporal niche overlap would increase in the presence of wolves, we compared temporal niche overlap between cougars and humans in areas with and without wolves. To test our predictions that cougar-human overlap would either be stable (2) or increase (4) as a function of wolf presence, we estimated the temporal activity patterns of cougars and humans over a 24 hour period with kernel density analysis, a non-parametric method for estimating the probability density function of a random variable (Ridout and Linkie 2009). We regarded detections of a species as a random sample from a distribution of its underlying continuous activity pattern (Meredith and Ridout 2014). In our analysis, kernel density estimators show the probability of a species being detected at any specific time of day. To estimate the overlap in temporal activity patterns between species, we used the R package "*overlap*" (Meredith and Ridout 2014) with a smoothing parameter of 1 and the overlap coefficient Δ_4, which the authors recommend for large sample sizes ($n > 75$). A smoothing parameter of 1 is optimal for the Δ_4 overlap coefficient, as determined by simulations described by Meredith and Ridout (2014). Δ_4 calculates temporal overlap between species by measuring the overlap of the two species' temporal activity density functions. We estimated 95%

confidence intervals for Δ_4 to compare differences in the overlap coefficients between areas with and without wolves from a smoothed bootstrapping distribution ($N = 10{,}000$). We concluded that temporal niche partitioning between cougars and humans differed between wolf and non-wolf treatments if the 95% confidence intervals did not overlap (Johnson 1999).

3.4 RESULTS

The cameras recorded 6,373 independent detections of humans, wolves, and cougars (Fig. 1). Humans were the most photographed species, with a total of 5,787 detections, wolves were detected on 306 occasions, and cougars were the least photographed species with 277 detections. In areas with wolf packs, numbers of photographs for humans, wolves, and cougars were 3991, 302 and 149, respectively. In areas without wolf packs, numbers of photographs for humans, wolves, and cougars were 1796, 4 and 129, respectively.

Changes in Cougar temporal activity

Cougars in the presence of wolves were significantly more active during the day (Table 1), when wolves were least active (Shores et al. 2019), as evidenced by a Wald test comparing the difference estimate of cougar activity during the day in wolf and non-wolf areas (z-score = 2.09, p = 0.04). Cougars were 3.3 times more likely to be photographed during the day in areas with wolves in comparison to non-wolf areas, as evidenced by a comparison of the incidence risk ratios of the *Day x Wolf* and *Day* coefficients. Wolf presence did not have a significant effect on overall cougar activity (Table 1). Changes in ungulate prey (mule and white-tailed deer) temporal activity between areas with and without wolves did not explain the changes in cougar temporal activity (Appendix 1).

Cougar-human temporal activity overlap

Cougars increased their temporal overlap (Δ_4) with humans significantly in areas with wolves (Fig. 2), as indicted by non-overlapping 95% confidence intervals for the wolf-present and wolf-absent Δ_4 overlap estimates. In areas without wolves, cougar and human temporal activity overlapped by 48% (95% CI = 40 – 53%, Fig. 2a), compared to 73% (95% CI = 0.65 – 0.76, Fig. 2b) in the presence of wolves. To account for possible changes in human activity in the wolf areas, we re-ran the analysis after substituting human activity from non-wolf areas for that in the wolf areas; for this analysis, overlap with cougar activity at wolf sites was still 14% higher than in non-wolf sites (Appendix 2). Notably, the confidence intervals for this estimate (62%; 95% CI = 55 –67 %; Appendix 2) do not overlap the human-cougar temporal overlap for non-wolf areas (Fig. 2; 48%, 40 – 53%). Cougars and wolves overlapped by 79% (95% CI = 71-85%'; Appendix 3).

