Ungulate Responses to Predators in Complex Landscapes of Northern Washington

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Abstract

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In 2008, after nearly 80 years of absence, gray wolves began to recolonize northern regions of Washington State. Wild ungulates comprise the majority of wolf diets, but the impact of recolonizing wolves on deer and elk in Washington is unknown. Cougars, bobcats, black bears, and coyotes compete with wolves for ungulate prey, while domestic dogs, vehicle collisions, human harvest, disease, and malnutrition also cause ungulate mortality. In my dissertation, I sought to determine how mule deer, white-tailed deer, and elk responded to predators through direct and indirect mechanisms within complex landscapes of wildfire, timber harvest, and human activity in northern Washington. Chapter 2 lays the methodological foundation in which I investigated how DNA evidence can improve the identification of predators at ungulate kill sites. I identified common errors in field-based mortality investigations and the factors contributing to these errors, informing when to prioritize genetic sampling. I also described key differences in predator signs associated with small prey (deer fawns and elk calves) versus adult deer kills. I applied these tools in subsequent chapters when identifying ungulate causes of mortality. In chapter 3, I examined how historic wildfires in north-central Washington shaped habitat structure and forage availability for mule deer, showing that mule deer use of burns depended on the season, wolf and cougar activity, and the characteristics of the fire that had burned there. In chapter 4, I modeled the demographic sensitivity of white-tailed deer to wolves, cougars, coyotes, bobcats, and human land management practices associated with forage availability. The population was co-limited by cougars, wolves, and forage, whereas bobcats and coyotes had less influence on population dynamics. Finally, I examined how elk navigated risk from cougars, wolves, and humans in Chapter 5, showing that elk altered habitat selection between day and night and depending on habitat structure to manage predation risk. Elk strongly avoided humans and predators rather than using areas of human activity as a refuge from predation risk. These findings illustrate how landscape context, particularly disturbance regimes and human presence, influence carnivore-ungulate interactions with important implications for wildlife management and conservation in anthropogenic landscapes.

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Chapter 1. INTRODUCTION

1.1 BACKGROUND

In 2008, gray wolves (*Canis lupus*) returned to Washington after nearly 80-years of absence (Wiles and Hayes 2011). Since then, these carnivores have recolonized northern regions of the state with additional territories in central and southeastern Washington. By the end of 2021, wolves had successfully established 33 packs across Washington (Washington Department of Fish and Wildlife et al. 2022). The return of wolves has led to broad questions about their impacts on ecosystems and created a rare opportunity to evaluate wildlife interactions across a range of wolf use and human activities. Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*) are all native to Washington and are expected to comprise the majority of wolf diets (Newsome et al. 2016). As a result, researchers, wildlife managers, and the public are interested in understanding the impact of wolves on these ungulates through predation (i.e., consumptive effects) and by influencing prey behavior (i.e., non-consumptive effects) (Lima and Dill 1990, Creel and Christianson 2008). Cougars (*Puma concolor*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*) compete with wolves for ungulate prey, leading to complex food web dynamics that have the potential to impact ungulates. Domestic dogs *(Canis lupus familiaris*), human harvest, vehicle collisions, disease, and malnutrition are other sources of ungulate mortality, adding further complexity. Within this system, human activities and natural disturbance regimes shape habitat structure, influencing primary productivity and predation risk with additional influences on ungulate population dynamics.

In 2016, the Washington State Legislature mandated that the Washington Department of Fish and Wildlife partner with the University of Washington to create the Washington Predator-Prey Project (WPPP; http://PredatorPreyProject.weebly.com). The WPPP aims to leverage the opportunity to study the impacts of recolonizing wolves in anthropogenic landscapes to inform the management and conservation of carnivores and their ungulate prey. The WPPP focuses on two study areas (Figure 1.1), where we outfitted bobcats, coyotes, cougars, and wolves with GPS collars from 2017 to 2021. We additionally deployed GPS and VHF collars on mule deer in the north-central Washington study area and elk and white-tailed deer in the northeast Washington study area, reflecting the predominant ungulate species in each region. Collectively, these data provided information about species' survival, distributions, and habitat use. My dissertation and the studies herein are one component of the larger WPPP. My goal was to disentangle the many interacting factors that influence mule deer, white-tailed deer, and elk populations, including forage, habitat structure, humans, and predators.

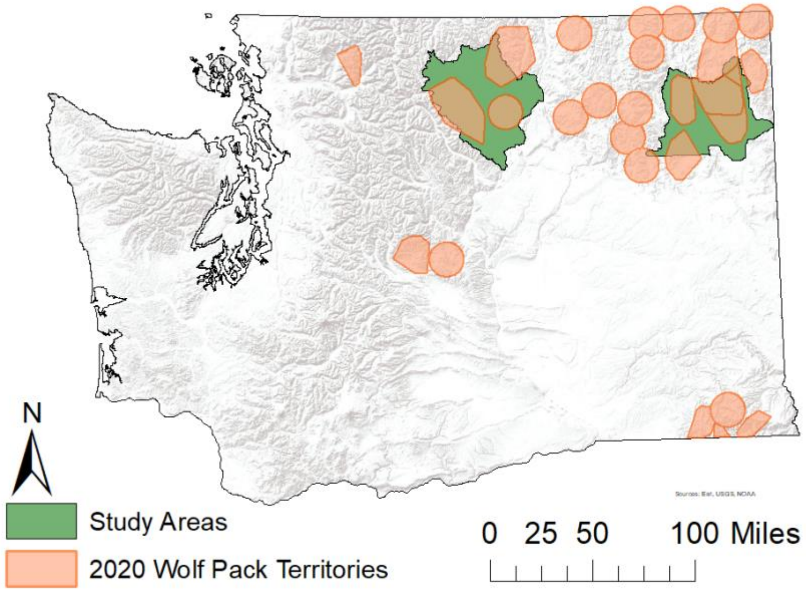

Figure 1.1 Washington Predator-Prey Project study areas and wolf pack territories across the state. Pack territories are delineated with 100% minimum convex polygons using locations from radio-marked wolves. Circles indicate known wolf packs without radio-collared individuals.

1.2 GOALS

One of the primary pathways through which predators impact prey is killing and consuming them (i.e., consumptive effects), and quantifying the rates and sources of mortality is a critical component in understanding the population dynamics of any species (Lotka 1925, Volterra 1926). In many studies of predator-prey interactions, including the WPPP, cause-specific mortality rates are estimated by monitoring a sample of radio-collared prey and identifying the cause when study animals die (Steigers and Flinders 1980, Ballard et al. 1981). When used in tandem with in-field kill-site investigations, genetic techniques improve the accuracy of mortality classifications by allowing for the identification of predators based on DNA evidence (Williams et al. 2003, Onorato et al. 2006, Mumma et al. 2014). However, genetic methods can be costly, and field investigators need guidance on when to prioritize DNA collection. In Chapter 2, I built a methodological foundation to improve mortality investigations of radio-collared prey, which I applied to subsequent chapters when assigning the cause of deer and elk mortalities. Specifically, I identified the factors influencing the efficacy of obtaining predator DNA and described the common errors associated with using in-field evidence alone. I then used genetic evidence as validation to improve the interpretation of in-field evidence by describing species-specific patterns of predation for prey of different sizes.

Predators not only influence prey through consumption but also alter prey vigilance, foraging, and habitat selection, with the potential to influence prey population dynamics via non-consumptive effects (Preisser et al. 2005). To mitigate predation risk, prey can exploit habitats with structural features disadvantaging the hunting mode of the predator (Preisser et al. 2007). Within the north-central study area of the WPPP, recent wildfires driven by climate change, fire suppression and loss of indigenous burning have drastically altered the landscape across which mule deer, cougars and wolves co-occur, shaping the interactions between them (Kimmerer and Lake 2001, Stavros et al. 2014, Jolly et al. 2015, Abatzoglou and Williams 2016). In Chapter 3, I examined how these burns shaped mule deer movement by enhancing forage in the summer and leading to deeper snow accumulating in the winter where the burned-away canopy cover no longer intercepted snowfall. Then, I considered how deer selection for or against these burns was altered by cougar and wolf activity and if predation was more likely in burned than unburned forests.

Like wildfires, land management practices such as logging can also impact the quality and availability of forage for deer. Bottom-up factors (i.e., forage resources) ultimately determine the potential carrying capacity of a landscape and influence the resilience of populations to top-down factors (i.e., predation), thus providing critical context when evaluating population regulation (Melis et al. 2009, Donadio and Buskirk 2016). In addition to inducing direct effects on prey species, apex predators can influence prey indirectly by changing the abundance or behavior of an intermediate species (Abrams et al. 1996). For example, in Wyoming, USA, the reintroduction of wolves suppressed coyotes, leading to increased survival of juvenile pronghorns (*Antilocapra americana*) and increased pronghorn abundance overall (Berger et al. 2008). In Chapter 4, I modeled the demographic sensitivity of white-tailed deer to land management practices associated with increased forage biomass for deer (as a proxy for a bottom-up effect), the direct effect of bobcats, cougars, coyotes, and wolves, and the potential indirect effect of apex predators on deer via mesopredator suppression.

Humans structure landscapes and influence wildlife dynamics through various pathways, though the outcome of such influences may be difficult to predict and context dependent (Dorresteijn et al. 2015). For instance, humans cause direct mortality of ungulates through vehicle collisions (Huijser et al. 2008) and hunting for recreational or subsistence purposes (Ballard et al. 2000), or humans may provide a refuge for ungulates species from human-averse carnivores (Berger 2007). Thus, human presence can substantially shape the landscape of fear (Ciuti et al. 2012) – the perception of predation risk that varies with time and space (Gaynor et al. 2019) – for wildlife. In Chapter 5, I examined whether elk exploit the human shield to mitigate risk from cougars and wolves or instead respond to humans as super predators (Darimont et al. 2015, Smith et al. 2017). I also showed how elk habitat selection shifted according to the diel cycle to reflect interactions between predator activity cycles and habitat structure, creating a dynamic landscape of fear (Palmer et al. 2022).

1.3 IMPLICATIONS

Populations of carnivores and their prey are declining worldwide (Estes et al. 2011, Ripple et al. 2014, 2015), and their long-term persistence increasingly depends on landscapes used by humans (Carter and Linnell 2016). This research adds important insights to the literature on predator-prey dynamics outside of protected areas, where humans manipulate landscapes, alter primary productivity, influence wildlife habitat selection (Bassing et al. 2022), and contribute to both predator and prey mortality (Ballard et al. 2000, Huijser et al. 2008). This research also adds compelling evidence to the existing literature demonstrating how the interactions between predator traits and habitat structure influence ungulate movement.

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Chapter 2. WILDLIFE WHODUNNIT: FORENSIC IDENTIFICATION OF PREDATORS TO INFORM WILDLIFE MANAGEMENT AND CONSERVATION

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Abstract: Genetic evidence at predation mortality sites is rapidly improving predator-prey interaction studies and can provide information beyond field-based investigations alone. However, factors contributing to the retention of genetic evidence have received limited investigation in a field setting, and researchers have yet to leverage genetic evidence to improve traditional field investigations. Using data from 61 mortality investigations of mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus canadensis*), we evaluated factors influencing predator DNA amplification success and misidentification of predators in field investigations. We found that predator DNA was detected more for prey with higher body mass (18.5% increase per standard deviation [23.1 kg] in carcass body mass above the mean [32.8 kg]). Predator DNA was also 27.0% more likely to amplify when collected from kill sites that had not undergone a freeze-thaw cycle between the mortality and the investigation.

The delay between the kill and the investigation, the swabbing surface, and the amount of precipitation did not influence amplification of predator DNA. Misidentifications of the predator based on the field ID were not influenced by the investigation delay or investigator confidence level, suggesting that investigators should collect genetic evidence even when they feel certain about the predator. Errors in identifying the predator during the field investigation increased for prey with smaller body mass, and the predator was actually more likely to be misidentified than correctly identified for fawns and calves <~21 kg. Black bears (*Ursus americanus*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and wolves (*Canis lupus*) were equally likely to be missed in a field investigation, but bobcats tended to be falsely assigned more than expected and cougars were falsely assigned as the predator less than expected. Using genetic evidence as validation, we showed how patterns of predation and the field signs left by predators differed for some species depending on the size of the prey. Our findings should help researchers and managers to optimize their use of genetics to enhance field investigations.

Keywords: carnivore, DNA, forensic analysis, genetic, mortality, predation, predator identification, saliva, ungulate

2.1 INTRODUCTION

Carnivores can affect the structure and dynamics of prey populations, with impacts extending throughout the ecological community (Sih et al. 1985, Sinclair et al. 2003). Researchers and wildlife managers are often interested in understanding food-web dynamics and identifying the factors regulating populations, with potential implications for predators and prey. For species below population targets that are limited by predation, management options have included increasing harvest of and relocating predators. For instance, the removal of bears (*Ursus* spp.) and wolves (*Canis lupus*) in Alaska increased survival and abundance of moose (*Alces alces*) and caribou (*Rangifer tarandus*; Boertje et al. 1996, Keech et al. 2011). For research to be informative, and management to be effective and ethical if predator removal is considered (Santiago-Ávila et al. 2018), it is essential to correctly identify the predators of prey.

To quantify the consumptive effects of predators on prey populations, cause-specific mortality rates are often estimated by monitoring a sample of radio-collared prey (Steigers and Flinders 1980, Ballard et al. 1981). When a mortality is detected, methods of inference such as evaluating carnivore tracks, scat, predator hair, associated predator signs (i.e. caching, scrapes, tree scratching), and the pattern of consumption of the prey are used to identify the most likely species of predator (Elbroch 2003, Eacker et al. 2016, Elbroch and McFarland 2019). Traditional field methods are imprecise at best, leading to unclassified mortality sites, and can contribute to misidentification of predator species (Onorato et al. 2006). Errors may result from investigator experience or over confidence, the challenge of distinguishing predator species based on scat and hair samples (Onorato et al. 2006, Morin et al. 2016), limited evidence available for examination (Peelle et al. 2019), interference of scavengers (Bauer et al. 2005), and similar carcass handling styles between predator species (Mumma et al. 2014, Elbroch and McFarland 2019).

Genetic techniques allow for the identification of predators based on DNA evidence at kill sites and can provide valuable insights when used in conjunction with field investigations (Williams et al. 2003, Onorato et al. 2006, Sundqvist et al. 2008). Predators can be identified from DNA left at kill sites in the form of saliva (Williams et al. 2003), hair (Onorato et al. 2006), and scats (Höss et al. 1992). Onorato et al. (2006) used genetic methods to identify predator hair and scats at elk (*Cervus canadensis*) calf mortality sites with 88.5% accuracy, while field-only methods were accurate for only 58% of predator hairs and 79% of predator scats. As a result, genetic identification is rapidly becoming a standard component of kill site investigations, particularly in predator-prey systems. Further, DNA can provide additional information such as sex and individual identification (Williams et al. 2003, Blejwas et al. 2006), yielding better management insight than field investigations alone.

Unfortunately, genetic identification can be costly, and there is little guidance on when and where to prioritize DNA collection if resources are limited. Additionally, knowledge about common misidentifications in kill site investigations can and should be leveraged to improve the training of field investigators and refine field investigations. To address these limitations, we collected predator DNA at the kill sites of collared deer (*Odocoileus* spp.) and elk by swabbing saliva from bite marks, collars and ear tags, and epithelial cells from predator scats. We aimed to (1) identify external factors such as weather, sample collection location, delays in sample collection, and the size of the individual prey that influence the efficacy of obtaining genetic material, (2) identify factors contributing to misidentifications of the predator species when using field evidence alone, (3) identify which predator species are most commonly misidentified in the field, and (4) describe species-specific patterns of predation for prey of different sizes.

We expected that DNA samples collected with the shortest time since mortality would have less time to degrade and have a higher rate of amplification success (Harms et al. 2015, Piaggio et al. 2020). We predicted that DNA collected from artificial surfaces (i.e. the collar and ear tags) would have higher rates of success in amplifying predator DNA (Peelle et al. 2019), and we expected that samples of predator DNA collected from the carcasses of larger prey (i.e., adult deer versus elk calves and deer fawns) would also be more successful in providing genetic information because the predator may spend more time handling and feeding on large prey, depositing more saliva. We expected that precipitation could wash away predator saliva and would reduce success of genetic identification (Brinkman et al. 2010), and that DNA undergoing a freeze-thaw cycle in the field would also be less likely to amplify (Takahara et al. 2015).

We expected that misidentifications would increase with the duration of time between the mortality and the field investigation because there would be more time for scavengers to destroy or contaminate the physical evidence at the site (Bauer et al. 2005). We also predicted that genetic evidence would be most beneficial where investigator confidence was low (i.e., misidentification rates would be lower with higher investigator confidence). If this were the case, it would indicate that researchers should prioritize collecting genetic information when they were uncertain about an investigation, but genetic information would be less important if investigators were confident in their classification of the predator. Additionally, we predicted that smaller prey (i.e., deer fawns and elk calves) would be more likely to have a misassigned predator from the field investigation because there should be less field evidence left to interpret compared to larger (i.e., adult) prey. We expected that predators would be most frequently misidentified for species within the same taxonomic family due to a similarity in prey handling styles, and that predators may handle smaller prey differently than larger prey due to shorter killing and feeding times.

2.2 METHODS

2.2.1 *Study Area*

We investigated mortalities of mule deer (*O. hemionus*), white-tailed deer (*O. virginianus*), and elk, in 2 northern Washington, USA, study areas (Figure 2.1). Black bears (*U. americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), cougars (*Puma concolor*), and wolves occurred in both study areas. Mule deer were captured in winter along the Methow Valley of Okanogan County (Okanogan Study Area) and ranged across the coniferous forests and shrub-steppe habitat of northcentral Washington through their annual migrations (latitude: *c.*

48.050° to 49.150°; longitude: *c.* −120.900° to −119.700°). Elevations ranged from 230–2830 m. In Mazama, WA, an average of 57 cm of rain and 292 cm of snow falls annually. Winters there were typically cold (average low of −7º C, average high of 1º C from December–March), while summers were warm (average low of 9º C to average high of 26º C from June–September; https://www.usclimatedata.com/climate/mazama/washington/united-states/uswa0264).

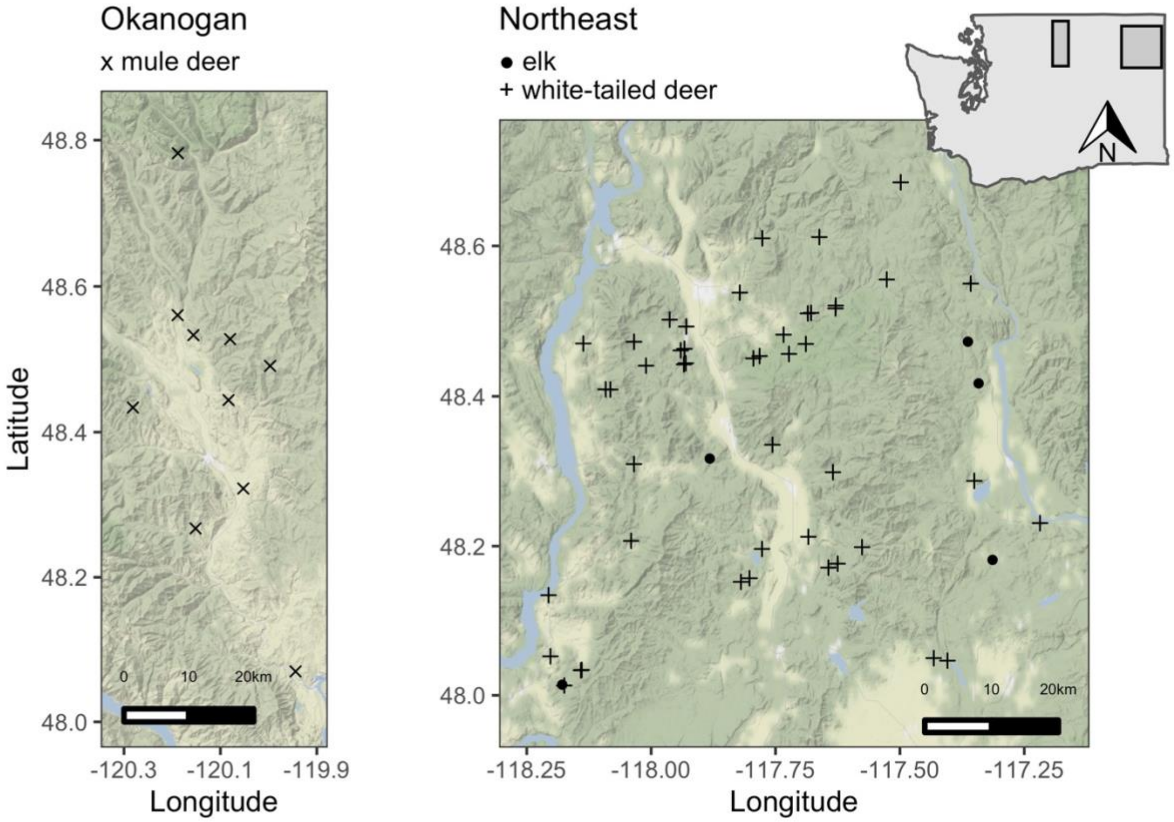

Figure 2.1 Locations of predation mortalities across northern Washington, USA, where lethal bite wounds (identified as hemorrhaged punctures) were swabbed for predator saliva DNA from 2017 to 2021.

Elk and white-tailed deer were captured in Stevens, Pend Oreille, and Spokane counties of northeastern Washington (northeast study area; latitude: *c.* 47.900° to 48.720°; longitude: *c.* −118.300° to −117.200°). Montane conifer forests managed for timber production dominated the mid-to-higher elevations of the region, while valley bottoms were predominately converted to agriculture. Elevations ranged from 370–2080 m. Chewelah, WA, at the center of the study area, received an average of 152 cm of rain and 114 cm of snow annually, with cool winters (average low of −6ºC, average high of 4º C from December–March) and warm summers (average low of 7º C to average high of 27º C from June–September; https://www.usclimatedata.com/climate/chewelah/washington/united-states/uswa0074).

2.2.2 *Field Methods*

From winter 2017 to spring 2021 we captured and collared adult female mule and white-tailed deer, white-tailed deer fawns, and elk calves. Adult female mule deer were captured by drive netting and aerial net-gunning (Kock et al. 1987) and fitted with GPS radiocollars (Model Vertex Plus, Vectronic Aerospace, Berlin, Germany). We captured adult female white-tailed deer and 6–8 month old white-tailed deer (both sexes) using a suspended net gun (Wildlife Capture Services, Flagstaff, Arizona, USA) or clover traps (Clover 1954, Hawkins et al. 1968, VerCauteren et al. 2000). Ground darting was also used to capture adult female white-tailed deer (Peterson et al. 2003). We fit adult female white-tailed deer with GPS radio-collars (Models Vertex Plus or Survey, Vectronic Aerospace, Berlin, Germany), and tested a subset of captured individuals for pregnancy with a portable ultrasound (Ibex Pro, E.I. Medical Imaging, Loveland, CO, USA). When pregnancy was detected, we inserted vaginal implant transmitters (VIT; VERTEX Natal-Link Vaginal Implant Transmitter, Vectronic Aerospace, Berlin, Germany) that triggered email and SMS notification on expulsion (Rice 2016). We used VIT expulsions to target neonates for capture, and we also captured white-tailed deer neonates opportunistically. White-tailed deer fawns were fitted with expandable, very high frequency (VHF) radio collars at capture (Model M4210, Advanced Telemetry Systems, Isanti, MN, USA and Model Vertex Natal-linked, Vectronic Aerospace, Berlin, Germany). We captured neonatal elk opportunistically and by targeting VIT expulsions from collared adult female elk (Bassing et al. 2022). Adult elk were not included in our study as none were confirmed to die by predation. Neonatal elk were fitted with expandable GPS (Model Survey, Vectronic Aerospace, Berlin, Germany) or VHF (Model M2230B, Advanced Telemetry Systems, Isanti, MN, USA) radiocollars. Neonatal deer and elk were weighed during capture. We used ANOVA to determine if the body mass of neonates varied by sex and year of capture and assigned the mean capture weight from the appropriate category if body mass at capture was unknown.

White-tailed deer, mule deer, and elk were captured in accordance with protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol No. 4226-01: Anti-Predator Behavior Effects) and adhered to the guidelines of the American Society of Mammologists for the use of live animals in research (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016).

Each GPS collar was equipped with mortality sensors that sent an email and SMS notification after 9 hours of inactivity. White-tailed deer fawn VHF collars were set to a 6-hour mortality delay, and elk calf collars were set to an 8-hour mortality delay. The VHF collars were programmed to transmit a code indicating the time of death. We monitored VHF collared individuals with radiotelemetry daily for the first 3 months of life, biweekly to 6-months old, and weekly from 6-months to 1-year old. Adults with GPS collars were monitored remotely. Mortalities were investigated as rapidly as possible upon detection to determine cause of death through June 2021.

We confirmed predation by skinning the carcass and finding evidence of lethal hemorrhage associated with bite marks (Williams et al. 2003). When predation was confirmed, we evaluated the predator tracks, sign and patterns of consumption following Elbroch (2003), Washington Department of Fish and Wildlife (2014), Stonehouse et al. (2016), and Elbroch and McFarland (2019) to determine the species of predator ostensibly responsible for the kill. We also noted the presence or absence of 12 indicators to identify the predator species. Indicators included blood on trails/vegetation, broken and crushed bones, caching or burial of the carcass, clipped or plucked hair, disarticulated limbs, a dispersed carcass, a drag trail, other dead animals, a peeled hide, an intact rumen, scratches on the hide, and predator tree scratching. Upon concluding the field investigation of the predation mortalities, investigators reported confidence in their assessment of the predator, ranging from 0 to 1, with a 0 assigned to cases where the predator was unidentifiable.

We swabbed the puncture wounds associated with the predation (identified by subcutaneous hemorrhage) for salivary DNA when these sites were uncovered in the skinning process to minimize the potential risk of contamination from scavenger DNA (Williams et al. 2003). Skinning knives were sterilized with bleach between mortality investigations and researchers wore sterile gloves while swabbing DNA; gloves were changed between swabbing sites if they became dirty or contamination was suspected. We wet sterile swabs (PurFlock Ultra®; Puritan Diagnostics LLC, Maine, USA) by dispensing 1 to 2 drops of phosphate buffered saline solution (pH 7.4) from a sterile eyedropper, and rolled the swabs over areas of predator saliva (Caniglia et al. 2013, Mumma et al. 2014) associated with lethal bites (i.e., the periphery of the hemorrhaged puncture), as well as collars, ear tags, and presumed predator scats. Presumed predator scats were identified by freshness, and importantly, collar, ear tag and predator scat swabs were collected as a supplement to salivary DNA collected from hemorrhaged punctures. Each swab was air dried and inserted individually into a coin envelope; the swab and envelope were preserved in desiccant before laboratory analysis. We did not sample bites without subcutaneous hemorrhage, as these could not be distinguished from the bites of scavengers. For each sampling site, swab replicates (labeled A and B) were collected. The first swab collected (A) was prioritized for extraction, and the second swab (B) was extracted if the A swab failed.

2.2.3 *Laboratory Analysis*

All DNA swabs were sent to the School of Environmental and Forest Sciences genetics lab at the University of Washington (http://sefsgeneticslab.weebly.com) that was specifically designed to process low-copy, degraded DNA (e.g., separate rooms for pre- and post-PCR processes to minimize contamination risk). The DNA was extracted from the swabs using Investigator Lyse&Spin and QIAamp DNA Investigator kits (Qiagen, Hinden, Germany) following the manufacturer's protocol. Species identification from samples was conducted using an assay that was optimized for detection of carnivore species that occur in Washington. The assay contained primers that amplified size-specific mitochondrial DNA fragments from different species of predators. Primers SIDL (Murphy et al. 2000) and Gulo1F (Dalén et al. 2004) were paired with reverse primer H3R (Dalén et al. 2004) to amplify canid, bear, and mustelid DNA at species-specific fragment lengths (De Barba et al. 2014). Primers FelidID F, Lruf R, and Pcon R (Davidson et al. 2014) were included to amplify cougar and bobcat DNA at species-specific lengths. Finally, primers DL1F and DL5R (Palomares et al. 2002) were included to amplify size-specific lynx DNA. The PCR reactions consisted of 0.12 µM FelidID F, 0.6 µM Lruf R, 0.6 µM Pcon R, 0.16 µM SIDL, 0.16 µM H3R, 0.08 µM Gulo1F, 0.16 µM DL1F, 0.16 µM DL5R, 4 µL of Qiagen Multiplex PCR Master Mix, 0.8 µL of Q solution, and 2 µL of extracted DNA for a final volume of 8 µL. The thermal cycling protocol consisted of an initial denaturation step of 95° C for 15 min, followed by 35 cycles of 94° C for 30 s, 46° C for 90 s, and 72° C for 60 s, followed by a final elongation step of 72° C for 15 min. Negative controls were used at both the DNA extraction and PCR stages to monitor for contamination, and positive controls were used to monitor the quality of PCR amplification. Two PCR replicates were amplified per sample, and PCR replicates were analyzed at Yale's DNA Analysis Facility using an ABI 3730 Fragment analyzer (Applied Biosystems, Foster City, CA, USA). The resulting sample electropherograms were checked for diagnostic species-specific amplification of predator DNA using GeneMapper 6 (Applied Biosystems, Foster City, CA, USA). Samples were assigned a genetic-based predator species ID if the electropherograms for both sample PCR replicates possessed the diagnostic amplified product for a particular predator species. If only 1 of the 2 PCR replicates for a sample exhibited amplification, 2 additional PCR replicates were run for that sample. Thus, we only accepted the species ID if at least 2 replicates returned the same ID. In cases where the initial genetic analysis yielded negative results or indicated the presence of multiple predator species, we processed additional swabs from the kill site using the same protocol. We then compared the predator species assigned during the field investigation to the species identified by the genetic evidence to find misidentifications. In cases where the genetic species identification did not match the field identification, we reviewed the investigation to ensure that the predator identified by genetics could be responsible for the evidence at the scene.

2.2.4 *Statistical Analysis*

To examine factors influencing the success of genetic testing (positive ID), we used logistic regression to test the influence of the delay between the mortality and the field investigation (days), the estimated body mass of prey at death (kg), the surface that was swabbed, the amount of precipitation, and if a freeze-thaw cycle had occurred between the deposition of predator DNA during the kill and the investigation. We considered a sample successful if either replicate amplified predator DNA and did not count A and B swabs from the same swabbing site separately. We classified the surface as hard if the saliva was collected from an ear tag or collar, and soft if it was collected from the carcass or a scat. All continuous variables in our models were standardized with a mean of 0 and standard deviation of 1 to improve model fit, and we confirmed that the Pearson's correlation between model covariates did not exceed 0.7 (Dormann et al. 2013).

To determine if DNA amplification success and misidentification rates depended on the size and associated age class of prey, we used estimated body mass as a continuous variable to describe prey size. Mule deer were not weighed in our study, so we used mean winter body mass of adult female mule deer captured in Ferry County, WA($\bar{x} =$ 70 kg, SD = 9, n = 25; J. Dellinger and A. Wirsing, The University of Washington, unpublished data). We assigned mean body mass of adult female white-tailed deer weighed in our study ($\bar{x} =$ 53, SD = 9 kg, n = 16; body mass recorded for 2017 captures only) if individual weight was not measured or used their individual weight if measured during captures. For white-tailed deer fawns, we estimated body mass at death given a rate of increase of 0.16 kg day^{-1} from 0–150 days old and a gain of 0.07 kg day^{-1} from 150–350 days old (Berry 2017). Similarly, elk calves gain 0.7–0.9 kg day^{-1} for the first 4 months of life (Cook 2002), which was the maximum age at which calves in this study died by predation. Thus, we estimated the body mass of calves at death as the capture mass + 0.8 kg days^{-1} since capture. Projected body mass for fawns captured at 6–8 months were estimated assuming those animals were born on the mean date of neonate birth for that year at mean capture weight.

We used precipitation and temperature data from the Parameter-elevation on Independent Slopes Model (PRISM) to describe weather conditions at kill sites, with data modeled on a daily basis at 800 m resolution (http://prism.oregonstate.edu; Daly et al. 2008). We summed the total amount of precipitation during the delay between the mortality and the investigation and determined if the predator DNA had been through a freeze-thaw cycle based on the minimum and maximum temperatures during the delay.

To investigate the drivers of predator misidentification in the field, we used logistic regression to examine the effects of estimated prey body mass at death, the delay between the mortality and the field investigation, and the confidence of the investigators in their physical evidence assessment. In this framework, predator misidentification was the response variable such that a 1 represented a misidentified predator and 0 represented a correctly identified predator. We also tested for an interaction between the time lag and the size of the carcass, because we hypothesized that larger carcasses would have lower rates of misidentification despite delays in the investigation as compared to smaller carcasses (i.e., the delay would be more consequential for smaller-bodied prey).

We used chi-squared tests to determine if misidentifications occurred for particular predator species at rates different than based on random chance. Misidentification was considered both from the perspective of false positives and false negatives. For example, a bobcat determined to be the predator from the field investigation but found through genetics to not be responsible for the kill would be classified as a false positive, whereas a kill genetically determined to be caused by a bobcat but assigned to another carnivore in the field would be classified as a false negative. To improve the interpretation of evidence at future field investigations, we summarized the field signs of predation and consumption that were associated with each carnivore species. To ensure we were not interpreting signs that may have been due to scavengers, we excluded cases where DNA from more than one predator species was detected.

2.3 RESULTS

We deployed mortality-sensitive tracking collars on 273 individual white-tailed deer (125 adults and 148 fawns), 148 adult mule deer, and 30 elk calves, for a total of 451 individual ungulates. There was no difference in body mass at capture for neonates between sexes (white-tailed deer: $F_{1,100} = 0.32$, $P = 0.6$; elk: $F_{1,21} = 1.8$, $P = 0.2$) or by year of capture (white-tailed deer: $F_{3,98} = 1.6$, $P = 0.2$; elk: $F_{2,20} = 0.25$, $P = 0.8$), so we assigned the mean neonate body mass at capture of that species across years if body mass at capture was unknown. Causes of mortality ($n = 215$ total mortalities investigated) included predation, malnutrition, disease, harvest, vehicle collision, and accidents (e.g., caught in a fence). Some causes of mortality remained unknown due to scavenger contamination, insufficient evidence remaining at the mortality site, or severe autolysis of tissues.

In total, we investigated 61 mortalities where genetic data were collected, and predation was confirmed as the proximate cause of death. We collected 202 samples, and on average, we were able to positively identify the predator for 76% of samples and 89% of all mortalities using DNA. On average, there was a 1.8-day delay (SD = 2.0, min–max = 0–10) between the mortality and the investigation. Genetic evidence improved inference at 21 mortalities using 3 different methods. First, there were 7 cases where the field evaluation was inconclusive, but we were able to identify the predator using genetics. Second, there were 13 cases where the predator was misidentified in the field but corrected with genetic information collected from swabbing lethal bites on the carcass. Third, there was one case where genetic methods identified 2 species of predator while the field investigators classified a different, third predator. In this case, we could not ultimately determine the responsible predator, but genetic evidence improved inference by avoiding a false positive.

2.3.1 *Drivers of DNA Amplification Success*

The DNA amplification success rates increased for larger prey, decreased if a freeze-thaw cycle occurred, and were unaffected by the delay, collection surface, and amount of precipitation. The likelihood of a positive genetic identification per sample increased by 18.5% (CI = 8.5–28.2%) with a standard deviation increase in carcass body mass (23.1 kg) above the mean (32.8 kg) (Figure 2.2; Appendix A, Table A1). If a freeze-thaw cycle occurred, the odds of success decreased by 27.0% (CI = 6.3–40.1%). Surprisingly, amplification success was not affected by the delay in the investigation (z = 1.41, *P* = 0.16; Appendix A, Table A2). Samples collected from ear tags and the collar (i.e., hard surfaces; *n* = 54) rather than the carcass (i.e., soft surfaces; *n* = 148), had a slightly higher success rate of detecting DNA (86.6% vs. 82.8%), but the effect was not significant (z = −0.73, *P* = 0.47; Figure 2.2; Appendix A, Table A1). Precipitation ranged from 0.0 to 5.0 cm ($\bar{x}$ = 0.3, SD = 0.7) and had no influence on DNA retention (z = 0.12, *P* = 0.91).

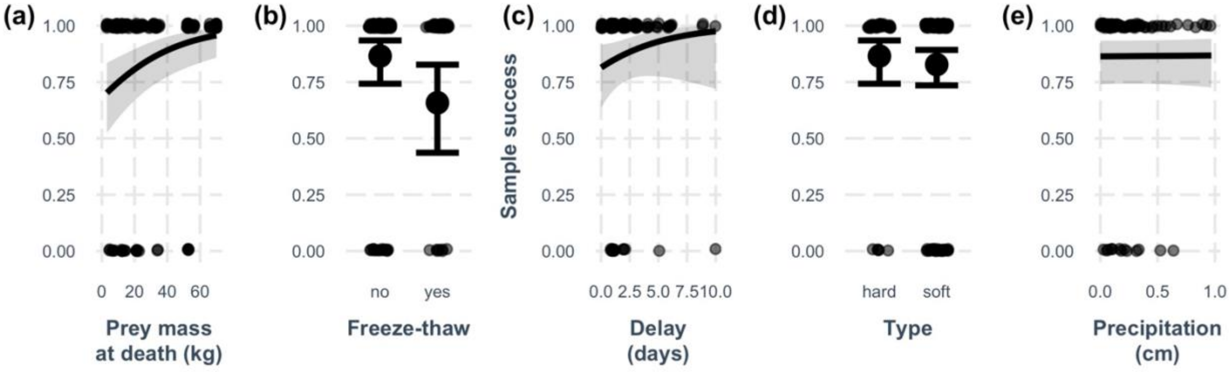

Figure 2.2 Factors influencing amplification of predator DNA at kill-sites of white-tailed deer (adult females and fawn), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021. Successful amplification was more likely for prey with larger mass at death (a)

and if a freeze-thaw cycle did not occur between the kill and investigation (b). The delay between the predation event and the investigation (c), the sample collection location (hard refers to samples collected from collars and ear tags, soft refers to samples collected from the carcass and scats) (d), and the amount of precipitation (e), did not influence if DNA was amplified from the sample. Coefficient estimates and odds ratios are presented in Appendix A, Table A1.

2.3.2 *Drivers of Misidentifications*

After excluding samples where the genetic ID was inconclusive and removing data where predator confidence was not recorded (6 mortalities), we had 48 predation mortalities to examine factors contributing to predator misidentifications. Estimated prey body mass at death was the only significant predictor of misidentification. For every standard deviation (22.8 kg) below the mean prey body mass at death (41.1 kg), investigators were 33.3% (CI = 13.8–46.0%) more likely to misidentify the predator (Figure 2.3; Appendix A, Table A3). Moreover, investigators at confirmed predation mortalities were more likely to misidentify the predator species when estimated prey body mass at death was below 21.26 kg, at which points fawns were approximately 3.5 months old whereas elk calves were 3–4 days old. Counter to our predictions, there was no significant effect of the delay between the mortality and the investigation ($z = -0.39$, $P = 0.70$) on rates of misidentification based on field evidence. Likewise, there was no effect of investigator confidence in their assessment of the predator ($z = 0.16$, $P = 0.87$), which ranged from 0 to 1 ($\bar{x} = 0.76$, SD = 0.35), nor was there an interaction between the investigation delay and prey body mass at death ($z = -1.17$, $P = 0.24$).

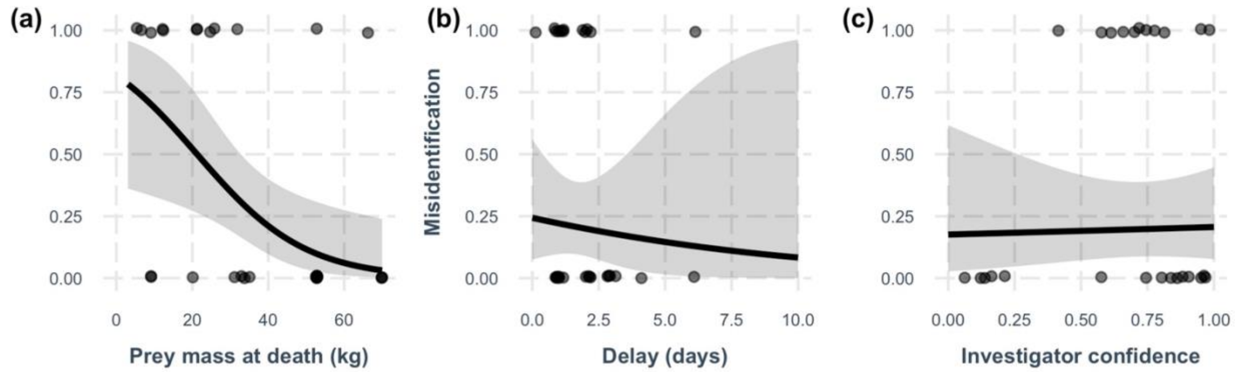

Figure 2.3 Factors influencing misidentifications of predators based on field evidence at mortalities of white-tailed deer (adult females and fawns), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021. The probability of misidentification of the predator from field evidence alone increased as prey mass at death decreased (a). The delay between the predation event and investigation (b) and the confidence of the investigator in their assessment of the predator (c) were unrelated to the misidentification of the predator when based on field evidence alone. Coefficient estimates and odds ratios are presented in Appendix A, Table A3.

2.3.3 *False Negatives and False Positives*

All predators were equally likely to be missed by the field investigators and assigned to a different, incorrect predator (i.e., a false negative) ($\chi^2 = 2.56$, df = 4, $P = 0.6$). Rates of being falsely assigned in the field when a different predator was responsible for the kill (i.e., false positives) varied significantly at the $\alpha = 0.10$ level ($\chi^2 = 8.87$, df = 4, $P = 0.06$) but not at the $\alpha = 0.05$ level. Bobcats were 2.4 times more likely to be misattributed as the predator than expected with 6 false positives observed and only 2.5 expected. The 6 mortalities misattributed to bobcats in the field had cougar ($n = 4$) and coyote ($n = 2$) DNA associated with hemorrhaged bite wounds, indicating that cougars and coyotes were the true predators (Table 2.1). Cougars were less likely to be misassigned as a predator in the field than was expected; false positives were 0.46 times the expected rate (3 observed, 6.5 expected) at kill sites.

Table 2.1 Cases of predations of white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021, where the genetic information from the predator differed from the assessment of the field investigators (i.e., misidentifications). False positives refer to species that were assigned in the field, but genetic information revealed that they were not associated with lethal bites. False negatives refer to the species identified by genetic information but misidentified in the field investigation. Where the genetic ID is inconclusive, more than one species of predator was positively identified on samples collected from hemorrhaged bites, but none were the species identified in the field investigation.

		Genetic ID						
		Bear	Bobcat	Cougar	Coyote	Wolf	Inconclusive	Total false positives
Field ID	Bear	0	0	1	0	0	1	2
	Bobcat	0	0	4	2	0	0	6
	Cougar	0	2	0	1	0	0	3
	Coyote	0	1	2	0	0	0	3
	Wolf	0	0	0	0	0	0	0
	Inconclusive	1	0	3	2	0	1	7
	Total false negatives	1	3	10	5	0	2	21

2.3.4 *Predator Sign*

We successfully amplified predator DNA at 54 kills. Of these, we detected DNA from more than one species of predator at 7.4% of mortalities, indicating scavengers may have contaminated these sites. Evidence of scavenging was detected only at kills of juvenile prey (<1 year old) and not at adult predations (>1 year old) but included fawns and calves ranging from 8 to 102 kg ($\bar{x}$ = 38.8, SD = 28.9 kg). After eliminating kills with evidence of scavenging and removing one mortality where no indicators of predator sign were recorded, we had a sample of 49 confirmed predations. Because the probability of misidentification was greater than 50% for prey <21.26 kg at death, we used this body mass as the threshold to categorize small versus large prey. A summary of predation sign (Table 2.2) associated with different species highlights the difference in the sign left from black bears, bobcats, cougars, and coyotes for large (>21.26 kg) and small (<21.26 kg) prey.

Table 2.2 Sign associated with each predator for confirmed mortalities of white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021, where there was no evidence of scavenging. Predator sign is compared for large prey (>21.26 kg) and for small prey (≤21.26 kg, the size of the average white-tailed deer fawn at 3.5 months old or a 3–4-day old elk calf) as this was the threshold below which investigators were more likely to misidentify the predator than correctly identify the predator if only using field evidence. The total number of predations is indicated as *n*, while each predation sign reports the number of cases where that sign was recorded/the number of cases where data was collected for that indicator. There were no confirmed wolf predations of small prey without evidence of scavenging.

	Predator	*n*	Blood trail/on vegetation	Broken and crushed bones	Buried/ cached	Clipped/ plucked hair	Disarticulated Limbs	Dispersed carcass	Drag trail	Other dead animals	Peeled hide	Rumen intact	Scratches on hide	Predator tree scratching
Large Prey (> 21.26 kg)	Bear	3	2/3	3/3	0/3	1/3	3/3	2/3	0/3	0/3	1/3	0/3	3/3	0/3
	Bobcat	5	3/5	2/5	4/5	4/5	3/5	0/5	3/5	0/5	0/5	4/5	2/5	0/5
	Cougar	23	5/23	6/23	17/23	17/23	8/23	2/18	11/23	2/23	1/13	19/20	13/23	3/23
	Coyote	2	½	½	0/2	0/2	2/2	2/2	½	0/2	1/1	½	½	0/2
	Wolf	1	1/1	0/1	0/1	0/1	1/1	0/0	0/1	0/1	0/0	0/0	0/1	0/1
Small Prey (≤ 21.6 kg)	Bear	2	½	2/2	0/2	0/2	2/2	½	0/2	0/2	2/2	0/2	½	½
	Bobcat	1	1/1	0/1	1/1	0/1	0/1	0/1	1/1	0/1	0/1	0/1	0/1	0/1
	Cougar	7	4/7	4/7	3/7	2/7	5/7	1/7	3/7	0/7	0/7	4/7	4/7	1/7
	Coyote	5	2/5	4/5	3/5	1/5	4/5	3/5	1/5	1/5	0/5	1/5	3/5	0/5

2.4 DISCUSSION

Our study adds to recent evidence indicating that genetic data markedly improves the classifications of predation mortalities by adding important data to that collected during field investigations (Onorato et al. 2006, Mumma et al. 2014). Our findings indicated that considering predator DNA in addition to the field evidence can be important in identifying the predator for smaller-bodied prey. We found that prey weighing less than ~21 kg at death (i.e., deer fawns ~3.5 months old and elk calves 3–4 days old) were more likely to be misidentified than correctly identified during field investigations despite well-trained field crews that systematically recorded 12 indicators of predator identity. Our findings highlight that genetic methods are especially valuable in regions with diverse carnivore assemblages due to the high likelihood of misidentification based on field sign alone. Overall, genetic evidence improved mortality investigations at 34% of kill sites, similar to rates observed by Onorato et al. (2006) and Mumma et al. (2014).