All species showed distinct temporal activity patterns (Fig. 2, Appendix 3). Humans were diurnal (Fig. 2). Wolves were crepuscular with peaks in activity before dawn and after dusk, little activity during the day, and higher levels of activity at night (Appendix 3; Shores et al. 2019). Cougars had crepuscular activity patterns in areas with and without wolves but had wider activity peaks that extended more into daytime hours in areas with wolves (Fig. 2) with increases in activity before and after mid-day (12:00). In the non-wolf areas, cougars exhibited a flat period of minimum activity between 11:00-13:00, whereas in the wolf areas they manifested a much shorter rest period, with increased activity between 9:00-15:00 hours. In the non-wolf areas, cougars also had a clear maximum activity peak immediately after dusk, while in the presence of wolves cougars decreased dusk activity to the point where activity levels at dusk and dawn were equal.

3.5 DISCUSSION

Our results support the hypothesis that large carnivores prioritize temporal niche partitioning with intraguild competitors over humans. Namely, where wolf packs were present, cougars displayed heightened activity during the daytime, when wolves were least active, and thereby significantly increased their temporal niche overlap with humans. These results differ from previous research indicating that, as a diurnal 'superpredator', humans can overwhelm the top-down ecological effects of carnivores (Darimont et al. 2015; Clinchy et al. 2016; Ordiz et al. 2013) and trigger increased nocturnality in large mammals (Gaynor et al. 2018). Accordingly, these findings have important implications for our understanding of how humans influence intraguild relationships among large carnivores and highlight the importance of the temporal dimension of carnivore niche partitioning.

There is growing evidence that humans can shape top-down effects in communities by changing apex predator abundance and traits (Ripple et al. 2014; Clinchy et al. 2016; Ordiz et al. 2013). No previous studies have asked whether humans affect intraguild relationships among apex carnivores (Kuijper et al. 2016; Elbroch et al. 2015). Our finding that cougars responded more strongly to wolves than to humans, at least in the temporal dimension, does not fit neatly into the human as superpredator paradigm. It is also surprising because our study took place in an anthropogenic, multi-use landscape where cougars were subject to year-round hound hunting, an effective harvesting method (Cooley et al. 2009) that produces clear risk cues and therefore might be expected to elicit marked avoidance. Notably, coyotes (a mesopredator) in the same system also exhibited elevated diurnality in areas with wolves despite high human diurnal activity and hunting (Shores et al. 2019). Collectively, these patterns of behavior in relation to wolves suggest that, under certain conditions, apex carnivores can retain their ecological effectiveness in anthropogenic landscapes, even when the human influence is lethal. They also reveal that we cannot always presume humans to be the dominant player within predator guilds.

Why did cougars apparently prioritize temporal avoidance of wolves over humans? Cougars may have avoided intraguild competitors instead of humans because, like other apex predators, they did not evolve to contend with top-down selection pressures such as hunting (Darimont et al. 2015). It is also possible that hound hunting in our study area is so lethal that cougars have little opportunity to survive it, and thus learn from it. Furthermore, there is substantial habitat overlap between mule and white-tailed deer in our system (Dellinger et al. 2018). Coupled with pervasive forest cover, this lack of spatial separation between their primary prey species may preclude wolves and cougars from spatially segregating, as suggested by the lack of a negative relationship between cougar and wolf detection rates. If so, then elevated risks of intraguild killing and kleptoparasitism due to spatial overlap with wolves may force cougars to exploit temporal niche space to decrease intraguild competition with wolves, at the expense of increased exposure to humans.

Humans are the primary cause of death for cougars (Thompson et al. 2014). Thus, cougar populations that become more diurnal in the presence of wolves could have increased mortality from humans that is additive to other natural causes. Furthermore, in the same study areas, cougars decreased activity at all times of the day during seasonal pulses of high human activity during deer hunting seasons (C. Shores, personal observation). By implication, cougars in our system are not insensitive to human disturbance. Rather, at least when and where both wolves and hunters are active, they are apparently being squeezed by conflicting pressures from intraguild competition and humans. The potential consequences of this predicament for cougar populations are not trivial. The greater temporal overlap with humans may lead to additive mortality in cougar populations, as humans are the primary cause of mortality for cougars, even in non-hunted populations (Thompson et al. 2014). Furthermore, a cougar dietary shift toward more diurnal prey, and increased overlap with more diurnal mesopredators such as coyotes (Shores et al. 2019), could have consequences for lower trophic levels. Accordingly, further research is needed to investigate the individual, population, and community consequences of changes to cougar temporal activity triggered by wolf and human presence.