Contrary to our expectation, we found that a delay in sample collection did not reduce DNA amplification success across our 0–10 day range. We investigated most carcasses within 2 days, but some investigations occurred up to 10 days after the mortality event. Our results demonstrates that genetic evidence can still be valuable even if the investigation is substantially delayed. Mumma et al. (2014) similarly investigated most carcasses within 1–2 days of mortality but some investigations occurred up to 6 days post-mortem, and they also found no effect of the delay on sample retention. Most studies documenting DNA degradation over time have focused on degradation from 0–48 hours since deposition (Blejwas et al. 2006, Sundqvist et al. 2008, Harms et al. 2015, Piaggio et al. 2020), a time frame that may be unachievable to access a carcass despite best efforts for many field studies. It is possible that samples degrade in the first 2 days and then stabilize, which could explain the difference between our findings and those of Blejwas et al. (2006), Sundqvist et al. (2008), Harms et al. (2015), and Piaggio et al. (2020). While our findings suggest that genetic evidence can still be useful even after a long delay, we emphasize that mortalities should be investigated as rapidly as possible because the evidence needed to confirm predation may be destroyed by consumption of the carcass and scavengers have more time to contaminate the site.

Of all the environmental and biological factors we hypothesized could affect the success of amplification and identification, prey size was most influential. Successful amplification of DNA decreased with prey size, and field investigators also misidentified predators most often for the smallest prey (i.e., deer fawns and neonatal elk). Thus, despite lower amplification success rates at neonatal mortality sites, DNA evidence is most valuable in investigating these mortalities. As Sundqvist et al. (2008) and Mumma et al. (2014) have pointed out, it is important to collect multiple samples at predation mortalities, and we further recommend that investigators focus on collecting additional samples at mortalities of smaller prey (i.e., younger age classes) to increase the chances of positively identifying a predator.

We found that in-field freeze-thaw cycles reduced DNA amplification success, indicating that investigators should prioritize rapid investigations of carcasses when temperatures fluctuate above and below 0°C. Takahara et al. (2015) similarly found that freezing and thawing reduced detection of eDNA in water samples. Surprisingly, increased precipitation did not reduce amplification success in our study, perhaps because many samples were cached or covered in snow which could have helped preserve DNA. To our knowledge, effects of precipitation on retention of salivary DNA have not been tested but could be considered in an experimental context. However, DNA collected from the exterior of deer scats has been shown to degrade marked with rainfall (Brinkman et al. 2010). We did not explore differences in rain versus snow because we could not distinguish which occurred when there was precipitation and temperatures fluctuated above and below freezing. Of the 202 samples, 105 were collected from mortalities receiving precipitation in the field, and half of those mortalities (52) were exposed to a minimum temperature below freezing, so the precipitation could have been snow. It is reasonable to expect that snow could help preserve DNA while rain could wash it away which may explain the lack of a net effect from precipitation.

Peelle et al. (2019) found that amplification success of predator DNA from snowshoe hare kills was more successful when samples were collected from hard surfaces, such as the plastic collar box, compared to soft surfaces such as bite wounds. In contrast, we did not detect an effect of the swabbing surface on amplification success. We therefore recommend that investigators swab both hard and soft surfaces to maximize the potential of obtaining predator DNA. Hemorrhaged bites are the best way to ensure DNA is collected from the predator and not a scavenger, and these samples should be weighted more heavily in the evaluation of the mortality if they positively identify a carnivore. However, DNA collected from the collar or ear tags can be exceedingly valuable if these are the only evidence found. Positive genetic classification from a hard surface can be used to indicate that a collar is from a probable mortality with the detection of predator or scavenger DNA rather than a potential dropped collar if no DNA is detected. This is especially important in studies of neonates, where expandable collars are designed to drop off the individual after a certain period. While not included in this study because they could not be confirmed as predation events, we documented 8 instances where carnivore DNA was amplified from the radio-collar when only the collar was found. While it is possible that DNA on a collar alone could occur when a carnivore finds and carries a dropped collar, such occurrences are likely rare (Windell et al. 2019), and it is far more likely that detection of DNA on collars represents cases where prey died and the saliva was from the predator or a scavenger.

Misidentification rates were not significantly affected by the delay between the mortality and the investigation or the confidence of the investigator. Delay may indeed be important, and the lack of significance could have reflected a small sample size (13 misidentifications out of 48 considered mortalities). We suspect that investigators were hesitant to make a classification for cases with long delay, and only assigned a predator in those cases when the evidence was exceptionally clear, otherwise classifying the cause of death as inconclusive. This would have reduced the misidentification rate associated with the delay between the kill and the investigation. Contrary to expectations, misidentifications rates were unaffected by investigator confidence. All investigators had been trained in ungulate necropsies, identifying predator tracks and sign, and identifying kill and consumption patterns for the predators in this study area, and they followed consistent protocols during predation investigations. The lack of effect is particularly important and implies that investigators are just as likely to misidentify the predator when they have high confidence in their field-based assessment. Thus, we recommend use of genetic methods to supplement field investigations regardless of investigator training or confidence.

We predicted that some predator species were more likely to be misidentified than others in the field. While we did not find a statistically significant difference, we suspect that the relatively small sample size of misidentifications limited our ability to detect such an effect and that species within the same taxonomic family are indeed more likely to be confused for one another. We noted frequent confusion between bobcats and cougars, which was likely due to their similar handling style of carcasses (Elbroch and McFarland 2019). In the field, investigators primarily differentiated between cougars and bobcats based on the size of their tracks and the distance between canine punctures (Stonehouse et al. 2016). One reason for a potential under identification of cougars in lieu of bobcats could be that juvenile cougars were mistaken to be bobcats due to their smaller size. We also saw that cougars more consistently cached larger adult deer and elk calves than fawns, and the rumen was more frequently found intact for large prey than small prey of cougars. Due to the small size of the prey, a cougar may consume most of a fawn in a single feeding bout rather than leaving signatures such as a cache. Intact rumens were ubiquitous at cougar and bobcat predations of adult deer, but this was only observed for half of cougar and bobcat predations of deer fawns and elk claves < ~21 kg at death (Table 2.1). Neonatal fawns dying from causes other than predators often had stomachs full of milk upon death, which may have been palatable to cougars while rumens of adult deer were not.

Although most misidentifications involved confusion among felids, bobcats and cougars were also mistaken for coyotes in several cases. In 3 out of 7 cases of predation mortality of fawns with no evidence of scavenging, coyotes buried carcasses after partial consumption. These can be mistaken for carcass caches typically found at bobcat and cougar kill sites. Also, coyotes tend to disperse carcass parts, which makes the investigation difficult when attempting to find lethal wounds or evidence of a struggle. These feeding characteristics could make it more challenging to identify predation events caused by coyotes.

When applying forensic techniques, researchers need to remain vigilant to minimize the risk of contamination. Contamination can occur due to scavenger activity at the site, sources introduced during the investigation, while samples are in transit, or in the lab. Swabbing bite wounds with lethal hemorrhage reduces the risk of detecting scavenger DNA but does not eliminate the possibility. Indeed, in our study we detected DNA from 2 species of predator on lethal wounds at 4 out of the 61 confirmed predations. In 2 cases, we deduced the responsible predator versus the scavenger based on physical signs at the site, but we were ultimately unable to classify the predator at the other 2 mortalities. Additionally, it is possible that field researchers could introduce predator DNA to a site (e.g., through dirty clothes or equipment), so using sterile gloves and appropriately cleaning equipment is essential. We also recommend that researchers occasionally collect blank samples of PBS buffer (if using) in the field to process and ensure that the solution has not been contaminated. All genetic lab work should be done in sterile conditions, with separate rooms for pre- and post-PCR processes, and negative and positive controls used at all steps of the process to monitor for any contamination.

2.5 MANAGEMENT IMPLICATIONS

Forensic DNA analysis is rapidly advancing the understanding of complex predator-prey interactions and improving information available to inform research, conservation, and management. However, it is critical to remember that genetic evidence alone cannot distinguish between a predator and a scavenger at a kill site, and the field investigation remains an essential component in determining the cause of death. With this in mind, we make the following recommendations regarding genetic evidence:

1. Genetic evidence consistently improves kill-site investigations and should be a standard component of predation mortality studies, especially where there is a rich community of carnivores that may prey on ungulates and regardless of the confidence or training level of the investigators.
2. More genetic samples should be collected for smaller prey (i.e., deer fawns and neonatal elk versus adult deer) because their predators are more frequently misidentified, yet DNA

samples are less likely to amplify. Additionally, investigators should be mindful that predator sign associated with small prey often differs from that of larger prey. For instance, cougars frequently cached the carcasses of large prey and left the rumen intact, while this was less common for small prey.

3. Rates of DNA amplification success decreased when a freeze-thaw cycle had occurred in the field. Investigators should collect more samples in these conditions to increase the likelihood of a positive identification.

Where the potential predators under consideration are in the same taxonomic family, collecting genetic evidence should be prioritized to help to distinguish the species and avoid misidentifications.

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Chapter 3. INTERACTIVE EFFECTS OF WILDFIRES, SEASON, AND PREDATOR ACTIVITY SHAPE MULE DEER MOVEMENTS

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Abstract: Wildfires are increasing in size, frequency, and severity due to climate change and fire suppression, but the direct and indirect effects on wildlife remain largely unresolved. Fire removes forest canopy, which can improve forage for ungulates but also reduce snow interception, leading to a deeper snowpack and potentially increased vulnerability to predation in winter. If ungulates exhibit predator-mediated foraging, burns should generally be selected for in summer to access high-quality forage and avoided in winter to reduce predation risk in deep snow. Fires also typically increase the amount of deadfall and initiate growth of dense understory vegetation, creating obstacles that may confer a hunting advantage to stalking predators and a disadvantage to coursing predators. To minimize risk, ungulates may therefore avoid burns when and where stalking predators are most active and use burns when and where coursing predators are most active. We used telemetry data from GPS-collared mule deer (*Odocoileus hemionus*), cougars (*Puma concolor*), and wolves (*Canis lupus*) to develop step selection functions to examine how mule deer navigated species-specific predation risk across a landscape in northern Washington, USA that has experienced substantial wildfire activity during the past several decades. We considered a diverse array of wildfire impacts, accounting for both the severity of the fire and time since the burn (1 to 35 years) in our analyses. We observed support for the predator mediating foraging hypothesis: mule deer generally selected for burned areas in summer and avoided burns in winter. In addition, deer increased use of burned areas when and where wolf activity was high and avoided burns when and where cougar use was high in winter, suggesting the hunting mode of resident predators mediated the seasonal response of deer to burns. Deer were not more likely to die by predation in burned than in unburned areas, indicating that they adequately manage fire-induced changes to predation risk. As fire activity increases with climate change, our findings indicate the impact on ungulates will depend on tradeoffs between enhanced summer forage and functionally reduced winter range, mediated by characteristics of the predator community.

Keywords: *Canis lupus*, magnet effect, *Odocoileus hemionus*, predator-prey interactions, *Puma concolor*, step selection function, ungulate, wildfire

3.1 INTRODUCTION

Across the globe, climate change, a history of fire suppression, and loss of indigenous burning practices have increased the frequency, size, and severity of wildfires, with the risk of catastrophic fires predicted to rise into the future (Kimmerer & Lake, 2001; Stavros et al., 2014; Jolly et al., 2015; Abatzoglou & Williams, 2016). Such changes in fire regime alter the distribution, structure, and composition of vegetation, with cascading impacts on the wildlife those habitats support (Hessburg et al., 2005; Geary et al., 2020). The impacts may be direct, by altering the food resources available to herbivores (Raynor et al., 2015; Westlake et al., 2020), or indirect, by influencing predation rates (Leahy et al., 2015), predator distributions (Jorge et al., 2020) or driving a behavioral response to changing predation risk (Cherry et al., 2017). The impacts of wildfire depend on both the time since the fire and the severity of the fire, though rarely are the diversity of the impacts considered simultaneously, leading to a variety of observed effects on wildlife (Volkmann et al., 2020). For instance, ungulates have been shown to avoid burned areas (Eckrich et al., 2019; Konkolics et al., 2021), select for burned areas (Keay & Peek, 1980; Pearson et al., 1995; Westlake et al., 2020), and show no response or a mixed response to burned areas (Long et al., 2008; Roerick et al., 2019; Gogan et al., 2019; Eckrich et al., 2020). To understand how herbivores repond to burns, it is necessary to consider both the spectrum of fire characteristics and the potential direct and indirect pathways of their effects.

Historically, low and mixed-severity fires of western North America burned frequently, reducing canopy cover and surface fuels while increasing light to the understory, facilitating the growth of the herbaceous understory (Arno & Fiedler, 2005; Hessburg et al., 2005). In xeric landscapes of western North America, the nutritional value of the understory improves immediately following a fire, though peak abundance of forage for ungulates occurs 6 – 15 years post fire before returning to near pre-fire levels after ~ 20 years (Proffitt et al., 2019; Hull et al., 2020; Hayes et al., 2022). Improved forage in burned areas often attracts herbivores, termed the magnet effect (Archibald et al., 2005). Such attraction to fire-affected areas can persist up to 20 years (Wan et al., 2014; Raynor et al., 2015; Westlake et al., 2020). Wildfire can also impact predation risk through structural changes in the landscape. Homogeneous burns can reduce hiding cover for prey (Germaine et al., 2004) and stalking predators, whereas heterogenous burns can create patchy refugia for prey (Skatter et al., 2017) and provide cover for stalking predators (Doherty et al. 2022). Fire may increase structural complexity through an accumulation of deadfall and initiating regeneration of serotinous vegetation, which could impact predator detection and evasion abilities for ungulates (Metsaranta et al., 2003). Predation risk management by ungulates in heterogenous landscapes, such as those impacted by wildfire, may depend on the hunting mode of the predator (Preisser et al., 2007; Kohl et al., 2019). Stalking predators such as cougars (*Puma concolor*) exploit complex landscapes where it is easier to approach prey undetected (Ruth et al., 2019), which may cause ungulates to avoid burned areas if fires increase deadfall and initiate the growth of dense understory vegetation. Alternatively, cursorial predators such as wolves (*Canis lupus*) favor open areas to hunt (Kauffman et al., 2007), and ungulates may utilize burned areas to minimize wolf predation risk. Thus, it may be necessary to account for characteristics of the predator community to predict how ungulates will respond to wildfires (Doherty et al. 2022).

Predation risk effects, particularly as related to wildfire, may also be seasonally dependent. Fire can increase snow depth by allowing falling snow that would have been intercepted by the canopy to accumulate to deeper levels (Musselman et al., 2008; Varhola et al., 2010; Maxwell et al., 2019). Studies from Isle Royale, USA (Post et al., 1999) and Banff National Park, Canada (Hebblewhite, 2005) have shown that snowpack strongly influences an ungulate’s ability to evade predators, favoring predators over prey in deep, low-density snow that may accumulate in recent burns. For example, deeper snow increased rates of predation from wolves and coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) because the higher ungulate foot load caused deer to sink deeper into the snow than carnivores, impeding escape from predators (Nelson & Mech, 1986; Olson et al., 2021). Because adult ungulates suffer the highest rates of predation mortality in winter relative to other seasons, snowpack characteristics could strongly influence their populations (Brodie et al., 2013; Forrester & Wittmer, 2013; van de Kerk et al., 2020; Cosgrove et al., 2021). Deeper snowpack also increases energetic output for ungulates and can hinder their ability to access key nutritional resources when forage is buried under deep or crusty snow (Parker et al., 1984; Gilbert et al., 2017; Penczykowski et al., 2017).

In navigating these complex, fire-affected landscapes, ungulates must balance the need to secure high quality nutrition while minimizing the risk of predation (i.e., risk sensitive foraging; Brown, 1988). Fear of predators can drive prey away from the highest quality food resources, with potential consequences for prey survival and distribution (Brown et al., 1999; Hernández & Laundré, 2005). For instance, white-tailed deer avoided burned areas with high quality forage to minimize predation risk when rearing fawns in Georgia, USA (Cherry et al., 2017). Understanding the responses of ungulates to wildfires therefore requires considering food resources, shifting predation risk, and the tradeoffs therein (Doherty et al., 2022).

Here, we examine the movement and survival of adult female mule deer (*O. Hemionus*) in northern Washington, USA from summer 2017 to winter 2020 – 2021 to determine how they respond to a diverse history of wildfire while being subject to cougar and wolf predation risk. We also used remotely sensed data to determine if fire reduced canopy cover, improved forage quality, and led to a deeper snowpack. This region experienced major wildfires in 2001, 2003, 2006, 2014, 2015, 2017 and 2018, creating a complex landscape to study the impacts of fire on predator-prey dynamics (MTBS Project, 2021). Wolves began to naturally recolonize this region in 2008 after nearly a century of extirpation and some areas remain unoccupied, providing a unique opportunity to examine predator-prey dynamics in areas with and without wolves.

We used global positioning system (GPS) telemetry data to model wolf, cougar, and mule deer activity to test three primary hypotheses of how ungulates could respond to a gradient of wildfire impacts and predator use. Under the *magnet effect hypothesis* (H1), ungulates should be attracted to the high-quality forage of low and moderate recent burns (< 20 years post fire) independent of predator use in the summer, selecting for these burns irrespective of predation risk. Under the 2-component *predation risk hypothesis* (H2), ungulate movement in response to burns should reflect the traits of the predator (*predation risk effect – predator traits hypothesis*, H2a); i.e., in periods with no or low snow, ungulates should avoid burned areas where stalking predators are more active and prefer burned areas where coursing predators are more active. In the winter, ungulates may increase avoidance of burned areas where both stalking and coursing predators have movement advantages in deep low-density snow and forage is harder to access (*predation risk effect – winter vulnerability hypothesis*, H2b). Finally, we hypothesized that ungulates could display *predator-mediated foraging* (H3) whereby they balance access to improved forage post fire (*magnet effect*, H1) with predation risk (*predation risk effect*, H2) such that they are no more likely to die by predation in burned areas than in unburned areas. We expected *predator-mediated foraging* (H3) to be supported based on risk-sensitive foraging theory and empirical evidence (Brown, 1988; Altendorf et al., 2001), but the dynamic nature of wildfire impacts could preclude an optimal response by ungulates and lead to either a strong forage-attraction or predator-avoidance response. Collectively, our analysis offers a comprehensive examination of a diversity of fire impacts on predator-prey interactions.

3.2 METHODS

3.2.1 *Study Area*

Our study encompassed the northern half of the Washington Department of Fish and Wildlife's East Slope Cascades Mule Deer Management Zone within Okanogan County, Washington, USA (11,040 km^2; latitude: *c.* 48.050° to 49.150°; longitude: *c.* -120.900° to -119.700°; Figure 3.1). Rolling shrub-steppe foothills at lower elevations (min: 230 m) transition to conifer forests at mid elevations, while the terrain becomes steep and rocky at high elevations (max: 2830 m). The region has a relatively low human population density (mean: 0.006 ± 0.173 people per km^2, min: 0, max: 59) that is primarily concentrated around valley bottoms. Cold winters (average low of -7ºC, average high of 1 ºC from December – March) and hot summers (average low of 9 ºC to average high of 26 ºC from June – September) are typical, with 57 cm of rain and 292 cm of snow estimated annually in Mazama, Washington, USA (based on data collected from 1981 – 2010; https://www.usclimatedata.com/climate/mazama/50ashington/united-states/uswa0264).

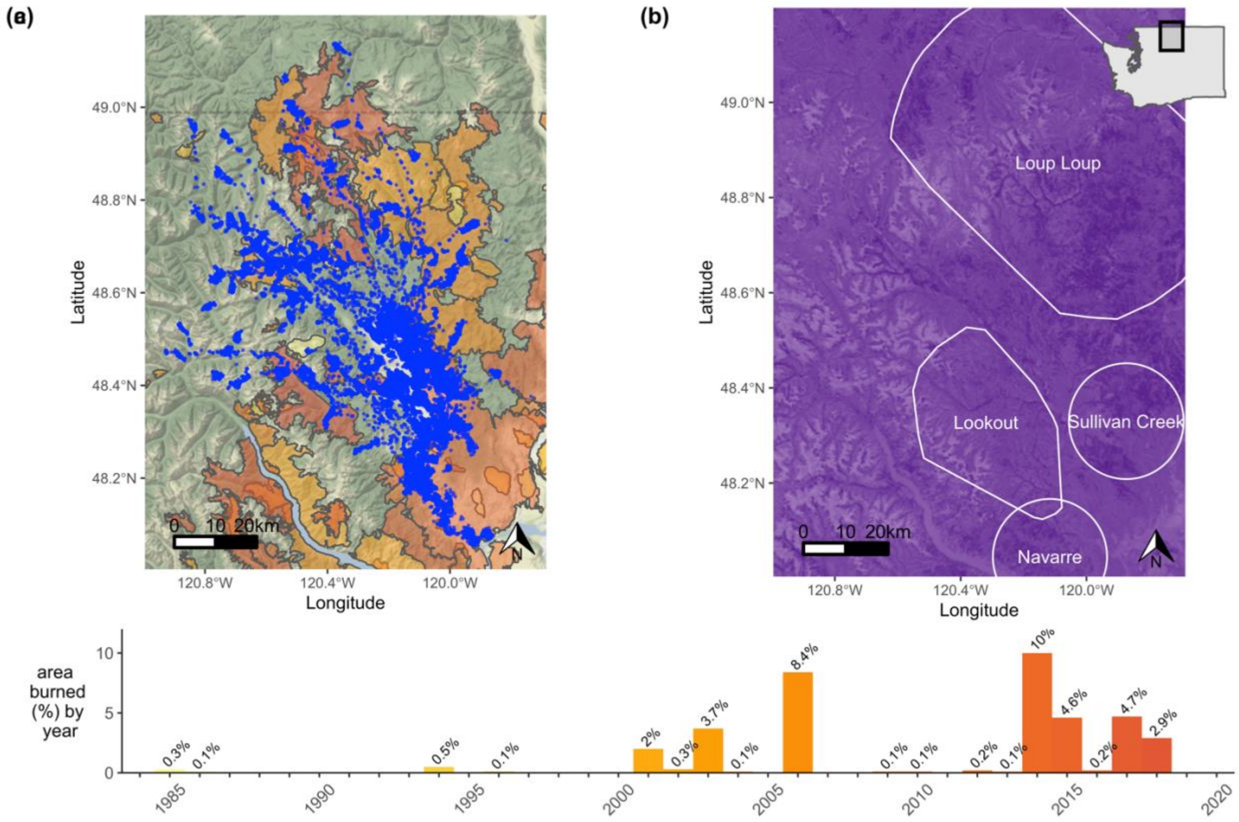

Figure 3.1 Mule deer (GPS locations from collared individuals shown in blue) in Okanogan County, Washington, USA (a) encounter a range of fire histories through their annual migrations. Orange shading in (a) illustrates the extent of the burn perimeter and corresponds to the year of the burn (c). Since collection of fire data began in 1984, (c) 38.4% of the 11,040 km^2 region burned, over half of which has occurred since 2014 (MTBS Project, 2021). (b) Predicted cougar use (summer 2019 displayed as example) is higher where colors are darker. Wolf pack territories during the study, shown as 95% minimum convex polygons, are overlaid. The Sullivan Creek (est. 2019) and Navarre (est. 2020) packs did not have collared wolves during our study, so their approximate territories are represented with circles.

Historically, low severity fires occurred every 1 – 25 years and mixed severity fires occurred every 25 – 100 years, but fires in this region are becoming increasingly severe and frequent (Hessburg et al., 2005; Arno & Allison-Bunnell, 2013). Since the Monitoring Trends in Burn Severity program (MTBS) began mapping fire perimeters in 1984, 38% of the region has burned, over half of which occurred since 2014 (MTBS Project, 2021). Prior to the start of the study, extreme fire years occurred in 2006 with the Tripod Complex (70,753 hectares) and Farewell (31,340 hectares) fires and in 2014 with the Carlton Complex (111,730 hectares) and Upper Falls (3,580 hectares) fires. These were followed by two major fire years during the study; the Canyon Creek (499 hectares), Diamond Creek (47,561 hectares), and Uno Peak (3593 hectares) fires burned in 2017, and the Crescent Mountain (21,553 hectares) and McLeod (10,011 hectares) fires burned in 2018. No major fires occurred in the region from 2019 through the end of our study.

The study area supported a wide array of both predators and prey. In addition to mule deer, white-tailed deer were common in the region, while elk (*Cervus canadensis*) and moose (*Alces alces*) were present but rare. Cougars occurred across the study area and preyed on mule deer, as did black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and coyotes, although these predators primarily prey on neonatal deer. Since 2008, wolves have naturally recolonized portions of the region, creating areas of presence and absence for comparison. The Lookout and Loup Loup packs occupied the southwest and northeast regions of the study area (Figure 3.1c) for the duration of the project (Washington Department of Fish and Wildlife et al., 2018, 2019, 2020, 2021). Over the study, the Loup Loup pack varied from 2 – 6 wolves (mean = 4.0) and the Lookout pack varied from 3 – 8 wolves (mean = 5.2). The Sullivan Creek pack formed along the eastern edge of the study area in 2019, and the Navarre pack established in the southern region of the study area in 2020. Aerial and in-field surveys as well as camera trap monitoring indicate that the Sullivan Creek and Navarre packs did not substantially overlap with the collared mule deer, though wolves from these packs were not collared so their precise range was unknown (Washington Department of Fish and Wildlife et al., 2020, 2021). Based on the reported minimum count of wolves from these packs from 2016 – 2020 (Washington Department of Fish and Wildlife et al., 2018, 2019, 2020, 2021), we estimated an averaged minimum density of 0.103 wolves per 100 km^2 (SD = 0.053, range: 0.045 – 0.190) during the study.

3.2.2 *Landscape Change*

We used linear regression to test if fire reduced canopy cover, increased forage quality and increased snow depth. Methods, results, and interpretation of the investigation are presented in Appendix B. For all analyses, fire timing and severity were sourced from MTBS, which maps the size and severity of fires > 1,000 acres across the United States from 1984 to the present (MTBS Project, 2021). MTBS classifies six categories of fire impacts based on a composite burn index at 30 m resolution: unburned to low, increased greenness, low severity, moderate severity, high severity, and mask (Key & Benson, 2006). We reclassified MTBS's "unburned to low" (unburned within a burned perimeter, or visible fire impacts affecting < 4.5 m^2 out of the 90 m^2 pixel) as "unburned," and pooled "increased greenness post fire" with "low severity" burns (hereafter low severity), leaving us with unburned, low, moderate, and high severity burn classifications for analysis. Masked values (burn severity unobtainable due to atmospheric or terrain factors) were removed from the analysis. In the MTBS classification system, low severity burns are characterized by significant consumption of vegetation < 1m and up to 25% mortality of overstory trees, whereas high severity burns are characterized by near complete consumption of the understory vegetation and > 75% tree mortality, and moderate severity burns either display characteristics between low and high severity burns or contain a mix of low and high severity burns (Key & Benson, 2006; https://burnseverity.cr.usgs.gov/glossary). We treated fire impact as a categorical covariate in the regression models with all combinations of time class (0 – 4 years, 5 – 9 years, 10 – 20 years, and 21 – 35 years) and the three severity classes (low, moderate, high), such that there were 13 categories including an unburned class. Time classes were selected based on the post fire stages of forest succession relevant to mammals (Fisher & Wilkinson, 2005), which aligned well with the distribution of our fire impacts across the study area.

3.2.3 *Animal Captures*

We captured cougars using wire-mesh cage traps or by ground-darting after treeing them with trained pursuit hounds (Hornocker, 1970; Kertson et al., 2011). We fit cougars with either an Iridium GPS-radio collar (Model Vertex Lite, Vectronic Aerospace, Berlin, Germany) or GPS-enabled accelerometer collar (Model G5-AL, Advanced Telemetry Systems, Inc., Minnesota, USA). Wolves were captured with padded leg-hold traps and by aerial darting (Jessup, 1982; Frame & Meier, 2007), and they were fit with GPS radio-collars (Models Vertex Lite and GPS Plus, Vectronic Aerospace). Adult female mule deer were captured on their wintering grounds in the Methow Valley, Washington, USA (c. 48.329°, -120.066°) using drive nets in 2017, and by aerial net-gunning from 2018 onward (Jessup, 1982), and fitted with GPS-radio collars (Model Vertex Plus, Vectronic Aerospace). All animal collars were programmed to record a GPS fix every 4 hours. Wolves were captured as part of existing management and conservation activities (Washington Department of Fish and Wildlife et al. 2021) by Washington Department of Fish and Wildlife personnel in accordance with their agency-approved wolf capture and handling protocols (Washington Department of Fish and Wildlife 2019) and the guidelines of the American Society of Mammalogists for the use of live animals in research

(Sikes et al. 2016). Cougar and mule deer captures and handling followed protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol #4226-01).

Mule deer collars transmitted mortality signals that triggered after 9 hours of inactivity, and mortalities were investigated as soon as possible to determine cause of death. Our investigations included: 1) an evaluation of the scene, 2) examination of predator tracks and signs where relevant (Elbroch & McFarland, 2019), 3) DNA swabbing of lethal bites in the event of predation (Caniglia et al., 2013; Mumma et al., 2014), and 4) necropsy with sample collection and testing when necessary. We recorded the location of the mortality using a handheld GPS receiver and confirmed the time of death with the telemetry data. Predation was confirmed at mortality sites if the carcass had lethal bite marks with hemorrhage, or clear signs of a chase or a struggle. In cases where there were no clear signs of hemorrhage due to consumption of the carcass, but all evidence clearly indicated a single species of predator responsible for the mortality, we classified the cause of death as "unknown – likely predation." If there were no clear signs of hemorrhage due to consumption of the carcass and the evidence weakly indicated a single species of predator, we classified the cause of death as "unknown – possible predation."

3.2.4 *Movement Models*

Our analyses included 4 summer seasons (2017, 2018, 2019 and 2020) and 4 winter seasons (2017-2018, 2018-2019, 2019-2020, and 2020-2021). Summer was defined as June 15 – September 30 and winter as December 1 – March 15 based on the seasonal range use of mule deer, which were identified using net squared displacement (Sawyer et al., 2009; Bunnefeld et al., 2011) in Migration Mapper (Merkle et al., 2017). We used resource selection functions (RSFs; Manly et al., 2002; Johnson et al., 2006) to describe cougar use and used Localized

Density Distributions (LDDs; Kittle et al., 2016) to describe wolf use, reflecting the different distributions and densities of these predator species. We used these predator layers to parameterize the mule deer step selection function. All analyses were performed in Program R version 4.1.0 (R Core Team, 2021).

3.2.5 *Cougars: Resource Selection Functions (RSF)*

Beausoleil et al., (2021) recently estimated cougar density as 1.55 ± 0.44 cougars per 100 km^2 in this study system. We used the *ctmm* package in R (Calabrese et al., 2016) to calculate 95% autocorrelated kernel density home ranges (Fleming et al., 2015) of collared adult cougars (≥ 2 years old and with > 3 months of data; Beausoleil et al., 2013), and found that home ranges varied from 102 to 7,792km^2 with a median of 836 km^2 ($n = 14$). As such, we assumed that the area was fully occupied by cougars and focused on modeling the probability of use within the home range (3rd order selection; Johnson, 1980) to describe cougar activity. We randomly selected 20 points for each telemetry location from within the 100% seasonal minimum convex polygon (MCP) for each cougar with an individual's data pooled across years using R package *amt* (Signer et al., 2019). We then combined the used and available locations for each cougar into a single dataset and used logistic regression in an RSF framework to model cougar use across the study area (Keating & Cherry, 2004). Because we were interested in producing the model with the best predictive fit rather than interpreting the effect of predictors, we did not eliminate predictive covariates based on correlation between them, nor did we use model selection to choose the most parsimonious model. We evaluated predictive performance of our models using leave one individual out cross validation (Boyce et al., 2002; Mahoney et al., 2018).

We modeled cougar space use with measures of terrain, landcover and human impacts (Kertson et al., 2011; Knopff et al., 2014). Specifically, we used elevation, elevation^2, heat load index, topographic position index, terrain roughness index, percent forest, percent shrub, percent open, distance to water, percent developed, human population density, distance to minor roads (logging and residential roads), and distance to major roads (freeways, highways, and secondary highways) as covariates. Continuous covariates were standardized to have a mean of zero and standard deviation of one. Elevation, heat load, topographic position index, terrain roughness index and landcover were available at 30 m resolution. Heat load incorporates slope, aspect, and latitude to estimate potential direct incident radiation at a location (McCune & Keon, 2002; McCune, 2007). Topographic position index identifies ridges and valleys by their difference in elevation from neighboring terrain and can be important for cougar movement (Peterson et al., 2021). Terrain roughness measures heterogeneity of the elevation, and cougars generally select rougher terrain over gentler terrain (Riley et al., 1999; Riley & Malecki, 2001). We obtained landcover from Terradapt:Cascadia (https://www.cascadiapartnerforum.org/terradapt), which provides spatial layers covering the entire annual range of the collared mule deer, including southern British Columbia. Simplified cover types were ground-truthed during vegetation surveys for a related study in northeastern Washington (T.R. Ganz et al., unpublished data) and resulted in open, shrub, forest and developed categories. Each landcover type was represented as percent cover (unstandardized) within a 250 m moving window at 30 m resolution. We selected a 250 m buffer because this approximated the mean step-length taken by deer for our focal periods (summer: mean = 253 m, SD = 281 m; winter: mean = 251 m, SD = 265 m), and thus represented the resources available to deer at each step.

3.2.6 *Wolves: Localized Density Distributions (LDD)*

To describe wolf pack activity while accounting for areas outside of known wolf pack territories, we created LDDs for summer and winter. LDDs are analogous to utilization distributions but incorporate multiple animals for social species such as wolves, representing a spatial distribution of pack use weighted by the number of individuals in the group (Kittle et al., 2016, 2017). Wolf pack size was based on aerial and in-field track surveys and camera trap monitoring (Washington Department of Fish and Wildlife et al. 2018, 2019, 2020, 2021). To create pack-level distributions, we first used an autocorrelated kernel density estimator to generate separate utilization distributions for each collared individual for each winter and summer. If more than one wolf was collared in a pack in a season of a year, we averaged the layers to describe pack use. For periods when a wolf was not collared within a pack, we used the average of that pack's layers from other years to approximate use in that season. For each season-year-pack combination, we set values < 0.05 in the distribution layer to 0.00 to approximate the 95% home range, then scaled the layer such that all values summed to one to account for variable intensity of use between different size home ranges (Kittle et al., 2016; Klauder et al., 2021). Finally, we multiplied the layer by minimum pack size for the year (Washington Department of Fish and Wildlife et al. 2018, 2019, 2020, 2021), and summed pack layers for the relevant period to create seasonal landscape level use layers for each season-year combination (Kittle et al., 2016).

3.2.7 *Mule Deer: Step Selection Functions*

Mule deer exhibit strong fidelity to their home ranges and movement corridors relative to other ungulates (Sawyer et al., 2018; Morrison et al., 2021; Kreling et al., 2021), so we expected that changes in selection owing to fire would be most evident at the finest spatial-temporal scale available in our GPS data (i.e., fixes collected every 4 hours). To validate this assumption, we calculated kernel density estimates (KDEs) of the 90% isopleth (Börger et al. 2006) using R package *amt* (Signer et al., 2019; Signer & Fieberg, 2021) for each deer with at least 200 locations on each seasonal range, corresponding to a minimum of about one month of data. We censored locations three weeks post-capture for all deer to minimize potential effects of capture on movement and survival (Northrup et al., 2014; van de Kerk et al., 2020). From these KDEs, we determined overlap of seasonal home ranges between subsequent years for individual deer by calculating the Bhattacharyya coefficient (Bhattacharyya 1943) in R package *amt* (Signer et al., 2019). The Bhattacharyya coefficient is a measure of overlap between two distributions that is well suited to comparing the volumetric overlap between home ranges and spans from 0 for no overlap to 1 for complete overlap (Fieberg & Kochanny, 2005). Only three deer in our study had fires burn within their home range between study seasons while they were monitored, so we were unable to statistically compare home range characteristics before and after fire. Each of these deer returned to the same summer home range after the fires that they had used before.

We used step selection functions (Fortin et al. 2005) to examine how mule deer responded to recent burns and predator use while accounting for other potentially important factors such as terrain, human impacts, and land cover. Step selection functions are a form of conditional logistic regression that compare landscape characteristics at the end of a taken step (the transition between two consecutive GPS points) to characteristics at the end of randomly generated steps that an animal could have accessed at that time (Thurfjell et al. 2014). We created separate population-level models for deer on summer and winter ranges (i.e., not while migrating) and restricted dates to match those used in modeling predator distributions. For each seasonal data set, we removed any individual with fewer than 50 fixes after the 3-week post-capture censor. Based on the seasonal movement characteristics of the deer, we generated 5 random steps with the turn angle drawn from a von Mises distribution and step-length drawn from a gamma distribution (Northrup et al. 2013, Thurfjell et al. 2014) using the *amt* package in R (Signer et al., 2019). Random steps were compared to taken steps with conditional logistic regression using the R package *mclogit* (Elff, 2016).

We developed a set of 11 candidate models to test our hypotheses that deer would respond to past fires, wolves, and cougars subject to additional influences from landscape factors. The candidate models were: (1) null, (2) null + wolf, (3) null + cougar, (4) null + wolf + cougar, (5) null + burn, (6) null + burn + wolf, (7) null + burn + cougar, (8) null + burn + wolf + cougar, (9) null + burn * wolf, (10) null + burn * cougar, and (11) null + burn * wolf + burn * cougar. As a null model, we used elevation, heat load index, terrain roughness index, percent open, percent forest, percent shrub and percent developed to explain mule deer selection. Elevation, heat load index, terrain roughness index, percent open, percent forest, percent shrub and percent developed covariates were used as previously described.

Wolf and cougar distributions were both standardized so covariate effects could be estimated at the mean level of predator use intensity. Because of the high density of cougars across the area, deer may not have been able to avoid cougars, but might have been able to avoid the areas with the highest cougar activity. To account for this possible non-linear effect of cougar use, we included an additive effect of cougar^2 in the models with cougar. A negative coefficient estimate for the cougar^2 covariate would indicate that deer increased avoidance (if the response to cougars was negative) or reduced the strength of selection (if the response to cougars was positive) for areas where cougar activity was more intense. In the summer, deer were not exposed to wolves in the 21 – 35 years since fire for low, moderate, or high severity burns, so this component of the burn * wolf interaction was excluded. We removed the 10 – 20 year burn classes from the winter wolf * burn interaction for the same reason.

Before running models, we checked Pearson's correlation between the covariates and eliminated covariates with |r| > 0.7 (Dormann et al., 2013). If correlation exceeded 0.7, we retained the covariate of primary interest and excluded the other. If the correlated covariates were of equal interest (e.g. landcover type), we used AIC to compare the null models excluding each of the correlated covariates, and retained the covariate producing a better model fit (Anderson & Burnham, 2002). We selected the most parsimonious model for each season based on AIC (Burnham & Anderson, 2002) and evaluated predictive performance of the best models with leave one individual out cross validation (Boyce et al., 2002; Mahoney et al., 2018).

3.2.8 *Spatial Predictors of Mortality*

We used a general linear model to test if deer were more likely to die from predation in burns relative to unburned areas. We coded each deer mortality location as ones and paired these with 20 locations randomly selected from their used telemetry points, which were coded as zeros following Olson et al. (2021). Locations were excluded for the first three weeks post capture so any deer dying in this window were likewise excluded. We constructed two separate models to account for uncertainty in cause of death: (1) confirmed predations only, and (2) confirmed, likely, and possible predation mortalities. Because of the small sample size, we treated burn as a binary predictor, where burns included low, moderate, and high severity burns since 1984. All burned locations in this dataset were < 20 years post fire.

3.3 RESULTS

3.3.1 *Movement Models*

We captured 24 cougars (16 females, 8 males) of which 20 were adults (≥ 2 years), and 4 were subadults (1.5 to < 2 years) at first capture (Beausoleil et al., 2013). All cougars contributed to the winter model and 17 cougars informed the summer model (Appendix B, Table B2.1 and Table B2.2, Figure B2.1). Both winter and summer models had good predictive performance ($r_{s\ winter} = 0.99$, $r_{s\ summer} = 0.95$; Appendix B, Figure B2.1). We used telemetry data from the five wolves that were GPS-collared during the project to model their distribution for each season of each year (Appendix B, Figure B2.3). Three wolves were from the Loup Loup pack (1 female, 2 males) and two were from the Lookout pack (2 males; Appendix B, Table B2.3). We captured and collared 149 adult female mule deer during our study. After censoring post-capture data and removing deer with < 50 locations per season from the step selection function, 143 deer informed the winter model and 116 deer informed the summer model (Appendix B, Table B3.1). We quantified 586 seasonal KDEs and found strong fidelity to seasonal ranges, with a median Bhattacharyya coefficient of 0.89 (range: 0.03 – 0.99).

Predicted cougar use and percent shrub were highly correlated in the summer (Pearson's correlation of 0.75), so we removed percent shrub from mule deer step selection summer models because we were more interested in interpreting the effect of cougar presence on deer than land cover per se. Likewise, terrain roughness and cougar use were highly correlated in the winter (Pearson's correlation of 0.72), so we removed terrain roughness from all winter models. Shrub and open were correlated by 0.76 in the winter, so we used AIC to compare the null models excluding shrub and excluding open. The model with open received 100% of model weight and an AIC score 259.44 points lower than the model with shrub, so we removed shrub from all

Winter models. In both summer and winter, the most complex mule deer model received 100% of the model weight (Appendix B, Table B3.2), indicating fire history, predator activity and the interactions therein were important drivers of deer selection. Both the highest ranked summer and winter models performed well ($r_{s,\ winter} = 1$, $r_{s,\ summer} = 0.988$; Appendix B, Figure B3.1).

Deer showed significant responses to nearly all the "null" habitat covariates with no difference in the direction of the effect by season (Table 3.1). Mule deer selected for areas with higher elevation, greater heat load, more open habitat, and greater terrain roughness (summer only) relative to what was available to them. We did not detect a significant relationship with percent forest cover in the summer, but areas of greater forest cover were avoided during winter (Table 3.1). The summer model revealed strong selection for developed areas by deer, but the population-level pattern appeared to be driven by 48 individuals that did not migrate into remote, wilderness areas in the summer where there was no exposure to development. We did not detect a significant relationship between deer use and development in the winter. Counterintuitively, both our summer and winter models revealed deer selection increased with greater predicted use by cougars. However, deer reduced selection of areas with the highest levels of predicted cougar use, particularly during the summer, as evidenced by the negative coefficient of the cougar^2 covariate. Deer avoided wolves throughout the year, and the effect was stronger in the winter than in the summer (Table 3.1).

Table 3.1 Non-burn related coefficient estimates for the seasonal step selection functions for mule deer with 95% confidence intervals. Terrain roughness was not considered in the winter model. Coefficient estimates for fire effects are provided in Appendix B, Table B3.3.

	Summer			Winter		
Covariate	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)
elevation	0.15	0.11	0.20	0.36	0.33	0.39
heat load	0.08	0.07	0.08	0.08	0.07	0.09

terrain roughness	0.08	0.06	0.09			
open	0.19	0.13	0.26	0.61	0.55	0.68
forest	-0.04	-0.11	0.02	-0.68	-0.81	-0.56
developed	1.20	0.91	1.50	0.19	-0.10	0.48
cougar	0.26	0.25	0.28	0.33	0.32	0.34
cougar^2	-0.052	-0.059	-0.045	-0.012	-0.018	-0.007
wolf	-0.07	-0.12	-0.03	-0.29	-0.36	-0.22

Deer responses to wildfire strongly depended on season, species-specific predator use, and the characteristics of the burned area. In the summer, deer primarily selected for burns, though not in all cases (Figure 3.2a). Cougar activity had little effect on use of low and high severity burns 0 – 4 years old, low severity burns 5 – 9 years old and moderate severity burns 10 – 20 years old in the summer (Figure 3.2b). As cougar activity increased in moderate severity burns 0 – 4 and 5 – 9 years old, deer increasingly selected for these areas, but avoided high severity burns 5 – 9 years old. Responses to cougars were mixed in 10 – 20 year old burns, but deer avoided the oldest burns (21 – 35 years) with increased cougar activity. Unlike the mixed response to cougars, deer consistently increased their use of post fire areas where wolf activity was higher in the summer, except for high severity burns 5 – 9 years post fire, which had no effect (Figure 3.2c).

The winter season presented more consistent trends as deer mostly avoided all burn classes at the mean levels of predator exposure (Figure 3.2a). With increasing levels of cougar activity, deer consistently strengthened their avoidance of all burn classes < 21 years old, while the oldest burn classes had non-significant effects (Figure 3.2b). Conversely, deer reduced avoidance of burns up to 9 years post fire with higher wolf activity, but increased avoidance of the oldest burns (Figure 3.2c).

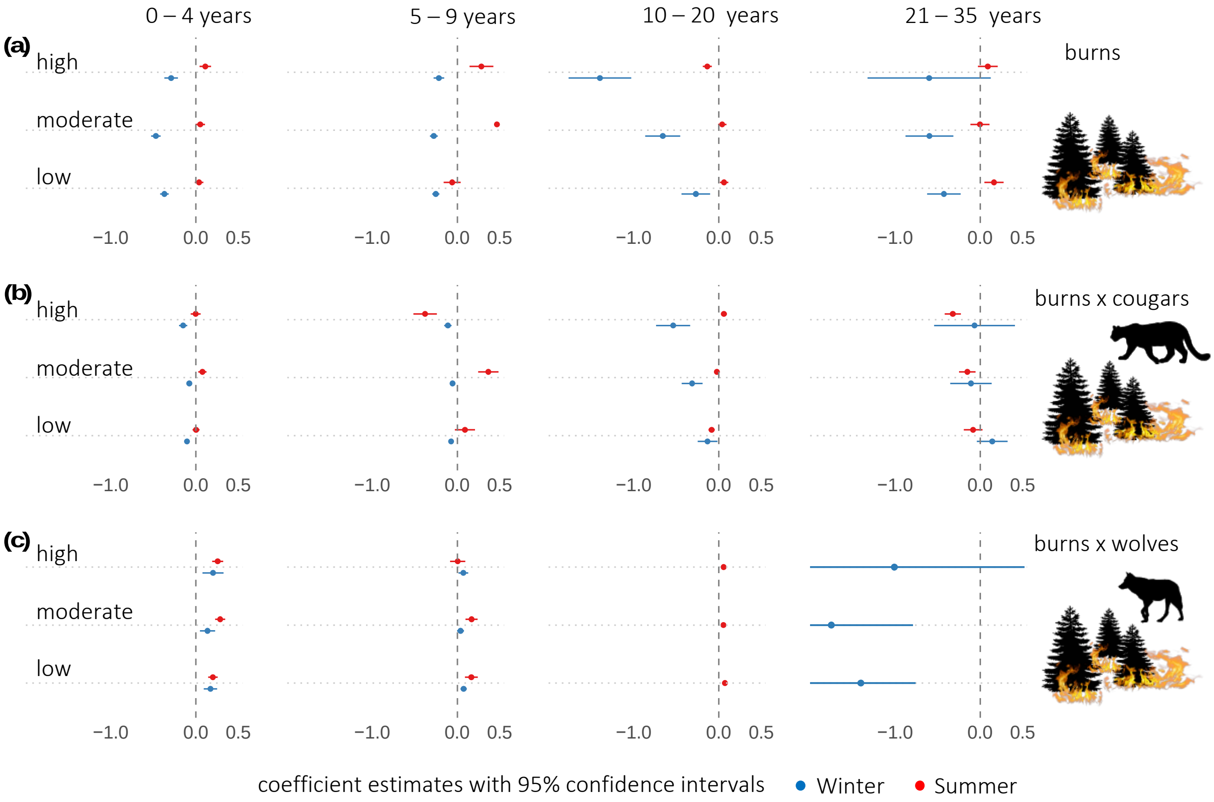

Figure 3.2 Coefficient estimates for deer selection for burned areas across fire severity and time since fire for (a) the main effect of burns and the additive effect of burns with a standard deviation increase in (b) cougar and (c) wolf activity above the mean. The net response of deer to a particular burn class with a standard deviation increase in wolf or cougar activity above the mean is the sum of the coefficient for the burn class at mean predator exposure plus the coefficient estimate representing the interaction with wolves or cougars in that burn class and the independent response to the predator. Dots indicate the estimated coefficient value, and corresponding lines display the 95% confidence intervals. Blue represents the winter model, and red represents the summer model. Negative coefficients show avoidance of the burn class, whereas positive coefficients indicate selection for the burn class at mean predator exposure (a), and interactions with the predator (b) and (c) indicate the degree to which the main effects of burns are strengthened or weakened by predator exposure. For instance, in the winter, deer avoided moderate severity burns 0 – 4 years post fire (a) and avoided these areas even more strongly when cougars were present because the interactive effect of cougars and moderate severity burns 0 – 4 years post fire was negative (b). Deer avoidance of these areas was

weakened when wolves were present because the interactive effect of wolves and moderate severity burns 0 – 4 years post fire was positive (b). Effects of wolf activity interacting with burn class could not be estimated in the winter for the period 10 – 20 years since fire or in the summer for the period 21 – 35 years since fire due to lack of exposure. In (c), the confidence intervals for all burns 21 – 35 years post fire extended beyond the lower x-axis limit, and beyond the upper x-axis limit for high severity fire. They have been cropped to improve the resolution of the figure.

3.3.2 *Spatial Predictors of Mortality*

We documented 52 deer mortalities over the course of the study, excluding three deer that were censored from analysis due to a mortality in the first three weeks post capture. In some cases, the cause of mortality was indeterminate owing to insufficient evidence remaining at the mortality site, severe autolysis of tissues, and contamination of the mortality site by scavengers. Of the 52 mortalities, 22 were confirmed to be the result of predation, nine resulted from an unknown cause of death that was likely to be predation, and one resulted from an unknown cause of death where predation was possible (n = 32; Table 3.2).

Table 3.2 Predation mortalities where the cause of death was confirmed, likely to be, or possibly predation. The likely predation from the unknown predator was due to a canid, but we could not distinguish between coyote or wolf.

	Black Bear	Bobcat	Cougar	Coyote	Wolf	Unknown
Confirmed	1	2	15	3	1	0
Likely	1	0	5	2	0	1
Possible	0	0	0	0	0	1
Total	2	2	20	5	1	2

Deer were not more likely to die at burned sites than unburned sites throughout the year (confirmed predations: $z_{460} = -0.65$, $p = 0.52$; confirmed, likely, and possible predations: $z_{670} = -0.03$, $p = 0.97$), nor in the winter (confirmed predations: $z_{165} = -0.53$, $p = 0.59$; confirmed, likely, and possible predations: $z_{268} = -0.14$, $p = 0.89$; Table 3.3). We conducted a *post hoc* analysis focused on deer mortality from cougars as these were their primary predator, and likewise did not detect differences in the predation risk with respect to burns (confirmed predations: $z_{313} = -0.51$, $p = 0.61$; confirmed, likely, and possible predations: $z_{418} = 0.47$, $p = 0.64$).

Table 3.3 Coefficient estimates from generalized linear models examining of the effect of burned versus unburned areas on mule deer predation risk in Okanogan County, Washington, USA. The models consider data from predation mortalities across the year (all year), only in the winter (winter), for deer killed by cougars (cougar, all year) and for deer killed by cougars in the winter (cougar, winter). Positive $\hat{\beta}$ estimates indicate a deer was more likely to die in a burned location than an unburned location, whereas negative $\hat{\beta}$ estimates indicate that a deer was less likely to die in a burned location than an unburned location for the dataset. Because of our small sample size of deer dying by confirmed predation (*n* = 22), we also ran the model with confirmed, likely, and possible predations (*n* = 32).

	Confirmed, likely, and possible predations						Confirmed predations					
Model	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	Odds Ratio	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	Odds Ratio	Lower CI (2.5%)	Upper CI (97.5%)
All year	0.0	-0.7	0.7	-1.0	-0.5	-2.0	-0.3	-1.2	0.6	-0.7	-0.3	-1.8
Winter	-0.1	-1.2	1.0	-0.9	-0.3	-2.8	-0.4	-2.0	1.0	-0.7	-0.1	-2.8
Cougar, all year	0.2	-0.7	1.1	-1.2	-0.5	-3.1	-0.3	-1.5	0.8	-0.7	-0.2	-2.2
Cougar, winter	0.8	-0.8	2.8	-2.3	-0.4	-17.2	0.4	-2.9	3.6	-1.4	-0.1	-37.1

3.4 DISCUSSION

As wildfires become more frequent, burn at higher intensity, and grow in size, it becomes increasingly important to understand their direct and indirect effects on wildlife populations (McKenzie et al., 2004; Volkmann et al., 2020). We found that mule deer response to burned areas depended on the season, predator activity and predator species, subject to the characteristics of the fire that had burned there. We observed the most support for the *predator mediated foraging hypothesis* (H3), which predicted that mule deer would be attracted to burned areas in the summer due to the forage-enhancing effects of fire, while also responding to predator exposure such that the likelihood of dying by predation did not increase in burned areas. In the winter, deer consistently avoided burned areas that we predicted would result from the accumulation of deeper, fluffier snow rendering deer more vulnerable to predators (*predation risk effect – winter vulnerability hypothesis*, H2b). However, the avoidance of burned areas in the winter was mediated by the traits of the predator (*predation risk effect – predator traits hypothesis*, H2a). Burned areas were avoided more in winter where activity from stalking predators (cougars) was higher, whereas the avoidance of burned areas was weakened under exposure to coursing predators (wolves). In the summer, deer increased use of burns where wolf activity increased but had a mixed response to burns where cougar activity was more intense. Collectively, our findings reveal an important context dependency of predator-prey interactions that has been previously unexplored and highlight the importance of accounting for the indirect effects of wildfires via predation risk to predict impacts on herbivores.

Fire effects on understory vegetation quality and abundance are a primary direct pathway through which wildfires impact herbivores, as has been documented in numerous studies of ungulates, forage quality, and fire (Allred et al., 2011; Eby et al., 2014). Deer were generally attracted to burned areas in the summer, as we predicted based on the *magnet effect hypothesis* (H1). Notably, we did not find an increase in the Normalized Difference Vegetation Index (NDVI; a remotely sensed measure of vegetation health) following fire in our landscape analysis, most likely because NDVI was highly correlated with canopy cover (Appendix B, Table B1.1 Figure B1.1; Pettorelli et al., 2005; Hull & Shipley, 2019). Previous studies in similar systems that directly measure vegetation consistently demonstrate that fire increases the quality and quantity of forage (e.g., Hobbs & Spowart, 1984; Proffitt et al., 2019; Roerick et al., 2019; Hayes et al., 2022), and it is most likely fire had similar effects on vegetation in our system. Further, deer showed the strongest selection for moderate and high severity burned areas 5 – 9 years post fire, which were also the areas where the most canopy cover was lost and thus would be expected to have the greatest increase in forage quality (Appendix B, Table B1.1 Figure B1.1a; Hull et al., 2020; Hayes et al., 2022). The observed decrease in canopy cover following fire and selection for burns indicate that the improvement in forage quality was the most likely driver of deer selection for burned areas in the summer.

Disentangling the effects of forage quality and predation risk on herbivore space use is challenging in the best of circumstances. Shrubs can be an important driver of mule deer habitat use (Cox et al., 2009; Gogan et al., 2019), but this cover class was excluded from the model due to its high correlation with cougar activity. The prey abundance hypothesis predicts that predators should select areas with a higher likelihood of encountering prey (Litvaitis et al., 1987; Palomares et al., 2001), which would present as the attraction of mule deer to cougars we observed if deer are attracted to shrubs, and cougars are attracted to areas of higher deer densities. This correlation increases the difficulty of distinguishing the effects of cougars from the shrub cover class on mule deer habitat selection. However, wildfires primarily burned areas classified as forest rather than shrub, and burns in shrub-dominated habitat tend to be patchier and less severe than in forests where they do occur (Meddens et al., 2016). Additionally, impacts of fires on the nutritional value of shrub- and grass- lands are short-lived relative to forests (Hobbs & Spowart, 1984; Green et al., 2015). Thus, the correlation between cougar activity and shrub-dominated habitat should not affect interpretation of our findings with respect to wildfires.

The dynamics of the cougar and wolf populations and the modeling frameworks we used to describe them should also be considered when interpreting these results. First, there were potentially 15-fold more cougars than wolves in the system, which almost certainly contributed to the stronger response of deer to cougars than to wolves. It is also possible that deer were relatively naïve to wolves given that wolves recolonized in 2008 after ~ 80 years of absence. However, the Loup Loup and Lookout packs recolonized ~ 10 years prior to the study, beyond the lifespan of most adult female deer in this system (Washington Department of Fish and Wildlife, *unpublished data*) and prey generally respond to recolonizing predators within a year (Atwood et al., 2007) to within a generation (Berger et al. 2001). As wolves continue to establish new packs in unoccupied regions (i.e., as with the establishment of the Sullivan Creek and Navarre packs in 2019 and 2020) and the size of the packs increase, effects of wolves on deer will likely intensify. It is also important to consider that we represented cougar activity with RSFs, which represent 3rd order selection (Johnson, 1980), whereas we used LDDs (Kittle et al. 2016) to describe wolf pack territories, which are inherently a 2nd order process (Johnson, 1980). These different approaches could influence our interpretation of deer responses to each predator. Given the patchy nature of wolf presence across the study area relative to the high density of cougars, we felt this approach best represented mule deer exposure to predators, though it may have oversimplified use within a wolf pack territory. It is also possible that we did not capture some wolf activity due to uncollared wolves, though movement from individual wolves in a pack tends to reliably describe pack level use (Benson and Patterson, 2014) and track and camera surveys indicate that transient wolves were rare. We believe this framework represents a reasonable approach for considering the interactive effects of these two predators and fire.

Mule deer response to wildfires was contingent on predator exposure therein, an important indirect effect of wildfires on mule deer. We found support for the *predation risk effect – predator traits hypothesis* (H2a), though our predictions were upheld more consistently for wolves compared to cougars and in winter compared to summer. Deer were more likely to use burned areas up to 20 years post fire with increased wolf activity in both the summer and the winter, likely because the regrowth of the understory could provide suitable hiding from wolves, and the coursing hunting style of wolves (Kauffman et al., 2007) would be impeded by obstacles such as deadfall in burns while the stotting gait of mule deer should facilitate escape (Dellinger et al., 2019). In contrast, deer avoided burns as cougar activity increased in the winter. Deadfall may enhance the hunting success of stalking predators like cougars by providing hiding cover for an ambush attack (Metsaranta et al., 2003; Ruth et al., 2019). Thus, our findings indicate the composition of the resident predator community may strongly affect how ungulates respond to wildfires and the resulting magnitude of predation risk effects (i.e., foregone foraging opportunities; Brown et al., 1999). In systems like ours, the presence of stalking predators like felids should lead to strong risk effects from prey avoiding recent burns that contain high-quality forage. In contrast, the presence of coursing predators like canids in fire-affected landscapes may induce negligible risk effects in the summer given that recent burns likely confer both food and relative safety rather than a trade-off between the two.

The direction of predation risk effects should depend on the structural changes to the landscape induced by fire, which may differ by system. For instance, fires in shrub- and grass-land dominated systems can decrease cover, which should cause herbivores to select for burns to reduce risk from staking predators (Eby et al., 2013; Jennings et al., 2016). In this study, mule deer in the summer did not respond to low severity burns 0 – 9 years post fire or moderate severity burns 10 – 20 years post fire both independent of predator exposure and with cougars. Fire may not have driven sufficient change in these areas to alter forage quality or perceived risk from cougars. Deer selected for moderate severity burns 0 – 9 years post-fire when cougar activity increased, so it may be that the primary effect of fire in these burn classes was to reduce stalking cover for cougars. Deer avoided older burns (10 – 35 years post burn) more consistently with increased cougar activity, when early successional habitat favored by cougars may have improved stalking cover (Kertson et al., 2011). Thus, the effects of burns on the hunting efficacy of predators via habitat alterations needs to be considered to predict impacts of fires on ungulates.

In the winter, we suspect that snow depth relative to the height of both forage plants and mule deer themselves played an important role in mule deer avoidance of burned areas. One reason for this was likely the movement advantages of both cougars and wolves in deep, low-density snow (*predation risk effect – winter vulnerability hypothesis,* H2b), although deer weakened their avoidance of burns with increased wolf exposure, indicating that habitat structure and predator hunting mode were still important in the winter (*predation risk effect – predator hunting mode,* H2a). Ungulates prefer areas of shallower snow when the depth of low density, fluffy snow exceeds half their chest height (Sweeney & Sweeney, 1984; Mahoney et al., 2018), and movement becomes severely impeded when snow depth exceeds 2/3 of chest height (Kelsall, 1969; Gilbert et al., 1970). Winter snow depth in Winthrop, Washington, USA (station ID: 9376, *c.* 48.47°, -120.18°, elevation 533 m) averaged 30 – 52 cm over the course of the study (USDA Natural Resources Conservation Service, 2021). Jones (1975) recorded an average chest heigh of 57 cm for mule deer, indicating that snow depths reported during our study could have driven the observed response, particularly if snow was deeper in burned areas. However, effects may have been conflated if lower elevations of the system had less snow, which may also explain why deer did not select for forests in the winter (Table 3.1). Shrubs up to 60 cm tall may be rendered 75% to 100% unavailable to deer at the snow depths estimated during our study, substantially limiting nutrient availability and further driving avoidance of burned areas if snow is deeper within them (White et al., 2009; Hanley et al., 2012; Gilbert et al., 2017). Most ungulates in snow dominated systems occupy a restricted range in the winter (including the mule deer in this study), so avoidance of burns in winter could functionally reduce the habitat available and thus the carrying capacity of the landscape, akin to avoidance of anthropogenic impacts (Sawyer et al., 2006; Dwinnell et al., 2019).

In systems like ours where mule deer were able to manage predation risk relative to burned areas (i.e., they were no more likely to die by predation in burned areas compared to unburned areas), the primary effects of wildfire should result from changes to the nutritional landscape and the risk effects influencing the use of those nutritional resources. In regions where snow is rare, fire may primarily improve the forage landscape for herbivores. However, at more northerly latitudes and higher elevations, deeper and more persistent snowpacks may reduce winter forage availability to an even greater extent, both by impeding access to forage and influencing predation risk for a longer duration. Future work examining how the use of burned areas influences body condition (Kreling et al., 2021), fetal rates, and survival could help to quantify the importance of the changing nutritional landscape and the impact of risk effects induced by the predator community (Volkmann et al., 2020).

We demonstrated that the response of mule deer to fire depended greatly on the season of consideration, the severity of fire impacts and stage of succession, and species-specific patterns of exposure to predators, highlighting key sources of context-dependency in predator-prey interactions. As researchers continue to investigate how prey such as herbivores respond to wildfire and climate change, direct measures of forage quality, snow depth and subsequent demographic impacts will improve our knowledge of wildlife dynamics in a changing world (Penczykowski et al., 2017; Boelman et al., 2019; Volkmann et al., 2020). Importantly, predicting impacts of wildfires on prey species depends not only on understanding changes to forage quality, but also understanding changes to landscape structure and risk effects from the predator community (Doherty et al., 2022).

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Chapter 4. FORAGE AVAILABILITY AND THE DIRECT EFFECTS OF TOP PREDATORS GOVERN POPULATION DYNAMICS OF WHITE-TAILED DEER IN A HUMAN DOMINATED LANDSCAPE OF NORTHEASTERN WASHINGTON, USA

Publication history: This study was co-authored with Sarah B. Bassing, Melia T. DeVivo, Beth Gardner, Brian N. Kertson, Lauren Satterfield, Lisa A. Shipley, Ben Y. Turnock, Savanah L. Walker, Derek Abrahamson, Aaron J. Wirsing and Laura R. Prugh. At the time this dissertation was submitted, no version of this manuscript was in review, accepted, or published elsewhere.

Abstract: Prey populations are governed by predation or other direct sources of mortality (i.e., top-down effects) and forage availability (i.e., bottom-up effects), but the relative importance of these factors is system specific, and both may reflect human activities. Apex predators can influence prey directly via consumptive and non-consumptive effects and indirectly by suppressing populations of mesopredators. The importance of mesopredator suppression has received limited study in human dominated systems, which are increasingly important to sustaining large terrestrial mammals. In northeastern Washington, USA, white-tailed deer (*Odocoileus virginianus*) are vulnerable to predation from cougars (*Puma concolor*) and recently recolonized wolves (*Canis lupus*) that may suppress bobcats (*Lynx rufus*), and coyotes (*C. latrans*). Across this landscape, timber harvest drives changes in habitat, initiating the growth of early seral vegetation and increased forage for deer. Using survival and GPS collar data collected between 2017 and 2021, we fit Cox Proportional Hazard models to evaluate how predator exposure, mesopredator suppression, and human activity associated with creation of early seral habitat influenced deer survival. We then parameterized a stage-structured matrix with the Cox Proportional Hazard models and simulated changes to forage, predator exposure and mesopredator suppression to evaluate the influence of these factors at the population level. The deer population was stable to possibly declining (lambda = 0.97, 95% CIs: 0.88, 1.05) during the four-year study period, and simulations indicated that the population was dually limited by the direct effects of wolf and cougar predation and forage quality. Coyotes had weak influence on deer population growth, and thus mesopredator suppression did not influence population dynamics. Given the dual limitation and top-down and bottom-up effects that we detected, a reduction in top predators would likely intensify forage regulation due to density dependent factors. Accordingly, our findings suggest that humans alter the carrying capacity of the landscape through the creation of early seral habitat by timber harvest and associated increases in forage for deer.

Keywords: *Canis lupus*, Carnivore, Mesopredator, *Odocoileus virginianus*, Population dynamics, Predator-prey interactions, *Puma concolor*, Survival analysis, Timber harvest, Ungulate

4.1 INTRODUCTION

Populations of carnivores and their prey are declining worldwide (Estes et al. 2011, Ripple et al. 2014, 2015), and their long-term persistence will depend on landscapes used by humans (Carter and Linnell 2016). However, much of the existing research on predator-prey interactions comes from protected areas, even though human activity can substantially influence these interactions through multiple pathways (Kuijper et al. 2016). For instance, predators tend to avoid areas of human activity, thus creating a refuge for prey (i.e., the human shield, Berger 2007, Muhly et al. 2011), but humans can cause substantial prey mortality through vehicle collisions (Etter et al. 2002, Huijser et al. 2008) and hunting (Ballard et al. 2000). Furthermore, human modifications of the landscape such as timber harvest are often associated with the construction of roads and other linear features that facilitate predator movement and thereby increase predation risk (Neilson and Boutin 2017, DeMars and Boutin 2018), but removal of forest cover can improve forage for herbivores (Hull et al. 2020). Thus, investigations into predator-prey dynamics in anthropogenic systems are necessary to identify the ecological role of predators when humans are present, understand community dynamics in managed systems, and guide conservation and management decisions in increasingly human dominated landscapes.

Ungulates provision carnivores (Elbroch and Wittmer 2012, Newsome et al. 2016), can alter vegetation (Hobbs 1996, Bernes et al. 2018), and provide valuable viewing and hunting opportunities for humans, so the dynamics of their relationships with predators are of broad interest to researchers, managers, and the public. Carnivore-ungulate interaction studies often overlook the complex impacts multiple sympatric predators have on prey (Montgomery et al. 2019), yet the overall composition of the wildlife community may be the strongest factor in determining how predation influences prey populations (Gervasi et al. 2012, Elbroch and Wittmer 2013, Prugh and Arthur 2015, Elbroch et al. 2015). The effects of predators on prey may be direct, whereby predators kill and consume prey or alter prey behavior, or indirect, where the presence of one predator influences the behavior or density of another, in turn influencing predation rates of prey (Schmitz et al. 2004). In some cases, interactions among predators can lead to seemingly paradoxical impacts on prey. For instance, in Wyoming, USA, the reintroduction of wolves (*Canis lupus*) suppressed coyote (*Canis latrans*) abundance, leading to increased survival of juvenile pronghorns (*Antilocapra americana*) and increased pronghorn abundance overall (Berger et al. 2008). Similarly, population models indicate that wolf population control can have positive or negative influences on Dall sheep (*Ovis dalli*) in Alaska, depending on the degree of mesopredator release (Prugh and Arthur 2015). Like wolves, cougars (*Puma concolor*) can also play a strong role in limiting coyote populations with potential indirect impacts on ungulates (Prugh and Sivy 2020, LaBarge et al. 2022). However, the extent of apex predator suppression of mesopredators in human dominated landscapes and subsequent impacts on prey species are currently unknown (Kuijper et al. 2016).

Human land management such as timber harvest may also influence the quantity, quality, and availability of forage on which prey species rely. The balance between intake of these nutritional resources and energetic output governs the body condition of individuals (Parker et al. 2009), in turn influencing survival, pregnancy and fetal rates (Eberhardt 2002). Ultimately, forage suitability and availability is the primary factor governing density dependent dynamics in ungulates (McCullough 1999). Whereas some human activities such as energy development functionally reduce available habitat, leading to population declines in Wyoming, USA (Dwinnell et al. 2019), creation of early seral habitat via timber harvest has led to booming deer populations in Alberta, Canada owing to increased forage (Latham et al. 2011).

Both bottom-up (i.e., the quality and availability of forage) and top-down factors (i.e., direct causes of mortality including predation, human hunting, and vehicle collision) influence ungulate population dynamics and these impacts frequently act simultaneously and interactively (Ballard et al. 2001, Forrester and Wittmer 2013). High primary productivity can increase prey population resilience to predation effects (Melis et al. 2009, Donadio and Buskirk 2016), but prey have been shown to reduce time foraging and intake rates in areas of high predation risk (Lima and Dill 1990). These examples highlight the dynamic interplay between top-down and bottom-up factors in influencing prey populations, which make the impacts of changing landscapes and predator guilds difficult to predict.

Since 2008, wolves have naturally recolonized northeastern Washington (Wiles and Hayes 2011), joining a rich community of sympatric predators including cougars, coyotes, and bobcats (*Lynx rufus*) and raising many questions about top-down impacts on prey populations. Overall, ungulate population dynamics are most sensitive to the mortality rates of adult females, but juvenile recruitment tends to be more variable such that reproductive rates and juvenile mortality usually have a stronger influence on population growth rates (λ) across populations (Gaillard et al. 1998, Ballard et al. 2001, Forrester and Wittmer 2013). Wolves and cougars are known to primarily prey on wild ungulates of all age classes, influencing ungulate populations through consumptive effects (i.e. predation) and non-consumptive effects (i.e. risk effects) (Elbroch and Wittmer 2012, Newsome et al. 2016). Coyotes are the primary predators of juvenile deer in many systems, and bobcats contribute additional juvenile mortality (Nelson et al. 2015). Thus, ungulate population dynamics may depend on the responses of coyotes and bobcats to dominant predators (Whittaker and Lindzey 2006, Ballard 2011). Recently, Prugh et al. (*unpublished data*) documented coyotes strongly avoiding areas of high cougar and wolf activity in this system, suggesting that such dynamics may be at play. In Washington, wolf abundance is relatively low compared to that of other carnivores (Washington Department of Fish and Wildlife 2019a), so we expected that wolves would influence white-tailed deer population dynamics most strongly via indirect effects. Across our study area, approximately a quarter of the forested area (~ 16% - 18% of the total area) has been harvested for timber since 2000 (Hansen et al. 2013), with the potential to enhance deer forage and ultimately influence deer population dynamics (Hull et al. 2020). Thus, this region provides an ideal system to examine how human modified landscapes alter the forage landscape and a complex carnivore guild interact to affect white-tailed deer population dynamics.

We tested two hypotheses on the factors driving white-tailed deer population dynamics in northeastern Washington from 2017 – 2021 by linking habitat use and survival data from collared white-tailed deer to model local population dynamics. According to the *bottom-up limitation hypothesis* (H1), we predicted that deer mortality risk would decrease with increased use of areas with forest cover loss associated with an increase in forage biomass. Subsequently, we expected that simulated increases in use of areas with more forage would result in an increase in λ. An alternative but not mutually exclusive hypothesis was that deer would be subject to *top-down limitation* (H2), either directly or indirectly. According to this hypothesis, we expected that deer mortality risk would increase with greater exposure to predators and that simulated increases in predator exposure would lead to a decrease in λ. To assess the potential for direct versus indirect effects of predators, we examined the spatial correlation between predators to determine if apex predators (cougars and wolves) suppressed mesopredator (bobcats and coyotes) activity. If the deer population was influenced by *top-down limitation via direct effects of predation* (H2a), then changes in λ resulting from simulated changes in predator exposure would not depend on the degree of mesopredator suppression. Alternatively, if the deer population was influenced by *top-down limitation via indirect effects of predation* (H2b), then we expected to observe a strong negative correlation between apex predators and mesopredators. We also expected that the strength of mesopredator suppression would influence estimates of population growth (λ) at varied levels of exposure to predators.

4.2 METHODS

4.2.1 *Study Area*

We defined the study area for this analysis (Figure 4.1) as the range of the collared white-tailed deer, which primarily occurred within Stevens and Pend Oreille Counties of northeastern Washington, USA (latitude: *c.* 47.900° to 48.720°; longitude: *c.* -118.300° to -117.200°, ~ 5,200 km^2). Cool winters (average low of -6ºC, average high of 4ºC from December – March) and warm summers (average low of 7ºC to average high of 27ºC from June – September) were typical of the region with an estimated 152 cm of rain and 114 cm of snow annually (values estimated for Chewelah, WA, USA at the center of the study area; https://www.usclimatedata.com/climate/chewelah/washington/united-states/uswa0074). Elevations ranged from 370 – 2080 m.

Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), and western red cedar (*Thuja plicata*) forests dominated the mid-to-higher elevations of the region, whereas valley bottoms were predominately converted to residential and agricultural use (1.3% and 3.5% of the study area, respectively; https://www.cascadiapartnerforum.org/terradapt). Snowberry (*Symphoricarpos albus*), Oregon grape (*Mahonia repens*), Common St. John's-wort (*Hypericum perforatum*), Shinyleaf spiraea (*Spiraea lucida*), Hawkweed (*Hieracium spp*.) were common species in the understory that were acceptable to white-tailed deer as forage (Berry et al. 2019). The majority of the region (77%) is privately owned and primarily managed for timber harvest, the US Forest Service manages 16% of the land, and US Fish and Wildlife Service, the Department of Natural Resources and the Bureau of Land Management manage 7%. Since 2000, 18% of the total area and 25% of the forest area have lost canopy cover, primarily owing to timber harvest (Hansen et al. 2013).

Elk (*Cervus canadensis*), moose (*Alces alces*), and mule deer (*O. hemionus*) occur across the area at low densities relative to white-tailed deer. Four wolf packs occupied the study area for the duration of the project (Wiles and Hayes 2011, Washington Department of Fish and Wildlife et al. 2021). Black bears (*Ursus americanus*), bobcats, cougars, and coyotes are also native to the area and prey on white-tailed deer. These white-tailed deer are managed in the Selkirk White-tailed Deer Management Zone, which has the highest population densities of white-tailed deer in the state (Washington Department of Fish and Wildlife 2016). The local population experienced several weather and disease-related events including severe winters during 2008-2011 and an outbreak of hemorrhagic disease in the fall of 2015. Generally, white-tailed deer populations rebound after such events owing to their high reproductive potential (DeYoung 2011), but the impact of these events is largely unknown because formal population surveys to determine abundance were not conducted for this herd (Washington Department of Fish and Wildlife 2016). During this study, there was a general season harvest of antlered deer from October – November, limited antlerless opportunities from 2017 – 2018, and no antlerless opportunities from 2019-2021.

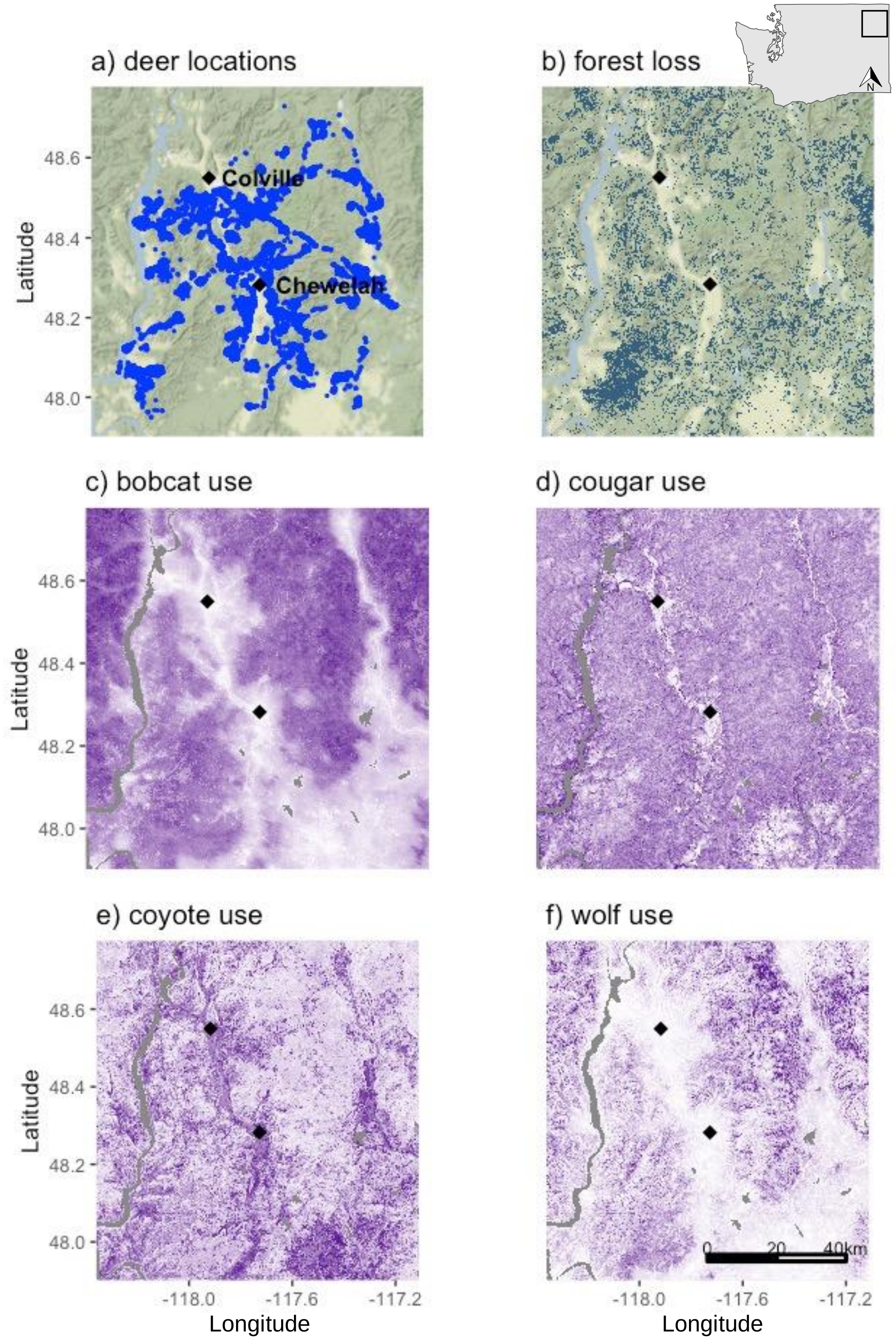

Figure 4.1 (a) Telemetry locations (blue) of white-tailed deer in northeastern Washington from 2017 – 2021. (b) Areas where forest cover has been lost since 2000 (dark shading) were detected

from remotely sensed data provided by Hansen et al. (2013) and had more biomass of forage acceptable to white-tailed deer on average than areas without forest cover loss. Relative likelihood of predator use, modeled from resource selection functions (RSF) using GPS collar data, was higher where colors are darker. The RSFs were constructed for each season of each year and are shown for (c) bobcats, (d) cougars, (e) coyotes, and (f) wolves for summer 2018. Each layer was scaled between 0 and 1 for best resolution. Grey shading in predator plots (c-f) indicates water bodies; selection was not predicted for these sites.

4.2.2 *Animal Capture and Handling*

To estimate vital rates and determine the factors influencing survival of white-tailed deer (hereafter: deer), we collared deer, bobcats, coyotes, cougars, and wolves. We conducted all wildlife captures and monitoring between February 2016 and June 2021. We captured 6-8-month-old and older deer in the winter between December 2016 and March 2020 using a suspended net gun (Wildlife Capture Services, Flagstaff, Arizona, USA) and clover traps (Clover 1954, Hawkins et al. 1968, VerCauteren et al. 1997) (Figure 4.1). Yearling and adult deer were also captured by ground darting. We fit global positioning system (GPS) radio-collars (Models Vertex Plus or Survey, Vectronic Aerospace, Berlin, Germany) to female yearling and adult deer. Collars were programmed to attempt a fix every 4-hours and were equipped with mortality sensors that sent an email and SMS notification after 9-hours of inactivity. During capture, we collected blood samples to determine pregnancy from blood serum by analyzing pregnancy-specific protein B concentration (PSPB; Bio-Tracking LLC, Moscow, ID, USA, Duquette et al. 2012). We also tested a subset of adult female deer for pregnancy during capture with a portable ultrasound (Ibex Pro, E.I. Medical Imaging, Loveland, CO) and inserted Vaginal Implant Transmitters (VIT; VERTEX Natal-Link Vaginal Implant Transmitter, Vectronic Aerospace) when pregnancy was detected (Johnson et al. 2006). We administered 1.00 cc of butorphanol-azaperone-medetomidine (BAM) to all deer receiving VITs during winter captures (Miller et al. 2009).

Expulsion of the VITs triggered an email and SMS notification, allowing us to target neonates for capture (Rice 2016). From May – June 2017-2020, we captured neonatal white-tailed deer by searching the area around a VIT expulsion, opportunistically, or by observing the behavior of adult female deer and searching the area if a neonate was suspected (White et al. 1972). Neonatal and 6–8-month-old deer were equipped with expandable very high frequency (VHF) radio collars (Model M4210, Advanced Telemetry Systems, Isanti, MN, USA and Model Vertex Natal-linked, Vectronic Aerospace) and weighed during capture. VHF collars were set to a 6-hour mortality delay, and juvenile deer were monitored with VHF radio-telemetry on a daily basis from capture to September, twice per week from October through December, and weekly from January until reaching 1-year of age around June. We assumed that 6-8-month-old deer that survived 365 days after the mean date of neonate captures the previous spring/summer reached 1-year of age. If any juvenile had a collared mother, we assumed their locations were the same as the mother. For juveniles with unmarked mothers, locations were triangulated ~ weekly. We censored the first 3 weeks post-capture for all deer captured > 6 months old to minimize the effects of capture on movement and survival estimates (Northrup et al., 2014; van de Kerk et al., 2020).

We investigated mortalities as rapidly as possible upon detection to determine cause of death. The investigations included a necropsy of the carcass and mortality scene inspection during which we collected DNA swabs associated with the potential predator when relevant (Ganz et al. 2022). We confirmed predation by skinning the carcass to identify lethal hemorrhage associated with bite marks (Williams et al. 2003) or by finding clear signs of a chase or struggle that indicate a kill site. Because these strict criteria may eliminate true predation mortalities that have been mostly consumed, we also classified likely or possible predation mortalities, though ultimately the cause of death was unconfirmed in these cases. “Likely predation” mortalities were cases where predation could not be confirmed and scavenging could not be ruled out, but there was no other apparent cause of death and the evidence pointed to a single potential predator. “Possible predation” mortalities were cases where predation could not be confirmed and scavenging could not be ruled out, but there was no other apparent cause of death, and the evidence revealed signs from multiple potential predators or vague evidence for a single predator. In these cases, we assigned the possible predator as the one that was most likely based on our investigation. Additionally, we classified “likely vehicle collisions” as cases where the carcass was found adjacent to a major road with no other apparent cause of death, but where vehicle collision could not be confirmed. When predation was determined to be the confirmed, likely, or possible cause of death, we evaluated the predator tracks, sign and patterns of consumption following Elbroch (2003), Washington Department of Fish and Wildlife (2014), Stonehouse et al. (2016), and Elbroch and McFarland (2019) to determine the species of predator responsible for the kill. We tabulated cause of death across age classes. To determine the fetal rate, we recorded the number of fetuses at the mortalities of collared deer when possible and for opportunistically encountered dead deer (e.g., road-kills).

Bobcats were captured using baited cage traps and then GPS collared (Model Gen4 GPS-Iridium, Telonics, Mesa, Arizona, USA). We captured cougars using trained dogs or baited cage traps and fit them with GPS collars (Model Vertex Lite, Vectronic Aerospace and GPS-enabled accelerometer collars, Advanced Telemetry Systems, Inc., Isanti Minnesota, USA) (Hornocker 1970, Kertson et al. 2011). Coyotes and wolves were captured with padded foot-hold traps and by aerial darting (Jessup 1982, Linhart 1993, Frame and Meier 2007), and then fit with GPS radio-collars (Model Gen4 GPS-Iridium, Telonics for coyotes, Models Vertex Lite and GPS Plus, Vectronic Aerospace for wolves). Carnivore collars were also programed to record a fix every 4 hours. White-tailed deer, bobcat, cougar and coyote capture and handling followed protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol #4226-01). Wolves were captured as part of existing management and conservation activities (Washington Department of Fish and Wildlife et al. 2021) by the Washington Department of Fish and Wildlife and the Spokane Tribe of Indians in accordance with their agency-approved wolf capture and handling protocols (Washington Department of Fish and Wildlife 2019b) and the guidelines of the American Society of Mammologists for the use of live animals in research (Sikes et al. 2016).

4.2.3 *Human Impacts*

We sought to capture both the potential primary negative and positive effects of human activities on deer in this region. Because preliminary investigations indicated that vehicle collisions were a primary source of deer mortality, we used distance to major roads (freeways, highways, and secondary highways) mapped at 1km resolution to represent this potential negative effect of human activity on deer. A greater distance to major roads was indicative of less human activity and a shorter distance to major roads indicated more human activity.

To capture a potential positive effect of humans on deer, we conducted vegetation surveys across the study area to evaluate the role of timber harvest in shaping the nutritional landscape. Canopy cover loss attributed to timber harvest was the primary driver of landscape change in the area and is associated with increased deer forage (Hull et al. 2020, Ulappa et al. 2020). It is possible that some loss was due to fire, but only 3% of the study area has burned since 2000 (MTBS Project 2022), and within the canopy cover loss areas only 12% of the loss could potentially be attributed to a fire (i.e., a wildfire occurred in the area in the year of, or years preceding, the loss).

Forest management practices ranged from small-scale selective thinning to large-scale clear cuts, but given the multitude of landowners and large portion of private land, we were unable to determine how specific harvest strategies influenced the biomass of forage acceptable to deer (Hull et al. 2020, Ulappa et al. 2020). Instead, we sought to determine if forest loss areas differed in biomass of forage acceptable to deer when compared to historically forested and historically unforested areas, allowing them to be used as a coarse proxy for bottom-up effects associated with land management.

To identify areas of forest loss, we used the Global Forest Cover Change dataset (http://glad.earthengine.app/view/global-forest-change; Hansen et al. 2013), a remotely sensed dataset that indicates if canopy cover has been lost since 2000, and the percent canopy cover in 2000 (though not proportion of cover loss) at 30 x 30m resolution. Forest cover loss indicated a stand-replacement disturbance (Hansen et al. 2013). We selected 201 unique sites by stratified random sampling across elevation, aspect, and forest harvest history, categorized as uncovered (< 50% forest cover in 2000), covered (≥ 50% forest cover in 2000 and no subsequent loss), and cover loss (≥ 50% forest cover in 2000 and subsequent canopy cover loss).

Surveys were conducted from July – September in 2019 and 2020 to capture the season when female ungulates are under high nutritional demands because of lactation requirements, and with the strongest effects on ungulate survival and reproductive success (Moen 1978, Tollefson et al. 2010, 2011, Cook et al. 2013, Johnson et al. 2019). Each 30 x 30 m site was oriented to the cardinal directions and placed in an area of contiguous habitat as close as possible to the randomly selected location. We validated the aspect, elevation, and harvest history by which the site was chosen, and measured point intercept canopy cover at 100 locations in a grid across the site (schematic available in Appendix C2). Nine 1 x 1 m quadrats were spread evenly across the site in which we documented the species and percent cover of each plant species with at least 1% cover and > 1 cm and < 2 m in height, as this is the forage available to ungulates as food (Rowland and Vojta 2013). Percent cover of the quadrat was estimated for each species independently such that total cover could exceed 100%.

To estimate the biomass of forage considered "acceptable" for white-tailed deer at each quadrat, we first classified each plant species measured on plots as avoided (significantly negative Ivlev's electivity index; Ivlev and Scott 1961), neutral (95% confidence intervals for Ivlev's index overlapped 0), or selected (significantly positive Ivlev's index) based on studies with tractable deer and elk (i.e. captive individuals that were habituated to observers) in similar habitats (Wagoner 2011, Wagoner et al. 2013, Ulappa 2015, Cook et al. 2016, Berry et al. 2019, Hull et al. 2020, Ulappa et al. 2020). For all acceptable plant species (neutral or selected), we used equations developed by Monzingo et al. (2022) for a similar study area to convert percent cover of acceptable forage to biomass (kg/ha). Species level equations were used when available, or else we used equations developed for the growth form of the plant, which generally performed comparably to species-specific equations (Monzingo et al. 2022). We then averaged values across the nine quadrats to estimate the biomass of acceptable forage (kg/ha) at each of the 201 sites. Finally, we used an ANOVA to compare acceptable biomass among covered, uncovered and harvested sites to determine if we could use these classifications as a proxy for the biomass of acceptable forage, thus allowing us to capture a component of bottom-up effects in analyses of the factors influencing deer population dynamics. We also ran a simple linear regression to determine if canopy cover (as sampled *in situ* and extracted from Cascadia Biodiversity Watch TerrAdapt:Cascadia [https://cascadiapartnerforum.org/terradapt] remotely sensed layers) would be a better proxy for forage biomass, as canopy cover has been shown to be inversely related to forage availability in some systems (Hull et al. 2020). All analyses were conducted in program R, version 4.1.2 (R Core Team 2021).

4.2.4 *Predator Exposure*

To describe an individual deer's exposure to bobcats, cougars, coyotes and wolves for the period under consideration, we used Resource Selection Functions (RSFs; Manly et al. 2002) adapted from Bassing et al. (2022) (methods detailed in the Appendix C1). While RSFs describe habitat selection or the relative probability of use rather than abundance, per se, predation risk increases with the increased likelihood of encountering a predator (Lima and Dill 1990, Hebblewhite and Merrill 2007), and abundance tends to reflect the strength of habitat selection such that RSFs can be used as an index of relative abundance (Boyce et al. 2016). RSFs were created for winter (December – February), spring (March – May), summer (June – September) and fall (October – November) and included covariates to describe human activity (global human modification index), terrain (elevation and slope) and environmental factors (distance to nearest water, canopy cover, landcover type, and distance to nearest habitat edge). To determine if mesopredators may be suppressed by wolves and cougars, we calculated Spearman's pairwise correlations between seasonal RSFs (each layer ranging from 0-1). Because the association between predators can vary depending on spatial scale (Prugh and Sivy 2020), we evaluated correlations from 30 x 30 m to 10,000 x 10,000 m resolution pixels, using the aggregate function in R package *raster* (Hijmans et al. 2015). We expected that mesopredators would avoid areas of high apex predator use if suppression occurred, evidenced by a negative correlation between their RSFs.

4.2.5 *Abiotic Factors*

Abiotic factors such as precipitation and temperature influence both top-down and bottom-up controls (Hopcraft et al. 2010). In North American ungulate populations, predation and winter severity are the primary drivers of juvenile mortality, whereas adult female mortality is most affected by winter severity across populations (Gaillard et al. 1998, Hewitt 2011, Griffin et al. 2011). To account for the influence of climate on deer winter/spring survival (Forrester and Wittmer 2013), we created a winter severity index (WSI) for the period from December to February following Johnson et al. (2013). The WSI incorporates standardized values of the mean monthly minimum temperature and the total monthly precipitation within the study area from winter 1965-1966 to winter 2020-2021 based on the Parameter-elevation Regressions on Independent Slopes Model (PRISM; https://prism.oregonstate.edu/; Daly et al. 2008). Severity of the previous winter was also used as a covariate in summer/fall survival models because the prior winter influences the body condition of ungulates during the subsequent year and thus their ability to meet lactation requirements (Eacker et al. 2016).