Time is increasingly being recognized as a key dimension of niche space that species use to manage predation risk (Kohl et al. 2018), including from humans (Gaynor et al. 2018), as well as relationships with fellow members of the carnivore guild (Brook et al. 2012; Shores et al. 2019). Although human-induced shifts toward nocturnality in carnivores are a global phenomenon (Gaynor et al. 2018), our results suggest that anthropogenic effects on the temporal behavioral of apex carnivores may hinge on which other members of carnivore community are present. Namely, and by contrast to other reports of increased cougar nocturnality in areas with increased human disturbance (Wang et al. 2015), cougars in our system increased their diurnality in the areas with wolves where they also faced hound hunting, ostensibly to avoid wolves. The nocturnal behavior exhibited by wolves in our study system may have been a response to human activity, thereby rendering the increased diurnality of cougars the result of a behavioral cascade from humans to wolves to cougars. Earlier work in our study system did not find a negative association between wolf and human activity (Shores et al. 2019). A meta-analysis of wolf temporal activity patterns, however, found road density (a possible proxy for human use) to be one of the best predictors of wolf nocturnality (Theuerkauf 2009). Hence, there is need for research examining how temporal relationships among apex carnivores, and between these species and humans, are mediated by landscape features.

We designed our study to minimize potential confounding factors in several ways. First, we took advantage of a natural experiment that leveraged spatial heterogeneity in wolf distribution across ecologically similar areas; the use of these quasi-experiments permits stronger inference than purely observational studies (Jachowski et al. 2020; Hille Ris Lambers; 2013). Second, we spatially replicated our sites in wolf present and wolf absent areas to help control for variables that may have otherwise influenced our results. Third, a comparison of habitat variables at camera sites between the study areas with and without wolves found no significant differences (Shores et al. 2019). Fourth, the use of a random effect in our statistical models helped to account for potential environmental variation that we did not quantify between camera locations. Nevertheless, the correlational nature of our study necessitates examination of alternative explanations. The changes in cougar activity patterns between areas with and without wolves could also have reflected changes in prey activity. However, changes in deer temporal activity in areas with wolves were opposite to the changes in cougar activity; both deer species decreased diurnality (Appendix 1), whereas cougars increased diurnality in the wolf areas. It is also possible that cougars avoided hound hunters, but not humans overall. This is a possibility we did not address because we were unable to quantify hound hunter activity. Differentiating between cougar responses to hound hunters and other human activity such as logging and motorized recreation would therefore help to clarify how cougars are managing risk from humans.

In addition, it is possible that changes in cougar diel activity could have owed to differences in black bear (*Ursus americanus*) activity between the study areas, as black bears are known to kleptoparasitize cougar kills (Ruth et al. 2019). To address this possibility, we examined differences in black bear temporal activity between the study areas (Appendix 4) and found that bears were significantly more likely to be photographed in areas with wolves, and were also diurnal in both the wolf and non-wolf areas. Although bears were less diurnal in the wolf areas, they maintained a significant positive association with the daytime in both study areas, and the difference in the degree of bear diurnality between study areas was not significant. These results agree with previous research showing bears to be primarily diurnal (Bridges et al. 2004, Elbroch and Rinehart 2011) and support our conclusion that wolves drove cougar shifts to higher levels of daytime activity, as cougars avoiding bears would have been expected to decrease diurnal activity in the wolf areas. However, further research on the degree of competition between cougars and black bears, particularly in relation to black bear kleptoparasitism of cougar kills, would help to clarify interspecific competition between these two members of the carnivore guild.

Recently, there has been a proliferation of research on how humans shape predator ecology (e.g., Clinchy et al. 2016; Kuijper et al. 2016; Gaynor et al. 2018). Our study expands this frontier as the first to examine how apex carnivores balance risk from both intraguild competitors and humans. Our results do not support the paradigm of humans as superpredators and instead reveal that, at least in terms of their temporal behavior, some apex predators may be more sensitive to other carnivore competitors than to humans. They also give rise to additional questions about how cougars, and by extension other apex predators, manage simultaneous risk from intraguild competitors and humans. It is possible, for instance, that cougars mitigated increased risk of human predation during the day by being more cryptic and using habitat such as denser forest farther from roads. A preliminary analysis of our camera trapping data did not show any changes in cougar habitat use between areas with and without wolves, but it is plausible that finer-scale spatial data from GPS collars might reveal such adjustments. In addition, our camera sites were all located along secondary roads and game trails, so the possibility that cougar responses to wolves and humans away from these movement corridors differed from those we observed remains to be examined. Finally, it is possible that there is a threshold beyond which human disturbance begins to negatively impact cougars (Bejder et al. 2006), and that human disturbance rarely reached this threshold over the course of our investigation. Studies either exploiting gradients of human disturbance or employing experimental approaches (e.g., different intensities of human and wolf playbacks) will be necessary to address this threshold scenario.

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3.7 TABLES AND FIGURES

Figure 1. Photographs of gray wolves (*Canis lupus*, a) and cougars (*Puma concolor*, b) from game cameras deployed in our study areas.

Table 1. Parameter coefficients (β) and 95% confidence intervals for a Zero-inflated Poisson (ZIP) GLMM comparing cougar activity during daytime hours between areas with and without wolves. Time is a binary variable with the categories Day and Night; wolf is a binary variable indicating wolf presence or absence. Night and wolf absence are the reference levels in the model. There was a significant increase in cougar activity during the day in areas with wolves, as indicated by a Wald difference estimate test (z-score = 2.09, p = 0.04). Note, Shores et al. (2019) showed that wolves in our study system were least active during the day and most active at dusk and night.

Conditional model		
Parameter	β	95% CI
Intercept	-3.57	-4.98 – -2.16
Day	-0.62	-1.01 – -0.23
Day x Wolf	0.57	0.06 – 1.08
Wolf	0.02	-0.43 – 0.47
Zero-inflation model		
Intercept	1.92	0.35 – 3.49