4.2.6 *Mortality Risk*

We used Cox Proportional Hazard models with staggered entry (Cox 1972, Pollock et al. 1989) to test the effects of exposure to predators, forest cover loss as an index of forage biomass, human activity, and winter severity on survival of individual adult female and juvenile (male and female) white-tailed deer using the *survival* package in R (Therneau and Lumley 2013). This model identifies factors influencing the time to an event (in our case, death) but does not incorporate the cause of death (Cox 1972). We chose this approach because the causes of mortality for many of the deer were unknown and we suspected that some causes of death (e.g., wolf predation) were more likely to remain unidentified than others (e.g., cougar predation and vehicle collision; Ganz et. al., 2022), which would lead to biased estimates of cause-specific mortality rates. Cox Proportional Hazard models assume that the baseline hazard is constant over the model timeframe, as are the effects of the model covariates (Fieberg and DelGiudice 2009), which we checked by inspecting diagnostic plots of the residuals and testing the proportionality assumption (Therneau and Grambsch 2000, Therneau and Lumley 2013). To meet these assumptions, we created 5 separate models for: juveniles (1) 0-6-months-old, (2) 6-9-months-old, (3) 9-12-months-old, and adult females in the (4) summer and fall (June – November) and in the (5) winter and spring (December – May). Because juveniles entered the model on the day of capture whereas the annual period for adults started June 1, the periods for 0-6-month-old deer and adults in the summer and fall were closely, but not exactly, temporally aligned. Likewise, the period for the adult female model from December – May was approximated by the juveniles 6-9-months-old and 9-12-months old models.

All models included exposure to bobcats, coyotes, cougars, and wolves to describe predation risk and distance to roads to describe human activity. Summer/fall models included severity of the previous winter and use of areas for forest loss during the growing season (June – September) as an indicator for higher biomass of acceptable forage. The 0-6-month-old model additionally included body mass at capture as larger neonates tend to have higher survival rates (Bishop et al. 2009, Bergman et al. 2014). Winter/spring models incorporated winter severity (Eacker et al. 2016). We used data from neonates captured with VITs to compare survival between neonates captured at 0 days old to those captured 1-3 days old, assuming that the neonate was born the day the VIT expelled, to determine if left-censoring influenced survival estimates (Gilbert et al. 2014). Survival did not differ between these neonates ($n_{\text{captured day 0}} = 23$; $n_{\text{captured day > 0}} = 11$; $\chi^2 = 0.6$, df =1, $P = 0.44$) so all 0-6-month-olds entered the survival models on the day of capture.

Deer were collared for varying lengths of time, prohibiting the estimation of annual home ranges, so we averaged the values of the spatially varying parameters (predator RSFs, canopy cover loss, and distance to roads) at each of their telemetry locations over the period of interest to parameterize the models (White et al. 2010, Eacker et al. 2016, Shuman et al. 2017). Locations were buffered with a 200 m radius moving window using the focal function in R package *raster* (Hijmans et al. 2015). We chose a 200 m buffer to reflect the resources available to each deer across each step (deer relocations: median = 188 m, mean = 265 m) and their vulnerability to wider ranging predators. All covariates in the survival models were scaled to have a mean of 0 and standard deviation of 1. Because adult deer surviving >1 year were included in multiple rows of the model, we calculated robust standard errors that accounted for the lack of independence between multiple records of the same individual (Therneau and Grambsch 2000). We checked correlation among covariates within the model, but because we were interested in using these models for predictive purposes, we did not exclude highly correlated covariates (Anderson and Burnham 2002). We verified that models met the assumptions of proportional hazard, and we adjusted model periods and considered polynomial forms of the covariates if necessary to meet model assumptions (Fieberg and DelGiudice 2009).

4.2.7 *Estimating Population Growth*

We created a female only post-birth-pulse matrix, including juvenile, yearling, and adult age classes as follows (Kendall et al. 2019) to evaluate λ across the population:

$$\begin{bmatrix} N_f(t+1) \\ N_y(t+1) \\ N_a(t+1) \end{bmatrix} = \begin{bmatrix} 0 & P_y * F_y * S_y & P_a * F_a * S_a \\ S_j & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} * \begin{bmatrix} N_f(t) \\ N_y(t) \\ N_a(t) \end{bmatrix}$$

Annual stage-specific survival rates (S_j: juvenile survival, S_y: yearling female survival, S_a: adult female survival) were determined using the staggered entry Kaplan and Meier technique (1958). Pregnancy rates of yearling females (P_y) and adult females (P_a) were determined via blood serum analysis or ultrasound at time of capture. We did not test juveniles for pregnancy and assumed their pregnancy rate was 0 (DeYoung 2011). The female-only fetal rate (F_y: yearling fetal rate, F_a: adult fetal rate) was half the fetal rate found during ante-mortem sampling, and we verified an equal sex ratio of juveniles with a χ^2 test. We also used a χ^2 test to confirm that the mortality rate of juveniles did not differ by sex. We calculated λ as the dominant eigenvalue, and the mean and variance of λ were determined by Monte Carlo simulation with 10,000 draws from the matrix, with survival and pregnancy drawn stochastically from a beta distribution.

4.2.8 *Simulating Population Growth*

We evaluated the elasticity (the relative influence of a matrix element on λ) and the sensitivity (how much λ would change in response to a change in that matrix element) of the matrix to the various parameters to determine which factors were most important to population dynamics, and then simulated changes to the values that managers would be able to manipulate (i.e., exposure to predators and forage quality). Specifically, we parameterized S for each period based on the Cox proportional hazard models such that S = 1- hazard(t) (Murray 2006) where t is the time, hazard(t) = $h_o e^{\boldsymbol{\beta X}}$ and h_o is the baseline hazard. The exponentiated $\boldsymbol{\beta X}$ represents the matrix of coefficients ($\boldsymbol{\beta}$) and covariates ($\mathbf{X}$). Annual survival was the product of model periods for each age class; i.e., $S_a = S_{\text{June – November}} * S_{\text{December – May}}$ and $S_j = S_{\text{0-6months}} * S_{\text{6-9months}} * S_{\text{9-12months}}$. To align simulations with the null estimate of λ, we set h_0 to 1 – the Kaplan Meier survival estimate for the survival period. The sample size of yearling females was too small to evaluate factors influencing survival, so survival was drawn stochastically from a beta distribution describing the null.

We simulated changes to λ by varying model parameters from -0.5 to 0.5 standard deviations in 0.01 standard deviation increments, with 1,000 repetitions at each value. Assuming a normal distribution, changes of 0.1, 0.2, 0.3, 0.4 and 0.5 standard deviations equate to 4.0%, 7.9%, 11.8%, 15.5% and 19.1% change, respectively, and we thought this was within the reasonable range of what managers might be able to influence. We did not simulate changes to harvest rates because antlerless harvest was limited during the study, our population model was female only, and no collared deer died by harvest. Simulations incorporated stochasticity from coefficient estimates, h_0, pregnancy rates, and yearling survival. We also simulated λ across the range of observed mesopredator suppression values for cougars and wolves because correlations between apex and mesopredators varied depending on scales. Finally, we used simple linear regression to evaluate how changes in predator exposure, mesopredator suppression, and use of areas of forest cover loss associated with improved forage influenced λ. We did not evaluate significance of the potential predictors of λ because significance would depend on the arbitrary choice of the number of simulations run.

4.3 RESULTS

We captured 280 white-tailed deer, of which 148 were juveniles. We found an additional two neonates dead during searches. Hoof wear indicated that these dead neonates were born alive such that 150 (73 female, 77 male; $\chi^2 = 0.06$, df = 1, $P = 0.81$) total juveniles were tracked. Of these, 108 were located as neonates (76 opportunistically and 32 from VITs) and 42 were captured in the winter at 6-8-months-old. Neonate captures ranged from 26 May to July 1 but generally occurred in early to mid-June (mean capture date $_{2017}$ = 11 June, SD $_{2017}$ = 3.7 days; mean capture date $_{2018}$ = 13 June, SD $_{2018}$ = 5.2 days; mean capture date $_{2019}$ = 15 June, SD $_{2019}$ = 6.1 days; mean capture date $_{2020}$ = 7 June, SD $_{2020}$ = 5.8 days). After censoring data from the first 3 weeks post capture (Northrup et al. 2014, van de Kerk et al. 2020) for 6-8-month-old juveniles, a total of 144 juveniles were included in the analysis (68 females, 76 males). Annual survival of juveniles did not differ by sex ($\chi^2 = 0.4$, df =1, $P = 0.51$) and thus both male and female juveniles informed the Cox Proportional Hazard survival models. We captured 131 deer as yearlings and adult females. After censoring post capture data, 117 individual deer (266 deer-years) informed the models of adult female survival. Female juveniles that survived beyond one year ($n = 18$), as well as deer GPS collared as yearlings ($n = 17$, $n = 14$ with post capture censor), were used to estimate yearling survival ($n = 31$).

Predation ($n = 45$) and vehicle collisions ($n = 21$) were the primary confirmed causes of mortality of collared deer (72 documented juvenile mortalities, 46 documented adult female mortalities, 1 documented yearling female mortality) while 50 mortalities were classified as unknown (Table 4.1). Of these unknown mortalities, 23 juveniles and 11 adult females likely or possibly died due to predation, while an additional 2 adult females likely died from vehicle collisions. Juvenile deaths were due to a range of predators. Cougars were the primary confirmed predator of juveniles (11 out of 30 confirmed predations), but coyotes were the primary predators when considering likely and possible mortalities (20 mortalities out of 53 confirmed, likely, and possible predations). Cougars were the primary predator of adult female deer when considering both confirmed (11 kills out of 15) and confirmed, likely, and possible mortalities (17 kills out of 26). We did not document any evidence of bobcats killing adult female deer, and there was only 1 instance where a wolf was a possible predator (1 juvenile mortality).

Table 4.1 Causes of death for white-tailed deer collared in northeast Washington, USA from 2017-2021. Predation was confirmed at mortality sites if the carcass had lethal bite marks with hemorrhage, or clear signs of a chase or a struggle. In cases where there were no clear signs of hemorrhage due to consumption of the carcass, but all evidence clearly indicated a single species of predator responsible for the mortality, we classified the cause of death as “likely predation.” If there were no clear signs of hemorrhage due to consumption of the carcass and the evidence weakly indicated a single species of predator, we classified the cause of death as “possible predation.” For juveniles, 1 unknown (*) predation was identified as felid, but it was unclear if a cougar or a bobcat was the predator. For adult females, 1 unknown (**) predation was identified as canid, but it was unclear if wolf or coyote. Only one yearling female died during the study - the mortality was attributed to vehicle collision.

	Juveniles				Adult Females			
	Confirmed	Likely	Possible	Total confirmed, likely, and possible	Confirmed	Likely	Possible	Total confirmed, likely, and possible
Unknown COD	29	0	0	29	21	0	0	21
Vehicle / other accident	10	0	0	10	10	2	0	12
Disease	3	0	0	3	1	0	0	1
Illegal Harvest	0	0	0	0	1	0	0	1
Total Predator	30	8	15	53	15	6	5	26
Bear	2	0	0	2	1	1	0	2
Bobcat	6	1	2	8	0	0	0	0
Cougar	11	3	2	17	11	4	2	17
Coyote	8	4	8	20	1	1	1	3
Wolf	0	0	1	1	0	0	0	0
Unknown predator	3	0	2*	5	2	0	3**	5

Annual survival was estimated to be 0.356 (SE: 0.045, 95% CIs: 0.279, 0.455) for juveniles, 0.900 (SE: 0.095, 95% CIs: 0.732, 1.00) for yearlings, and 0.728 (SE: 0.034, 95% CIs: 0.665, 0.798) for adult females. All tested yearlings (*n* = 11) were pregnant at capture, so we pooled yearling and adult pregnancy rates to avoid overestimating yearling pregnancy (yearling pregnancy rates are typically lower than those of adults; DeYoung 2011), resulting in a combined yearling and adult pregnancy rate of 0.958 (SE: 0.019, *n* = 113). Yearlings averaged 1.33 fetuses per pregnant female (*n* = 3) whereas adults averaged 1.60 (*n* = 20). Incorporating demographic rates into the null matrix model, we found that λ did not differ from 1 (mean = 0.969, median = 0.970, 95% CIs: 0.882, 1.049) over 10,000 simulations, indicating that the population was stable to possibly declining between 2017-2021. Estimates of λ were most sensitive to adult female survival (mean sensitivity = 0.615, SD = 0.035) followed by juvenile survival (mean sensitivity = 0.526, SD = 0.047) and likewise most elastic to adult female survival (mean elasticity = 0.464, SD = 0.044) followed by juvenile survival (mean elasticity = 0.193, SD = 0.017).

4.3.1 *Factors Influencing Mortality Risk*

Predator RSFs (Figure 4.1) adapted from Bassing et al. (2022) incorporated data from 37 bobcats, 60 cougars, 23 coyotes and 15 wolves (Bassing et al. 2022; Appendix C Tables C1.1 & C1.2). Predator correlations (Figure 4.2) revealed that bobcats were generally positively associated with cougars and wolves across seasons, suggesting that they were not spatially suppressed by apex predators. As such we did not simulate bobcat suppression by top predators in the matrix. Coyotes were strongly negatively correlated with cougars in the fall (mean = -0.80, SD = 0.03, range: -0.84 at 8,400 m to -0.68 at 30 m) but less so in other seasons. Coyotes had a near neutral relationship to wolves at a fine spatial scale in the summer (0.08 at 30 m) and fall (-

0.01 at 30 m) but strongly negatively correlated with wolves at coarse spatial scales (summer min: -0.65 at 9,150 m; fall min: -0.72 at 9,150 m).

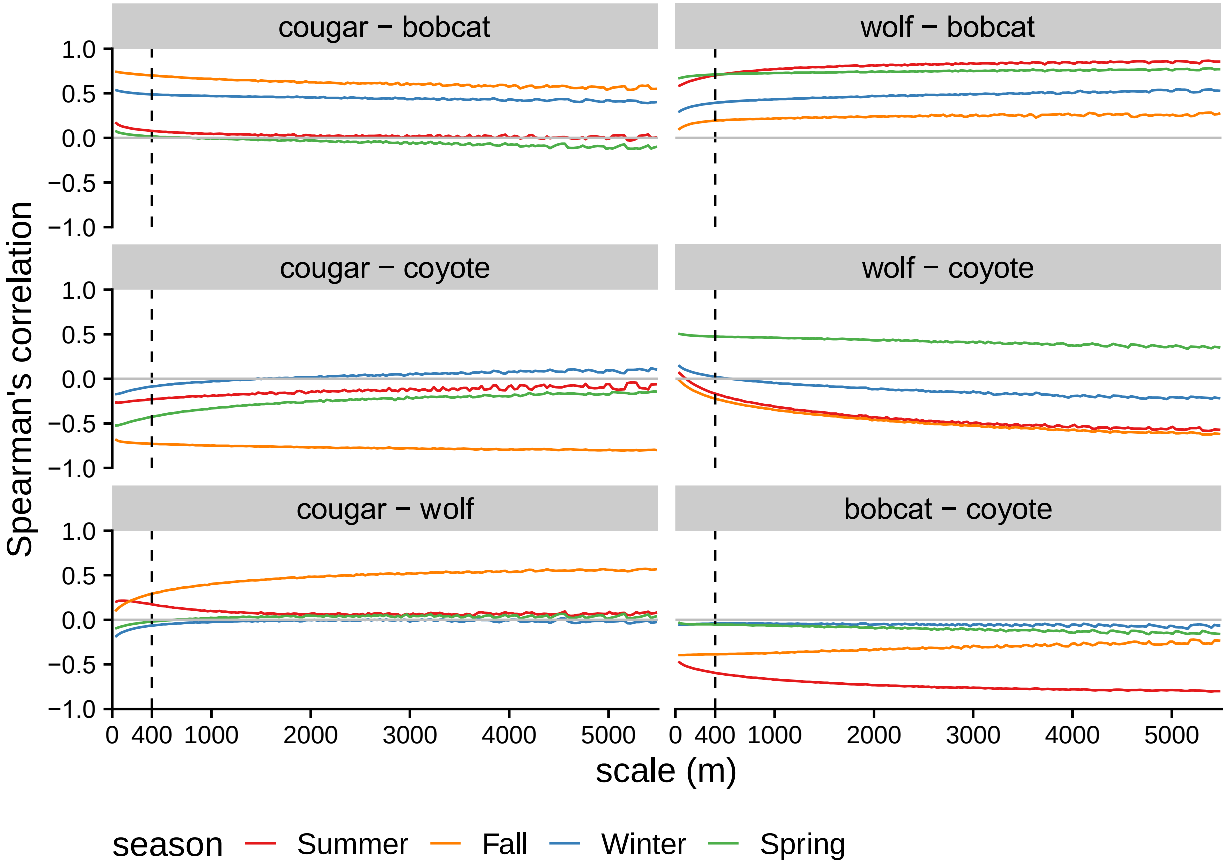

Figure 4.2 Spearman's correlations between predator RSFs plotted from a 30 x 30 m pixel to a 5,000 x 5,000 m pixel illustrate the scale dependence of spatial associations between predators in northeastern Washington, USA. Dashed lines at 400 m resolution approximate the scale of the 200 m radius buffer used to estimate predator exposure at each telemetry location, from which predator exposure covariates in the Cox Proportional Hazard models were derived. Correlations asymptote before ~5,000 m so more coarse spatial scales are not displayed. The RSFs were constructed from predator telemetry data collected between 2016 and 2021.

We documented 330 individual species of understory vegetation across the 201 sites surveyed. Canopy cover performed poorly as a predictor of acceptable forage biomass (remotely sensed canopy cover: $R^2 = 0.03$, *in situ* canopy cover: $R^2 = 0.09$), so we relied on differences between site classes. Biomass of acceptable forage was highest in sites with cover loss, ranging from 23.0 – 852.4 kg/ha (mean = 334.3, median = 321.1, SD = 150.0), compared to forested sites (range: 0.3 – 796.1 kg/ha, mean = 212.6, SD = 165.7) and uncovered sites (range: 0.0 – 1021.9 kg/ha, mean = 256.0, SD = 217.3). Because there was no difference in acceptable forage biomass between forested sites without recent cover loss and historically uncovered sites ($F_{1,135} = 1.6$, df = 1, $P = 0.2$), we pooled these sites to compare areas of cover loss to no cover loss. Estimated biomass of acceptable forage was an average of 40.9% higher in cover loss sites ($F_{1,199} = 12.17$, df = 1, $P < 0.001$), compared to sites with no cover loss (range: 0.0 – 1021.9 kg/ha, mean = 237.3, median = 177.5, SD = 197.2), confirming that the use of remotely sensed data on forest loss can serve as a coarse index of acceptable forage biomass. Winter was most severe the first year of the study ($WSI_{2016\text{-}2017} = 2.07$), the most mild during 2019 – 2020 ($WSI_{2019\text{ – }2020} = -0.31$) and relatively moderate the other years of the study ($WSI_{2017\text{ – }2018} = 0.39$, $WSI_{2018\text{-}2019} = 0.68$, $WSI_{2020\text{-}2021} = 0.08$) relative to all winters since 1965-1966.

Bobcats were highly correlated with wolves in the summer/fall model for adult females ($\rho = 0.87$) and in the model for 0–6-month-old deer ($\rho = 0.85$), but we retained both covariates to prioritize predictive performance of these models (Anderson and Burnham 2002). In the adult model of summer-fall survival, hazard from cougars and WSI of the prior year varied over time, violating the assumption of proportional hazard, but inclusion of a $cougar^2$ covariate and removing the WSI covariate resolved the issue. Likewise, canopy $loss^2$ was included in the 0-6-month-old model to meet the assumptions of proportional hazard of the covariates.

Mortality risk (Figure 4.3, Appendix C, Table C3.1) increased with exposure to cougars for adult female deer and juveniles 0-6-months-old, but not for 6-12-month-old deer. When modeled over the range of observed cougar values, the addition of the $cougar^2$ covariate for adult females in the summer-fall indicates that these deer were especially vulnerable to increased mortality risk in areas of the highest cougar activity. Exposure to areas with high wolf activity increased mortality risk for females in the summer/fall but not winter/spring. Likewise, mortality risk tended to increase for deer $\leq$ 9 months old but not 9-12-month-olds. Exposure to bobcats apparently increased survival of fawns 0-6-months-old while having no effect in other models, but this effect could be due to the correlation with wolves. Coyote exposure tended to increase mortality risk for adult females in the winter, but reduced mortality risk for 9-12-month-old deer. Survival of adult females tended to increase with use of forest cover loss areas, but the effect was not significant. Addition of canopy cover loss^2 to the 0-6-month-old model indicates that the highest levels of use of the areas with canopy cover loss reduced survival probability when modeled over the range of observed uses. Proximity to roads did not influence deer survival at the 1 km resolution at which it was evaluated. More severe winters tended to increase the mortality risk for adult females and juveniles 9-12-months-old. There did not appear to be a carryover effect of winter severity while fawns were in utero to survival the next summer for juveniles 0-6-months-old. Neonates with larger body mass at capture were less likely to die.

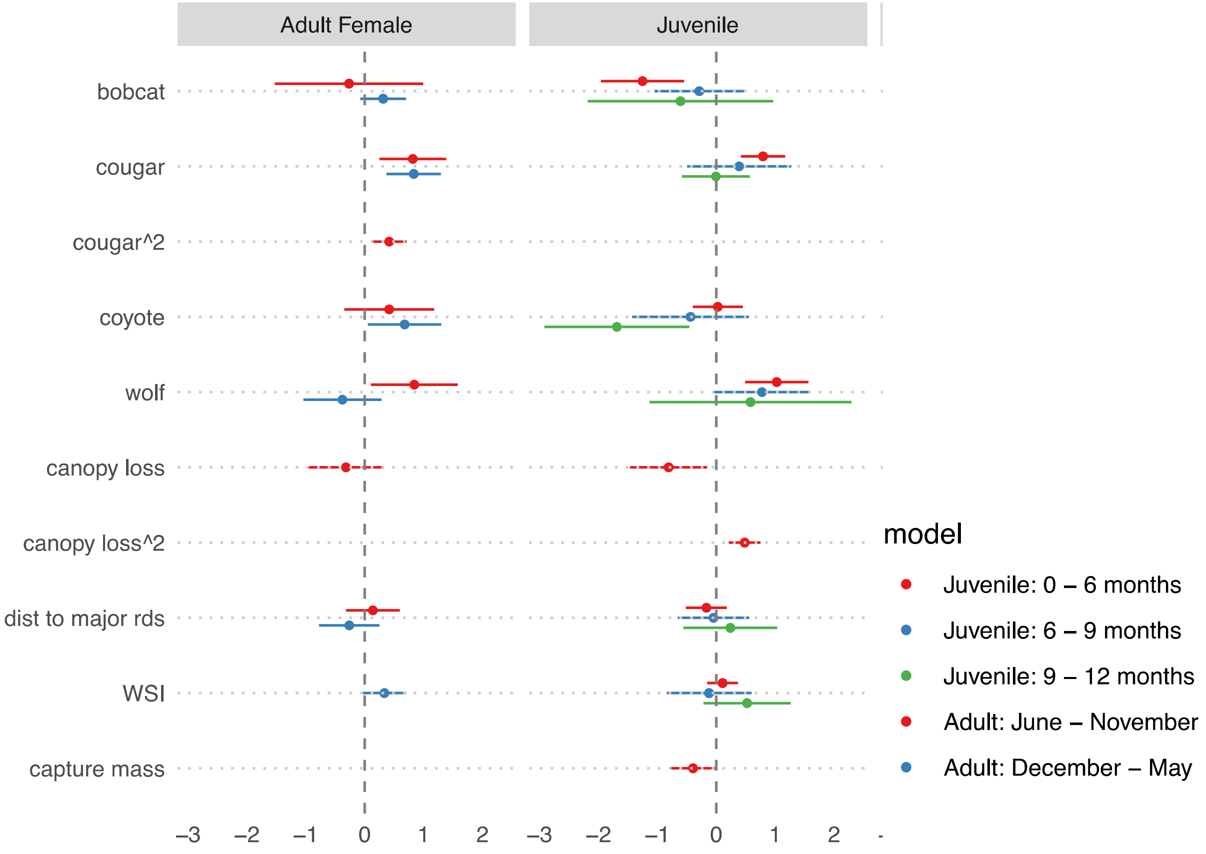

Figure 4.3 Factors influencing risk of mortality for adult female and juvenile white-tailed deer in northeast Washington from 2017-2021. Covariate estimates > 0 increase the risk of mortality, while covariate estimates < 0 reduce the risk of mortality. Dots indicate estimated coefficient values and corresponding lines display the 95% confidence intervals. Because juveniles enter models on the day of capture, the 0-6-month period and June – November period are closely, but not exactly, aligned. Likewise, the 6-9 and 9-12-month models are approximately the same time span as the adult December – May model. The WSI in the 0-6-month model refers to the previous winter (i.e., while fawns are in utero), and WSI of the prior year was excluded from the adult June – November model because it violated model assumptions. Only neonates were weighed at capture. Covariate estimates are included in the Appendix C, Table C3.1.

4.3.2 *Simulations*

The growth rate of the white-tailed deer population increased most strongly with increased forage quality and bobcats and decreased most strongly with increased cougar and wolf exposure (Figure 4.4). Coyotes had a weakly negative effect on λ. The strength of coyote suppression by apex predators modeled over the range of observed values (Figure 4.2) did not influence λ, suggesting minimal indirect effects of apex predators on white-tailed deer λ via coyote suppression. Bobcats were not suppressed by apex predators (Figure 4.2) and thus not incorporated into simulations.

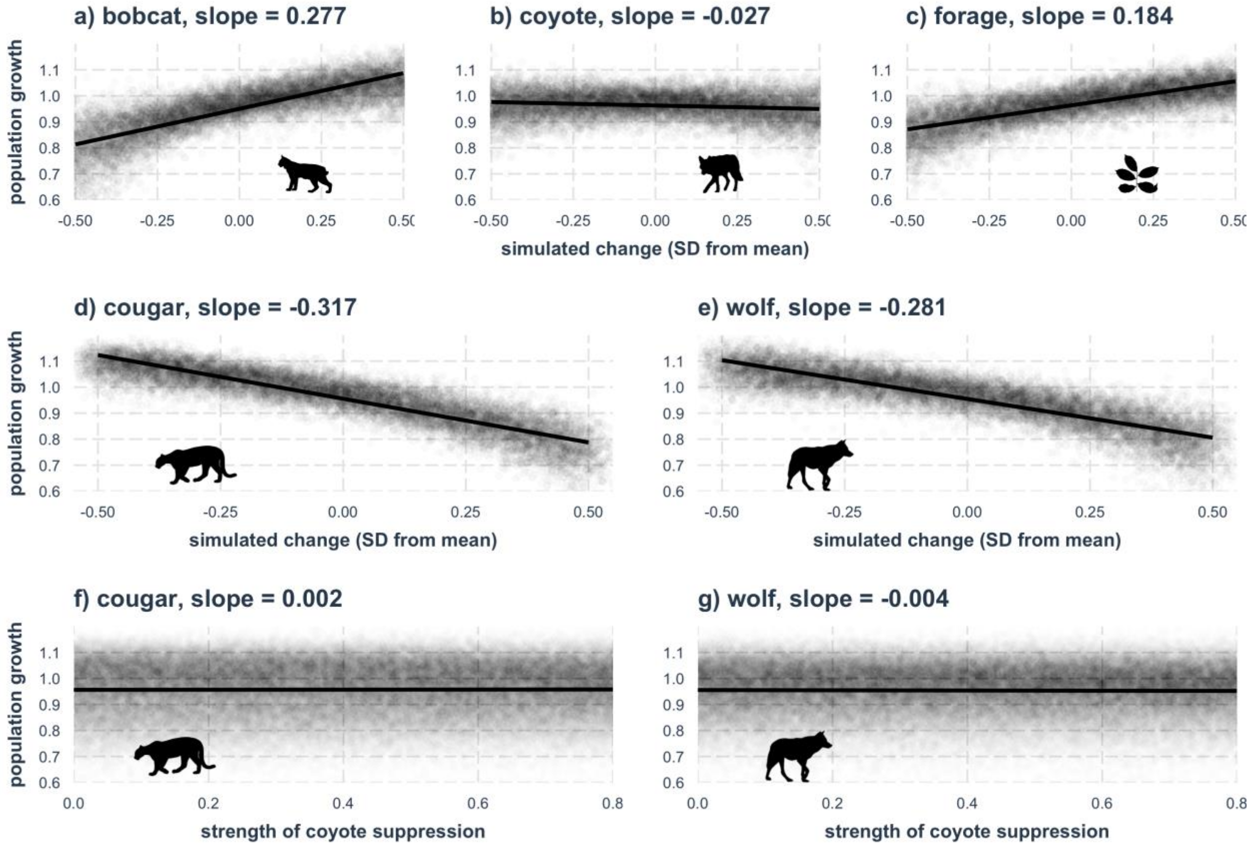

Figure 4.4 Modeled estimates of white-tailed deer population growth in relation to simulated changes to bobcat (a), coyote (b), cougar (d) and wolf (e) exposure and use of areas of canopy cover loss associated with more biomass of acceptable forage (c). Assuming a normal distribution, changes of 0.1, 0.2, 0.3, 0.4 and 0.5 standard deviations equate to 4.0%, 7.9%,

11.8%, 15.5% and 19.1%, respectively. Changes in λ following simulated changes in cougar (d) and wolf (e) exposure account for coyote suppression, however λ was not influenced by the degree of suppression by cougars (f) or wolves (g). Silhouettes were sourced from R package *rphylopic* (Chamberlain 2018) and created by Margot Michaud (a, b, e, g), Ferran Sayol (c), and Gabriela Palomo-Munoz (d, f).

4.4 DISCUSSION

As landscapes become increasingly dominated by anthropogenic activities (Fischer and Lindenmayer 2007), understanding the factors influencing interspecific interactions and population dynamics of wildlife in the human context will be critical for management and conservation (Carter and Linnell 2016, Kuijper et al. 2016). In our study area, which supports cougars, wolves, bobcats, and coyotes and where timber harvest dominates landscape change, we found that the growth rate of the white-tailed deer population was co-limited by bottom-up (H1) and top-down (H2) effects; both simulated increases in use of areas with canopy loss associated with more forage and simulated decreases in exposure to top predators led to increases in population growth. Whereas we observed strong negative spatial correlation between cougars and coyotes in the fall and wolves and coyotes in the summer and fall, these patterns were evidently not strong enough to induce an indirect effect on prey via mesopredator suppression, counter to hypothesis H2a (*top-down limitation via indirect effects of predation*). Cougars were the primary predator of adult female white-tailed deer and influenced population growth regardless of the degree of mesopredator suppression, as did wolves – despite a lack of confirmed predations – indicating that *top-down limitation via direct effects of predation* (H2b) was the dominant effect of these apex predators. Notably, by quantifying exposure to predators, we accounted for both the potential consumptive and non-consumptive effects direct effects of carnivores. The dual limitation of forage and top carnivores suggests that a reduction in deer exposure to apex predators would likely increase the role of forage in limiting deer due to density dependent factors (Wang et al. 2009). In this system and others like it, population dynamics reflected differences in top-predator densities and their response to humans, direct causes of mortality, the role of mesopredators in the system, and forage dynamics.

Both cougars and wolves rely on wild ungulates as a primary source of prey (Elbroch and Wittmer 2012, Newsome et al. 2016), but changes in cougar exposure had a somewhat stronger effect on the population growth rate of white-tailed deer (Figure 4.4). This disparity likely reflects differences in predator population densities across the study area and responses to human activity. In an adjacent area north of our study system, Beausoleil et al. (2021) estimated 1.96 cougars / 100 km^2 (SD = 0.20), whereas wolf densities at the time of our study were approximately 0.19 (SD = 0.03) wolves / 100 km^2 based on the minimum count of wolves in the region from 2016-2021 (Washington Department of Fish and Wildlife et al. 2016, 2018, 2019, 2020, 2021, 2022). Moreover, RSFs showed that cougars had a weakly positive response to human modification of the landscape whereas wolves strongly avoided areas with high levels of human modification across seasons (Appendix C, Table C1.1). These patterns suggest that human activity may have created a refuge for deer from wolves but not cougars. If so, then the role of wolves in limiting prey populations may be dampened in human dominated systems (Hebblewhite et al. 2005, Kuijper et al. 2016).

We did not confirm wolf predation of any collared deer (Table 4.1), yet we know from empirical data wolves did kill deer in our study area (L. Satterfield, *unpublished data*). The efficiency with which a pack of wolves can consume a carcass combined with wolves' tendency to widely disperse a carcass (Elbroch and McFarland 2019) make it much more difficult to confirm wolf predation than that of cougars, bobcats or coyotes during deer mortality investigation (Ganz et al. 2022). Despite the lack of confirmed wolf predation events of collared deer, hazard models indicated that wolf exposure increased mortality risk for adult female deer in the summer/fall and for 6-9-month-old deer, but there was not an effect of wolves on adult female mortality risk in the winter/spring or for 9-12-month-old deer. Analysis of wolf diets in the study area suggests that packs increased relative use of moose in the winter/spring while continuing to feed on deer (L. Satterfield, *unpublished data*), which may explain this lack of effect. Other studies have likewise shown that wolves prefer moose and elk to deer when available (Popp et al. 2018). Deer in this area tend to winter in lower elevation areas close to humans, which may reduce wolf mortality risk via the human shield (Berger 2007), and RSF analysis showed wolves strongly avoided areas with high levels of human modification across seasons (Appendix C, Table C1.1) as have Prugh et al. (*unpublished data*). Notably, distance to roads did not affect mortality (Figure 4.3), indicating that an increase in the risk of vehicle collision could be counteracted by reduced predation risk when wolves avoid roads due to human activities (i.e. the human shield) (Table 4.1). An additional reason that wolves could have influenced deer survival despite the lack of confirmed wolf predations is that by summarizing prey exposure to wolves, the Cox Proportional Hazard framework incorporates the direct risk of mortality from predators as well as the non-consumptive risk effects of wolves (Lima and Dill 1990). If this were the case, deer with greater exposure to wolves may have increased their vigilance, or other defensive behaviors, at the expense of foraging time, in turn reducing body condition and increasing vulnerability to other sources of mortality (Altendorf et al. 2001). Notably, if deer avoided areas of high wolf activity the habitat and resources therein would be functionally unavailable, with the potential to ultimately reduce the carrying capacity of white-tailed deer.

Cougars were a leading source of white-tailed deer mortality across age-classes (Table 4.1) and contributed to increased deer mortality risk for adult females and deer 0-6-months-old. In the spring, pre-parturient adult females are more vulnerable to cougar predation than juveniles (Knopff et al. 2010), presumably because pregnancy increases energetic demands and hinders locomotion, which could possibly explain why 6-12-month-old deer were not at increased risk of mortality with exposure to cougars. This could also reflect increased vulnerability of older deer to cougar predation (Ackerman et al. 1984). Reflecting their role as the primary predator of deer in the system, changes in exposure to cougars had the strongest impacts on population growth of the considered top-down and bottom-up effects (Figure 4.4).

Surprisingly, apex predator suppression of mesopredators, particularly coyotes, played little role in the deer population dynamics we observed, potentially owing to the high diversity of the predator community and the low density of wolves in our study area. In addition, coyotes had a relatively weak impact on deer population dynamics (Figure 4.4). When wolf recolonization led to an increase in the pronghorn population growth rate following coyote suppression in Wyoming, USA, neonate mortality was dominated by coyotes absent wolves, the wolf population was much higher (up to 6.1 wolves / 100 km^2), and wolves did not directly prey on pronghorn (Berger and Conner 2008, Berger et al. 2008). Coyotes in our system were responsible for a substantial proportion of confirmed, likely and possible juvenile mortalities (Table 4.1), but cougars, bobcats and vehicle collisions were also large sources of mortality, dampening the effect of coyotes.

Identifying the appropriate framework and scale to consider the strength of mesopredator suppression poses challenges, as we found the association between wolves and coyotes to be scale- and season-dependent, which has also been documented in Alaska (Sivy et al. 2017, Klauder et al. 2021) and globally for associations between large and small carnivores (Prugh and Sivy 2020). Apex predators can suppress mesopredators behaviorally (i.e., causing mesopredators to avoid areas of apex predator use) and numerically (i.e., by reducing mesopredator density) (Prugh et al. 2009, Ritchie and Johnson 2009), and it may be that behavioral suppression alone is insufficient to drive an indirect effect on prey population growth. Although RSFs are suitable to describe relative abundance (Boyce et al. 2016), correlations between mesopredators and apex predators more likely represent the behavioral response. Additionally, mesopredators in this system avoided areas of high wolf and cougar activity (Prugh et al., *unpublished data*), and if deer did the same, then abundance and predation rates of mesopredators relative to deer may not have changed. Nevertheless, even simulating maximum observed values of wolf and cougar suppression of coyotes (0.8) across the year, effects on population growth were minimal. In regions where mesopredator release or suppression has been an important component of the food web, predator-prey pairings tend to be strongly linked and driven by prey specialization rather than the broad diversity of generalist predators with multiple prey species as in this system (Prugh et al. 2009, Brashares et al. 2010).

Unexpectedly, increased coyote exposure reduced mortality risk for 9-12-months-olds. Likewise, bobcat activity tended to reduce mortality risk for juveniles in the Cox Proportional Hazard models, and apparently led to increased population growth of deer. These counterintuitive results may reflect the numeric effect of apex predators on mesopredators that we were unable to capture by evaluating spatial correlations as bobcats tended to correlate positively with cougars and wolves in all seasons, and coyotes were positively associated with wolves in the spring (Figure 4.2). Given the small proportion bobcat mortality on deer, their effects on the population were minimal with or without suppression. More likely, the bobcat RSFs reflected an unmeasured factor affecting deer survival, and indeed, the bobcat RSFs had the poorest predictive performance of all predator RSFs and were largely driven by the human modification index (Appendix C, Table C1.2).

We found that increased use of areas of canopy cover loss in the growing season (associated with high biomass of acceptable forage) decreased deer mortality risk and simulated increases in use of areas of these canopy cover loss areas increased population growth (Figure 4.4). Because all captures of deer > 6-months-old occurred in the winter, and thus we did not have data on summer habitat use of these deer, we were unable to account for the effects of summer forage on winter/spring survival. However, spring and summer nutrition dictates body condition over the year and ultimately survival and reproductive rates (Côté and Festa-Bianchet 2001, Cook et al. 2004, 2013, Tollefson et al. 2011, Monteith et al. 2014). Additionally, neonates with larger capture mass were at lower risk of mortality, which reflects the quality of forage available to mothers (Côté and Festa-Bianchet 2001). As a result, we likely underestimated the beneficial effects of forage on population growth. Given that forage availability in the summer played a role comparable to that of apex predators in governing the population across the year, this means that forage availability – not top predators – may actually be the primary factor governing the population. This is consistent with Forrester and Wittmer's (2013) finding that predation is the primary proximate cause of death in mule deer populations but predation is generally compensatory, and nutrition is the primary driver of population dynamics. Similarly, Melis et al. (2009) found that impacts of Eurasian lynx (*Lynx lynx*) predation on population growth of roe deer (*Capreolus capreolus*) were reduced in areas of high primary productivity.

It is possible that the growth of early seral vegetation in timber harvest areas may have influenced predator hunting success by disadvantaging wolves' and coyotes coursing hunting style (Kauffman et al. 2007), which could partially explain the effect of canopy loss on population growth. However, a post-hoc analysis showed no change in horizontal visibility at 1.5 m between harvested and unharvested forest sites (F= 0.34, df = 1, P = 0.56), nor did summer predator RSFs correlate with areas of timber harvest, indicating that improved forage is the most likely explanation. Early seral habitat should favor the stalking hunting style of cougars (Ruth and Murphy 2009), which may explain why juvenile deer with the highest use of forest loss areas were more vulnerable to mortality (Figure 4.3, Appendix C, Table C3.1).

Owing to the observational nature of this study, we were unable to fully account for all the pathways through which predators, humans, and forage can influence deer population dynamics, which should be considered when interpreting these results. Using RSFs to describe predation risk assumes that mortality risk is directly related to likelihood of predator use. Whereas predation risk does increase with the probability of an encounter (Lima and Dill 1990, Hebblewhite and Merrill 2007), other factors such as interactions between habitat structure and predator hunting mode (Coon et al. 2020) add additional contigencies that we could not consider here. However, RSFs are a suitable index of relative abundance (Boyce et al. 2016), so even with these limitations our framework is still informative. We did not account for predation risk from black bears in this system because they were not monitored. Bear predations of deer were rare (Table 4.1) and we do not believe bear predation was undercounted (counter to wolf predations). Thus black bears were likely of limited importance to deer population dynamics in such a rich predator community. Forage dynamics and ungulate nutrition are complex processes (Merems et al. 2020) and shaped by many factors in addition to the human land management practices we considered here, which themselves are multifacted (Hayes et al. 2022). However, our finding that even a simplified forage proxy influenced population growth highlights the important role of bottom-up effects in this system, which are likely even stronger than we were able to quantify for the aformentioned reasons. It is also important to consider that this study occurred over a relatively short duration (4-years), and we could not assess the impacts of predation and forage on longer-term ungulate dynamics. Conintued moritoring and longer-term assessment of these relationships here and in other systems will be key to understanding temporal trends in top-down limitation and bottom-up regulation.

Even with these limitations, our findings suggest that in diverse multi-predator multi-prey systems dominated by humans, the direct effects of apex predators on prey overwhelm indirect effects transmitted via mesopredator suppression. Additionally, our study builds on previous work showing that despite top down effects, forage is critical to population dynamics (Forrester and Wittmer 2013) and indicates potential for strong effects in response to drivers of resource dynamics like climate change or active forage management, whether by timber harvest or habitat restoration (Bergman et al. 2014). These findings of co-limitation likewise have important implications in the context of potential predator management. Namely, in other systems co-limited by forage and predation, predator reduction efforts only led to short-lived increases in ungulate abundance (Proffitt et al. 2020). However, habitat modifications can have unanticipated consequences, as in British Columbia, Canada where creation of early seral habitat for timber harvest supported a booming deer population, in turn supporting a larger predator population that negatively impacted rarer ungulates (i.e., caribou [*rangifer tarandus*] Wittmer et al. 2007). As apex predators return to anthropogenic landscapes, more explicit examination of the influence of humans on prey population dynamics via effects on predators (i.e., the human shield; Berger 2007), forage landscapes, and prey mortality (i.e., via hunting and vehicle collisions) will provide important insights to sustaining wildlife across diverse landscapes.

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Chapter 5. COUGARS, WOLVES AND HUMAN SUPER PREDATORS DRIVE A DYNAMIC LANDSCAPE OF FEAR FOR ELK

Publication history: This study was co-authored with Laura Prugh and Melia DeVivo. At the time this dissertation was submitted, no version of this manuscript was in review, accepted or published elsewhere.

Abstract: Human dominated areas are increasingly critical to sustaining wildlife populations, and wildlife dynamics may be starkly different in anthropogenic landscapes than in protected areas, where most research has focused. Humans can function as a shield, providing a refuge for ungulates from human-averse carnivores, or as a super predator, causing mortality through hunting and vehicle collisions and eliciting a fear response akin to that of non-human predators. To manage risk from predators, prey navigate the landscape of fear, which describes risk perception across space and time. Emerging research shows that the landscape of fear can reflect variation at fine temporal scales, such as between day and night, or over longer durations, such as between seasons. We used telemetry data collected from GPS-collared elk (*Cervus canadensis*), cougars (*Puma concolor*) and wolves (*Canis lupus*) between 2017 and 2021 to examine how elk habitat selection changed in relation to each of these predators, as well as human density, across diel and seasonal cycles. We predicted elk would respond most strongly to cougars (nocturnal hunters) and wolves (nocturnal in the presence of humans) at night. We expected elk would either avoid humans, with the strongest avoidance during the day, or exploit areas of higher human density as a shield against predators. Elk adjusted their movement between day and night to reflect the activity cycles of cougars, wolves, and humans, in ways we generally predicted would reduce encountering predators in places and times they would confer the largest threat. Specifically, elk strongly avoided cougars in the night, but displayed a weak response to cougars in the day, and elk were more likely to use open areas where cougar activity was higher. Elk avoided wolves more strongly in the night than the day in the hunting season, but the opposite was true in the summer, which we think reflected crepuscular activity relative to daylight hours. Elk also reduced use of open areas where wolf activity was higher, reflecting the coursing hunting style of wolves. Humans caused nearly 80% of adult female elk mortality, and elk strongly avoided areas of higher human density, especially during the day, supporting the human super predator hypothesis. Elk movement was apparently adequate to manage risk and access resources, as a stage-structured matrix model showed that the population was growing during the four years of the study ($\lambda = 1.098$, 95% CIs: 1.036, 1.152). Our results add to the mounting evidence that humans act as super predators outside of protected landscapes, highlighting the importance of studying prey in multi-predator systems in anthropogenic areas.

Keywords: *Canis lupus*, *Cervus canadensis*, Carnivore, Dynamic landscape of fear, Landscape of fear, Human shield, Human super predator, Predator-prey interactions, *Puma concolor*, Step Selection Function, Ungulate

5.1 INTRODUCTION

To succeed at the individual level, prey species must balance securing access to the resources needed for energetic requirements and reproduction with managing predation risk (Creel 2018). The perception of predation risk across time and space reflects a dynamic interplay between predator habitat use, predator activity cycles, and habitat structure, collectively referred to as a landscape of fear (Laundré et al. 2001, 2010, Gaynor et al. 2019). To navigate the landscape of fear, prey alter behavior or traits to manage risk, for instance by shifting vigilance levels and habitat use to forage in places and times of lower risk (Lima and Dill 1990, Brown et al. 1999, Lima and Bednekoff 1999). However, prey are often subject to multiple predators (Montgomery et al. 2019) that have contrasting patterns of activity and habitat use, making the landscape of fear difficult to navigate. Additionally, humans can profoundly influence predators, prey, and the interactions among them (Sarmento and Berger 2017, Guiden et al. 2019, Lamb et al. 2020). Yet, because most large terrestrial vertebrates primarily occur and are studied within protected areas, the influence of humans on ungulate-carnivore interactions outside protected areas remains largely unknown (Pacifici et al. 2020).

Predator-prey interactions, and thus the landscape of fear, are strongly shaped by contextual factors, including the features of the landscape, the traits of the predator, and characteristics of the prey (Wirsing et al. 2021). For instance, prey are expected to move into more open landscapes when subject to higher risk from stalking predators that rely on cover for ambush, whereas prey should avoid open habitat and take refuge in areas of higher cover or more rough terrain to mitigate risk from coursing predators (Preisser et al. 2007). For example, when predation risk from wolves (*Canis lupus*) – a cursorial predator – was high, elk (*Cervus canadensis*) in Yellowstone National Park, USA selected for dense forests and rough terrain away from the open areas where wolves are more successful hunters (Fortin et al. 2005, Mao et al. 2005, Creel et al. 2005). Conversely, under the threat of cougar (*Puma concolor*) predation – a stalking predator – elk moved into flatter, more open areas and away from dense cover and rough terrain where cougars hunt most successfully (Ruth et al. 2019, Kohl et al. 2019). Such behaviors allow prey to navigate risk from multiple sources, but in a multi-predator system within a human dominated landscape, avoidance of one predator could result in increased exposure to other threats.

One way that prey manage multiple threats is by making movement adjustments to respond to temporal variations in risk, reflecting a dynamic landscape of fear (Palmer et al. 2022). Diel cycles and light availability have been shown to play a strong role in predation risk-sensitive foraging across a wide variety of taxa (Lima and Dill 1990, Prugh and Golden 2014). The dynamic landscape of fear can reflect short-term shifts in predation risk that vary with the diel cycle, or longer term variation across seasons reflecting differences in habitat use, migratory movement, life cycle and abiotic factors such as climate and weather (Prugh et al. 2019, Palmer et al. 2022). Kohl et al. (2018, 2019) recently showed that by responding to a dynamic landscape of fear, elk exploit forage resources in high-risk landscapes by using risky but profitable areas when predators are least active. Specifically, elk avoid cougars – primarily a nocturnal predator – at night and avoid wolves – primarily crepuscular hunters – at dawn and at dusk, creating windows of opportunity to use these otherwise high-quality but risky foraging areas (Kohl et al. 2018, 2019).

Human activity also shows strong temporal patterns and may itself influence a dynamic landscape of fear (Gaynor et al. 2019). However, the ways in which ungulates respond to humans can be difficult to predict because herbivores can benefit from human activity but are also at risk of human-caused mortality. Ungulates can use the ‘human shield’ of anthropogenic areas to avoid human-averse carnivores (Hebblewhite et al. 2005, Berger 2007, Muhly et al. 2011), but may also respond to humans with a fear response that can exceed that of sympatric predators (Crosmary et al. 2012, Ciuti et al. 2012, Lone et al. 2014). Accordingly, predators and prey alike may view humans as a ‘super predator’ (Darimont et al. 2015, Smith et al. 2017). Because humans kill ungulates through vehicle collisions (Huijser et al. 2008) and hunting (Ballard et al. 2000), utilizing the human shield to avoid predators could lead to an increase in human caused mortality (Kautz et al. 2022). Alternatively, ungulates could be at increased risk of predation if fear of the human super predator leads to increased overlap with non-human predators. How ungulates manage risk from multiple predators has yet to be evaluated in a human dominated system.

To examine how prey respond to a multi-predator landscape in the context of humans, we collared and monitored elk in northeastern Washington, USA between 2017-2021 across a landscape occupied by cougars, wolves, and humans. We developed step selection functions to determine if elk movement reflected the dynamic landscape of fear created by humans, cougars, and wolves, hypothesizing that elk would make temporal adjustments in habitat selection to reflect the dynamic landscape of fear on a diel cycle (*H1 – dynamic landscape of fear*) (Palmer et al. 2022). Specifically, because cougars are primarily nocturnal hunters (Ruth et al. 2019) and wolves tend to be more nocturnal than crepuscular in areas with human activity (Theuerkauf 2009), we expected that elk would avoid predators most strongly at night while avoiding humans most strongly during the day when elk are more likely to encounter humans and predators are less active (*H1a – daily dynamic landscape of fear*). We additionally hypothesized that elk would navigate the dynamic landscape of fear according to the season (*H1b – seasonally dynamic landscape of fear*) to reflect shifting vulnerability to human and non-human predators. Because elk were vulnerable to human harvest in this area, we expected avoidance of humans to be strongest during the fall hunting season. Neonatal elk are most vulnerable to predation, so we expected elk to respond to predators more strongly in the summer than in the hunting season as most adult female elk have calves at heel during the former interval (Brodie et al. 2013, Eacker et al. 2016). Additionally, we expected elk with a calf would have a stronger response to predators than elk without a calf in the summer. Such a pattern would suggest that humans function as a super predator (*H2a*), whereas if elk with calves used areas of higher human activity in the summer to avoid cougars and wolves, it may suggest that elk are using humans as a shield to reduce predation risk (*H2b*). We expected that elk would increasingly use open areas where cougar activity was higher, while avoiding open areas where wolf activity was higher, reflecting the hunting traits of the predator (*H3 – predator hunting mode*). If habitat selection failed to reflect risk, it would be possible that the population could decline as a result as evidenced by population growth (λ) < 1.

5.2 METHODS

5.2.1 *Study Area*

This research occurred within Stevens and Pend Oreille Counties of northeastern Washington, USA (latitude: *c.* 47.90° to 48.72°; longitude: *c.* -118.30° to -117.20°; ~ 5,200 km^2; Figure 5.1). Elevations ranged from 370 m to 2080 m. At the center of the study area in Chewelah, WA, cool winters (average low of -6ºC, average high of 4ºC from December – March) and warm summers (average low of 7ºC to average high of 27ºC from June – September; https://www.usclimatedata.com/climate/chewelah/washington/united-states/uswa0074) are typical with an estimated 152 cm of rain and 114 cm of snow annually. Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), and western red cedar (*Thuja plicata*) forests dominate the region, but valley bottoms are predominately converted to residential and agriculture use (1.3 % and 3.5% of the study area, respectively). The human population averages 4.3 people / km^2 (SD: 0.3; range: 0 to 542).

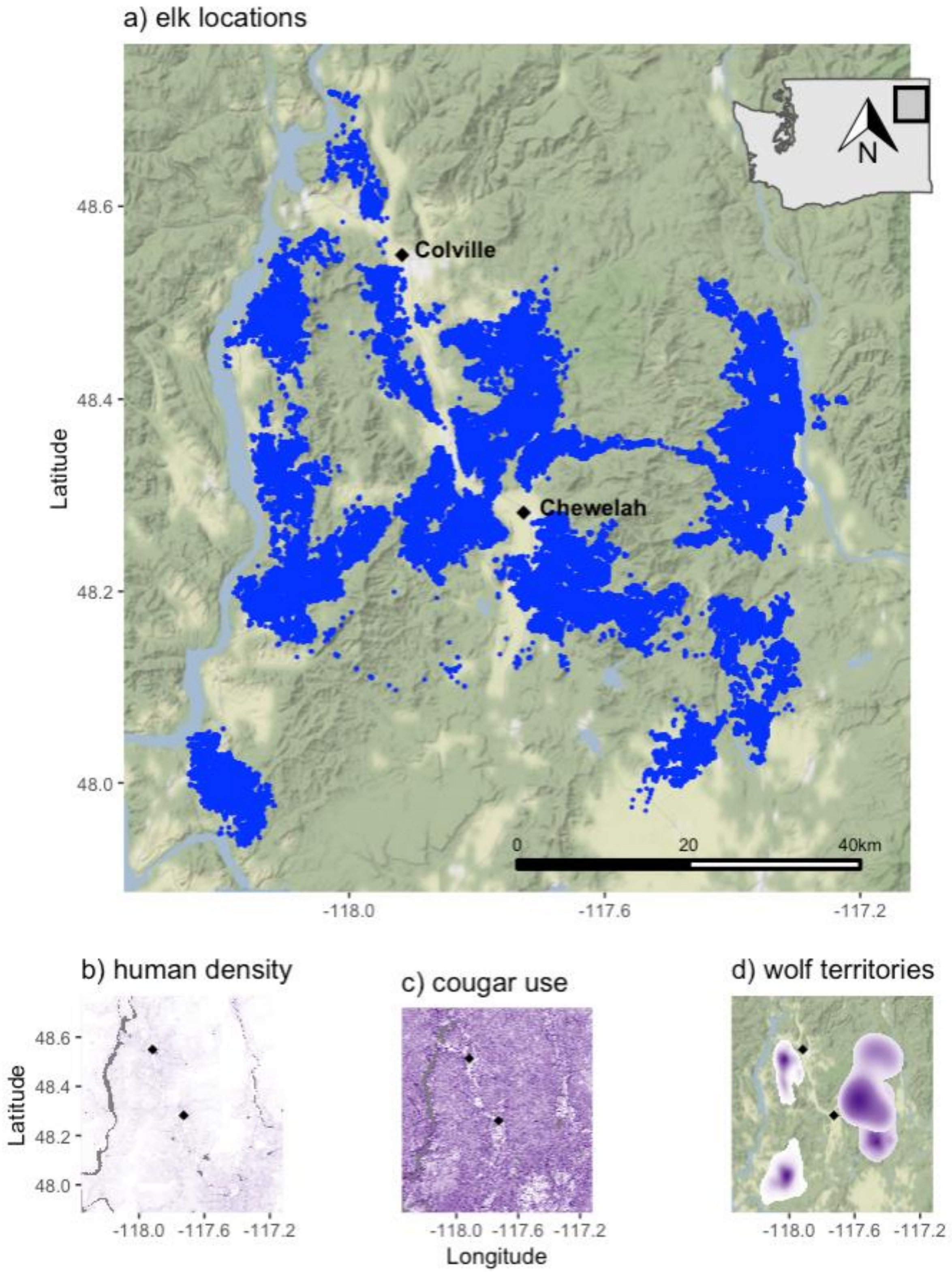

Figure 5.1 Locations of GPS collared elk shown in blue (a). Human density (people per 100 m grid cell, range: 1-50, b), relative likelihood of cougar use (c) and wolf pack activity (summer

2018 as example, d) are higher for deeper purples. Grey shading in (b and c) show water bodies where human density (b) and cougar use (c) were not estimated.

In addition to elk, white-tailed deer (*Odocoileus virginianus*) occur at a relatively high density in this area, whereas moose (*Alces alces*), and mule deer (*O. hemionus*) are present at relatively lower densities. Cougars occur at high density relative to other regions and Beausoleil et al. (2021) recently estimated 1.96 cougars / 100 km^2 (SD = 0.20) directly north of our study system. Four wolf packs occupied the study area for the duration of the project (Wiles and Hayes 2011, Washington Department of Fish and Wildlife et al. 2021). Wolves occurred at lower density than cougars (approximately 0.19 wolves / 100 km^2 [SD = 0.03]) based on the minimum count of wolves in the region from 2016-2021 (Washington Department of Fish and Wildlife et al. 2016, 2018, 2019, 2020, 2021, 2022). Black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) are also native to the area. Archery hunting of male and female elk was permitted for ~ 2-weeks in mid-September and adult male elk were hunted from early October through early December (https://www.eregulations.com/washington/hunting/elk-general-seasons). Exact dates of seasons varied by year, and additional permits were issued outside of the hunting season (generally 1 July – 31 March; A. Prince, *personal communication*) for crop depredations.

5.2.2 *Animal Capture and Handling*

To evaluate elk movement and estimate vital rates, we captured, collared, and monitored neonatal and adult female elk between January 2017 and June 2021. We aerial darted (Jessup 1982) female elk > 1 year old in the winter between January 2017 and January 2020 and fit them with global positioning system (GPS) radio-collars (Model Survey, Vectronic Aerospace, Berlin, Germany). Elk were immobilized with 10mg Thiafentanil and 50 mg xylazine and reversed with

150 mg naltrexone and 500 mg tolazoline. Adult GPS collars were programmed to attempt to record a location every 4 hours. During capture, we extracted a vestigial upper canine for cementum annuli aging (Hamlin et al. 2000) and collected blood to determine pregnancy by analyzing pregnancy-specific protein B concentration (Bio-Tracking LLC, Moscow, ID, USA; Duquette et al. 2012). In 2018, we tested a subset of adult female elk for pregnancy during capture with a portable ultrasound (Ibex Pro, E.I. Medical Imaging, Loveland, Co, USA), and inserted vaginal implant transmitters (VIT; model M3960 Advanced Telemetry Systems, Isanti, MN, USA) when pregnancy was detected (Johnson et al. 2006). From mid-May – early-June, when parturition was expected, VITs were monitored daily with telemetry. When a VIT expulsion was detected, we searched the area around a VIT expulsion site and the mother's location to locate and capture neonatal elk. Calves were also captured opportunistically and by searching the vicinity of GPS collared cow elk when telemetry locations were indicative of parturition, identified by short (<250 m) relocation distances and clustering around a central location (T.R. Ganz, *unpublished data*). In 2019 and 2020, we captured neonates without the use of VITs. Neonatal elk were fit with a combination of expandible GPS collar (Model Survey, Vectronic Aerospace, Berlin, Germany) that transmitted 1 fix daily and very high frequency (VHF) tracking collars (Models M2230B and M4210, Advance Telemetry Systems, Isanti, Michigan, USA).

GPS collars were equipped with mortality sensors that sent emails and SMS notifications after 9 hours of inactivity that were monitored remotely. VHF collars were set to 8-hour mortality delay, and calves were monitored with radio-telemetry on a daily basis from capture to the end of summer, twice per week through the fall, and weekly through the winter and spring until reaching 1-year of age. We truncated the first 3-weeks post-capture for all elk captured > 1 year old to minimize the potential effect of capture on movement (Northrup et al. 2014, van de Kerk et al. 2020).

We investigated mortalities as rapidly as possible upon detection to determine cause of death (median = 2 days, SD = 5, range: 1-16). The investigation included a necropsy of the carcass and mortality scene assessment where we collected DNA swabs associated with the predator when relevant (Ganz et al. 2022). We confirmed predation by skinning the carcass to identify lethal hemorrhage associated with bite marks (Williams et al. 2003) or by finding clear signs of a chase or struggle that indicate a kill site. Because these strict criteria may eliminate true predation mortalities that have been mostly consumed, we also classified likely or possible predation mortalities. “Likely predation” mortalities were cases where predation could not be confirmed, but there was no other apparent cause of death and the evidence pointed to a single potential predator without confounding evidence. “Possible predation” mortalities were cases where predation could not be confirmed but there was no other apparent cause of death, and the evidence revealed signs from multiple potential predators or vague evidence for a single predator. In these cases, we assigned the possible predator as the one that was most likely based on our investigation. When predation was determined to be the confirmed, likely, or possible cause of death, we evaluated the predator tracks, sign and patterns of consumption following Elbroch (2003), Washington Department of Fish and Wildlife (2014), Stonehouse et al. (2016), and Elbroch and McFarland (2019) to determine the species of predator responsible for the kill. We tabulated causes of death by life-stage based on these assessments.

We captured cougars using trained dogs or baited cage traps (Hornocker 1970, Kertson et al. 2011) and fit them with GPS collars (Model Vertex Lite, Vectronic Aerospace and GPS-enabled accelerometer collars, Advanced Telemetry Systems, Inc., Isanti Minnesota, USA).

Wolves were captured with padded leg-hold traps and by aerial darting (Jessup 1982, Linhart 1993, Frame and Meier 2007), and then fit with GPS radio-collars (Models Vertex Lite and GPS Plus, Vectronic Aerospace). Cougar collars were programed to record a fix every 4 hours and wolf collars were programmed to collect locations every 4-12 hours. Elk and cougar capture and handling followed protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol #4226-01). Wolves were captured as part of existing management and conservation activities (Washington Department of Fish and Wildlife et al. 2021) by the Washington Department of Fish and Wildlife and the Spokane Tribe of Indians in accordance with their agency-approved wolf capture and handling protocols (Washington Department of Fish and Wildlife 2019) and the guidelines of the American Society of Mammologists for the use of live animals in research (Sikes et al. 2016).

5.2.3 *Step Selection Functions*

We used step selection functions (Fortin et al. 2005) to examine how elk navigated risk from predators and humans while accessing forage resources. Step selection functions are a form of conditional logistic regression that compare landscape characteristics at the end of a taken step (the transition between two consecutive GPS points) to characteristics at the end of randomly generated steps that an animal could have taken at that time (Thurfjell et al. 2014). We created separate population-level models for elk in the summer (June – August) and in the primary hunting season (September – December). We excluded locations associated with migratory movement from the models, which we identified in Migration Mapper (Merkle et al. 2022) using net squared displacement (Sawyer et al. 2009, Bunnefeld et al. 2011). We also removed any individual with fewer than 100 fixes from each seasonal dataset. To determine if selection reflected maternal behavior to mitigate calf predation risk, we also created and compared summer step selection functions for cow elk known to have a calf (collared calves that survived through summer) to those known not to have a calf (either the cow was not pregnant at capture, or the calf died before reaching 10-days old). We included only elk with > 300 used locations (~50 days of data) in the comparison of the response of elk with and without a calf to ensure that selection differences were not driven by movements of elk with only very young calves.

For the step selection function, we generated 20 random steps per taken step with the turn angle drawn from a von Mises distribution and step-length drawn from a gamma distribution (Northrup et al. 2013, Thurfjell et al. 2014) using the *amt* package in R (Signer et al. 2019). Random steps were compared to taken steps with conditional logistic regression in a Cox proportional hazard framework (Cox 1972) in R package *amt* (Signer et al. 2019). All analyses were conducted in program R (R Core Team 2021).

Seasonal models contained the following covariates: elevation, slope, open x time of day, human population density x time of day, wolf x time of day, cougar x time of day, open x wolf and cougar x wolf. The interaction with time of day allowed us to test if the strength and selection for a particular covariate depended on day versus night (H1a), as we expected that elk would avoid cougars and wolves more strongly at night while responding to humans more strongly in the day, reflecting their respective activity cycles. If elk avoided humans, it would suggest that humans functioned as a super predator (H2a), whereas if elk selected for humans, it could indicate that elk were exploiting the human shield as a refuge (H2b). Due to a lack of overlap between areas of high human use and high predators use (Appendix D, Figure D1.1) we were unable to include an interaction between humans and predators in the model. We included the interaction between non-human predators and open habitat to test for an effect of predator hunting mode (H3), expecting that elk would avoid open areas more strongly where wolves were more active and increase selection for open areas where cougars were more active.

We classified the location at the end of each step as day (between sunrise and sunset) or night (after sunset and before sunrise) using R package *suncalc* (Thieurmel and Elmarhraoui 2019). We included elevation and slope as covariates as they are known to influence elk movement (Long et al. 2008, Rowland et al. 2018), but we did not expect elk responses to elevation and slope to depend on the time of day, so no interactive effect was considered. We sourced elevation and slope values from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM; Farr and Kobrick 2000), and scaled them to have a mean of 0 and standard deviation of 1. To describe human activity that elk should respond to most strongly, we used the unconstrained United Nations adjusted estimates of human population density (Sorichetta et al. 2015, Bondarenko et al. 2020). Human population density was untransformed and represented the number of people in a 100 m x 100 m grid cell (range 0 – 28 across used and available elk locations).

We took different approaches to describe cougars and wolf activity to account for differences in their density and distribution. Beausoleil et al. (2021) recently estimated 1.96 cougars / 100 km^2 (SD = 0.20) directly north of our study system. We used the *ctmm* package in R (Calabrese et al. 2016) to calculate 90% autocorrelated kernel density home ranges (Börger et al. 2006, Fleming et al. 2015) of collared adult cougars (≥ 2 years old and with > 3 months of data; Beausoleil et al. 2013), and found that home ranges varied from 31 to 644 km^2 with a median of 135 km^2 (mean = 226, SD = 190, *n* = 28). As such, we assumed that the area was fully occupied by cougars and used resource selection functions (RSF; Manly et al. 2007) to describe cougar risk to elk as the probability of use within the home range (3rd order selection; Johnson, 1980). Layers were used as adapted for chapter 4 from Bassing et al. (2022), where they are described in more detail. Cougar RSF values ranged from 0 to 1.

Because we collared wolves from all wolf packs in the study area and movement from individual wolves within a pack tends to reliably describe pack level use (Benson and Patterson, 2014), we effectively had a census of wolf packs. Additionally, track and camera surveys indicated that transient wolves outside of known wolf pack territories were rare (Washington Department of Fish and Wildlife et al. 2022). To describe wolf pack activity while accounting for areas outside of pack territories, we created Localized Density Distributions (LDDs; Kittle et al. 2016, 2017) for summer and the elk hunting season. The LDDs are analogous to utilization distributions but incorporate multiple animals for social species such as wolves, representing a spatial distribution of pack use weighted by the number of individuals in the group (Kittle et al. 2016, 2017). Wolf pack size was based on aerial and in-field track surveys and camera trap monitoring (Washington Department of Fish and Wildlife et al. 2017, 2018, 2019, 2020). To create pack-level distributions, we first used an autocorrelated kernel density estimator to generate separate utilization distributions for each collared individual with > 200 locations per season (minimum 1 month of data) for summer and the elk hunting season. To increase sample size and because wolf pack use was largely consistent across years, we also included 2021 wolf telemetry data in creating seasonal pack layers. For each pack, we then averaged the individual layers to describe pack use for each season.

For each season-pack combination, we set values < 0.1 in the distribution layer to 0 to approximate the 90% home range (Börger et al. 2006) and then scaled the layer such that all values summed to one to account for variable intensity of use between different size home ranges (Kittle et al. 2016, Klauder et al. 2021). Next, we multiplied the layer by minimum pack size for that year (Washington Department of Fish and Wildlife et al. 2018, 2019, 2020, 2021), and summed pack layers for the relevant period to create seasonal landscape level use layers for each season-year combination (Kittle et al. 2016). Finally, we scaled wolf values at elk locations from 0 to 1 so that the wolf covariates were on a similar scale as cougars.

We created a continuous covariate describing the proportion of open terrain within a 250 m moving window at 30 m resolution as open terrain was associated with more forage (Appendix D2) and hypothesized to influence predation risk. Open habitat was defined by pooling Terradapt:Cascadia (https://www.cascadiapartnerforum.org/terradapt) landcover classification of agriculture, mesic grass, xeric grass and xeric shrub, based on in-field observations (Appendix D2). We selected a 250 m buffer because this approximated the median step-length taken by elk (summer: median = 243 m, hunting season: median = 255 m). Elk primarily prefer graminoids, which primarily grow outside of densely forested areas, so open habitat generally confers better foraging opportunities for elk (Merrill et al. 1995, Cook et al. 2016, Robatcek 2019). Open habitat should disadvantage the stalking hunting style of cougars that rely on dense cover to approach prey undetected, while favoring the coursing hunting style of wolves (Kohl et al. 2018, 2019). Using vegetation survey data gathered in this study area in 2019 and 2020, described in chapter 4, we verified that open habitat had higher biomass of forage suitable for elk and less horizontal cover relative to other habitat classifications (Appendix D2).

All covariates were available at 30 m resolution, except for human population density which was calculated at 100 m resolution. Before running models, we checked Pearson's correlation between the covariates to ensure correlation did not exceed $|r| > 0.7$ (Dormann et al.

2013). We evaluated predictive performance of the models with leave one individual out cross validation (Boyce et al. 2002, Mahoney et al. 2018).

5.2.4 *Demographics*

To evaluate the growth rate (λ) of the elk population, we created a female only post-birth-pulse matrix with calf, yearling, prime age adult (2 – 9), old adult (10 – 14), and senescent adult (15+) age classes as vital rates differ between these groups (Raithel et al. 2007, Kendall et al. 2019):

$$\begin{vmatrix} 0 & 0 & fa * Sa & fo * So & fs * Ss \\ Sc & 0 & 0 & 0 & 0 \\ 0 & Sy & (1 - to) * Sa & 0 & 0 \\ 0 & 0 & to * Sa & (1 - ts) * So & 0 \\ 0 & 0 & 0 & ts * So & Ss \end{vmatrix}$$

Annual stage-specific survival rates (S_c: calf survival, S_y: yearling survival, S_a: prime adult female survival, S_o: old adult female survival, S_s: senescent female survival) were determined using the staggered entry Kaplan and Meier technique (1958). Annual survival started on June 1 for all yearling and adult elk, while calves entered the model on the day of capture (~June 1). To verify that left censoring of calves did not influence the survival estimate, we assumed that calves captured by VIT were born on the day of VIT expulsion and used a χ^2 test to compare survival between elk captured at ≤ 1 day old to those of unknown age at capture (Gilbert et al. 2014). Only 2 yearling elk were captured, so we pooled their data with adult females to estimate survival and assumed yearling survival was the same as prime age females, an assumption generally corroborated by Raithel et al. (2007). Transitions probabilities were the inverse of the number of years that elk were included in each multi-year age class such that probability of transitioning from an adult to an old elk (t_o) = 0.128 and the probability of transitioning from an old elk to a senescent elk (t_s) = 0.2.

Pregnancy rates were determined from blood serum collected during capture. The female-only fetal rate (f_a: prime adult fetal rate, f_o: old adult fetal rate, f_s: senescent adult fetal rate) was taken to be half the pregnancy rate of the respective age class, and we used a χ^2 test to validate an equal sex ratio of calves at birth. No adult female elk were captured in the senescent age class prohibiting estimation of a pregnancy rate for this class, so we used pregnancy values reported by Raithel et al. (2007) in a review of elk vital rates across 37 populations of Rocky Mountain Elk. We assumed that calves and yearlings did not get pregnant (Raedeke et al. 2002).

We calculated λ as the dominant eigenvalue of the matrix, and the mean and variance of λ were determined by Monte Carlo simulation with 10,000 draws from the matrix, with survival and fetal rates drawn stochastically from a beta distribution. We evaluated the elasticity (the relative influence of a matrix element on λ) and the sensitivity (how much λ would change in response to a change in that matrix element) of the matrix to the various parameters to identify which factors were most important to population dynamics.

5.3 RESULTS

We captured and collared 30 neonatal calves (16 female, 14 male) and 63 female elk ranging from 1.5 to 14 years old. Eleven calves were collared from 18 VITs that were deployed in 2018, and the remaining 19 calves were captured opportunistically (*n* = 4) and from GPS collared cows without VITs (*n* = 15). Calf captures occurred from 18 May to 6 June (mean = May 28, SD = 5 days). Fifteen elk calves survived to 1 year old, 11 died and 4 had unknown outcomes due to dropped collars (Table 5.1). Fourteen adult female elk died over the course of the study, primarily owing to human causes (3 vehicle collision, 2 wounding loss and 6 were legally harvested). Predation due to bears (2) and cougars (3) accounted for nearly half the confirmed calf mortalities while an additional 3 calves likely (2) or possibly (1) died from bear predation. One elk calf likely died by coyote predation and another elk possibly died from an unknown predator, but the investigation was substantially delayed due to GPS malfunction and the cause of death was undeterminable.

Table 5.1 Causes of death of elk collared in Northeastern Washington, USA from 2017-2021. No yearlings died in the study and so are not included here. Likewise, no elk died by wolf predation nor were there any cases where wolf predation was classified likely or possible, though we cannot rule out wolf predation where the cause of death was unknown. We detected evidence of wolf scavenging on one of the calf carcasses, evidenced by DNA not associated with lethal bites. The elk calf that died by starvation(*) was entangled in a fence and abandoned by its mother.

	Calves				Adult Females
	Confirmed	Likely	Possible	Total confirmed, likely, and possible	Confirmed
Unknown COD	5	0	0	5	1
Disease	0	0	0	0	2
Starvation*	1	0	0	1	0
Vehicle	0	0	0	0	3
Human	0	0	0	0	8
Total Predator	5	3	2	10	0
Bear	2	2	1	5	0
Cougar	3	0	0	3	0
Coyote	0	1	0	1	0
Unknown predator	0	0	1	1	0

5.3.1 *Step Selection Functions*

We captured and collared 42 cougars (24 female, 18 male) across both Washington Predator-Prey Project study areas (Bassing et al. 2022), which were used to create RSFs (see chapter 4 and Bassing et al. 2022 for details). We captured and collared 16 wolves (8 female, 8 males) from all 4 packs in the study area. From these wolves we generated 25 wolf x season x year utilization distributions, which were used to construct LDDs of pack activity. Sixty elk informed the summer and fall elk step selection functions (summer: 77,988 used locations; fall: 98,357 used locations; Appendix D, Table D3.1). Step selection functions performed well, evidenced by Spearman's correlation coefficients of 0.963 for the summer and 0.987 for the fall model. We used data from 15 elk to model selection of elk with calves (7,566 used locations) and compared these coefficient estimates to selection of 12 elk (6,013 used locations) without calves.

Elk responded to nearly all considered covariates with pronounced effects of time of day (Table 5.2, Figure 5.2). Elk showed strong avoidance of cougars at night in both seasons (though the strongest avoidance was in the fall hunting season), but weak daytime avoidance of cougars during the hunting season and slight daytime selection for cougars in the summer. Elk avoided wolves most strongly in the day rather than the night in the summer but avoided wolves more strongly at night than day in the hunting season. The strongest avoidance of wolves occurred at night in the hunting season. Elk avoided humans more strongly in the hunting season than the summer, and elk avoided humans more strongly during the day than night in both seasons. We could not explicitly test for an interaction between humans and predators, but the lack of overlap between areas of high predator and high human use indicate that predators strongly avoided areas of human activity. Thus, elk selection for human areas would suggest that elk were leveraging a human shield to avoid predators, and there was no case where elk selected for high human density areas.

Presence of a calf increased avoidance of cougars ($\hat{\beta}_{\text{calf}} = -0.53$, $\text{SE}_{\text{calf}} = 0.14$; $\hat{\beta}_{\text{no calf}} = 0.35$, $\text{SE}_{\text{no calf}} = 0.14$), wolves ($\hat{\beta}_{\text{calf}} = -10.39$, $\text{SE}_{\text{calf}} = 4.56$; $\hat{\beta}_{\text{no calf}} = -7.55$, $\text{SE}_{\text{no calf}} = 0.99$) and humans ($\hat{\beta}_{\text{calf}} = -20.96$, $\text{SE}_{\text{calf}} = 2.09$; $\hat{\beta}_{\text{no calf}} = -2.04$, $\text{SE}_{\text{no calf}} = 0.85$) relative to elk without a calf (Appendix D, Table D3.2 and Figure D3.1). Elk selected for open areas at night but avoided them in the day. Elk responded divergently to the interaction between cougars and % open and wolves and % open, reflecting shifting vulnerability to predators according to their hunting mode (Appendix D, Figures D3.2 and D3.3). That is, elk were more likely to use open areas where cougars had higher activity and less likely to use open areas where wolves were more active.

Table 5.2 Model output for step selection functions of elk movement in the summer (June – August) and the hunting season (September – December) for GPS-collared elk in northeastern, Washington, USA from 2017-2020. Because time of day was modeled as an interactive effect, the effect of night is additive to the daytime effect. That is, adding the coefficient estimates for day and night together for a covariate represents the response of elk at night.

	Summer				Hunting season			
covariate	$\hat{\beta}$	SE	z-score	*P*	$\hat{\beta}$	SE	z-score	*P*
elevation	0.36	0.01	31.1	< 0.001	0.58	0.01	55.3	< 0.001
slope	-0.10	0.01	-19.1	< 0.001	-0.02	0.00	-3.9	< 0.001
cougar - day	0.21	0.04	5.2	< 0.001	-0.10	0.04	-2.4	0.016
cougar x night	-2.97	0.06	-46.1	< 0.001	-3.47	0.06	-62.8	< 0.001
wolf - day	-4.09	0.36	-11.5	< 0.001	-2.98	0.39	-7.5	< 0.001
wolf x night	1.91	0.59	3.3	0.001	-6.75	0.55	-12.3	< 0.001
human - day	-9.31	0.36	-26.1	< 0.001	-12.24	0.43	-28.3	< 0.001
human x night	6.33	0.43	14.8	< 0.001	11.21	0.44	25.2	< 0.001
open - day	-3.02	0.06	-54.2	< 0.001	-3.77	0.05	-69.5	< 0.001
open x night	4.17	0.06	74.5	< 0.001	4.65	0.05	86.9	< 0.001
open x cougar	2.15	0.11	19.5	< 0.001	1.77	0.09	19.0	< 0.001
open x wolf	-3.26	0.67	-4.9	< 0.001	1.35	0.49	2.7	0.006

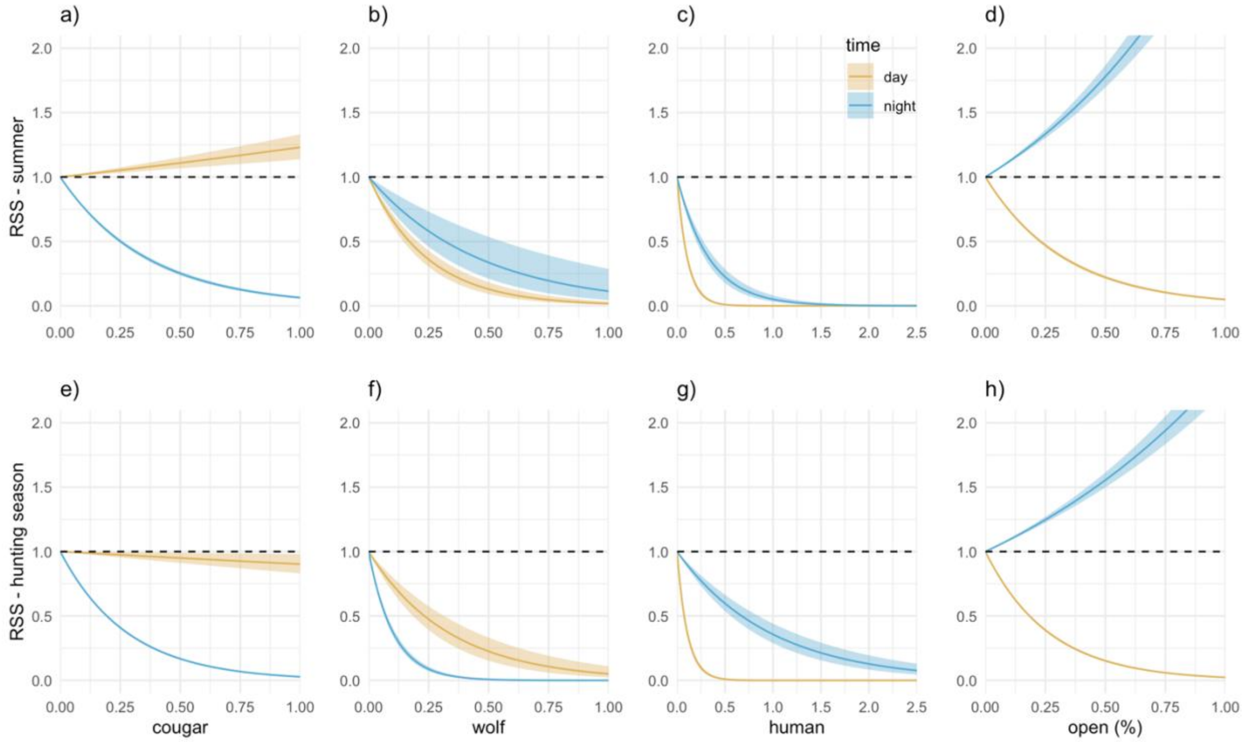

Figure 5.2 Relative strength of selection (RSS; Avgar et al. 2017) for day (yellow) and night (blue) in the summer (top row) and hunting season (bottom row) for elk movement in response to cougars (a, e), wolves (b, f), humans (c, g) and open habitat (d, h). The RSS is the probability of selection for the given covariate value with all other covariates at 0, relative to the probability of selection if all covariates are set to 0. Relative selection occurs when the RSS is > 1 (above the dashed horizontal line) whereas relative avoidance occurs when the RSS is < 1 (below the dashed horizontal line). Elk did not use areas with human density > 2.5 people per 100 m grid cell, so the x-axis is truncated beyond 2.5.

5.3.2 *Demographics*

Survival was relatively high across age classes (Table 5.3). Calf survival did not differ between those captured at ≤ 1 day old and those captured at unknown age ($\chi^2 = 0.20$, df = 1, $P = 0.69$), so all calves entered the survival model on the day of capture (Gilbert et al. 2014). Because there was an equal sex ratio between female (*n* = 16) and male (*n* = 14) calves ($\chi^2 = 0.133$, df = 1, $P = 0.72$) and survival did not vary by sex ($\chi^2 = 0.80$, df = 1, $P = 0.36$), we included both male and female calves in juvenile survival estimates. Based on the observed vital rates (Table 5.3), the population was increasing during the study period ($\lambda = 1.098$, 95% CIs: 1.036, 1.152). Elasticity was highest for survival of prime-aged adults (mean $_{\text{elasticity}}$ = 0.385, SD $_{\text{elasticity}}$ = 0.049) followed by survival of calves (mean $_{\text{elasticity}}$ = 0.137, SD $_{\text{elasticity}}$ = 0.014) and yearling females (mean $_{\text{elasticity}}$ = 0.137, SD $_{\text{elasticity}}$ = 0.014). The population was most sensitive to survival of prime-aged adult females (mean $_{\text{sensitivity}}$ = 0.522, SD $_{\text{sensitivity}}$ = 0.058) followed by the pregnancy rate of prime-aged adult females (mean $_{\text{sensitivity}}$ = 0.253, SD $_{\text{sensitivity}}$ = 0.042) and the survival of calves (mean $_{\text{sensitivity}}$ = 0.241, SD $_{\text{sensitivity}}$ = 0.024).

Table 5.3 Vital rates and standard errors (SE) used to parameterize the matrix of elk population growth, based on elk captured and collared in northeast Washington USA from 2017 – 2021. No adult female elk were captured while in the senescent age class from which to estimate pregnancy, so we populated the matrix with values reported by Raithel et al. (2007) in a review of elk vital rates across 37 populations of rocky mountain elk.

Age Class	*n* (survival)	survival (SE)	*n* (pregnancy)	pregnancy (SE)
Calf	30	0.632 (0.088)	0	0
Yearling female	2	0.926 (0.023)	2	0
Prime-aged adult (2-9 years)	182	0.926 (0.023)	51	0.911 (0.040)
Old (10 - 14 years)	37	0.884 (0.063)	6	0.857 (0.133)
Senescent (15+ years)	7	0.833 (0.152)	values from Raithel et al. (2007)	0.530 (0.126)

5.4 DISCUSSION

Human impacts on landscapes are pervasive, expanding, and increasingly impacting wildlife, making management human-dominated areas critical to sustaining wildlife populations (Fischer and Lindenmayer 2007). However, wildlife dynamics in anthropogenic landscapes may be starkly different than inter-specific interactions in protected areas (Carter and Linnell 2016, Kuijper et al. 2016), and research on predator-prey dynamics in human dominated systems is necessary to understand the wildlife interactions therein to manage wildlife accordingly. In northeastern Washington, we found that elk shifted movement according to the time of day and the season to navigate risks from human and non-human predators, reflecting a dynamic landscape of fear (H1a and H2b; Palmer et al. 2022). Predators avoided areas of high human activity (Appendix D, Figure D1.1). However, rather than exploiting areas of higher human activity as a refuge from predators (i.e., the human shield, H2b), elk strongly avoided humans at all times of day in both seasons examined, likely indicating that elk perceive humans as a super predator (H2a; Darimont et al. 2015, Smith et al. 2017). Elk also moderated selection with respect to habitat structure in ways that would reduce risk depending on predator hunting mode (H3; Preisser et al. 2007, Kohl et al. 2018). The elk population was increasing by ~ 10% per year during the study period ($\lambda = 1.098$, 95% CIs: 1.036, 1.152). Although we were unable to directly evaluate factors influencing population dynamics, population growth suggests that temporally dynamic elk movement contributes to allowing elk to balance risk from human and non-human predators. Our study highlights the importance of accounting for diel variation in animal movement and the landscape of fear and expands the understanding of how species manage risk from multiple contrasting threats.

We observed pronounced effects when considering how elk moved between day and night, highlighting the importance of accounting for diurnal variation in animal movement (Palmer et al. 2022). Elk tended to show a weak response to cougars in the day, but strong avoidance of areas of high cougar activity at night, when cougars actively hunt (Ruth et al. 2019), as was similarly observed by Kohl et al. (2018). This may also contribute to the strong response of elk to open habitat, which disadvantages cougars' stalk and ambush style of hunting, as elk selected open areas at night but strongly avoided them in the day. In contrast to cougars, elk avoided wolves to more similar degrees between the day and night. While we assumed wolves would be primarily nocturnal in the presence of humans (Theuerkauf 2009), camera trap data from an adjacent study area found that wolves were primarily crepuscular, though the area was largely remote and the role of humans was not explicitly considered (Shores et al. 2019). Indeed, elk response to wolves may be explained by primarily crepuscular activity. Specifically, elk avoided wolves more strongly in the day than night in the summer, but the reverse occurred in the hunting season. Summer days receive up to ~16 hours of daylight in northern Washington, while late fall has only ~ 8 hours of daylight (https://www.timeanddate.com/sun/@5789920). If wolves hunted crepuscularly and avoided times of greatest human activity, they would be most active in daylight hours in the summer and at night by the fall, which could have driven the observed effect.

Elk strongly avoided areas of higher human population density, especially during the day, in accordance with the human super predator hypothesis (H2a). Human activities may have additionally contributed to the strong avoidance of open areas in the day, as ungulates have been shown to perceive higher risk from humans where sightlines are increased (Gaynor et al. 2022). Thus, elk apparently manage risk by avoiding humans in the day, cougars and night, and wolves at dawn and dusk, reflecting the activity cycles of the predators. While ungulates have been shown to use temporally dependent habitat selection to manage risk from multiple non-human predators (Kohl et al. 2018), and humans in contrast to a non-human predator (Crosmary et al. 2012, Bonnot et al. 2020), we are the first to our knowledge to evaluate contrasting risk from human and multiple non-human predators on the diel cycle.

Seasonal effects likewise influenced elk movement, but differences between seasons tended to be weaker than between day and night. One reason could be that mortality rates were relatively low, and juvenile survival was high compared to other populations (Raithel et al. 2007), so shifts in seasonal vulnerability to non-human predators reflecting elk calf size and escape capacity may have been less relevant. Nevertheless, neonatal mortality was primarily due to non-human predators, whereas humans were the primary source of mortality for adult elk (Table 5.1). Counter to our predictions, elk tended to avoid cougars and wolves more strongly in the hunting season than in the summer. This finding may reflect seasonal changes in human activity, which may have increased in remote areas during the hunting season compared to other times of year (Bassing 2022). If elk, cougars, and wolves sought to reduce encounters with humans using remote areas, the overlap between predators and elk may have increased. As a result, elk may have increased the strength of avoidance of predators at fine spatial scales to reduce predation risk. In contrast, elk may have been able to avoid cougars and wolves at coarser scales in the summer to reduce predation risk. Given that our models focused on relatively fine scale movements (4-hour fix rate), the effect of scale may have therefore contributed to the stronger response to cougars and wolves during the hunting season than in the summer.

Elk strongly avoided humans, indicating that humans function as a super predator (H2a) rather than a refuge from predators (human shield hypothesis H2b) for elk even though wolves, and to a lesser extent, cougars, also avoided humans in this system (Bassing et al. 2022, Prugh et al. *unpublished data*). Nearly 80% of adult mortalities were due to human causes (i.e., vehicle collisions and hunting), and no adult elk were confirmed to have been killed by predators. While elk avoided humans more strongly in the daytime during the hunting season than in the summer, they avoided humans at night to a weaker degree in the hunting season than in the summer (Figure 5.2). This seasonal effect could be weak evidence of the human shield whereby elk reduce avoidance of humans at night to manage risk from non-human predators. More likely, the stronger avoidance of humans in the summer reflects increased avoidance of humans while elk calves are most vulnerable as elk with calves avoided humans ten times more strongly than elk without calves (Appendix D Table D3.2 and Figure D3.1). By avoiding humans, elk calves may have been subject to increased overlap with predators, as most known causes of death for calves were predation, but we were unable to test for this.

Despite potential tradeoffs that may be conferred from increased risk of one predator due to avoidance of another, population growth ($\lambda = 1.098$, 95% CIs: 1.036, 1.152) derived from vital rates observed during the 4-year period indicate the population was growing. Adult female survival was comparable to other populations, but calf survival was generally at the upper end of the range of what has been observed in other populations of Rocky Mountain elk (Raithel et al. 2007, Brodie et al. 2013, Eacker et al. 2016). Adult female survival typically has the largest influence on population growth as we similarly observed here, but juvenile survival can be highlight variable and tends to drive differences in population growth between populations (Gaillard et al. 1998, Raithel et al. 2007). As such, high juvenile survival likely drove population growth in this system. Notably, juvenile mortality was only observed for calves between 0 – 3.5 months old (mean = 4.2 weeks, median = 1.6, SD = 4.7 weeks), though it is possible that some calves died after collar failure when they were censored from the study, indicating that predation had minimal impact on the survival of all but the youngest elk.

The approach we used to quantify human presence, the predators included in the movement models, and the models describing predator distribution should be considered when interpreting our results. First, population density reflects one aspect of human activity, but it might not account for an increase in human activity in remote areas during the hunting season. However, if this were the case, we might expect weakened avoidance of human population density in the hunting season rather than the strengthened avoidance of humans we observed. Second, our models did not account for black bear activity because we did not collar bears, even though black bears may have been responsible for up to ~50% of neonatal mortalities (Table 5.1). However, only very young elk are vulnerable to black bear predation (Griffin et al. 2011) and all elk calves were born and captured within a 3-week window, so the time period when bears should have affected elk movement would have been limited. Finally, we used different modeling frameworks to describe cougar and wolf activity, reflecting differences in their density and distribution within the study area which may have influenced our findings. Cougars occur at relatively high density (Beausoleil et al. 2021) and home range estimates indicated they fully occupied the landscape, whereas collar data and track and camera surveys indicate wolf activity was generally restricted to wolf pack territories (Washington Department of Fish and Wildlife et al. 2018, 2019, 2020, 2021). As such, we used RSFs (Manly et al. 2007) to describe cougar activity, which represents a habitat use within the home range (Johnson 1980), while we used LDDs to describe wolf activity, which represents location of pack territories and intensity of use of use within them (Kittle et al. 2016). However, these different modeling frameworks likely align with the ability of elk to navigate these threats. Elk can select habitat outside of a wolf pack territory where the risk of encounter is low but must use areas of low likelihood of cougar use within cougar home ranges to reduce risk of encountering a cougar. It is also possible that both cougars and wolves responded to humans contingent on the time of day, but we did not account for this when quantifying predator space use.

Our study indicates that temporal variation in habitat use, especially reflecting the diel cycle, is a critical component of how animals navigate the dynamic landscape of fear and balance risk from multiple threats. Although temporally dependent habitat selection has been examined as a strategy for ungulates to manage risk from multiple non-human predators (Kohl et al. 2018), we are the first to our knowledge to evaluate contrasting risk from human and multiple non-human predators on the diel cycle, and we emphasize the importance of accounting for the temporal component of risk. Rather than providing a refuge from predation risk, as has been documented in protected areas (Berger 2007), our findings add weight to research indicating that humans function as a super predator in human dominated ecosystems (Darimont et al. 2015, Smith et al. 2017, Crawford et al. 2022), indicating that human presence alone is enough to alter wildlife dynamics. While elk habitat selection was apparently adequate to balance mitigating predation risk with accessing resources necessary to maintain positive population growth in this system, outcomes may differ in other anthropogenic systems. If ungulate mortality risk from non-human predators increased following increased overlap due to avoidance of the human super predator, demographic effects could follow. Thus, future research focusing on the potential indirect effects of humans on predator-prey interactions is likely key to sustaining wildlife populations outside of protected areas.

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Chapter 6. CONCLUSIONS

From 2016 through 2021, the Washington Predator-Prey Project fit 670 tracking collars on mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and wolves (*C. lupus*). Additionally, we deployed over 500 motion-sensitive cameras to document animal movement and scavenging, surveyed vegetation at over 260 sites, collected over 2,500 scat samples, and investigated over 600 potential carnivore kills. Collectively, these data streams provided rich insights into the complex dynamics of ungulate–predator interactions in human dominated landscapes of northern Washington.