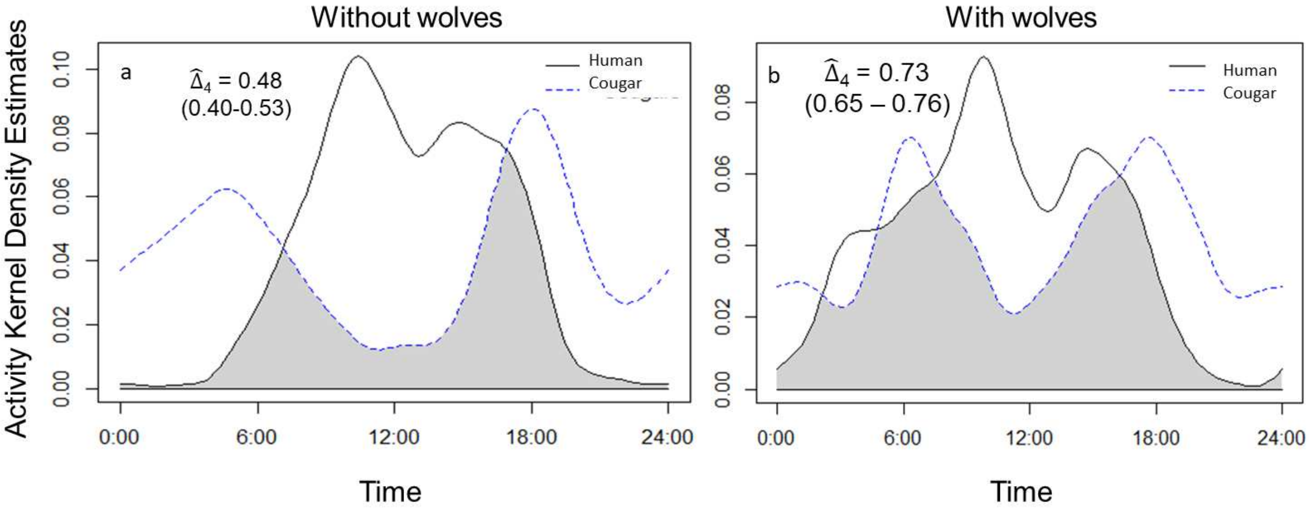


Figure 2. Kernel density estimates of temporal overlap (Δ_4) between humans and cougars in areas without wolf packs (a; 48% overlap) and with wolf packs (b; 73% overlap). 95% confidence intervals are indicated in parentheses.

3.8 APPENDICES

Appendix 1. Zero-inflated Poisson generalized linear mixed model results comparing white-tailed deer and mule deer temporal activity between areas with and without wolves with 95% confidence intervals. Night is the reference level in the 2-level binary variable of time (Day, and Night). Both white-tailed deer and mule deer had significantly decreased diurnality (z-score = 3.93, $p < 0.0001$ and z-score = -2.63 and $p < 0.01$, respectively) in areas with resident wolf packs, which is opposite the increased diurnality of cougars in the presence of wolves. This further supports the hypothesis that increased cougar diurnality in the presence of wolves is a response to intraguild competition. The zero inflation models for white tailed deer and mule deer had intercepts of 1.17 (standard error (SE) = 0.04) and 1.34 (SE = 0.04), respectively.

	White-tailed deer		Mule deer	
Coefficient	Estimate	SE	Estimate	SE
Intercept	-2.440	0.260	-1.080	0.190
Wolf	1.370	0.360	-0.660	0.270
Day	0.340	0.050	0.290	0.030
Wolf x Day	0.040	0.060	-0.030	0.060

Appendix 2. **Changes in human activity between areas with and without wolves.**

While every effort was made to control for confounding factors between our study sites in order to isolate the effects of wolves on other carnivores, human activity patterns were beyond our control. Any attempt to explain why human behavior might vary between the two areas is beyond the scope of our study, but there is little reason to believe that the presence of wolves would drive that variation. In order to address this, we performed two additional analysis steps to 1) quantify the difference in human activity patterns between the two groups and 2) estimate the relative contributions of differences in cougar and human activity to the increase in overlap between the two study areas.

To address the above objectives, we compared the temporal density functions of humans in wolf and non-wolf areas, and the temporal density functions of cougars in wolf areas and humans in non-wolf areas using the methods described in the manuscript, detailed again below for ease of reference. We estimated temporal activity of humans and cougars over a 24 hour period from camera trap photographs seperated by at least 30 minutes with kernel density analysis, a non-parametric method for estimating the probability density function of a random variable (Ridout and Linkie 2009). In our analysis, kernel density estimators show the probability of a species being detected at any specific time of day. To estimate the overlap in temporal activity patterns between species, we used the R package "*overlap*" (Meredith and Ridout 2014) with a smoothing parameter of 1 and the overlap coefficient Δ_4 , recommended for sample sizes over 75. Δ_4 calculates temporal overlap between species by measuring the overlap of the two species' temporal activity density functions. We estimated the average overlap coefficient (Δ_4) and 95% confidence intervals (CIs) for Δ_4 from a smoothed bootstrapping distribution (N = 10,000).

Human temporal activity overlapped by an average coefficient value of 80.5% (Figure A2_1, 95% confidence interval (CI) = 78.3-82.7%) between areas with and without wolves. In non-wolf areas human activity was more concentrated, with higher peaks during daytime hours and minimal activity between dusk and dawn, and in wolf areas humans were somewhat more likely to be active in the pre-dawn hours leading to a less concentrated density curve. The overall similarity and high overlap between the two indicate that the study sites were comparable, but the differences suggest that changes in human activity may have contributed to part of the increase in overlap between cougars and humans in the wolf areas.