As part of the broader Washington Predator-Prey Project, my dissertation focused on analysis of collar data to examine the factors influencing mule deer, white-tailed deer, and elk, especially predators, habitat, and humans. Chapters 3-5 each focused on different ungulate species (mule deer, white-tailed deer, and elk, respectively), yet consistent themes emerged from these chapters regarding wildlife dynamics in northern Washington. First, as I described in chapter 2, mortality investigations are a critical component in determining population dynamics, but some predators are more likely to be accurately identified than others. Second, deer and elk responded to both predators and forage, and both are critical factors to consider when examining ungulate movement and population dynamics. Third, ungulate responses to predators depended on the environmental context over space and time. Finally, humans profoundly influenced ungulate-predator dynamics through direct and indirect mechanisms, yielding important insights into wildlife dynamics in working landscapes.

The Washington Predator-Prey Project was initiated to study the broad impact of wolves in Washington, yet few of the deer and elk mortalities we investigated were attributed to wolves. There were multiple reasons for this. In chapters 3 and 4, I estimated that there may have been 15 times as many cougars as wolves in the study areas. Based on this numerical effect alone, wolf predations of deer were likely low compared to cougars or other sources of mortality. Second, a pack of wolves can quickly consume and widely disperse a carcass, making it challenging to find the hemorrhaged bite wounds necessary to differentiate predators from scavengers. Genetic evidence can help identify wolf presence at a kill, as I detailed in chapter 2, but does not distinguish between a scavenger and the predator responsible for the kill. We could not identify the cause of death for a relatively large portion of ungulate mortalities, largely reflecting scavenging and carcass degradation that occurred during delays in accessing carcasses, which limited the ability of investigators to confirm predation. In the north-central study area where mule deer predominate (chapter 3), rugged terrain sometimes delayed investigators. In the northeast study area (chapters 4 and 5), nearly 80% of the land was privately owned, requiring permission from property owners to investigate mortalities when marked animals died on private property.

Even though confirmed predations by wolves were rare and rates of unclassified mortalities were relatively high, the ungulates I studied did respond to wolves and cougars in addition to habitat and forage. In chapters 3 and 5, I showed how mule deer and elk, respectively, altered habitat selection to reflect wolf and cougar activity in ways that I predicted would reduce risk from these predators. In chapter 4, I found that population growth of white-tailed deer depended on the abundance of wolves and cougars, whereas bobcats and coyotes were relatively unimportant to population dynamics. I also found strong evidence that deer and elk were influenced by forage. In chapter 3, I found that mule deer selected for fire-affected forests in the summer to access the flush of vegetation that follows a burn. Likewise, in chapter 5, I showed that elk adjusted their movement to access areas associated with higher forage biomass at times of lower risk. And in chapter 4, I found that white-tailed deer using habitat associated with early seral vegetation had an increased likelihood of survival with subsequent impacts on population growth, suggesting that forage contributed to regulating the population.

The interplay between predator traits and environmental context was critical to understanding how ungulates responded to risk. Wolves are coursing predators that hunt most successfully by chasing prey in open landscapes, whereas cougars are stalking predators that rely on cover to approach prey undetected. When examining the movement of mule deer (chapter 3) and elk (chapter 5), I found that mule deer reduced selection for areas with more stalking cover where cougar activity was higher and avoided open areas where wolf activity was higher. Elk further adjusted habitat selection by the time of day, strongly avoiding cougars at night when cougars hunt and having a relatively weak response to cougars during the day. Likewise, elk strongly avoided humans during the day when people were active but reduced their avoidance of humans at night. It is likely that deer similarly moderated activity by time of day to reflect predator and human activity, but I did not investigate that here.

Finally, I showed that humans profoundly influenced ungulates and their interactions with predators and habitat through direct and indirect pathways. For instance, in chapter 5, elk strongly avoided people, even though predators were relatively unlikely to use areas associated with humans. Humans additionally caused most of the adult female elk mortality through hunting and vehicle collisions, evidencing a direct effect of humans on elk dynamics. In chapter 4, white-tailed deer survival increased with the use of early seral habitat created by land management activities (i.e., timber harvest), suggesting that human activities may indirectly increase the carrying capacity of deer in northeastern Washington. And in chapter 3, mule deer adjusted movements to account for shifting forage and predation risk in wildfire burns driven by human-caused climate change and fire suppression, highlighting the pervasiveness of human impacts across scales.

As wolves recolonize the American West, there is considerable interest in quantifying their impact on ungulates. Like others before me, this research highlights the complexity of factors influencing ungulates and their response to predators and the importance of simultaneously considering habitat and climate. Evaluating wildlife dynamics in the context of habitat and under the influence of humans can help inform management and conservation of predators and prey alike in the diverse landscapes of the Washington and beyond.

APPENDIX A

Supplemental Information for Chapter 2

Wildlife Whodunnit: forensic identification of predators to inform wildlife management and conservation

Table A1 Factors contributing to the positive identification of a predator at the sample level for predations of white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington state from 2017 to 2021. Out of 202 samples, 153 successfully amplified predator DNA. Predator DNA was more likely to amplify when collected from larger prey, while amplification success decreased if a freeze-thaw cycle occurred between the kill and the investigation. The delay between the kill and the investigation, the sample collection location and the amount of precipitation were unimportant in predator DNA amplification. Confidence limits (CL, 95%) are presented for the odds ratios.

Variable	Estimate	SE	*P*	Odds Ratio	Lower CL	Upper CL
Delay	0.40	0.28	0.16	1.50	0.90	2.75
Weight	0.78	0.24	0.001	2.18	1.41	3.58
Type-soft	-0.29	0.40	0.47	0.75	0.33	1.61
Freeze-thaw	-1.21	0.49	0.01	0.30	0.11	0.78
Precipitation	0.02	0.21	0.91	1.03	0.70	1.63

Table A2 DNA amplification success rates over time for samples collected from predation mortalities of collared white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington state from 2017 to 2021.

Delay (days)	Success Rate	Samples (*n*)
0 days	67.9%	28
1 day	67.7%	99
2 days	87.2%	39
3 – 5 days	95.8%	24
6 – 10 days	83.3%	12

Table A3 Factors contributing to misidentification of the predator when only using field evidence to assess predations of white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington state from 2017 to 2021. Out of 61 predation mortalities, the predator was misidentified in 13 cases when only using field evidence. Predators of smaller prey (i.e., deer fawns and elk calves) were more likely to be misidentified than larger prey (i.e., adult deer), while they delay between the kill and the investigation, the confidence of the investigator, and the interaction between the delay and investigator confidence were all unimportant. Confidence limits (CL, 95%) are presented for the odds ratios.

Variable	Estimate	SE	*P*	Odds Ratio	Lower CL	Upper CL
Delay	-0.26	0.68	0.70	0.77	0.16	2.19
Weight	-1.61	0.64	0.01	0.20	0.04	0.57
Confidence	0.07	0.42	0.87	1.07	0.49	2.80
Delay x Weight	-1.25	1.08	0.24	0.29	0.02	1.46

APPENDIX B

Supplemental Information for Chapter 3

Interactive effects of wildfires, season, and predator activity shape mule deer movements

B.1 LANDCOVER ANALYSIS

B1.1 *Analysis*

We expected fire to reduce canopy cover, increase forage quality, and increase snow depth, which in turn may explain how fire influenced mule deer selection. To test our predictions of the impacts of fire on the landscape, we drew a random sample of 1040 points stratified across aspect, elevation and our 13 burn classes and used linear to regression to examine how canopy cover, forage quality and snow depth responded to burns across these points. Agricultural and developed areas, snow/ice, and water were unlikely to reflect fire impacts, so we excluded these areas from the analysis, leaving 1037 points. Effects were tested with 2019 layers describing canopy cover, Normalized Difference Vegetation Index (NDVI) and Snow Disappearance Date. We chose 2019 to evaluate the layers because 2018 was the last study year with major wildfires, and as such remotely sensed layers did not reflect actively burning fires and allowed us to examine a minimum of 1 year since fire. We obtained canopy cover (%) and a composite summer NDVI from Terradapt:Cascadia (https://www.cascadiapartnerforum.org/terradapt). Rather than a temporally varying NDVI, the composite value amalgamated NDVI scores for each 30 m pixel from July 5 – September 22, 2019 to approximate summer nutritional value of each location. We standardized NDVI for use in the models such that the mean was zero and standard deviation was one. In constructing these analyses, we were aware that NDVI can be highly correlated with canopy cover in densely forested areas, where it may be a less reliable indicator of forage quality (Hull & Shipley 2019, Pettorelli et al. 2005). However, given the lack of ground validation data, we were interested in testing if remotely sensed data would reflect changes in the understory vegetation due to a flush of new growth following a fire. If this were the case, we expected that the linear regression would reveal that recently burned areas had lower canopy cover and higher NDVI than unburned areas.

For this analysis, we treated landcover as a categorical covariate. Elevation and burn class were used as described in the manuscript, and we also included elevation^2 to account for the fact that canopy cover and NDVI could be highest at mid elevations and lower at the extremes. Aspect was treated as a categorical covariate with the four cardinal directions as categories. Snow depth data were not available for this area at a sufficiently fine-grained resolution for our analyses. We used snow disappearance date as a proxy for snow depth because deeper snow typically takes longer to melt in the spring (Schneider et al. 2019). We used a daily snow disappearance date product derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) data that represents the last day of the year when snow is detected in a 500 m pixel (Crumley et al. 2020, Nolin et al. 2021). We included elevation, aspect, and land cover in the models to account for their effects on canopy cover, forage quality, and snow, resulting in the three following models:

(1) Canopy Cover (%) ~ elevation + elevation^2 + aspect + burn class + landcover

(2) NDVI ~ elevation + elevation^2 + aspect + burn class + landcover + canopy cover

(3) Snow Disappearance Date ~ elevation + elevation^2 + aspect + burn class + landcover + canopy cover

We ran models with all possible combinations of landscape predictors and chose the most parsimonious based on the Akaike Information Criterion (Burnham & Anderson, 2002). If models were within 2 AIC points, we considered them the same and chose the simpler model (Arnold, 2010).

B1.2 *Results and Interpretation*

The best model for canopy cover ($R^2 = 0.61$) included burn class, elevation^2, aspect, and land cover, but not elevation, supporting our prediction that fire would reduce canopy cover. All burn classes had a negative effect on canopy cover, though not all effects were statistically significant at the $\alpha = 0.05$ level (Table B1.1; Figure B1.1). Canopy cover was lowest 5-9 years post fire rather than immediately after the fire, with 12.3% (CIs: -16.3%, -8.4%) less cover than unburned areas in high severity burns. Canopy cover trended toward pre-fire levels after the 5-9 year low as expected, returning to pre-fire levels after 20 years (Table B1.1; Figure B1.1).

The best model for NDVI ($R^2 = 0.78$) included elevation, burn class, land cover and canopy cover and excluded elevation^2 and aspect (Table B1.1; Figure B1.1). We found that NDVI primarily reflected canopy cover rather than a flush of new understory growth, even for new burns. NDVI was no different after 10 years than in unburned areas, except for the oldest (21-35 year) high severity burns. The strong correlation of canopy cover with NDVI (Pearson's correlation of 0.81) suggests that NDVI did not capture ungulate forage quality in this system and instead reflected canopy cover at large scale (Pettorelli et al. 2005). However, ample studies measuring understory vegetation change following fire and canopy cover loss consistently indicate that the forage base for deer does improve (Hobbs & Spowart 1984, Proffitt et al. 2019, Roerick et al. 2019, Hull et al. 2020, Hayes et al. 2022).

The most parsimonious model for snow disappearance date ($R^2 = 0.60$) included elevation, elevation^2, aspect, burn class, and canopy cover, and excluded landcover (Table B1.1; Figure B1.1). Snow disappeared later in burned areas, although results were mostly non-significant (Table B1.1). Counter to our expectations that lower canopy cover would yield deeper snow and longer retention, snow disappearance date advanced 1 day for every 1.25 % (95% CIs: .25%, 1.75%) increase in canopy cover across our randomly sampled points. Forest structure can accelerate spring snowmelt by increasing longwave radiation in climates with mean December – February temperatures > -1°C, which may be the case for lower elevation regions of our study system, whereas forest cover delays snowmelt in cooler areas by shading snow (Lundquist et al. 2013). With such a wide span of elevations and temperatures across our study, it is hard to determine the true impact of fire on snow depth, highlighting the need for high resolution data describing snow characteristics like depth to better understand how wildlife are responding to changing snowscapes (Penczykowski et al. 2017, Boelman 2019).

Table B1.1 Predictors for the models of landscape metrics that we expected to be impacted by fire. Empty rows in the table represent covariates that were excluded from the model based on AIC, except for first model where the canopy cover was the response.

	Canopy Cover			NDVI			Snow Disappearance Date		
Covariate	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	37.0	33.6	40.4	-1.3	-1.4	-1.2	98.1	93.2	103.1
elevation				-0.11	-0.14	-0.08	17.4	16.4	18.4
elevation^2	-5.5	-6.2	-4.9				3.4	2.4	4.3
aspect - N	2.9	0.9	4.9				2.5	0.1	4.9
aspect - S	-1.7	-3.7	0.3				-3.9	-6.3	-1.5
aspect - W	-1.3	-3.4	0.7				-3.8	-6.2	-1.3
0-4 yrs low	-1.3	-5.1	2.6	-0.2	-0.4	-0.1	2.8	-1.6	7.3
0-4 yrs mod	-4.4	-8.4	-0.3	-0.3	-0.5	-0.2	3.1	-1.6	7.7
0-4 yrs high	-6.0	-10.0	-2.0	-0.2	-0.4	-0.1	5.4	0.7	10.0
5-9 yrs low	-7.5	-11.3	-3.6	-0.2	-0.4	-0.1	1.2	-3.3	5.7
5-9 yrs mod	-10.6	-14.5	-6.6	-0.3	-0.4	-0.1	0.1	-4.6	4.8
5-9 yrs high	-12.3	-16.2	-8.4	-0.158	-0.318	0.001	4.4	-0.3	9.1
10-20 yrs low	-4.6	-8.4	-0.8	-0.03	-0.19	0.12	-0.8	-5.2	3.7
10-20 yrs mod	-6.8	-10.7	-3.0	0.04	-0.12	0.19	0.8	-3.6	5.3
10-20 yrs high	-7.2	-11.2	-3.3	-0.02	-0.18	0.14	3.2	-1.4	7.7
21-35 yrs low	-2.0	-5.8	1.8	0.0	-0.2	0.2	5.1	0.6	9.6
21-35 yrs mod	-4.3	-8.1	-0.4	0.11	-0.05	0.26	8.7	4.2	13.1
21-35 yrs high	-2.1	-5.9	1.8	0.18	0.03	0.34	5.0	0.6	9.5
shrub	8.6	6.8	10.4	0.5	0.5	0.6			
forest	31.0	28.5	33.6	0.3	0.2	0.4			
canopy2019				0.037	0.035	0.040	0.08	0.02	0.14

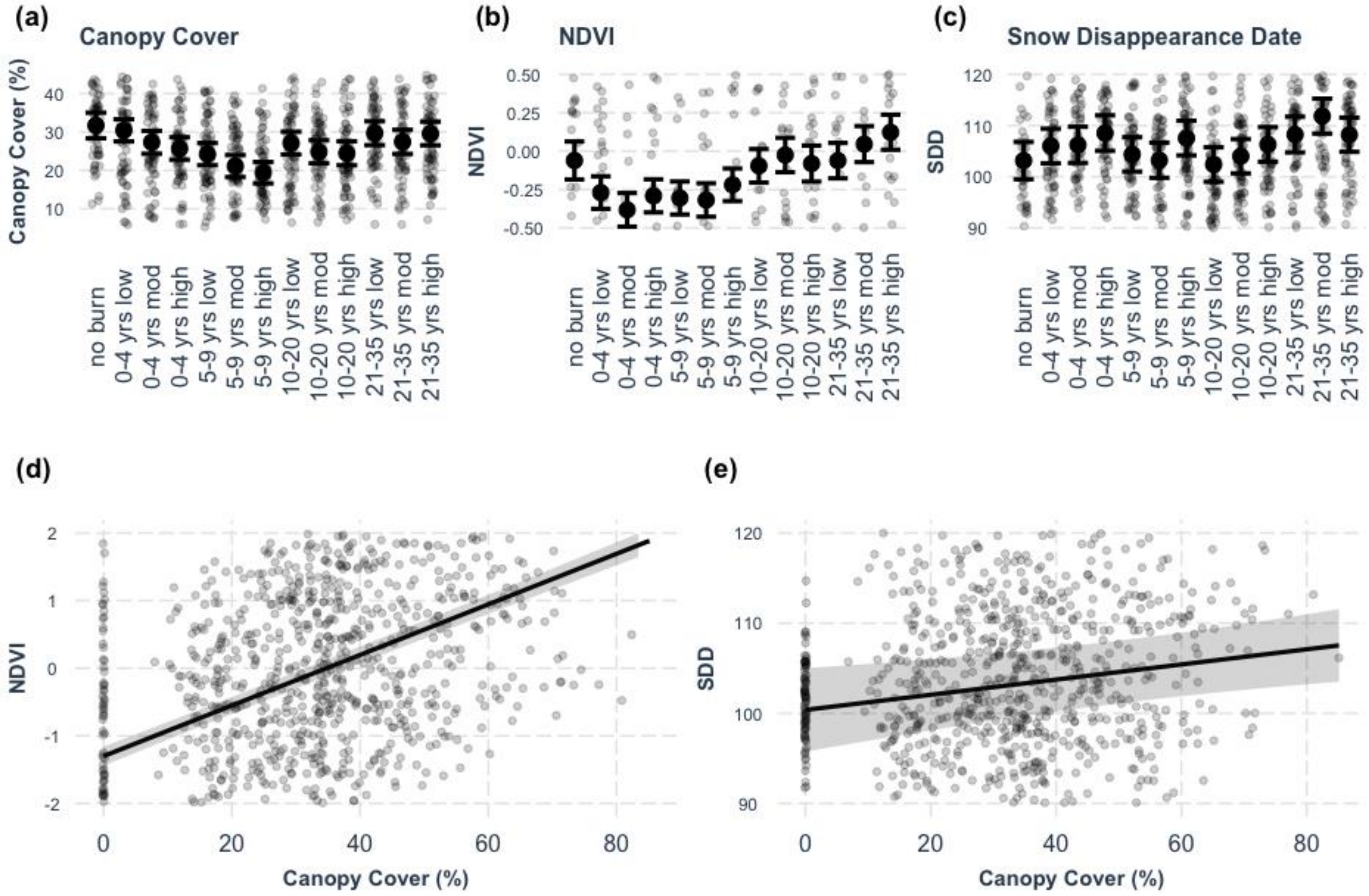

Figure B1.1 Fire generally (a) reduced canopy cover, with more severe fires having stronger effects. (b) NDVI decreased 0-9 years post fire and was no different 10-35 years post fire compared to unburned areas. (c) Snow disappeared later following wildfires, but the effects were generally non-significant. (d) NDVI was highly correlated with canopy cover. (e) Snow disappearance date increased with canopy cover.

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B.2 PREDATOR DATA AND DISTRIBUTION MODELS

Table B2.1 Characteristics of collared cougars. End date is the date of mortality, collar failure, or the last transmission as of July 15, 2021. A total of 17,233 used locations (minimum: 132, maximum: 1,775, mean: 783, SD: 419 per individual) were incorporated into the summer model and 15,330 used locations (minimum: 50, maximum: 1,167, mean: 529, SD: 348 per individual) were included in the winter model. Individuals with no locations in a model were excluded from calculations of summary statistics.

ID	Sex	Capture Date	End Date	Locations in the summer model	Locations in the winter model
MVC202F	Female	2017-01-04	2019-01-15	1253	1022
MVC204F	Female	2017-01-30	2017-07-09	132	216
MVC205F	Female	2017-01-30	2019-03-05	1055	1167
MVC206F	Female	2017-02-13	2021-01-04	1347	828
MVC207F	Female	2017-02-13	2017-10-20	498	157
MVC208M	Male	2017-02-14	2018-01-16	550	406
MVC221M	Male	2018-01-07	2020-10-25	605	969
MVC222F	Female	2018-01-16	2019-01-23	601	613
MVC223F	Female	2018-01-22	2018-10-18	550	283
MVC224M	Male	2018-02-20	2018-11-05	606	108
MVC225F	Female	2018-03-07	2019-12-17	1210	693
MVC226F	Female	2018-03-10	2020-01-09	608	508
MVC227F	Female	2018-03-10	2021-01-08	1775	1041
MVC229M	Male	2019-01-12	2020-04-22	587	945
MVC230F	Female	2019-02-01	2020-03-23	551	717
MVC231M	Male	2019-02-16	2019-11-21	596	130
MVC232F	Female	2019-02-28	2019-08-11	259	75
MVC201F	Female	2016-12-14	2016-12-26	0	50
MVC228F	Female	2018-12-16	2019-01-26	0	203
MVC233F	Female	2019-12-20	2020-01-23	0	204

MVC234M	Male	2019-12-21	2020-02-19	0	358
MVC235M	Male	2019-12-27	2020-02-25	0	359
MVC236F	Female	2020-01-17	2020-03-18	0	348
MVC237M	Male	2020-02-25	2020-04-25	0	104

Table B2.2 Coefficient estimates for the cougar RSF and their 95% confidence intervals for the summer and winter resource selection functions. Predictors with confidence intervals overlapping zero were excluded when creating probability of use layers. Elevation and distance to major roads was correlated by 0.78, though neither was excluded because we were interested in prediction rather than interpretation of the covariates. Landcover layers were available by year, while the randomly drawn points in the RSF were not assigned a time. To account for this, we assigned the mean value of % landcover from the years of the study to estimate the effects of the predictor covariates, but we predicted cougar use annually using the landcover data available for that year.

	Winter			Summer		
Covariate	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)
intercept	-0.001	-0.009	0.006	-0.098	-0.109	-0.086
shrub	0.093	0.086	0.101	0.075	0.064	0.087
open	0.039	0.032	0.045	0.058	0.047	0.068
forest	0.043	0.036	0.050	0.073	0.062	0.085
water	-0.004	-0.005	-0.003	-0.008	-0.009	-0.007
human population density	0.001	-0.001	0.002	-0.001	-0.001	0.000
developed	-0.078	-0.244	0.088	0.121	0.072	0.170
major roads	-0.001	-0.002	0.000	-0.008	-0.011	-0.006
minor roads	-0.003	-0.004	-0.002	-0.002	-0.004	0.000
elevation	0.002	0.000	0.003	-0.016	-0.018	-0.014
elevation^2	0.008	0.007	0.009	0.014	0.012	0.015
heat load	-0.016	-0.021	-0.012	0.089	0.084	0.094
terrain roughness	-0.007	-0.008	-0.006	0.025	0.024	0.026
terrain position	-0.003	-0.004	-0.002	-0.003	-0.004	-0.002

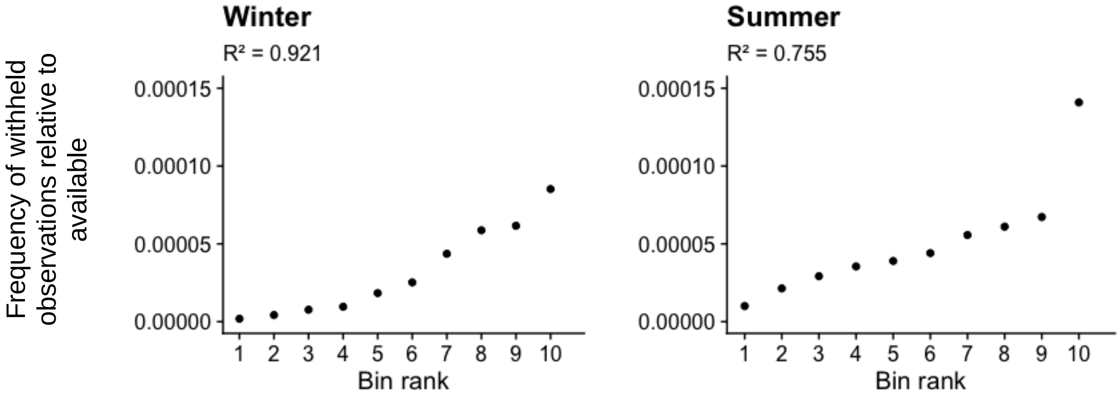


Figure B2.1 Correlation between the binned RSF score and the area adjusted relative frequency of the cross-validated used locations from the withheld individual used in testing the cougar resource selection function, following Boyce et al. 2020. Spearman-rank correlation for the winter model ($r_s = 0.99$) and summer model ($r_s = 0.95$) were high, indicating that the models performed well.

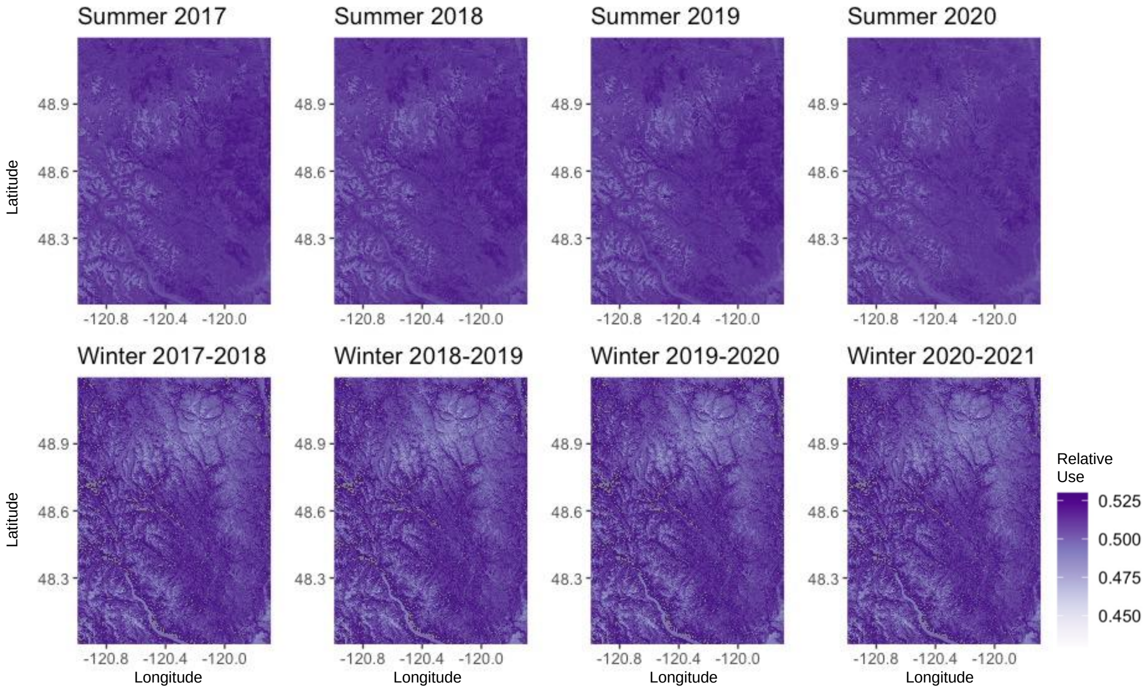


Figure B2.2 Relative probability of cougar use mapped across the study area by season and year.

Table B2.3 Summary of the number of locations from collared wolves used to inform the LDDs for each pack for each season by each year. Years and seasons without wolves were estimated based on average layers from other years, adjusted for pack size. The Lookout pack primarily used winter range to the north and east of the study system in the later years of the project. Wolves W71F and W93 dispersed out of the study area prior to their end date, and these dispersal locations were excluded from LDDs. As such, there were no locations for summer 2017 or winter 2020-2021 so these columns were excluded from the table.

ID	**Pack**	**Sex**	**Capture Date**	**End Date**	**Summer 2018**	**Summer 2019**	**Summer 2020**	**Winter 2016-2017**	**Winter 2017-2018**	**Winter 2018-2019**	**Winter 2019-2020**
W61M	Loup Loup	Male	2018-02-08	2019-09-07	609	54	0	0	199	624	0
W71F	Loup Loup	Female	2017-02-10	2017-07-18	0	0	0	195	0	0	0
W88M	Loup Loup	Male	2019-03-01	2020-10-31	0	536	492	0	0	75	531
W93M	Lookout	Male	2019-05-30	2020-09-01	0	637	0	0	0	0	633
W94M	Lookout	Male	2019-06-01	2020-10-31	0	643	637	0	0	0	632

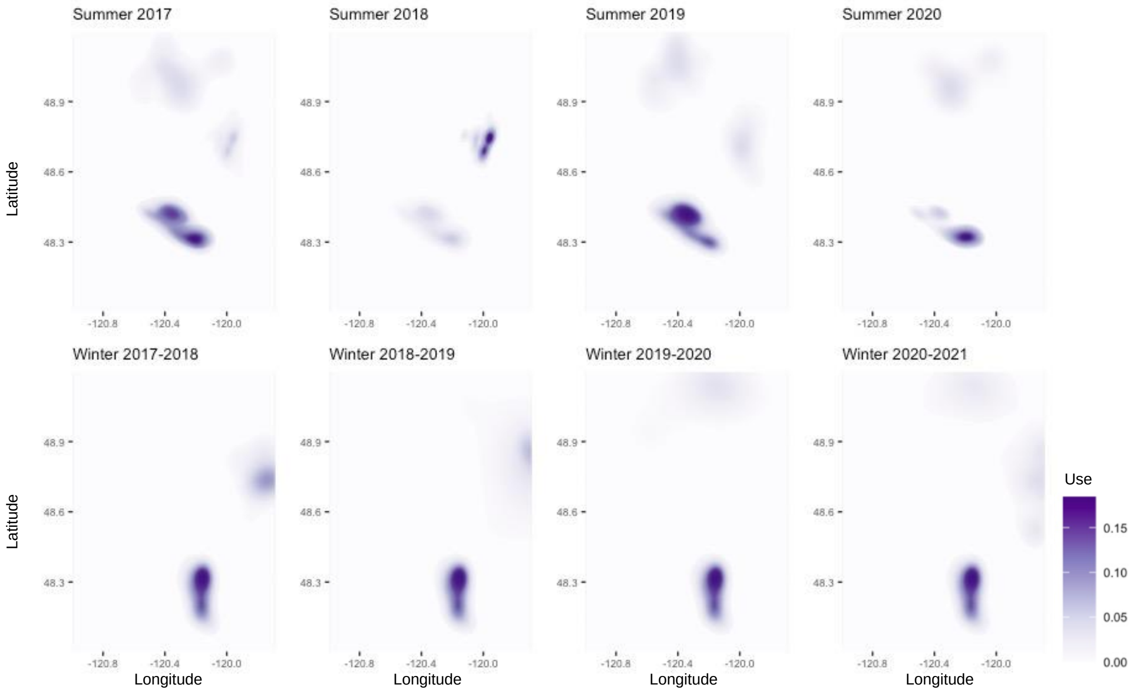


Figure B2.3 Localized density distributions (LDDs) across the study area for wolves. LDDs measure intensity of use for social animals, with the sum of all locations equaling 1. We scaled LDDs between 0 and 1 to improve interpretability of the plots, since they represent relative probability of use within a raster cell.

B.3 MULE DEER MOVEMENT

Table B3.1 Summary information for mule deer that contributed to the model. Censored locations from the first 3 weeks post capture are excluded. End date is the date of mortality, collar failure, or the last transmission as of July 15, 2021. In total 145,229 used locations were included in the summer model (minimum: 292, maximum: 2,565, mean: 1,252, SD: 649 per individual). The winter model incorporated 150,280 used mule deer locations (minimum: 50, maximum: 2,449, mean: 1,051, SD: 699 per individual). Deer with no locations in a model were excluded from calculations of summary statistics.

ID	Capture Date	End Date	Locations in the summer model	Locations in the winter model
12MD18	2018-01-19	2018-11-30	292	208

14MD18	2018-01-19	2020-07-10	1308	1423
151MD18	2018-01-19	2018-10-10	578	204
152MD18	2018-01-19	2018-06-04	0	208
153MD18	2018-01-19	2021-07-07	1276	1986
15MD18	2018-01-19	2020-05-31	1262	1395
176MD20	2020-01-09	2021-07-05	545	861
177MD20	2020-01-09	2021-07-10	353	781
178MD20	2020-01-09	2021-07-08	445	823
179MD20	2020-01-08	2021-07-10	630	867
180MD20	2020-01-11	2021-07-10	545	829
181MD20	2020-01-08	2021-07-08	610	585
182MD20	2020-01-08	2021-07-09	632	869
183MD20	2020-01-11	2020-03-25	0	103
184MD20	2020-01-12	2021-07-10	630	822
185MD20	2020-01-11	2020-10-21	435	214
186MD20	2020-01-09	2021-07-05	562	843
188MD20	2020-01-11	2021-07-11	629	797
189MD20	2020-01-11	2021-07-06	583	865
18MD18	2018-01-19	2021-07-11	1841	1982
190MD18	2018-01-18	2018-12-20	626	324
194MD20	2020-01-11	2021-07-07	580	845
195MD20	2020-01-11	2021-07-09	612	853
196MD20	2020-01-11	2021-07-03	566	420
197MD20	2020-01-11	2021-07-11	530	825
198MD20	2020-01-11	2020-06-18	0	250
199MD20	2020-01-11	2021-07-10	608	839
200MD18	2018-01-18	2020-03-29	1236	1424
200MD20	2020-01-12	2021-07-11	638	585
201MD20	2020-01-12	2020-04-01	0	246
202MD20	2020-01-11	2021-07-10	579	846
203MD20	2020-01-12	2021-07-10	624	847
204MD20	2020-01-12	2021-02-27	634	622
205MD20	2020-01-08	2020-10-23	644	272
206MD20	2020-01-09	2021-07-08	518	874
207MD20	2020-01-09	2021-07-11	586	876
208MD20	2020-01-12	2021-07-11	583	855
209MD20	2020-01-11	2021-07-11	565	843
20MD18	2018-01-20	2020-02-02	1075	1186
210MD18	2018-01-18	2021-07-11	1887	1996
210MD20	2020-01-11	2021-07-11	611	855

211MD20	2020-01-11	2021-07-11	550	844
212MD20	2020-01-12	2021-07-05	544	862
213MD20	2020-01-11	2021-07-10	328	813
220MD18	2018-01-18	2021-02-24	1870	1866
223MD20	2020-01-11	2021-07-08	507	610
22MD18	2018-01-18	2018-04-18	0	203
230MD18	2018-01-20	2021-07-05	1695	2036
23MD18	2018-01-19	2019-08-08	963	682
251MD20	2020-01-11	2021-07-09	349	784
25MD18	2018-01-20	2021-07-11	1811	2020
27MD18	2018-01-20	2021-03-07	1706	1968
28MD18	2018-01-19	2019-05-10	634	682
29MD18	2018-01-19	2018-12-24	636	338
30MD18	2018-01-19	2019-09-18	1159	825
31MD18	2018-01-26	2021-07-11	1920	1469
325MD21	2021-01-15	2021-07-05	0	212
326MD21	2021-01-15	2021-07-05	0	214
327MD21	2021-01-16	2021-07-11	0	218
328MD21	2021-01-15	2021-02-27	0	128
329MD21	2021-01-15	2021-07-11	0	224
32MD18	2018-01-20	2021-07-09	1802	1986
330MD21	2021-01-15	2021-07-05	0	202
331MD21	2021-01-15	2021-07-09	0	200
332MD21	2021-01-15	2021-07-05	0	216
333MD21	2021-01-16	2021-07-11	0	206
334MD21	2021-01-16	2021-07-10	0	196
335MD21	2021-01-16	2021-07-03	0	216
33MD18	2018-01-20	2021-07-05	1633	2037
35MD18	2018-01-19	2018-04-20	0	208
36MD18	2018-01-20	2021-07-09	1742	2001
37MD18	2018-01-19	2021-07-11	1922	1317
38MD18	2018-01-19	2021-07-09	1910	1489
3926MD17	2017-02-01	2021-07-05	2296	2449
3934MD17	2017-02-01	2019-03-11	1279	675
3951MD17	2017-01-31	2018-06-16	582	622
3954MD17	2017-01-31	2019-04-17	1255	1220
3956MD17	2017-01-31	2020-03-01	1513	1767
3957MD17	2017-01-31	2018-11-14	1186	605
3959MD17	2017-01-31	2018-08-20	1014	613
3960MD17	2017-02-02	2021-01-28	2357	2153

3961MD17	2017-01-31	2021-01-27	2356	2173
3963MD17	2017-02-01	2021-01-28	2499	2180
3966MD17	2017-02-02	2020-10-30	2271	1859
3967MD17	2017-02-02	2020-05-19	1892	1518
3976MD17	2017-02-01	2018-02-06	630	386
3981MD17	2017-02-01	2021-01-28	2562	1866
3982MD17	2017-02-01	2021-01-28	2466	2170
3983MD17	2017-02-01	2021-01-28	2392	2195
3987MD17	2017-02-01	2019-09-17	1854	770
3988MD17	2017-02-01	2021-07-11	2565	1393
39MD18	2018-01-19	2020-06-07	1260	1447
3MD18	2018-01-19	2018-11-08	612	112
40MD18	2018-01-19	2021-07-11	1825	1988
41MD18	2018-01-19	2021-07-10	1784	2028
42MD18	2018-01-26	2019-08-24	1059	774
43MD18	2018-01-20	2021-06-29	1835	2036
44MD18	2018-01-20	2019-01-06	636	416
45MD18	2018-01-26	2018-05-24	0	164
46MD18	2018-01-26	2018-09-08	500	164
47MD18	2018-01-20	2018-06-13	0	202
48MD18	2018-01-26	2019-04-25	512	780
49MD18	2018-01-26	2021-02-26	1910	1047
50MD18	2018-01-26	2019-05-17	634	464
52MD18	2018-01-20	2021-07-11	1868	1996
53MD18	2018-01-26	2020-07-10	1212	1390
54MD18	2018-01-26	2020-05-06	1264	1406
55MD18	2018-01-20	2021-06-21	1794	1968
59MD18	2018-01-20	2021-07-11	1917	1490
5MD18	2018-01-20	2020-08-06	1329	1436
60MD18	2018-01-19	2021-07-07	1809	2022
61MD18	2018-01-19	2020-05-08	1107	1431
64MD18	2018-01-20	2018-06-07	0	198
65MD18	2018-01-20	2021-07-11	1877	2007
66MD18	2018-01-18	2019-12-28	1256	987
67MD18	2018-01-19	2021-02-04	1834	1685
68MD18	2018-01-18	2021-07-11	1874	1953
69MD18	2018-01-20	2018-04-09	0	200
70MD18	2018-01-20	2019-06-25	669	809
72MD18	2018-01-19	2020-02-14	878	1245
73MD18	2018-01-20	2018-03-03	0	124

74MD18	2018-01-19	2021-07-11	1893	1253
75MD18	2018-01-18	2019-02-25	646	720
76MD18	2018-01-20	2018-06-24	0	198
77MD18	2018-01-20	2021-07-09	1800	1994
78MD18	2018-01-18	2018-02-17	0	50
79MD18	2018-01-19	2021-07-05	1750	1595
82MD18	2018-01-19	2021-07-11	1838	2025
83MD18	2018-01-19	2021-07-09	1863	1971
84MD18	2018-01-18	2021-07-11	1902	1463
85MD18	2018-01-20	2021-03-23	1772	2022
87MD18	2018-01-26	2021-07-05	1847	1976
88MD18	2018-01-19	2018-03-21	0	208
89MD18	2018-01-26	2018-05-06	0	165
90MD18	2018-01-19	2018-12-23	390	333
91MD18	2018-01-20	2021-01-18	1818	1692
92MD18	2018-01-20	2021-07-09	1868	1984
94MD18	2018-01-26	2018-03-27	0	164
95MD18	2018-01-18	2021-07-09	1775	2023
96MD18	2018-01-26	2021-07-07	1854	1841
97MD18	2018-01-19	2021-07-11	1928	1544
98MD18	2018-01-19	2021-06-29	1608	2053
99MD18	2018-01-19	2021-07-11	1914	1803

Table B3.2 Model selection table for the mule deer step selection functions. The most complex model was strongly favored for both summer and winter seasons. The null habitat model for winter included elevation, heat load and open, forest and developed cover types and the null habitat model for summer additionally included terrain roughness.

	Model	Covariates	parameters	logLik	AICc	delta	weight
Winter SSF	full	Null + burn * cougar + burn * wolf	41	-263978	528037	0	1
	coug x burn	Null + burn * cougar	31	-264040	528143	105	0
	burn + coug + wolf	Null + burn + cougar + wolf	20	-264100	528239	202	0
	coug + burn	Null + burn + cougar	19	-264125	528288	251	0
	coug + wolf	Null + cougar + wolf	8	-264374	528764	727	0
	coug	Null + cougar	7	-264394	528802	764	0
	wolf x burn	Null + burn * wolf	27	-265727	531509	3471	0
	wolf + burn	Null + burn + wolf	18	-265762	531560	3523	0
	burn	Null + burn	17	-265780	531594	3557	0
	wolf	Null + wolf	6	-266024	532060	4023	0
	null	Null	5	-266037	532084	4047	0
Summer SSF	full	Null + burn * cougar + burn * wolf	42	-259032	518148	0	1
	coug x burn	Null + burn * cougar	32	-259110	518284	136	0
	coug + burn	Null + burn + cougar	20	-259201	518441	293	0
	burn + coug + wolf	Null + burn + cougar + wolf	21	-259200	518443	294	0
	coug	Null + cougar	8	-259362	518740	592	0
	coug + wolf	Null + cougar + wolf	9	-259361	518741	592	0
	wolf x burn	Null + burn * wolf	28	-259841	519738	1590	0
	wolf + burn	Null + burn + wolf	19	-259910	519857	1709	0
	burn	Null + burn	18	-259911	519858	1709	0

wolf	Null + wolf	7	-260077	520168	2020	0
null	Null	6	-260079	520170	2022	0

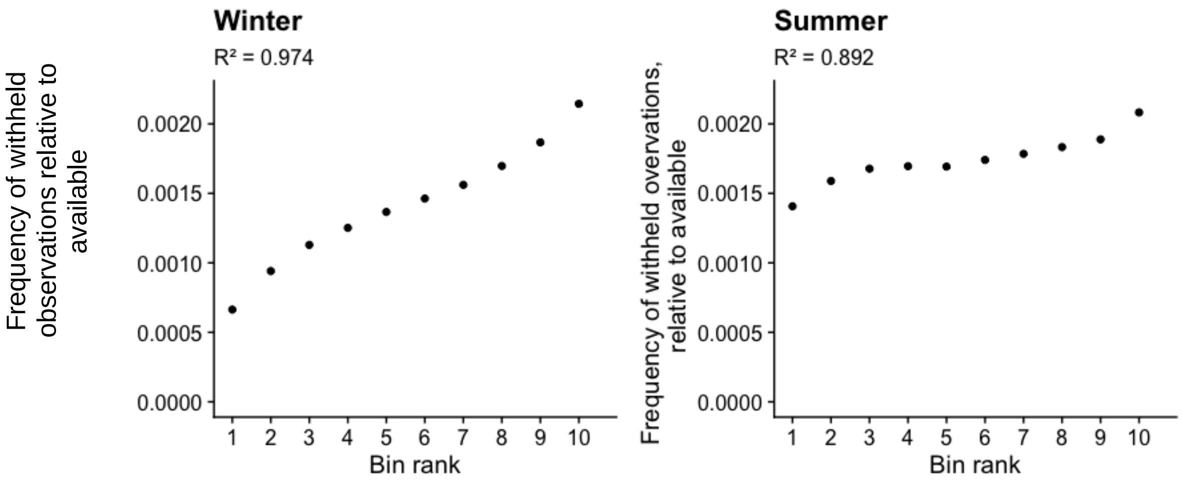


Figure B3.1 Correlation between the binned RSF score and the area adjusted relative frequency of the cross-validated used locations from the withheld individual used in testing the mule deer selection function, following Boyce et al. 2020. Spearman-rank correlation for the winter model ($r_s = 1.000$) and summer model ($r_s = 0.988$) were high, indicating that the models performed well.

Table B3.3 Coefficient estimates for fire related covariates in the seasonal step selection functions. The interactive effect of wolf:21-35 years since burn could not be estimated in the summer due to lack of exposure, as with the interactive effect of wolf:10-20 years since burn in the winter.

	Summer			Winter		
Covariate	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)
0-4 yrs low	0.04	-0.01	0.09	-0.37	-0.42	-0.32
0-4 yrs mod	0.05	0.00	0.11	-0.47	-0.53	-0.41
0-4 yrs high	0.11	0.04	0.18	-0.29	-0.37	-0.21
5-9 yrs low	-0.06	-0.16	0.04	-0.25	-0.30	-0.21
5-9 yrs mod	0.46	0.37	0.56	-0.28	-0.32	-0.23
5-9 yrs high	0.28	0.14	0.42	-0.22	-0.28	-0.16
10-20 yrs low	0.06	0.01	0.11	-0.27	-0.44	-0.10
10-20 yrs mod	0.04	-0.01	0.09	-0.66	-0.86	-0.45
10-20 yrs high	-0.14	-0.19	-0.08	-1.40	-1.76	-1.03
21-35 yrs low	0.16	0.05	0.28	-0.43	-0.62	-0.23
21-35 yrs mod	0.00	-0.12	0.12	-0.60	-0.88	-0.32
21-35 yrs high	0.09	-0.03	0.20	-0.60	-1.32	0.12
cougar:0-4 yrs low	0.00	-0.04	0.04	-0.10	-0.13	-0.08
cougar:0-4 yrs mod	0.08	0.03	0.12	-0.08	-0.10	-0.05
cougar:0-4 yrs high	0.00	-0.06	0.05	-0.15	-0.20	-0.10
cougar:5-9 yrs low	0.09	-0.03	0.21	-0.07	-0.09	-0.05
cougar:5-9 yrs mod	0.36	0.24	0.48	-0.06	-0.08	-0.03
cougar:5-9 yrs high	-0.38	-0.52	-0.24	-0.11	-0.15	-0.07
cougar:10-20 yrs low	-0.08	-0.12	-0.05	-0.13	-0.25	-0.02
cougar:10-20 yrs mod	-0.02	-0.06	0.01	-0.31	-0.44	-0.19
cougar:10-20 yrs high	0.06	0.03	0.09	-0.54	-0.74	-0.34
cougar:21-35 yrs low	-0.08	-0.19	0.03	0.14	-0.04	0.32
cougar:21-35 yrs mod	-0.15	-0.25	-0.05	-0.11	-0.35	0.13
cougar:21-35 yrs high	-0.32	-0.42	-0.23	-0.07	-0.54	0.41
wolf:0-4 yrs low	0.20	0.14	0.25	0.17	0.09	0.25
wolf:0-4 yrs mod	0.29	0.23	0.34	0.14	0.05	0.23
wolf:0-4 yrs high	0.26	0.19	0.32	0.20	0.08	0.33
wolf:5-9 yrs low	0.16	0.09	0.24	0.07	0.04	0.11
wolf:5-9 yrs mod	0.17	0.10	0.24	0.04	0.00	0.08
wolf:5-9 yrs high	0.00	-0.09	0.09	0.07	0.01	0.13
wolf:10-20 yrs low	0.07	0.04	0.10			
wolf:10-20 yrs mod	0.05	0.02	0.08			

wolf:10-20 yrs high	0.06	0.03	0.08			
wolf:21-35 yrs low				-1.40	-2.05	-0.76
wolf:21-35 yrs mod				-1.75	-2.71	-0.79
wolf:21-35 yrs high				-1.01	-3.31	1.29

APPENDIX C

Supplemental Information for Chapter 4

Forge availability and the direct effect of top predator govern population dynamics of white-tailed deer in a human dominated landscape of northeastern Washington, USA.

C.1 RESOURCE SELECTION FUNCTIONS

Adapted, with permission, from: Bassing, S. B., M. Devivo, T. R. Ganz, B. N. Kertson, L. R. Prugh, T. Roussin, L. Satterfield, R. M. Windell, A. J. Wirsing, and B. Gardner. 2022. Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring. Ecological Applications. e2745.

C1.1 *Methods*

To describe an individual deer's exposure to various predators, we developed resource selection functions (RSFs) from the GPS collar data for bobcats, cougars, coyotes, and wolves. These layers predict the relative probability of each predators' habitat selection across the study area and were originally developed by Bassing et al. (2022) using locations from carnivores collared as part of the Washington Predator-Prey Project across northern Washington. Although selection is not synonymous with presence, predation risk increases with probability of predator use (Hebblewhite and Merrill 2007), and abundance tends to reflect the strength of habitat selection such that RSFs can be used as an index of relative abundance (Boyce et al. 2016). For each individual predator, we censored telemetry relocation data for 3 weeks post capture (Northrup et al. 2014, van de Kerk et al. 2020) and excluded relocations associated with dispersal events (L. Satterfield and R. Wendell, University of Washington, *pers. comm.*). We then pooled all remaining location data for a given species across years (2017 – 2021) to create seasonal RSFs (summer: June – Sept; fall: October – November; winter: December – February; spring: March - May) for each species. All data preparation and statistical analyses were conducted in Program R (R Core Team 2021) unless otherwise noted.

We defined the spatial extent of what was used and available to each collared individual based on 3rd-order resource selection (i.e., resources used within an animal's home range; Johnson 1980). We created utilization distributions for each collared individual's annual home range using a 95% kernel density estimator (KDE; Worton 1989, Hooten et al. 2017) with the adehabitatHR package (Calange 2006). We masked water bodies as unavailable, then randomly sampled 20 available resources units per 1 used location within the 95% KDE (Fieberg et al. 2021) and extracted covariate values at each used (1) and available (0) location. We assigned a weight of 1 to used locations and 5,000 to available locations following Fieberg et al. (2021).

We used eight covariates to represent environmental features and human impacts that we expected would influence habitat selection. This included elevation, slope, an index for human-modified landscape, distance to nearest water, road density, canopy cover, landcover type, and distance to nearest habitat edge (Koehler and Hornocker 1991, Long et al. 2009, Smereka et al. 2020, Peterson et al. 2021, Staudenmaier et al. 2021). We extracted elevation and slope from the Shuttle Radar Topography Mission (SRTM) 30 m resolution digital elevation model (DEM; Farr and Kobrick 2000). We extracted an index of human modification to the landscape from the Global Human Modification map (Kennedy et al. 2019). We calculated distance to nearest water in ArcGIS using the Euclidean Distance tool (ESRI 2020) and the National Hydrology Dataset for Washington (Washington State Department of Ecology 2019). We calculated road density (road length/1 km^2) using the Cascadia Biodiversity Watch TerrAdapt:Cascadia tool (https://cascadiapartnerforum.org/terradapt) roads layer. We calculated percent canopy cover for each year from the Global Forest Change data (Hansen et al. 2013). We reclassified annual landcover data from the Cascadia Biodiversity Watch TerrAdapt:Cascadia tool (30 m resolution) into 6 landcover types (developed, forest, open grass, shrub mix, wetlands, and other). Due to few observations in the developed landcover classes for some species, we further reclassified the developed category into the other category for cougar winter models, and for bobcat, coyote, and wolf summer and winter models. Finally, we derived distance to nearest edge by reclassifying the annual Cascadia landcover data into binary forested and non-forested categories and calculated the distance from each pixel to the edge of forested and non-forested habitat for each year in ArcGIS using the Euclidean Distance tool (ESRI 2020). Because percent canopy cover, landcover type, and distance to edge varied annually, we extracted these covariate values from annual data sets that matched the year each used and available location arose. We centered and scaled all continuous variables and checked for collinearity, excluding human-modified landscape when correlated ($r \geq 0.60$) with elevation. We used the remaining variables to create a global model, including a quadratic term on elevation. Finally, we included a random effect for individual in all models to account for pseudo-replication in sequential telemetry locations from the same animal.

We fit the species and season specific RSFs using the lme4 package (Bates et al. 2015). We then predicted annual RSFs across the extent of the study area at 30m pixel resolution. We scaled the predicted relative probability of resource selection between 0 and 1 by subtracting each predicted value from the maximum predicted value. To minimize the effect of large outliers skewing the scaled predictions, we considered all predicted RSF values above the 99% percentile to be outliers and forced these values to the RSF value at the 99th percentile. We used these annual season- and species-specific predictions as covariates in the movement analyses to represent the relative probability of species presence across the landscape.

Lastly, we used the (Boyce et al. 2002) method for K-fold cross-validation to evaluate the predictive capacity of the RSFs to ensure they were predictive of animal presence throughout the study areas. To do this, we reclassified the landcover data and standardized the continuous covariates for all used and available locations as described above. We then randomly partitioned each season- and species-specific dataset into 5 folds, balancing each fold proportional to the number of used and available locations in the original dataset with the groupdata2 package (Olsen 2021). Each fold comprised 4/5ths of the data for model training and 1/5th of the data for model testing. We fit the season- and species-specific RSFs (Table C1.1) to each of the 5 training datasets, withholding the corresponding testing data from each model run. We then predicted the RSF results from each training model across the study areas for each year, adjusted for outliers, and rescaled the RSF values between 0 and 1 as described above. For each trained RSF, we then reclassified the scaled RSF predictions into 10 ranked bins based on its quantiles (Boyce et al. 2002, Morris et al. 2016). To cross-validate the binned predictions, we plotted the used locations from the testing datasets and extracted the binned RSF values from these locations and area-weighted the frequency of each bin by the number of pixels representing that bin (Boyce et al. 2002, Morris et al. 2016). Finally, we calculated the Spearman's rank-order correlation (ρ) between each bin rank and the area-weighted frequency of used locations to evaluate the predictive ability of the RSFs (Boyce et al. 2002, Morris et al. 2016).

Before extracting RSF values for each predator species at deer locations, we scaled each validated RSF such that the total sum of the pixels was 1. Because we used these layers as a proxy for relative abundance, this ensured that differences in seasonal layers for each predator represented a similar total use across the area by each predator species, rather that changes in relative abundance.

C1.2 *Results*

In total, we captured and collared 37 bobcats, 60 cougars, 23 coyotes and 15 wolves. From their data, we fit 16 RSFs (Table C1.1) accounting for summer, fall, winter and spring probability of use for bobcats, cougars, coyotes, and wolves. In general, distance to water, elevation, road density, slope, and landcover type were significant in most or all models. Landcover class had the strongest effect on resource selection for most species, where the "Other" and "Developed" landcover classes were strongly avoided relative to the "Forest" landcover class by almost all species. Conversely, most species were more likely to select for the "Shrub mix" and "Wetland" landcover classes relative to the "Forest" landcover class, although not as strongly compared to their avoidance of "Other" and "Developed" landcover classes. The effect of the "Open grass" landcover class and road density varied by species and season. Most species selected for flatter slopes and mid-elevations within each study area. In addition, most species avoided areas with increasing distance to nearest edge, canopy cover, and human modification to the landscape but selected for areas as distance to water increased.

Table C1.1 Model outputs for resource selection functions fit to bobcats, cougars, coyotes, and wolves for summer (June – September), fall (October – November), winter (December – February) and spring (March – May) with telemetry data collected between 2017 and 2021 in northern Washington.

Species	Season	Parameter	Estimate	SE	z	*P*
Bobcat	Summer	Intercept	-11.42	0.03	-417.77	0.000
Bobcat	Summer	Elev	0.03	0.02	1.86	0.063
Bobcat	Summer	Elev^2	-0.06	0.01	-5.16	0.000
Bobcat	Summer	Slope	-0.02	0.01	-1.59	0.111

Bobcat	Summer	RoadDen	-0.03	0.01	-2.55	0.011
Bobcat	Summer	Dist2Water	0.03	0.01	2.45	0.014
Bobcat	Summer	HumanMod	-0.17	0.02	-10.08	0.000
Bobcat	Summer	CanopyCover	0.05	0.01	3.85	0.000
Bobcat	Summer	Dist2Edge	-0.08	0.01	-6.6	0.000
Bobcat	Summer	Landcover_typeOpen Grass	-0.27	0.03	-8.26	0.000
Bobcat	Summer	Landcover_typeOther	-0.61	0.1	-6.09	0.000
Bobcat	Summer	Landcover_typeShrub Mix	0.15	0.03	5.57	0.000
Bobcat	Summer	Landcover_typeWetland	0.36	0.13	2.66	0.008
Bobcat	Fall	Intercept	-11.44	0.06	-204.32	0.000
Bobcat	Fall	Elev	-0.05	0.03	-1.51	0.132
Bobcat	Fall	Elev^2	-0.01	0.02	-0.46	0.645
Bobcat	Fall	Slope	0.03	0.02	1.45	0.146
Bobcat	Fall	RoadDen	-0.14	0.02	-6.56	0.000
Bobcat	Fall	Dist2Water	-0.07	0.02	-3.16	0.002
Bobcat	Fall	HumanMod	0.03	0.03	0.89	0.373
Bobcat	Fall	CanopyCover	0.08	0.02	3.68	0.000
Bobcat	Fall	Dist2Edge	-0.26	0.03	-9.17	0.000
Bobcat	Fall	Landcover_typeOpen Grass	-0.27	0.06	-4.71	0.000
Bobcat	Fall	Landcover_typeOther	-1.91	0.36	-5.28	0.000
Bobcat	Fall	Landcover_typeShrub Mix	0	0.05	0.07	0.942
Bobcat	Fall	Landcover_typeWetland	0.54	0.2	2.76	0.006
Bobcat	Winter	Intercept	-11.53	0.07	-159.78	0.000
Bobcat	Winter	Elev	-0.81	0.03	-28.64	0.000
Bobcat	Winter	Elev^2	0.12	0.01	7.97	0.000
Bobcat	Winter	Slope	0.18	0.02	11.25	0.000
Bobcat	Winter	RoadDen	-0.07	0.02	-4.38	0.000
Bobcat	Winter	Dist2Water	-0.03	0.02	-1.69	0.091
Bobcat	Winter	HumanMod	-0.46	0.03	-16.32	0.000
Bobcat	Winter	CanopyCover	0.1	0.02	5.3	0.000
Bobcat	Winter	Dist2Edge	-0.05	0.02	-3.08	0.002
Bobcat	Winter	Landcover_typeOpen Grass	-0.38	0.05	-7.74	0.000
Bobcat	Winter	Landcover_typeOther	-1.42	0.2	-7.27	0.000
Bobcat	Winter	Landcover_typeShrub Mix	-0.22	0.04	-5.28	0.000
Bobcat	Winter	Landcover_typeWetland	0.28	0.13	2.13	0.034
Bobcat	Spring	Intercept	-11.43	0.03	-409.61	0.000
Bobcat	Spring	Elev	-0.03	0.02	-1.96	0.050
Bobcat	Spring	Elev^2	-0.06	0.01	-6.28	0.000
Bobcat	Spring	Slope	-0.01	0.01	-0.51	0.613
Bobcat	Spring	RoadDen	-0.03	0.01	-2.72	0.007

Bobcat	Spring	Dist2Water	0.03	0.01	3.5	0.000
Bobcat	Spring	HumanMod	-0.19	0.02	-11.99	0.000
Bobcat	Spring	CanopyCover	0.06	0.01	4.84	0.000
Bobcat	Spring	Dist2Edge	-0.1	0.01	-8.85	0.000
Bobcat	Spring	Landcover_typeOpen Grass	-0.25	0.03	-8.73	0.000
Bobcat	Spring	Landcover_typeOther	-0.58	0.1	-6.01	0.000
Bobcat	Spring	Landcover_typeShrub Mix	0.18	0.03	6.93	0.000
Bobcat	Spring	Landcover_typeWetland	0.33	0.12	2.78	0.005
Cougar	Summer	Intercept	-11.75	0.02	-604.89	0.000
Cougar	Summer	Elev	-0.09	0.01	-9.56	0.000
Cougar	Summer	Elev^2	0.14	0.01	27.17	0.000
Cougar	Summer	Slope	-0.05	0.01	-9.28	0.000
Cougar	Summer	RoadDen	-0.07	0.01	-11.82	0.000
Cougar	Summer	Dist2Water	-0.15	0.01	-27.03	0.000
Cougar	Summer	CanopyCover	0.24	0.01	35.6	0.000
Cougar	Summer	Dist2Edge	-0.21	0.01	-29.91	0.000
Cougar	Summer	Landcover_typeOpen Grass	-0.16	0.02	-8.58	0.000
Cougar	Summer	Landcover_typeOther	-1.37	0.05	-25.6	0.000
Cougar	Summer	Landcover_typeShrub Mix	0.25	0.01	18.13	0.000
Cougar	Summer	Landcover_typeWetland	1.55	0.03	55.06	0.000
Cougar	Fall	Intercept	-11.51	0.03	-399.45	0.000
Cougar	Fall	Elev	0.04	0.02	2.52	0.012
Cougar	Fall	Elev^2	-0.02	0.01	-2.44	0.015
Cougar	Fall	Slope	0.07	0.01	7.09	0.000
Cougar	Fall	RoadDen	-0.05	0.01	-5.39	0.000
Cougar	Fall	Dist2Water	-0.06	0.01	-6.45	0.000
Cougar	Fall	HumanMod	0.04	0.02	2.65	0.008
Cougar	Fall	CanopyCover	0.23	0.01	19.63	0.000
Cougar	Fall	Dist2Edge	-0.11	0.01	-10.14	0.000
Cougar	Fall	Landcover_typeOpen Grass	-0.28	0.03	-8.52	0.000
Cougar	Fall	Landcover_typeOther	-1.83	0.15	-12.43	0.000
Cougar	Fall	Landcover_typeShrub Mix	0.09	0.02	3.81	0.000
Cougar	Fall	Landcover_typeWetland	1.47	0.06	25.95	0.000
Cougar	Winter	Intercept	-11.4	0.03	-336.03	0.000
Cougar	Winter	Elev	-0.3	0.01	-23.06	0.000
Cougar	Winter	Elev^2	-0.02	0.01	-3.56	0.000
Cougar	Winter	Slope	0.35	0.01	48.47	0.000
Cougar	Winter	RoadDen	-0.01	0.01	-1.06	0.289
Cougar	Winter	Dist2Water	-0.07	0.01	-9.77	0.000
Cougar	Winter	HumanMod	0.09	0.01	7.73	0.000

Cougar	Winter	CanopyCover	0.16	0.01	16.6	0.000
Cougar	Winter	Dist2Edge	-0.02	0.01	-1.93	0.054
Cougar	Winter	Landcover_typeOpen Grass	-0.49	0.03	-18.24	0.000
Cougar	Winter	Landcover_typeOther	-2.53	0.13	-18.99	0.000
Cougar	Winter	Landcover_typeShrub Mix	-0.17	0.02	-8.86	0.000
Cougar	Winter	Landcover_typeWetland	0.7	0.05	13.24	0.000
Cougar	Spring	Intercept	-11.37	0.04	-262.35	0.000
Cougar	Spring	Elev	-0.21	0.01	-16.49	0.000
Cougar	Spring	Elev^2	-0.14	0.01	-19.31	0.000
Cougar	Spring	Slope	0.19	0.01	30.49	0.000
Cougar	Spring	RoadDen	-0.03	0.01	-4.91	0.000
Cougar	Spring	Dist2Water	-0.05	0.01	-8.17	0.000
Cougar	Spring	HumanMod	0.12	0.01	12.05	0.000
Cougar	Spring	CanopyCover	0.21	0.01	25.88	0.000
Cougar	Spring	Dist2Edge	-0.04	0.01	-5.52	0.000
Cougar	Spring	Landcover_typeOpen Grass	-0.46	0.02	-18.98	0.000
Cougar	Spring	Landcover_typeOther	-2.68	0.13	-20.55	0.000
Cougar	Spring	Landcover_typeShrub Mix	-0.05	0.02	-2.82	0.005
Cougar	Spring	Landcover_typeWetland	0.74	0.05	14.9	0.000
Coyote	Summer	Intercept	-11.96	0.04	-287.48	0.000
Coyote	Summer	Elev	0.07	0.02	3.81	0.000
Coyote	Summer	Elev^2	0	0.01	-0.3	0.767
Coyote	Summer	Slope	-0.33	0.01	-30.67	0.000
Coyote	Summer	RoadDen	0.04	0.01	4.69	0.000
Coyote	Summer	Dist2Water	0.05	0.01	4.85	0.000
Coyote	Summer	Dist2Edge	-0.03	0.01	-2.6	0.009
Coyote	Summer	CanopyCover	-0.19	0.01	-16.39	0.000
Coyote	Summer	Landcover_typeOpen Grass	0.6	0.03	20.8	0.000
Coyote	Summer	Landcover_typeOther	0.19	0.06	3.42	0.001
Coyote	Summer	Landcover_typeShrub Mix	0.51	0.03	19.28	0.000
Coyote	Summer	Landcover_typeWetland	0.91	0.08	11.99	0.000
Coyote	Fall	Intercept	-11.68	0.04	-280.95	0.000
Coyote	Fall	Elev	-0.03	0.02	-1.54	0.125
Coyote	Fall	Elev^2	-0.12	0.01	-8.71	0.000
Coyote	Fall	Slope	-0.24	0.01	-17.78	0.000
Coyote	Fall	RoadDen	0.11	0.01	10.47	0.000
Coyote	Fall	Dist2Water	0.09	0.01	7.26	0.000
Coyote	Fall	Dist2Edge	-0.05	0.01	-3.76	0.000
Coyote	Fall	CanopyCover	-0.1	0.01	-6.94	0.000
Coyote	Fall	Landcover_typeOpen Grass	0.39	0.04	10.75	0.000

Coyote	Fall	Landcover_typeOther	0.04	0.07	0.55	0.585
Coyote	Fall	Landcover_typeShrub Mix	0.32	0.03	9.78	0.000
Coyote	Fall	Landcover_typeWetland	1	0.09	10.77	0.000
Coyote	Winter	Intercept	-11.5	0.03	-410.94	0.000
Coyote	Winter	Elev	-0.07	0.02	-3.87	0.000
Coyote	Winter	Elev^2	-0.08	0.01	-7.32	0.000
Coyote	Winter	Slope	-0.12	0.01	-12.26	0.000
Coyote	Winter	RoadDen	0.06	0.01	7.08	0.000
Coyote	Winter	Dist2Water	0.1	0.01	11.16	0.000
Coyote	Winter	Dist2Edge	-0.04	0.01	-3.34	0.001
Coyote	Winter	CanopyCover	-0.02	0.01	-1.48	0.140
Coyote	Winter	Landcover_typeOpen Grass	0.1	0.03	3.32	0.001
Coyote	Winter	Landcover_typeOther	-0.35	0.06	-6.13	0.000
Coyote	Winter	Landcover_typeShrub Mix	0.06	0.03	2.44	0.015
Coyote	Winter	Landcover_typeWetland	0.5	0.08	6.12	0.000
Coyote	Spring	Intercept	-11.67	0.05	-233.52	0.000
Coyote	Spring	Elev	0.35	0.03	13.35	0.000
Coyote	Spring	Elev^2	-0.12	0.01	-8.49	0.000
Coyote	Spring	Slope	-0.31	0.01	-24.05	0.000
Coyote	Spring	RoadDen	0.04	0.01	3.98	0.000
Coyote	Spring	Dist2Water	0.09	0.01	7.97	0.000
Coyote	Spring	Dist2Edge	-0.08	0.01	-5.96	0.000
Coyote	Spring	CanopyCover	-0.12	0.01	-9.46	0.000
Coyote	Spring	Landcover_typeOpen Grass	0.29	0.03	8.37	0.000
Coyote	Spring	Landcover_typeOther	-0.18	0.07	-2.62	0.009
Coyote	Spring	Landcover_typeShrub Mix	0.43	0.03	14.58	0.000
Coyote	Spring	Landcover_typeWetland	0.64	0.1	6.51	0.000
Wolf	Summer	Intercept	-12.21	0.08	-146.19	0.000
Wolf	Summer	Elev	0.08	0.02	3.91	0.000
Wolf	Summer	Elev^2	-0.37	0.01	-25.58	0.000
Wolf	Summer	Slope	-0.8	0.01	-59.7	0.000
Wolf	Summer	RoadDen	-0.04	0.01	-3.8	0.000
Wolf	Summer	Dist2Water	-0.28	0.01	-21.11	0.000
Wolf	Summer	HumanMod	-0.42	0.02	-23.26	0.000
Wolf	Summer	CanopyCover	-0.04	0.01	-2.74	0.006
Wolf	Summer	Dist2Edge	-0.22	0.01	-15.41	0.000
Wolf	Summer	Landcover_typeOpen Grass	-0.01	0.03	-0.29	0.770
Wolf	Summer	Landcover_typeOther	0.02	0.07	0.34	0.735
Wolf	Summer	Landcover_typeShrub Mix	-0.02	0.03	-0.76	0.446
Wolf	Fall	Intercept	-12.14	0.04	-285.87	0.000

Wolf	Fall	Elev	0.32	0.03	10	0.000
Wolf	Fall	Elev^2	-0.37	0.02	-18.06	0.000
Wolf	Fall	Slope	-0.5	0.02	-25.2	0.000
Wolf	Fall	RoadDen	-0.07	0.02	-4.25	0.000
Wolf	Fall	Dist2Water	-0.09	0.02	-4.69	0.000
Wolf	Fall	HumanMod	-0.34	0.03	-12.17	0.000
Wolf	Fall	CanopyCover	-0.1	0.02	-4.8	0.000
Wolf	Fall	Dist2Edge	-0.27	0.02	-12.17	0.000
Wolf	Fall	Landcover_typeOpen Grass	0.31	0.05	5.88	0.000
Wolf	Fall	Landcover_typeOther	0.24	0.12	1.98	0.048
Wolf	Fall	Landcover_typeShrub Mix	0.15	0.04	3.4	0.001
Wolf	Winter	Intercept	-11.45	0.09	-128.94	0.000
Wolf	Winter	Elev	0.01	0.03	0.47	0.637
Wolf	Winter	Elev^2	-0.33	0.02	-19.62	0.000
Wolf	Winter	Slope	-0.2	0.02	-13.1	0.000
Wolf	Winter	RoadDen	-0.15	0.02	-9.58	0.000
Wolf	Winter	Dist2Water	-0.05	0.01	-3.44	0.001
Wolf	Winter	HumanMod	-0.23	0.02	-10.71	0.000
Wolf	Winter	CanopyCover	-0.08	0.02	-4.4	0.000
Wolf	Winter	Dist2Edge	-0.31	0.02	-15.79	0.000
Wolf	Winter	Landcover_typeOpen Grass	0.32	0.04	7.25	0.000
Wolf	Winter	Landcover_typeOther	-0.29	0.13	-2.28	0.022
Wolf	Winter	Landcover_typeShrub Mix	0.23	0.04	5.87	0.000
Wolf	Spring	Intercept	-11.21	0.07	-168.76	0.000
Wolf	Spring	Elev	0.36	0.02	15.23	0.000
Wolf	Spring	Elev^2	-0.58	0.02	-33.69	0.000
Wolf	Spring	Slope	-0.31	0.01	-22.7	0.000
Wolf	Spring	RoadDen	0.01	0.01	0.94	0.348
Wolf	Spring	Dist2Water	0	0.01	-0.22	0.829
Wolf	Spring	HumanMod	-0.14	0.02	-7.01	0.000
Wolf	Spring	CanopyCover	-0.05	0.02	-3.26	0.001
Wolf	Spring	Dist2Edge	-0.26	0.02	-15.54	0.000
Wolf	Spring	Landcover_typeOpen Grass	0.1	0.04	2.46	0.014
Wolf	Spring	Landcover_typeOther	-0.72	0.16	-4.56	0.000
Wolf	Spring	Landcover_typeShrub Mix	0.23	0.03	6.71	0.000

We found that the testing data withheld during the K-fold process were highly correlated with the binned RSF predictions in the K-fold cross-validation analyses (Table C1.2), indicating the RSFs were predictive of the relative probability of resource selection for each species. The mean Spearman's rank-order correlation coefficient (ρ) for each species, season, and year-specific RSF ranged from 0.87 (Bobcats - summer 2002) to 1.00 (All spring cougar models, coyotes -fall 2020 and wolves – winter 2018-2019).

Table C1.2 Spearman's rank-order correlation coefficient (ρ) and standard error (SE) for each season x year x predator RSF in northern Washington for 2017-2021.

Species	Season	Year	ρ	SE
Bobcat	Summer	2017	0.884	0.012
Bobcat	Summer	2018	0.888	0.017
Bobcat	Summer	2019	0.898	0.020
Bobcat	Summer	2020	0.867	0.028
Bobcat	Fall	2017	0.930	0.021
Bobcat	Fall	2018	0.903	0.021
Bobcat	Fall	2019	0.925	0.016
Bobcat	Fall	2020	0.918	0.015
Bobcat	Winter	2017-2018	0.971	0.005
Bobcat	Winter	2018-2019	0.976	0.008
Bobcat	Winter	2019-2020	0.971	0.007
Bobcat	Winter	2020-2021	0.968	0.008
Bobcat	Spring	2018	0.903	0.008
Bobcat	Spring	2019	0.910	0.011
Bobcat	Spring	2020	0.908	0.012
Bobcat	Spring	2021	0.918	0.018
Cougar	Summer	2017	0.995	0.003
Cougar	Summer	2018	0.995	0.003
Cougar	Summer	2019	0.978	0.006
Cougar	Summer	2020	0.988	0.000
Cougar	Fall	2017	0.956	0.014
Cougar	Fall	2018	0.973	0.010
Cougar	Fall	2019	0.961	0.015
Cougar	Fall	2020	0.968	0.011
Cougar	Winter	2017-2018	0.998	0.002
Cougar	Winter	2018-2019	0.988	0.000
Cougar	Winter	2019-2020	0.998	0.002
Cougar	Winter	2020-2021	0.988	0.004

Cougar	Spring	2018	1.000	0.000
Cougar	Spring	2019	1.000	0.000
Cougar	Spring	2020	1.000	0.000
Cougar	Spring	2021	1.000	0.000
Coyote	Summer	2017	0.988	0.000
Coyote	Summer	2018	0.985	0.002
Coyote	Summer	2019	0.983	0.005
Coyote	Summer	2020	0.985	0.002
Coyote	Fall	2017	0.995	0.003
Coyote	Fall	2018	0.995	0.003
Coyote	Fall	2019	0.998	0.002
Coyote	Fall	2020	1.000	0.000
Coyote	Winter	2017-2018	0.985	0.002
Coyote	Winter	2018-2019	0.982	0.003
Coyote	Winter	2019-2020	0.982	0.003
Coyote	Winter	2020-2021	0.982	0.003
Coyote	Spring	2018	0.988	0.000
Coyote	Spring	2019	0.990	0.002
Coyote	Spring	2020	0.990	0.002
Coyote	Spring	2021	0.988	0.007
Wolf	Summer	2017	0.993	0.003
Wolf	Summer	2018	0.988	0.004
Wolf	Summer	2019	0.990	0.005
Wolf	Summer	2020	0.988	0.005
Wolf	Fall	2017	0.976	0.005
Wolf	Fall	2018	0.993	0.003
Wolf	Fall	2019	0.981	0.007
Wolf	Fall	2020	0.985	0.002
Wolf	Winter	2017-2018	0.998	0.002
Wolf	Winter	2018-2019	1.000	0.000
Wolf	Winter	2019-2020	0.995	0.003
Wolf	Winter	2020-2021	0.993	0.003
Wolf	Spring	2018	0.988	0.005
Wolf	Spring	2019	0.985	0.005
Wolf	Spring	2020	0.990	0.002
Wolf	Spring	2021	0.993	0.005

C.2 VEGETATION SAMPLING

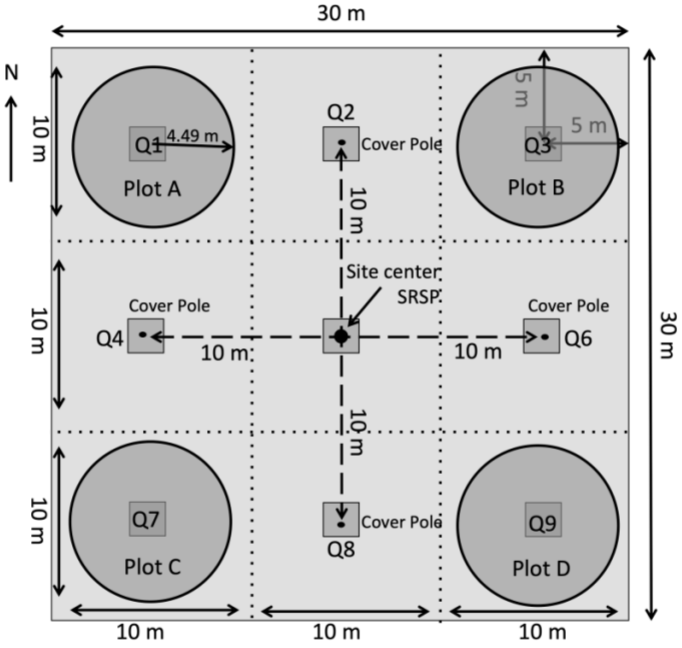
WPPP Vegetation Survey Protocol and Guide to the Data Collection Form

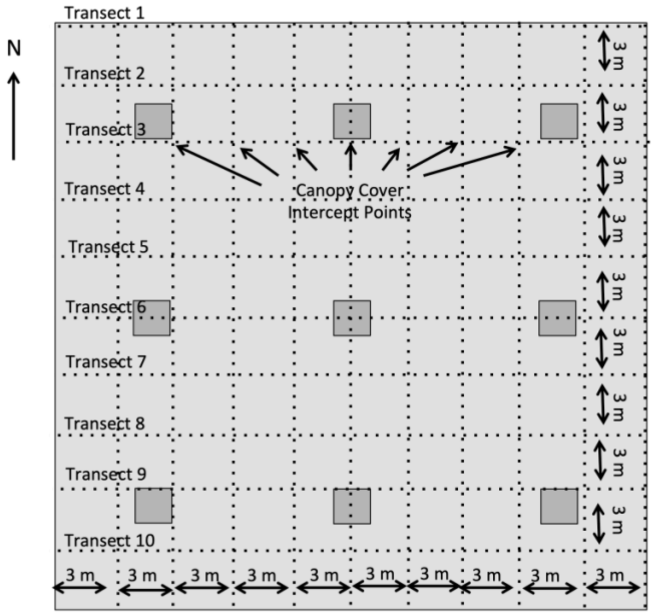
Created by T.R. Ganz 5/6/2019

These data are collected so that researchers of the WPPP can describe the vegetation and forest structure available to ungulates to identify spatial predictors of ungulate movement and mortality. Each 30m x 30m site is composed of 4 forest structure plots, 9 vegetation quadrats, and 100 canopy intercept points

Helpful Distances:
Site Center to Corner = 21.1m
Site Center to Q1 = 14.14m
Q1 to Corner = 7.07m

A. Site Orientation





Confirm that the characteristics of the site match the strata (elevation, aspect and forest cover) of the Stratified Random Sampling Point (SRSP).

Center the plot on the given SRSP, and it orient it to the cardinal directions. Ensure that the 30m x 30m area encompasses a single habitat type and is not on edge habitat. If the identified location is on edge habitat, relocated the plot the minimum distance so that it is entirely within the targeted habitat type.

All measures are recorded with a single 30 x 30m site but are broken into 2 visuals here for clarification. Each 30 x 30m site is composed of nine 1m^2 quadrats to survey vegetative cover (labeled Q1-Q9), and four fixed-radius circular plots (labeled plot A – plot D; r=4.49m; area = 62.5 m^2; total area of the 4 plots = 250m^2), and 100 canopy cover interception points to evaluate forest structure. Please follow the schematic to label each quadrat and plot, such that quadrat 1 (Q1) and plot A are always in the northwest corner of the site. Only record trees and plants originating from within the plot or quadrat. If they fall on the boundary, include them if more than 50% is in the survey area, and exclude them if less than 50% falls within the survey area.

Table C2.1 Understory vegetation and white-tailed deer acceptance (*O. virginianu*s) for the associated species documented during habitat surveys conducted across northeastern Washington, USA July – September, 2020 and 2021. Plants are alphabetized by genus within species. We first determined white-tailed deer response based on Berry et al. (2019). If deer response to a particular species was not noted, but there was a suitability classification for another plant in the same genus, we assumed deer exhibited the same response. If we could not find a response for white-tailed deer, we used the pooled response of mule deer (*O. hemionus*) and white-tailed deer (Hull et al. 2020) or subsequently the response of mule deer (Wagoner 2011, Wagoner et al. 2013, Ulappa 2015, Ulappa et al. 2020). If there was not a measured response for any *Odocoileus spp.*, we assumed the response was the same as that of elk *(Cervus canadensis*; Cook et al. 2016). Finally, if we could find no information about the plant species, we assumed that deer avoided ferns, evergreen shrubs, conifers, grass and annual forbs and accepted deciduous shrubs and perennial forbs based on general trends among plant functional groups (Wagoner et al. 2013, Berry et al. 2019, Hull et al. 2020, Ulappa et al. 2020).

Growth Form	Species Code	Common Name	Genus	Species	Preference	Species Referenced
Tree	ABI-AMA	Pacific silver fir	Abies	amabilis	avoided	*O. spp.*
Tree	ABI-GRA	Grand fir	Abies	grandis	avoided	*O. virginianus*
Tree	ABI-LAS	Subalpine fir	Abies	lasiocarpa	avoided	*O. spp.*
Tree	ACE-GLA	Rocky mountain maple	Acer	glabrum	selected	*O. virginianus*
Tree	ACE-RUB	Red maple	Acer	rubrum	selected	*O. virginianus*
Tree	ACE-SPP	Unknown maple	Acer	spp.	selected	*O. virginianus*
Forb/herb	ACH-MIL	Yarrow	Achillea	millefolium	avoided	*O. virginianus*
Forb/herb	ACM-AME	American bird's-foot trefoil	Acmispon	americanus	avoided	*O. spp.*
Forb/herb	ACM-DEN	Riverbar bird's-foot trefoil	Acmispon	denticulatus	avoided	*O. spp.*
Forb/herb	ACM-NEV	Nevada deervetch	Acmispon	nevadensis	avoided	*O. spp.*
Forb/herb	ADE-BIC	American trailplant	Adenocaulon	bicolor	neutral	*O. virginianus*
Graminoid	AEG-CYL	Jointed goat grass	Aegilops	cylindrica	avoided	*O. spp.*
Forb/herb	AGA-URT	Nettleleaf giant hyssop	Agastache	urticifolia	selected/neutral	*O. spp.*

Graminoid	AGR-GIG	Black bent	Agrostis	gigantea	avoided	*O. virginianus*
Tree	ALN-INC	Mountain alder	Alnus	incana	neutral	*O. virginianus*
Tree	ALN-RUB	Red Alder	Alnus	rubra	neutral	*O. virginianus*
Tree	ALN-SPP	Unknown Alder	Alnus	spp.	neutral	*O. virginianus*
Tree	ALN-VIR	Green alder	Alnus	viridis	neutral	*O. virginianus*
Graminoid	ALO-PRA	Field meadow-foxtail	Alopecurus	pratensis	avoided	*O. spp.*
Shrub	AME-ALN	Serviceberry	Amelanchier	alnifolia	selected	*O. virginianus*
Forb/herb	ANA-MAR	Pearly everlasting	Anaphalis	margaritacea	neutral	*O. spp.*
Forb/herb	ANC-ARV	Small bugloss	Anchusa	arvensis	selected/neutral	*O. spp.*
Forb/herb	ANG-ARG	Lyall's angelica	Angelica	arguta	neutral	*C. canadensis*
Forb/herb	ANT-NEG	Field pussytoe	Antennaria	neglecta	neutral	*O. spp.*
Forb/herb	ANT-SPP	Unknown pussytoe	Antennaria	spp.	neutral	*O. spp.*
Forb/herb	ANT-UMB	Umber pussytoes	Antennaria	umbrinella	neutral	*O. spp.*
Forb/herb	ANT-COT	Stinking chamomile	Anthemis	cotula	avoided	*O. spp.*
Forb/herb	APO-AND	Spreading dogbane	Apocynum	androsaemifolium	selected/neutral	*O. spp.*
Forb/herb	APO-CAN	Cemp dogbane	Apocynum	cannabinum	selected/neutral	*O. spp.*
Forb/herb	APO-SPP	Unknown dogbane	Apocynum	spp.	selected/neutral	*O. spp.*
Forb/herb	APO-FLO	Western dogbane	Apocynum	xfloribundum	selected/neutral	*O. spp.*
Forb/herb	AQU-FOR	Red columbine	Aquilegia	formosa	selected/neutral	*O. spp.*
Forb/herb	ARA-NUD	Wild sarsaparilla	Aralia	nudicaulis	selected	*O. spp.*
Shrub	ARC-UVA	Kinnikinnick	Arctostaphylos	uva-ursi	avoided	*O. virginianus*
Forb/herb	ARN-COR	Heartleaf arnica	Arnica	cordifolia	neutral	*O. virginianus*
Forb/herb	ART-DRA	Wild tarragon	Artemisia	dracunculus	neutral	*C. canadensis*
Forb/herb	ART-FRI	Prairie sagewort	Artemisia	frigida	neutral	*C. canadensis*
Forb/herb	ART-SPP	Unknown artemisia	Artemisia	spp.	neutral	*C. canadensis*
Forb/herb	ASA-CAU	Wild ginger	Asarum	caudatum	neutral	*C. canadensis*
Forb/herb	AST-SPP	Unknown aster	Asteraceae	spp.	selected/neutral	*O. spp.*
Forb/herb	AST-CAN	Canada milk-vetch	Astragalus	canadensis	selected	*O. virginianus*
Forb/herb	BAL-SAG	Arrowleaf balsalm root	Balsamorhiza	sagittata	selected/neutral	*O. hemionus*

Forb/herb	BAS-SCO	Summer cypress	Bassia	scoparia	avoided	*O. spp.*
Forb/herb	BER-INC	Hoary alyssum	Berteroa	incana	avoided	*O. spp.*
Forb/herb	BIS-VIV	Alpine bistort	Bistorta	vivipara	selected/neutral	*O. spp.*
Graminoid	BRO-CIL	Fringed brome	Bromus	ciliatus	avoided	*O. virginianus*
Graminoid	BRO-COM	Meadow brome	Bromus	commutatus	avoided	*O. virginianus*
Graminoid	BRO-HOR	Soft brome	Bromus	hordeaceus	avoided	*O. virginianus*
Graminoid	BRO-INE	Smooth brome	Bromus	inermis	avoided	*O. virginianus*
Graminoid	BRO-JAP	Japanese brome	Bromus	japonicus	avoided	*O. virginianus*
Graminoid	BRO-SIT	Alaska brome	Bromus	sitchensis	avoided	*O. virginianus*
Graminoid	BRO-SPP	Unknown brome	Bromus	spp.	avoided	*O. virginianus*
Graminoid	BRO-SQU	Corn brome	Bromus	squarrosus	avoided	*O. virginianus*
Graminoid	BRO-STE	Poverty brome	Bromus	sterilis	avoided	*O. virginianus*
Graminoid	BRO-TEC	Cheat grass	Bromus	tectorum	avoided	*O. virginianus*
nonvascular	MOS-SPP	Unknown moss	Bryphyta	spp.	avoided	*C. canadensis*
Graminoid	CAL-RUB	Pinegrass	Calamagrostis	rubescens	avoided	*O. virginianus*
Tree	CAL-NOO	Alaskan cedar	Callitropsis	nootkatensis	avoided	*O. spp.*
Forb/herb	CAL-SEP	Hedge bindweed	Calystegia	sepium	selected/neutral	*O. spp.*
Forb/herb	CAM-MIC	Littlepod false flax	Camelina	microcarpa	selected/neutral	*O. hemionus*
Forb/herb	CAM-ROT	Harebell	Campanula	rotundifolia	neutral	*O. hemionus columbianus*
Forb/herb	CAP-BUR	Shepherd's-purse	Capsella	bursa-pastoris	avoided	*O. spp.*
Graminoid	CAR-CUS	Cusick's sedge	Carex	cusickii	avoided	*O. virginianus*
Graminoid	CAR-PRA	Meadow sedge	Carex	praticola	avoided	*O. virginianus*
Graminoid	CAR-SPP	Unknown sedge	Carex	spp.	avoided	*O. virginianus*
Shrub	CEA-SAN	Redstem ceanothus	Ceanothus	sanguineus	selected	*O. virginianus*
Shrub	CEA-VEL	Snowbrush ceanothus	Ceanothus	velutinus	avoided	*O. spp.*
Forb/herb	CEN-DIF	Diffuse knapweed	Centaurea	diffusa	avoided	*O. hemionus*
Forb/herb	CEN-MEL	Malta starthistle	Centaurea	melitensis	avoided	*O. hemionus*
Forb/herb	CEN-MON	Mountain bluet	Centaurea	montana	avoided	*O. hemionus*
Forb/herb	CEN-NIG	Black knapweed	Centaurea	nigra	avoided	*O. hemionus*

Forb/herb	CEN-SPP	Unknown centaurea	Centaurea	spp.	avoided	*O. hemionus*
Forb/herb	CEN-STO	Spotted knapweed	Centaurea	stoebe	avoided	*O. hemionus*
Forb/herb	CEN-ERY	Common centaury	Centaurium	erythraea	avoided	*O. spp.*
Forb/herb	CHA-ANG	Fireweed	Chamerion	angustifolium	selected	*O. virginianus*
Forb/herb	CHE-ALB	Lambsquarters	Chenopodium	album	avoided	*O. spp.*
Forb/herb	CHI-UMB	Pipsissewa	Chimaphila	umbellata	avoided	*O. virginianus*
Forb/herb	CHO-JUN	Rush skeletonweed	Chondrilla	juncea	selected/neutral	*O. spp.*
Graminoid	CIN-LAT	Slender wood-reed	Cinna	latifolia	selected	*C. canadensis*
Forb/herb	CIR-ALP	Enchanters nightshade	Circaea	alpine	avoided	*C. canadensis*
Forb/herb	CIR-ARV	Canadian thistle	Cirsium	arvense	avoided	*O. virginianus*
Forb/herb	CIR-EDU	Edible thistle	Cirsium	edule	avoided	*O. virginianus*
Forb/herb	CIR-VUL	Bull thistle	Cirsium	vulgare	avoided	*O. virginianus*
Forb/herb	CLA-LAN	Lanceleaf springbeauty	Claytonia	lanceolata	selected/neutral	*O. spp.*
Forb/herb	CLE-OCC	Rock clematis	Clematis	occidentalis	selected	*O. virginianus*
Forb/herb	CLI-DOU	Yerba buena	Clinopodium	douglasii	neutral	*C. canadensis*
Forb/herb	CLI-UNI	Queen's cup	Clintonia	uniflora	neutral	*O. virginianus*
Forb/herb	COL-PAR	Maiden blue eyed mary	Collinsia	parviflora	avoided	*O. virginianus*
Forb/herb	COL-GRA	Large-flowered collomia	Collomia	grandiflora	selected	*O. spp.*
Forb/herb	COL-LIN	Narrow leaved collomia	Collomia	linearis	selected	*O. spp.*
Forb/herb	COP-TRI	Threeleaf goldthread	Coptis	trifolia	selected/neutral	*O. spp.*
Forb/herb	COR-STR	Striped coralroot	Corallorhiza	striata	selected/neutral	*O. spp.*
Shrub	COR-CAN	Canada bunchberry	Cornus	canadensis	neutral	*O. spp.*
Tree	COR-NUT	Mountain dogwood	Cornus	nuttalli	neutral	*O. spp.*
Shrub	COR-STO	Red-osier dogwood	Cornus	stolonifera	neutral	*O. spp.*
Forb/herb	COR-UNA	Western bunchberry	Cornus	unalaschkensis	neutral	*O. spp.*
Shrub	COR-COR	Beaked hazelnut	Corylus	cornuta	avoided	*O. spp.*
Shrub	CRA-DOU	Black hawthorn	Crataegus	douglasii	selected	*C. canadensis*
Forb/herb	CRE-TEC	Narrowleaf hawksbeard	Crepis	tectorum	neutral	*O. hemionus columbianus*
Forb/herb	CYN-OFF	Common hound's-tongue	Cynoglossum	officinale	selected/neutral	*O. spp.*