To examine that influence, we compared cougar activity from the wolf sites with human activity from the non-wolf sites. In this scenario temporal overlap between cougars and humans was 61.9% (Figure A2_2; 95% CI = 54.7-66.7%), or 14% greater than the overlap of cougar and human activity in the non-wolf areas, compared to the 25% reported in Chapter 3. Notably the confidence intervals for this estimate still do not overlap those for non-wolf areas (Fig 2; 40 – 53%). This finding suggests that in a hypothetical study area where cougar activity matched that observed in the presence of wolves, but human activity remained unchanged, the increase in overlap between the two species would still be significant.

Figure A2_1. Kernel density estimates of human intraspecific temporal activity overlap ($\widehat{\Delta}_4$) in areas with and without resident wolf packs. Human activity was similar between areas with and without wolves and overlapped by an average of 80.5% (95% confidence interval = 78.3 - 82.7%).

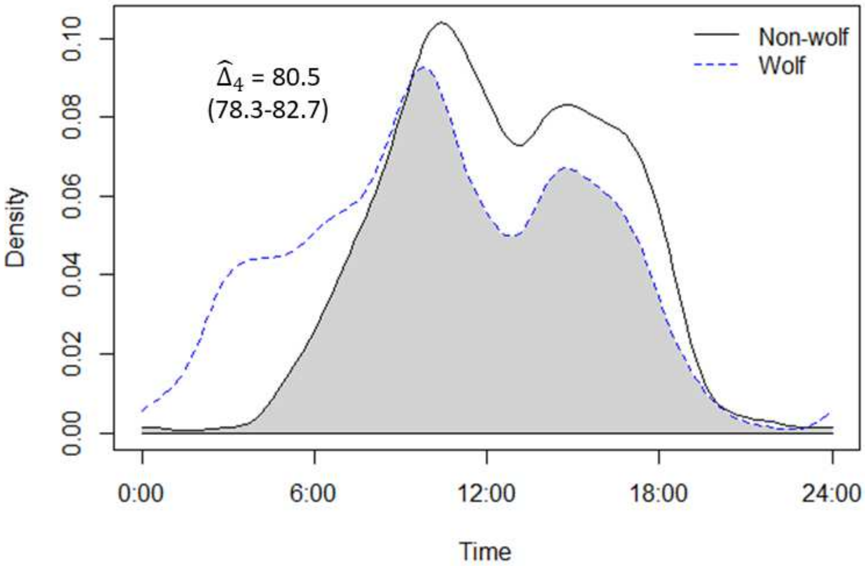
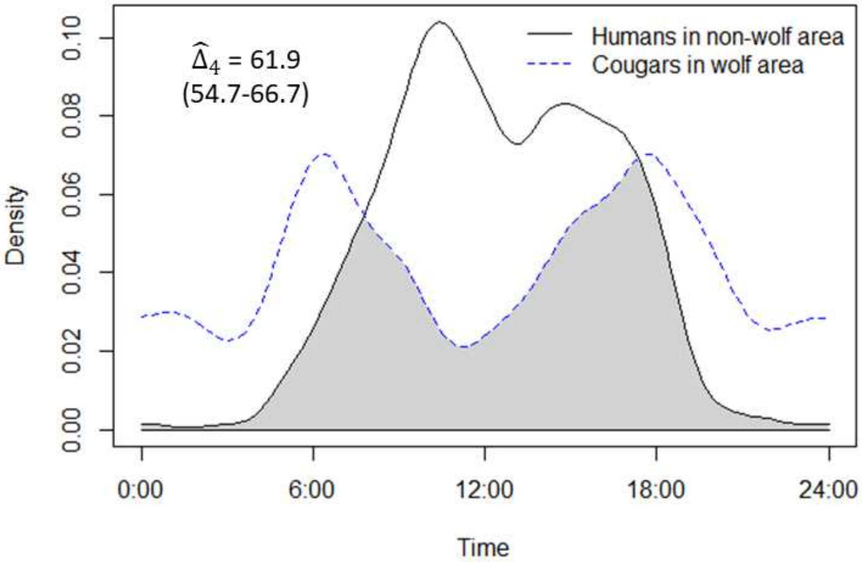
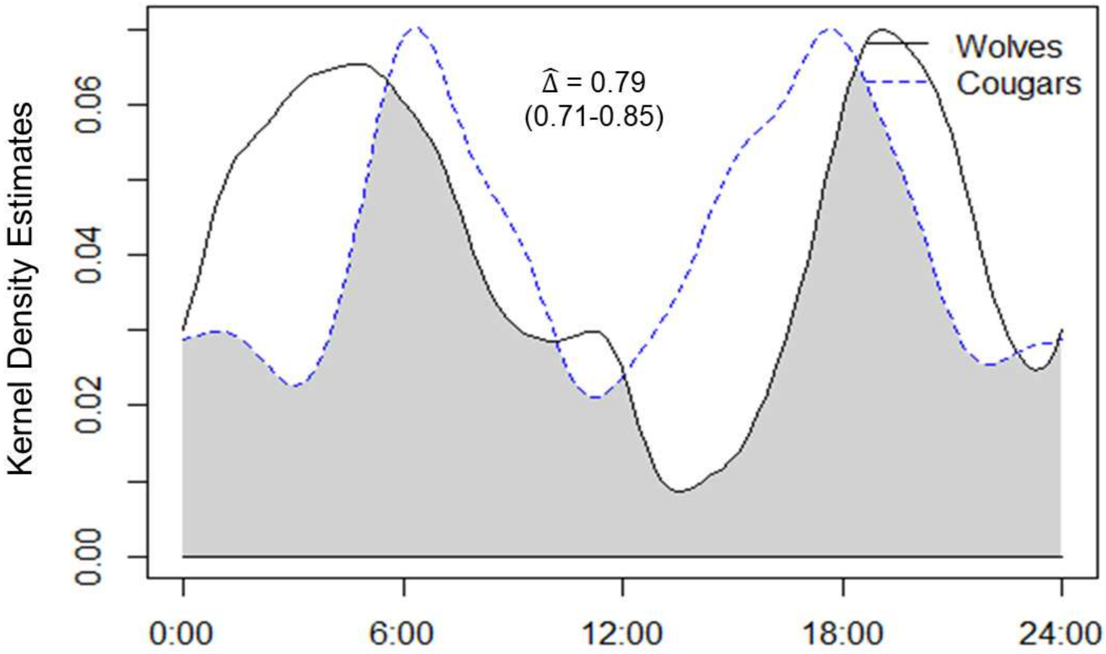


Figure A2_2. Kernel density estimates of temporal overlap ($\widehat{\Delta}_4$) of human activity in areas without wolves and cougar activity in areas with wolves. The average overlap was 61.9% (95% CI = 54.7–66.7).



Appendix 3. **Temporal activity overlap of cougars and wolves**

Kernel density estimates of temporal overlap (Δ_4) between wolves and cougars in areas with resident wolf packs. The average temporal overlap was 79% (95% CI = 71-85%).



Appendix 4. Differences in black bear (Ursus americanus) temporal activity between wolf and non-wolf areas

Table 1. Parameter coefficients (β) and 95% confidence intervals for a Zero-inflated Poisson (ZIP) GLMM comparing black bear diurnal activity between areas with and without wolves. Time is a binary variable with the categories Day and Night; wolf is a binary variable indicating wolf presence or absence. Night and wolf absence are the reference levels in the model. * indicates the coefficient is significantly ($p < 0.05$) different from zero. Black bears were significantly more likely to be photographed in the study areas with wolves (*Wolf presence* coefficient).Although black bears were less diurnal in areas with wolves, they were strongly diurnal in both study areas ($p<0.01$), and there was not a significant difference in black bear diurnal activity between the wolf and non-wolf areas.

Conditional model		
Parameter	β	95% CI
Intercept*	-3.54	-3.95 – -3.13
Day*	0.94	0.69 – 1.20
Day x Wolf*	0.41	0.25 – 0.72
Wolf Presence*	0.70	0.49 – 1.11
Zero-inflation model		
Intercept*	1.84	1.69 – 2.13