Graminoid	DAC-GLO	Orchard grass	Dactylis	glomerata	avoided	*O. spp.*
Forb/herb	DES-SOP	Flixweed	Descurainia	sophia	avoided	*O. spp.*
Forb/herb	DIA-ARM	Deptford pink	Dianthus	armeria	neutral	*C. canadensis*
Graminoid	DIS-SPI	Alkaline grass	Distichlis	spicata	avoided	*O. spp.*
Forb/herb	DRY-ARG	Tall cinquefoil	Drymocallis	arguta	selected/neutral	*O. spp.*
Forb/herb	DRY-GLA	Sticky cinquefoil	Drymocallis	glandulosa	selected/neutral	*O. spp.*
Forb/herb	DRY-CAR	Toothed woodfern	Dryopteris	carthusiana	avoided	*O. spp.*
Graminoid	ELY-GLA	Blue wild-rye	Elymus	glaucus	neutral	*O. virginianus*
Graminoid	ELY-REP	Quackgrass	Elymus	repens	avoided	*O. spp.*
Forb/herb	EPI-BRA	Autumn willowherb	Epilobium	brachycarpum	selected/neutral	*O. hemionus*
Forb/herb	EPI-CIL	Ciliate willowherb	Epilobium	ciliatum	neutral	*O. spp.*
Forb/herb	EQU-ARV	Common horsetail	Equisetum	arvense	neutral	*C. canadensis*
Forb/herb	EQU-HYE	Scouringrush horsetail	Equisetum	hyemale	neutral	*C. canadensis*
Forb/herb	ERI-FIL	Threadleaf fleabane	Erigeron	filifolius	neutral	*O. spp.*
Forb/herb	ERI-SPE	Showy daisy	Erigeron	speciosus	neutral	*O. spp.*
Forb/herb	ERI-SPP	Unknown daisy	Erigeron	spp.	neutral	*O. spp.*
Forb/herb	ERI-HER	Parsnipflower buckwheat	Eriogonum	heracleoides	selected/neutral	*O. hemionus*
Forb/herb	ERY-SPP	Unknown monkey flower	Erythranthe	spp.	avoided	*O. spp.*
Forb/herb	EUR-CON	Western showy aster	Eurybia	conspicua	selected	*O. virginianus*
Forb/herb	EUT-OCC	Western goldenrod	Euthamia	occidentalis	neutral	*C. canadensis*
Forb/herb	FAL-CON	Black bindweed	Fallopia	convolvulus	avoided	*O. spp.*
Graminoid	FES-CAM	Prairie fescue	Festuca	campestris	avoided	*O. virginianus*
Graminoid	FES-IDA	Idaho fescue	Festuca	idahoensis	avoided	*O. virginianus*
Graminoid	FES-OCC	Western fescue	Festuca	occidentalis	avoided	*O. virginianus*
Graminoid	FES-RUB	Red fescue	Festuca	rubra	avoided	*O. virginianus*
Graminoid	FES-SPP	Unknown fescue	Festuca	spp.	avoided	*O. virginianus*
Forb/herb	FRA-VES	Woodland strawberry	Fragaria	vesca	avoided	*O. virginianus*
Forb/herb	FRA-VIR	Mountain strawberry	Fragaria	virginiana	neutral	*O. virginianus*
Shrub	FRA-PUR	Buckthorn	Frangula	purshiana	selected	*O. hemionus columbianus*

Forb/herb	GAI-ARI	Blanket flower	Gaillardia	aristata	selected/neutral	*O. spp.*
Forb/herb	GAL-BOR	Northern bedstraw	Galium	boreale	neutral	*O. virginianus*
Forb/herb	GAL-TRI	Fragrant bedstraw	Galium	triflorum	neutral	*O. virginianus*
Forb/herb	GAY-DEC	Deceptive groundsmoke	Gayophytum	decipiens	avoided	*O. spp.*
Forb/herb	GAY-DIF	Spreading groundsmoke	Gayophytum	diffusum	avoided	*O. spp.*
Forb/herb	GER-BIC	Northern crane's-bill	Geranium	bicknelli	neutral	*O. hemionus columbianus*
Forb/herb	GER-ROB	Stinky-Bob	Geranium	robertianum	neutral	*O. hemionus columbianus*
Forb/herb	GER-VIS	Sticky purple geranium	Geranium	viscosissimum	neutral	*O. hemionus columbianus*
Forb/herb	GEU-MAC	Large-leaved avens	Geum	macrophyllum	neutral	*O. hemionus columbianus*
Forb/herb	GEU-RIV	Water avens	Geum	rivale	neutral	*O. hemionus columbianus*
Forb/herb	GEU-TRI	Prairie smoke	Geum	triflorum	neutral	*O. hemionus columbianus*
Forb/herb	GOO-OBL	Western rattlesnake-plantain	Goodyera	oblongifolia	neutral	*O. virginianus*
Forb/herb	GRI-SPP	Unknown gumweed	Grindelia	spp.	selected/neutral	*O. spp.*
Forb/herb	HED-SUL	Yellow sweet-vetch	Hedysarum	sulphurescens	selected/neutral	*O. spp.*
Forb/herb	HER-SPP	Unknown herb/forb	Herb	spp.	selected/neutral	*O. spp.*
Forb/herb	HEU-CYL	Roundleaf alumroot	Heuchera	cylindrica	neutral	*O. virginianus*
Forb/herb	HIE-ALB	White hawkweed	Hieracium	albiflorum	neutral	*O. virginianus*
Forb/herb	HIE-AUR	Orange hawkweed	Hieracium	aurantiacum	neutral	*O. virginianus*
Forb/herb	HIE-CAE	Meadow hawkweed	Hieracium	caespitosum	neutral	*O. virginianus*
Forb/herb	HIE-SCO	Scouler's hawkweed	Hieracium	scouleri	neutral	*O. virginianus*
Forb/herb	HIE-SPP	Unknown hawkweed	Hieracium	spp.	neutral	*O. virginianus*
Forb/herb	HIE-TRI	Slender hawkweed	Hieracium	triste	neutral	*O. virginianus*
Forb/herb	HIE-UMB	Narrowleaf hawkweed	Hieracium	umbellatum	neutral	*O. virginianus*
Shrub	HOL-DIS	Ocean-spray	Holodiscus	discolor	neutral	*O. virginianus*
Forb/herb	HYD-CAP	Ballhead waterleaf	Hydrophyllum	capitatum	neutral	*O. spp.*
Forb/herb	HYP-PER	Common St. John's-wort	Hypericum	perforatum	neutral	*O. virginianus*
Forb/herb	IPO-AGG	Scarlet gilia	Ipomopsis	aggregata	selected/neutral	*O. spp.*
Graminoid	JUN-EFF	Soft rush	Juncus	effusus	avoided	*O. hemionus columbianus*

Graminoid	KOA-MAC	Prairie Junegrass	Koeleria	macrantha	avoided	*O. spp.*
Forb/herb	LAC-SER	Prickly lettuce	Lactuca	serriola	neutral	*O. hemionus columbianus*
Tree	LAR-LYA	Subalpine larch	Larix	lyallii	avoided	*O. spp.*
Tree	LAR-OCC	Western larch	Larix	occidentalis	avoided	*O. spp.*
Tree	LAR-SPP	Unknown larch	Larix	spp.	avoided	*O. spp.*
Forb/herb	LAT-NEV	Sierra peavine	Lathyrus	nevadensis	selected	*O. hemionus columbianus*
Forb/herb	LAT-OCH	Cream-flowered peavine	Lathyrus	ochroleucus	selected	*O. hemionus columbianus*
Forb/herb	LAT-PAU	Few-flowered peavine	Lathyrus	pauciflorus	selected	*O. hemionus columbianus*
Forb/herb	LAT-SPP	Unknown peavine	Lathyrus	spp.	selected	*O. hemionus columbianus*
Forb/herb	LEU-VUL	Oxeye daisy	Leucanthemum	vulgare	selected/neutral	*O. spp.*
Forb/herb	LIG-GRA	Gray's lovage	Ligusticum	grayi	selected	*C. canadensis*
Forb/herb	LIG-POR	Bear root	Ligusticum	porteri	selected	*C. canadensis*
Forb/herb	LIN-DAL	Dalmatian toadflax	Linaria	dalmatica	selected/neutral	*O. spp.*
Forb/herb	LIN-VUL	Butter and eggs	Linaria	vulgaris	selected/neutral	*O. spp.*
Forb/herb	LIN-BOR	Twinflower	Linnaea	borealis	avoided	*O. virginianus*
Forb/herb	LON-CIL	Orange honeysuckle	Lonicera	ciliosa	selected	*O. virginianus*
Forb/herb	LON-CON	Purple-flower honeysuckle	Lonicera	conjugialis	selected	*O. virginianus*
Forb/herb	LON-SPP	Unknown honeysuckle	Lonicera	spp.	selected	*O. virginianus*
Forb/herb	LON-UTA	Utah honeysuckle	Lonicera	utahensis	selected	*O. virginianus*
Forb/herb	LUP-ARG	Silvery lupine	Lupinus	argenteus	selected	*O. virginianus*
Forb/herb	LUP-LAT	Broadleaf lupine	Lupinus	latifolius	selected	*O. virginianus*
Forb/herb	LUP-SER	Silky lupine	Lupinus	sericeus	selected	*O. virginianus*
Forb/herb	LUP-SPP	Unknown lupine	Lupinus	spp.	selected	*O. virginianus*
Graminoid	LUZ-PAR	Small-flowered woodrush	Luzula	parviflora	selected	*C. canadensis*
nonvascular	LYC-SPP	Clubmoss	Lycopodiaceae	spp.	avoided	*C. canadensis*
Forb/herb	LYS-AME	Skunk cabbage	Lysichiton	americanus	neutral	*C. canadensis*
Forb/herb	MAD-GRA	grassy tarweed	Madia	gracilis	avoided	*O. spp.*
Shrub	MAH-REP	Creeping Oregon-grape	Mahonia	repens	neutral	*O. virginianus*
Forb/herb	MAI-RAC	Large false Solomon's seal	Maianthemum	racemosum	selected	*O. spp.*

Forb/herb	MAL-NEG	Dwarf mallow	Malva	neglecta	avoided	*O. spp.*
Forb/herb	MED-LUP	Black medic	Medicago	lupulina	avoided	*O. spp.*
Forb/herb	MED-SAT	Alfalfa	Medicago	sativa	selected/neutral	*O. spp.*
Forb/herb	MEN-CAN	Wild mint	Mentha	canadensis	avoided	*C. canadensis*
Forb/herb	MER-PAN	Tall bluebell	Mertensia	paniculata	selected/neutral	*O. spp.*
Forb/herb	MIC-SPP	Unknown saxifrage	Micranthes	spp.	selected/neutral	*O. spp.*
Forb/herb	MIC-GRA	Slender phlox	Microsteris	gracilis	avoided	*O. spp.*
Forb/herb	MOE-LAT	Bluntleaf sandwort	Moehringia	lateriflora	neutral	*C. canadensis*
Forb/herb	MYO-LAX	Small forget-me-not	Myosotis	laxa	avoided	*O. spp.*
Forb/herb	NEP-CAT	Catnip	Nepeta	cataria	selected/neutral	*O. spp.*
Forb/herb	ONO-VIC	Saintfoin	Onobrychis	viciifolia	selected/neutral	*O. spp.*
Shrub	OPL-HOR	Devil's club	Oplopanax	horridus	selected/neutral	*C. canadensis and O. spp.*
Forb/herb	ORT-SEC	One-sided pyrola	Orthilia	secunda	avoided	*C. canadensis*
Forb/herb	OSM-BER	Mountain sweet-cicely	Osmorhiza	Berteroi	avoided	*O. spp.*
Forb/herb	PAC-MAC	Siskiyou Mountain ragwort	Packera	macounii	neutral	*C. canadensis*
Shrub	PAX-MYR	Oregon boxleaf	Paxistima	myrsinites	avoided	*O. virginianus*
Forb/herb	PEC-BRE	Brewer's mitrewort	Pectiantia	breweri	selected/neutral	*O. spp.*
Forb/herb	PEN-CON	Yellow penstemon	Penstemon	confertus	neutral	*O. virginianus*
Forb/herb	PEN-FRU	shrubby penstemon	Penstemon	fruticosus	neutral	*O. spp.*
Forb/herb	PEN-PRO	Small-flowered penstemon	Penstemon	procerus	neutral	*O. spp.*
Forb/herb	PEN-SPP	Unknown penstemon	Penstemon	spp.	neutral	*O. spp.*
Forb/herb	PER-WAL	Himalayan knotweed	Persicaria	wallichii	selected/neutral	*O. spp.*
Forb/herb	PET-FRI	Sweet coltsfoot	Petasites	frigidus	selected	*C. canadensis*
Forb/herb	PET-SAG	Arrow-leaved coltsfoot	Petasites	frigidus	selected	*C. canadensis*
Forb/herb	PHA-HAS	Silverleaf phacelia	Phacelia	hastata	neutral	*C. canadensis*
Graminoid	PHA-ARU	Reed canary grass	Phalaris	arundinacea	selected	*C. canadensis*
Shrub	PHI-LEW	Lewis' mock orange	Philadelphus	lewisii	neutral	*O. spp.*
Graminoid	PHL-PRA	Timothy	Phleum	pratense	avoided	*O. spp.*
Shrub	PHY-MAL	Mallow ninebark	Physocarpus	malvaceus	avoided	*O. virginianus*

Tree	PIC-ENG	Engelmann spruce	Picea	engelmannii	avoided	*O. spp.*
Tree	PIC-MAR	Black spruce	Picea	mariana	avoided	*O. spp.*
Tree	PIC-SIT	Sitka spruce	Picea	sitchensis	avoided	*O. spp.*
Tree	PIC-SPP	Unknown spruce	Picea	spp.	avoided	*O. spp.*
Tree	CON-SPP	Unknown conifer	Pinaceae	spp.	avoided	*O. spp.*
Tree	PIN-CON	Lodgepole pine	Pinus	contorta	avoided	*O. spp.*
Tree	PIN-MON	Western white pine	Pinus	monticola	avoided	*O. spp.*
Tree	PIN-PON	Ponderosa pine	Pinus	ponderosa	avoided	*O. spp.*
Forb/herb	PLA-LAN	English plantain	Plantago	lanceolata	neutral	*C. canadensis*
Forb/herb	PLA-MAJ	Common plantain	Plantago	major	neutral	*C. canadensis*
Forb/herb	PLA-PAT	Wooly plantain	Plantago	patagonica	neutral	*C. canadensis*
Forb/herb	PLA-SPP	Unknown plantain	Plantago	spp.	neutral	*C. canadensis*
Forb/herb	PLA-ORB	Round leaved orchid	Platanthera	orbiculata	selected/neutral	*O. spp.*
Forb/herb	PLA-UNA	Alaska rein orchid	Platanthera	unalascensis	selected/neutral	*O. spp.*
Graminoid	POA-PRA	Kentucky bluegrass	Poa	Pratensis	avoided	*O. spp.*
Graminoid	POA-SPP	Unknown bluegrass	Poa	spp.	avoided	*O. spp.*
Graminoid	GRA-SPP	Unknown grass	Poaceae	spp.	avoided	*O. virginianus*
Forb/herb	POL-AVI	Common knotweed	Polygonum	aviculare	avoided	*O. spp.*
Forb/herb	POL-DOU	Douglas's knotweed	Polygonum	douglasii	avoided	*O. spp.*
Tree	POP-TRE	Quaking aspen	Populus	tremuloides	selected	*O. spp.*
Tree	POP-TRI	Black cottonwood	Populus	trichocarpa	selected	*O. spp.*
Forb/herb	POT-ARG	Silver cinquefoil	Potentilla	argentea	neutral	*O. virginianus*
Forb/herb	POT-GRA	Slender cinquefoil	Potentilla	gracilis	neutral	*O. virginianus*
Forb/herb	POT-REC	Sulphur cinquefoil	Potentilla	recta	neutral	*O. virginianus*
Forb/herb	POT-SPP	Unknown cinquefoil	Potentilla	spp.	neutral	*O. virginianus*
Forb/herb	PRO-HOO	Hooker's fairy-bells	Prosartes	hookeri	neutral	*C. canadensis*
Forb/herb	PRO-TRA	Roughfruit fairybells	Prosartes	trachycarpa	neutral	*C. canadensis*
Forb/herb	PRU-VUL	Self-heal	Prunella	vulgaris	neutral	*O. spp.*
Tree	PRU-ARM	Apricot	Prunus	armeniaca	selected	*O. hemionus columbianus*

Shrub	PRU-PEN	Pin cherry	Prunus	pensylvanica	selected	*O. hemionus columbianus*
Shrub	PRU-VIR	Chokecherry	Prunus	virginiana	selected	*O. hemionus columbianus*
Graminoid	PSE-SPI	Bluebunch wheatgrass	Pseudoroegneria	spicata	avoided	*O. hemionus*
Tree	PSE-MEN	Douglas fir	Pseudotsuga	menziesii	avoided	*O. virginianus*
Forb/herb	PTE-AQU	Bracken fern	Pteridium	aquilinum	avoided	*O. hemionus columbianus*
Forb/herb	PTE-SPP	Unknown bracken	Pteridium	spp.	avoided	*O. spp.*
Forb/herb	RAN-BUL	Bulbous buttercup	Ranunculus	bulbosus	neutral	*O. hemionus columbianus*
Forb/herb	RAN-SPP	Unknown buttercup	Ranunculus	spp.	neutral	*O. hemionus columbianus*
Shrub	RHA-ALN	Alder-leaf buckthorn	Rhamnus	alnifolia	selected	*O. hemionus columbianus*
Shrub	RIB-ACE	Maple-leaf currant	Ribes	acerifolium	selected	*O. virginianus*
Shrub	RIB-AUR	Golden currant	Ribes	aureum	selected	*O. virginianus*
Shrub	RIB-CER	Wax currant	Ribes	cereum	selected	*O. virginianus*
Shrub	RIB-LAC	Swamp currant	Ribes	lacustre	selected	*O. virginianus*
Shrub	RIB-VIS	Mountain currant	Ribes	viscosissimum	selected	*O. virginianus*
Forb/herb	RIG-LEP	Wireweed	Rigiopappus	leptocladus	avoided	*O. spp.*
Forb/herb	ROR-PAL	Marsh yellowcress	Rorippa	palustris	avoided	*O. spp.*
Shrub	ROS-ACI	Prickly rose	Rosa	acicularis	selected	*O. virginianus*
Shrub	ROS-GYM	Bald-hip rose	Rosa	gymnocarpa	selected	*O. virginianus*
Shrub	ROS-NUT	Nootka rose	Rosa	nutkana	selected	*O. virginianus*
Shrub	ROS-SPP	Unknown rose	Rosa	spp.	selected	*O. virginianus*
Shrub	ROS-WOO	Pearhip rose	Rosa	woodsii	selected	*O. virginianus*
Shrub	RUB-IDA	Red rasberry	Rubus	idaeus	neutral	*O. virginianus*
Shrub	RUB-PAR	Thimbleberry	Rubus	parviflorus	neutral	*O. virginianus*
Forb/herb	RUM-ACE	Sheep sorrel	Rumex	acetosa	selected	*O. hemionus columbianus*
Forb/herb	RUM-CRI	Curly dock	Rumex	crispus	selected	*O. hemionus columbianus*
Tree	SAL-BAR	Barclay's willow	Salix	barclayi	neutral	*O. virginianus*
Tree	SAL-BEB	Bebb's willow	Salix	bebbiana	neutral	*O. virginianus*
Tree	SAL-LAS	Pacific willow	Salix	lasiandra	neutral	*O. virginianus*
Shrub	SAL-PLA	Plane-leaf willow	Salix	planifolia	neutral	*O. virginianus*

Tree	SAL-SCO	Scouler's willow	Salix	scouleriana	neutral	*O. virginianus*
Tree, Shrub	SAL-SIT	Sitka willow	Salix	sitchensis	neutral	*O. virginianus*
Tree, Shrub	SAL-SPP	Unknown willow	Salix	spp.	neutral	*O. virginianus*
Shrub	SAM-NIG	Black elderberry	Sambucus	nigra	selected	*O. hemionus columbianus*
Graminoid	SCO-FES	Common rivergrass	Scolochloa	festucacea	avoided	*O. spp.*
Graminoid	SEC-CER	Cultivated rye	Secale	cereale	avoided	*O. spp.*
Forb/herb	SED-LAN	Lance-leaved stonecrop	Sedum	lanceolatum	neutral	*O. spp.*
Forb/herb	SED-STE	Wormleaf stonecrop	Sedum	stenopetalum	neutral	*O. spp.*
Graminoid	SET-PUM	Yellow foxtail	Setaria	pumila	avoided	*O. spp.*
Shrub	SHE-CAN	Russet buffaloberry	Shepherdia	canadensis	neutral	*O. virginianus*
Shrub	SHR-SPP	Unknown shrub	Shrub	spp.	selected/neutral	*O. spp.*
Forb/herb	SIL-LAT	White campion	Silene	latifolia	selected/neutral	*O. spp.*
Forb/herb	SIL-MEN	Menzies' catchfly	Silene	menziesii	selected/neutral	*O. spp.*
Forb/herb	SIS-ALT	Tumble mustard	Sisymbrium	altissimum	selected/neutral	*O. hemionus*
Forb/herb	SOL-SPP	Unknown goldenrod	Solidago	spp.	selected	*O. hemionus columbianus*
Forb/herb	SOR-SCO	Western mountain-ash	Sorbus	scopulina	selected	*O. spp.*
Forb/herb	SPE-ARV	Corn spurry	Spergula	arvensis	avoided	*O. spp.*
Shrub	SPI-DOU	Douglas's spiraea	Spiraea	douglasii	neutral	*O. virginianus*
Shrub	SPI-LUC	Shinyleaf spiraea	Spiraea	lucida	neutral	*O. virginianus*
Shrub	SPI-PYR	Pyramid spiraea	Spiraea	pyramidata	neutral	*O. virginianus*
Forb/herb	SPI-SPL	Rosy spiraea	Spiraea	splendens	neutral	*O. virginianus*
Shrub	SPI-SPP	Unknown spiraea	Spiraea	spp.	neutral	*O. virginianus*
Forb/herb	STA-SPP	Unknown hedge-nettle	Stachys	spp.	neutral	*C. canadensis*
Forb/herb	STE-CRI	Crisped starwort	Stellaria	crispa	avoided	*O. hemionus columbianus*
Forb/herb	STE-MED	Common chickweed	Stellaria	media	avoided	*O. hemionus columbianus*
Forb/herb	STR-AMP	Clasping twisted stalk	Streptopus	amplexifolius	neutral	*C. canadensis*
Forb/herb	STR-STR	Small twisted stalk	Streptopus	streptopoides	neutral	*C. canadensis*
Shrub	SYM-ALB	Common snowberry	Symphoricarpos	albus	neutral	*O. virginianus*
Shrub	SYM-OCC	Western snowberry	Symphoricarpos	occidentalis	neutral	*O. virginianus*

Shrub	SYM-SPP	Unknown snowberry	Symphoricarpos	spp.	neutral	*O. virginianus*
Forb/herb	SYM-FOL	Leafy aster	Symphyotrichum	foliaceum	selected/neutral	*O. spp.*
Forb/herb	TAN-VUL	Common tansy	Tanacetum	vulgare	avoided	*C. canadensis*
Forb/herb	TAR-OFF	Common dandelion	Taraxacum	officinale	neutral	*O. virginianus*
Forb/herb	TAR-SPP	Unknown dandelion	Taraxacum	spp.	neutral	*O. virginianus*
Forb/herb	THA-OCC	Western meadow rue	Thalictrum	occidentale	neutral	*O. spp.*
Tree	THU-PLI	Western red cedar	Thuja	plicata	neutral	*O. virginianus*
Forb/herb	TIA-TRI	Three-leaf foamflower	Tiarella	trifoliata	neutral	*O. hemionus columbianus*
Shrub	TOX-RAD	Poison ivy	Toxicodendron	radicans	selected/neutral	*O. spp.*
Forb/herb	TRA-DUB	Yellow salsify	Tragopogon	dubius	selected/neutral	*O. hemionus*
Forb/herb	TRI-AUR	Large hop clover	Trifolium	aureum	neutral	*O. virginianus*
Forb/herb	TRI-CAM	Hop clover	Trifolium	campestre	neutral	*O. virginianus*
Forb/herb	TRI-PRA	Red clover	Trifolium	pratense	neutral	*O. virginianus*
Forb/herb	TRI-REP	White clover	Trifolium	repens	neutral	*O. virginianus*
Forb/herb	TRI-OVA	Western trillium	Trillium	ovatum	selected	*O. hemionus columbianus*
Forb/herb	TRIL-SPP	Unknown Trillium	Trillium	spp.	selected	*O. hemionus columbianus*
Graminoid	TRI-CAN	Tall false oat	Trisetum	canescens	neutral	*C. canadensis*
Graminoid	TRI-AES	Common wheat	Triticum	aestivum	avoided	*O. spp.*
Graminoid	TRI-SPP	Unknown Wheat	Triticum	spp.	avoided	*O. spp.*
Tree	TSU-HET	Western hemlock	Tsuga	heterophylla	avoided	*O. hemionus columbianus*
Tree	BRN-SPP	Burned trees	Unknown	spp.	avoided	*O. spp.*
Graminoid	GRA-MOW	Mowed grass	Unknown	spp.	avoided	*O. spp.*
Forb/herb	URT-DIO	Stinging nettle	Urtica	dioica	avoided	*C. canadensis*
Shrub	VAC-CES	Dwarf huckleberry	Vaccinium	cespitosum	avoided	*O. virginianus*
Shrub	VAC-MEM	Black huckleberry	Vaccinium	membranaceum	avoided	*O. virginianus*
Shrub	VAC-MYR	Velvet-leaf blueberry	Vaccinium	myrtilloides	avoided	*O. virginianus*
Shrub	VAC-OVA	Alaska blueberry	Vaccinium	ovalifolium	avoided	*O. virginianus*
Shrub	VAC-SCO	Grouseberry	Vaccinium	scoparium	avoided	*O. spp.*
Shrub	VAC-SPP	Unknown vaccinium	Vaccinium	spp.	avoided	*O. virginianus*

Forb/herb	VER-THA	Great mullein	Verbascum	thapsus	avoided	*O. spp.*
Forb/herb	VER-AME	American brooklime	Veronica	americana	selected	*O. hemionus columbianus*
Forb/herb	VER-OFF	Common speedwell	Veronica	officinalis	selected	*O. hemionus columbianus*
Forb/herb	VER-SPP	Unknown Veronica	Veronica	spp.	selected	*O. hemionus columbianus*
Shrub	VIB-ELL	Common viburnum	Viburnum	ellipticum	selected/neutral	*O. spp.*
Forb/herb	VIC-AME	American vetch	Vicia	americana	selected	*O. hemionus columbianus*
Forb/herb	VIC-HIR	Tiny vetch	Vicia	hirsuta	selected	*O. hemionus columbianus*
Forb/herb	VIC-SPP	Unknown vetch	Vicia	spp.	selected	*O. hemionus columbianus*
Forb/herb	VIC-VIL	Wooly vetch	Vicia	villosa	selected	*O. hemionus columbianus*
Forb/herb	VIO-ADU	Early blue violet	Viola	adunca	neutral	*O. virginianus*
Forb/herb	VIO-CAN	Canadian violet	Viola	canadensis	neutral	*O. virginianus*
Forb/herb	VIO-GLA	Stream violet	Viola	glabella	neutral	*O. virginianus*
Forb/herb	VIO-NUT	Nuttall's violet	Viola	nuttalli	neutral	*O. virginianus*
Forb/herb	VIO-ORB	Round-leaved violet	Viola	orbiculata	neutral	*O. virginianus*
Forb/herb	VIO-SEM	Evergreen violet	Viola	sempervirens	neutral	*O. virginianus*
Forb/herb	VIO-SPP	Unknown violet	Viola	spp.	neutral	*O. virginianus*

C.3 COX PROPORTIONAL HAZARD MODELS

Table C3.1 Covariate estimates for Cox proportional hazard models (Cox 1972) for fawn and adult female mortality risk in northeast Washington from 2017 – 2021. Positive $\hat{\beta}$ estimates increase the risk of mortality, whereas negative $\hat{\beta}$ estimates reduce risk of mortality. Robust standard errors (SEs) result from the cluster term in the models for adult females.

Life Stage	Model	Covariate	β	SE	Robust SE (Adults)	*P*
Juvenile	0-6 months	bobcat	-1.253	0.361	-	0.001
Juvenile	0-6 months	cougar	0.793	0.192	-	0.000
Juvenile	0-6 months	coyote	0.025	0.216	-	0.906
Juvenile	0-6 months	wolf	1.026	0.274	-	0.000
Juvenile	0-6 months	capture mass	-0.396	0.190	-	0.037
Juvenile	0-6 months	WSI prior year	0.106	0.133	-	0.424
Juvenile	0-6 months	canopy loss	-0.809	0.334	-	0.015
Juvenile	0-6 months	canopy loss^2	0.481	0.138	-	0.000
Juvenile	0-6 months	dist to major rds	-0.169	0.177	-	0.341
Juvenile	6-9 months	bobcat	-0.289	0.386	-	0.454
Juvenile	6-9 months	cougar	0.388	0.451	-	0.391
Juvenile	6-9 months	coyote	-0.438	0.506	-	0.387
Juvenile	6-9 months	wolf	0.774	0.413	-	0.061
Juvenile	6-9 months	WSI	-0.122	0.368	-	0.740
Juvenile	6-9 months	dist to major rds	-0.048	0.311	-	0.878
Juvenile	9-12 months	bobcat	-0.608	0.804	-	0.450
Juvenile	9-12 months	cougar	-0.006	0.294	-	0.983
Juvenile	9-12 months	coyote	-1.688	0.627	-	0.007
Juvenile	9-12 months	wolf	0.581	0.875	-	0.507
Juvenile	9-12 months	WSI	0.523	0.378	-	0.167
Juvenile	9-12 months	dist to major rds	0.238	0.406	-	0.557
Adult Female	June - November	bobcat	-0.266	0.643	0.772	0.731
Adult Female	June - November	wolf	0.841	0.377	0.497	0.090
Adult Female	June - November	cougar	0.817	0.290	0.329	0.013
Adult Female	June - November	cougar^2	0.415	0.152	0.147	0.005
Adult Female	June - November	coyote	0.416	0.389	0.568	0.464
Adult Female	June - November	dist to major rds	0.139	0.233	0.217	0.522

Adult Female	June - November	canopy loss	-0.320	0.330	0.389	0.411
Adult Female	December - May	bobcat	0.313	0.199	0.181	0.084
Adult Female	December - May	cougar	0.832	0.236	0.205	0.000
Adult Female	December - May	coyote	0.677	0.318	0.352	0.054
Adult Female	December - May	wolf	-0.378	0.339	0.302	0.211
Adult Female	December - May	dist to major rds	-0.263	0.262	0.247	0.286
Adult Female	December - May	WSI	0.335	0.187	0.170	0.050

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APPENDIX D

Supplemental Information for Chapter 5

Cougars, wolves, and human super predators drive a dynamic landscape of fear for elk.

D.1 HUMAN PREDATOR OVERLAP

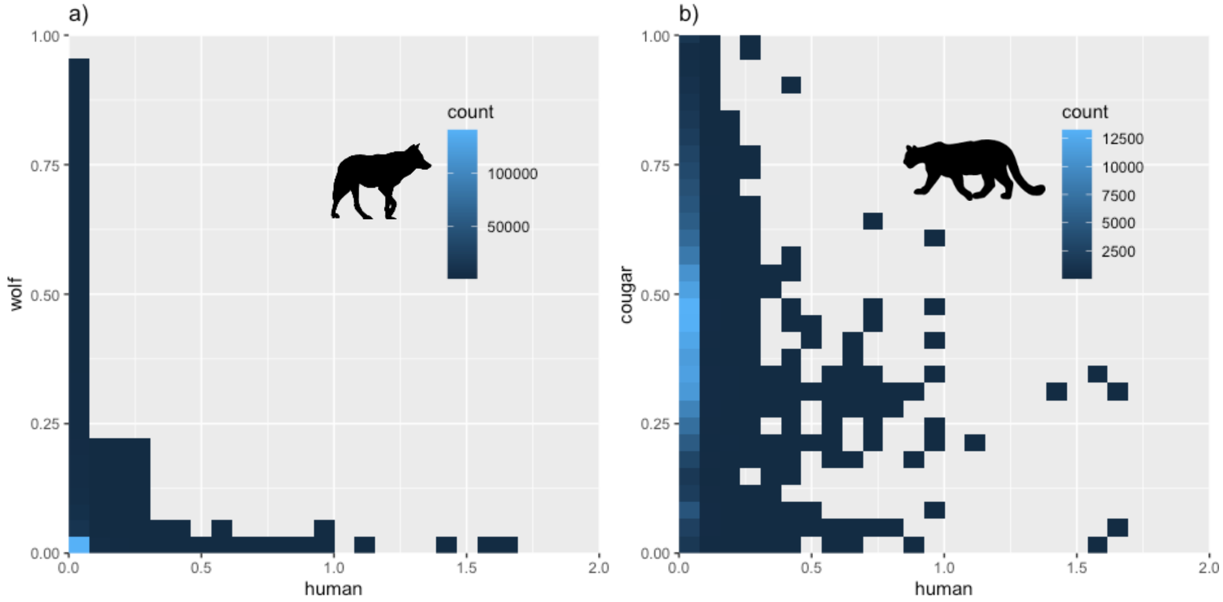

Figure D1.1 Distribution of locations used by elk across wolf (a), and cougar (b) habitat use across human population density. The lack of overlap between areas of high predator and high human use prohibited a direct inclusion of the interaction between humans and predators that could describe a human shield in the step selection functions.

D.2 VEGETATION

D2.1 *Methods*

We leveraged vegetation surveys from chapter 4 which were conducted in the same study area and at the same time, to identify differences in habitat types that might influence elk movement and vulnerability to predation. Specifically, we compared habitat classifications based on (1) forest cover history versus (2) landcover type to determine which remotely sensed habitat classification scheme reflected more pronounced differences in forage availability and visual cover for parameterizing step selection functions. We considered timber harvest because it is a primary driver of landscape change in this study area which can influence both forage and visual cover available to ungulates (Hull et al. 2020). We considered 3 classification of forest cover history, which were uncovered (<50% cover in 2000), covered (>50% cover in 2000) with no cover loss in the past 20 years, and cover loss within the past 20 years, where cover loss reflects a stand replacing disturbance (http://glad.earthengine.app/view/global-forest-change; Hansen et al. 2013). In total, 201 unique sites were identified by stratified random sampling across elevation, aspect, and forest cover history to evaluate how a land management strategy could influence forage availability. Because factors influencing elk movement may differ from those affecting deer, we also considered differences in visual cover and forage biomass based on landcover type according to Terradapt:Cascadia (https://www.cascadiapartnerforum.org/terradapt) cover classifications. We pooled Terradapt:Cascadia cover types into simplified classifications of open (agriculture, mesic grass, xeric grass and xeric shrub), shrub (mesic shrub and woody wetland) and forest habitat (forest) and residential landcovers based on visual assessment of landscape structure during surveys. Because there were only 2 residential sites and these represented a small proportion of the study area, we removed these locations from analysis for a total of 199 randomly sampled sites classified as open, shrub or forest.

Surveys were conducted from July – September in 2019 and 2020 to capture the season when ungulates are under high nutritional demands due to lactation requirements, and with the strongest effects on ungulate survival and reproductive success (Moen 1978, Tollefson et al. 2011, Cook et al. 2013, Johnson et al. 2019). Each 30 x 30 m site was oriented to the cardinal directions and placed in an area of contiguous habitat as close as possible to the randomly selected location. Nine 1 x 1 m quadrats were spread evenly across the site in which the species and percent cover of each plant species with at least 1% cover and > 1 cm and < 2 m in height was recorded, as this is the forage available to elk as food (Rowland and Vojta 2013). A cover pole was placed 10 m from site center in the four cardinal directions to determine percent horizontal cover to 2 m and averaged these values to create a single metric of visual cover for each site.

To estimate the biomass of forage considered "acceptable" to elk at each quadrat, we first classified each plant species measured on plots as avoided (significantly negative Ivlev's electivity index; Ivlev and Scott 1961), neutral (95% confidence intervals for Ivlev's index overlapped 0), or selected (significantly positive Ivlev's index) based on studies with tractable deer and elk in similar habitats (Cook et al. 2016, Robatcek 2019; Table D2.1). If that information was unavailable, we assumed that elk accepted forbs, deciduous shrubs and graminoids while avoiding ferns, conifers and evergreen shrubs (Merrill et al. 1995, Cook et al. 2016, Robatcek 2019). For all acceptable plant species (neutral or selected), we used equations developed by Monzingo et al. (2022) for a similar study area to convert percent cover of acceptable forage to biomass (kg/ha). Species level equations were used when available, or else we used equations developed for the growth form of the plant, which generally performed comparably to species-specific equations (Monzingo et al. 2022). We then averaged values across the nine quadrats to estimate the biomass of acceptable forage (kg/ha) at each site.

We used ANOVA to test for differences in the (1) biomass of acceptable forage and (2) horizontal cover. Differences in biomass and horizontal cover were compared for a forest harvest history (covered, uncovered, and loss) classification scheme versus simplified landcover type (open, shrub, forest) classification scheme to identify which was a stronger driver of nutrition and habitat structure that would influence elk predation risk.

Table D2.1 Understory vegetation and elk acceptance (*Cervus elaphus*) of plants documented during habitat surveys conducted across northeastern Washington, USA July – September, 2019 and 2020. Plants are alphabetized by genus within species. We first determined elk response based on Cook et al. (2016) and Robatcek (2019). If elk response to a particular species was unreported, but suitability was classified for another plant in the same genus, we assumed elk exhibited the same response. If that information was unavailable, we assumed that elk accepted forbs, deciduous shrubs and graminoids while avoiding ferns, conifers and evergreen shrubs (Merrill et al. 1995, Cook et al. 2016, Robatcek 2019).

Form	Code	Common Name	Genus	Species	Preference	Source	Notes
tree	ABI-AMA	Pacific silver fir	Abies	amabilis	avoided	Cook et al. 2016	
tree	ABI-GRA	Grand fir	Abies	grandis	avoided	Cook et al. 2016	Assume the same as A. amabilis
tree	ABI-LAS	Subalpine fir	Abies	lasiocarpa	avoided	Cook et al. 2016	Assume the same as A. amabilis
forb/herb	AGA-URT	Nettleleaf giant hyssop	Agastache	urticifolia	avoided	Robatcek 2019	
graminoid	ALO-PRA	Field meadow-foxtail	Alopecurus	pratensis	avoided	Robatcek 2019	Assume the same as A. geniculatus
forb/herb	ARA-NUD	Wild sarsaparilla	Aralia	nudicaulis	avoided	Robatcek 2019	Assume the same as Araliaceae Oplopanax horridus
forb/herb	AST-SPP	Unknown aster	Asteraceae	spp.	avoided	Robatcek 2019	Asteraceae avoided
forb/herb	BER-INC	Hoary alyssum	Berteroa	incana	avoided	Robatcek 2019	Brassicaceae avoided
graminoid	BRO-TEC	Cheat grass	Bromus	tectorum	avoided	Robatcek 2019	Bromus generally selected
nonvascular	MOS-SPP	Unknown moss	Bryphyta	spp.	avoided	Cook et al. 2016	
forb/herb	CAL-SEP	Hedge bindweed	Calystegia	sepium	avoided	Robatcek 2019	Convolvulaceae avoided
forb/herb	CAM-MIC	Littlepod false flax	Camelina	microcarpa	avoided	Robatcek 2019	Brassicaceae avoided
forb/herb	CAP-BUR	Shepherd's-purse	Capsella	bursa-pastoris	avoided	Robatcek 2019	Brassicaceae avoided
shrub	CEA-SAN	Redstem ceanothus	Ceanothus	sanguineus	avoided	Cook et al. 2016	

shrub	CEA-VEL	Snowbrush ceanothus	Ceanothus	velutinus	avoided	Robatcek 2019	
forb/herb	CEN-DIF	Diffuse knapweed	Centaurea	diffusa	avoided	Robatcek 2019	Assume the same as C. stoebe
forb/herb	CEN-MEL	Malta starthistle	Centaurea	melitensis	avoided	Robatcek 2019	Assume the same as C. stoebe
forb/herb	CEN-MON	Mountain bluet	Centaurea	montana	avoided	Robatcek 2019	Assume the same as C. stoebe
forb/herb	CEN-NIG	Black knapweed	Centaurea	nigra	avoided	Robatcek 2019	Assume the same as C. stoebe
forb/herb	CEN-SPP	Unknown centaurea	Centaurea	spp.	avoided	Robatcek 2019	Assume the same as C. stoebe
forb/herb	CEN-STO	Spotted knapweed	Centaurea	stoebe	avoided	Robatcek 2019	
forb/herb	CHI-UMB	Pipsissewa	Chimaphila	umbellata	avoided	Robatcek 2019	
forb/herb	CHO-JUN	Rush skeletonweed	Chondrilla	juncea	avoided	Robatcek 2019	
forb/herb	CIR-ALP	Enchanters nightshade	Circaea	alpine	avoided	Cook et al. 2016	
forb/herb	CIR-ARV	Canadian thistle	Cirsium	arvense	avoided	Robatcek 2019	
forb/herb	CIR-EDU	Edible thistle	Cirsium	edule	avoided	Robatcek 2019	Cirsium spp. Avoided
forb/herb	CIR-VUL	Bull thistle	Cirsium	vulgare	avoided	Robatcek 2019	Cirsium spp. Avoided
forb/herb	COL-PAR	Maiden blue eyed mary	Collinsia	parviflora	avoided	Robatcek 2019	
forb/herb	COL-GRA	Large-flowered collomia	Collomia	grandiflora	avoided	Robatcek 2019	
forb/herb	COL-LIN	Narrow leaved collomia	Collomia	linearis	avoided	Robatcek 2019	
forb/herb	COR-STR	Striped coralroot	Corallorhiza	striata	avoided	Robatcek 2019	Assume the same as C. maculata
forb/herb	CYN-OFF	Common hound's-tongue	Cynoglossum	officinale	avoided	Robatcek 2019	
forb/herb	DES-SOP	Flixweed	Descurainia	sophia	avoided	Robatcek 2019	Assume the same as D. pinnata
forb/herb	DRY-CAR	Toothed woodfern	Dryopteris	carthusiana	avoided	Robatcek 2019	
graminoid	ELY-REP	Quackgrass	Elymus	repens	avoided	Robatcek 2019	

forb/herb	EPI-BRA	Autumn willowherb	Epilobium	brachycarpum	avoided	Robatcek 2019	
forb/herb	EPI-CIL	Ciliate willowherb	Epilobium	ciliatum	avoided	Robatcek 2019	
forb/herb	ERY-SPP	Unknown monkey flower	Erythranthe	spp.	avoided	Robatcek 2019	
forb/herb	GAI-ARI	Blanket flower	Gaillardia	aristata	avoided	Robatcek 2019	
forb/herb	GAL-BOR	Northern bedstraw	Galium	boreale	avoided	Robatcek 2019	
forb/herb	GAY-DEC	Deceptive groundsmoke	Gayophytum	decipiens	avoided	Robatcek 2019	Assume the same as G. humile
forb/herb	GAY-DIF	Spreading groundsmoke	Gayophytum	diffusum	avoided	Robatcek 2019	Assume the same as G. humile
forb/herb	GRI-SPP	Unknown gumweed	Grindelia	spp.	avoided	Robatcek 2019	Assume the same as G. squarrosa
tree	LAR-LYA	Subalpine larch	Larix	lyallii	avoided	Robatcek 2019	Assume the same as L. occidentalis
tree	LAR-OCC	Western larch	Larix	occidentalis	avoided	Robatcek 2019	
tree	LAR-SPP	Unknown larch	Larix	spp.	avoided	Robatcek 2019	Assume the same as L. occidentalis
forb/herb	LIN-DAL	Dalmatian toadflax	Linaria	dalmatica	avoided	Robatcek 2019	Plantaginaceae avoided
forb/herb	LIN-VUL	Butter and eggs	Linaria	vulgaris	avoided	Robatcek 2019	Plantaginaceae avoided
nonvascular	LYC-SPP	Clubmoss	Lycopodiaceae	spp.	avoided	Cook et al. 2016	
forb/herb	MAD-GRA	grassy tarweed	Madia	gracilis	avoided	Robatcek 2019	Assume the same as M. glomerata
forb/herb	MAI-RAC	Large false Solomon's seal	Maianthemum	racemosum	avoided	Robatcek 2019	
forb/herb	MEN-CAN	Wild mint	Mentha	canadensis	avoided	Cook et al. 2016	
forb/herb	MIC-SPP	Unknown saxifrage	Micranthes	spp.	avoided	Robatcek 2019	Saxifrage spp. avoided
forb/herb	MIC-GRA	Slender phlox	Microsteris	gracilis	avoided	Robatcek 2019	
forb/herb	ORT-SEC	One-sided pyrola	Orthilia	secunda	avoided	Cook et al. 2016	Reported for Pyrola spp.
forb/herb	OSM-BER	Mountain sweet-cicely	Osmorhiza	Berteroi	avoided	Cook et al. 2016	
tree	PIC-ENG	Engelmann spruce	Picea	engelmannii	avoided	Robatcek 2019	

tree	PIC-MAR	Black spruce	Picea	mariana	avoided	Robatcek 2019	
tree	PIC-SIT	Sitka spruce	Picea	sitchensis	avoided	Robatcek 2019	
tree	PIC-SPP	Unknown spruce	Picea	spp.	avoided	Robatcek 2019	
tree	PIN-CON	Lodgepole pine	Pinus	contorta	avoided	Robatcek 2019	
tree	PIN-MON	Western white pine	Pinus	monticola	avoided	Robatcek 2019	
tree	PIN-PON	Ponderosa pine	Pinus	ponderosa	avoided	Robatcek 2019	
forb/herb	PLA-ORB	Round leaved orchid	Platanthera	orbiculata	avoided	Robatcek 2019	
forb/herb	PLA-UNA	Alaska rein orchid	Platanthera	unalascensis	avoided	Robatcek 2019	
graminoid	POA-PRA	Kentucky bluegrass	Poa	Pratensis	avoided	Robatcek 2019	
graminoid	POA-SPP	Unknown bluegrass	Poa	spp.	avoided	Robatcek 2019	
forb/herb	POL-DOU	Douglas's knotweed	Polygonum	douglasii	avoided	Robatcek 2019	
forb/herb	PRU-VUL	Self-heal	Prunella	vulgaris	avoided	Cook et al. 2016	
tree	PSE-MEN	Douglas fir	Pseudotsuga	menziesii	avoided	Cook et al. 2016	
forb/herb	PTE-AQU	Bracken fern	Pteridium	aquilinum	avoided	Cook et al. 2016	
forb/herb	PTE-SPP	Unknown bracken	Pteridium	spp.	avoided	Cook et al. 2016	Assume the same as P. aquilinum
forb/herb	SIL-LAT	White campion	Silene	latifolia	avoided	Robatcek 2019	
forb/herb	SIL-MEN	Menzies' catchfly	Silene	menziesii	avoided	Robatcek 2019	
forb/herb	SIS-ALT	Tumble mustard	Sisymbrium	altissimum	avoided	Robatcek 2019	Brassicaceae avoided
forb/herb	TAN-VUL	Common tansy	Tanacetum	vulgare	avoided	Cook et al. 2016	
tree	THU-PLI	Western red cedar	Thuja	plicata	avoided	Cook et al. 2016	
tree	TSU-HET	Western hemlock	Tsuga	heterophylla	avoided	Cook et al. 2016	
graminoid	GRA-MOW	Mowed grass	Unknown	spp.	avoided		Assume mowed grass too short to be valuable
forb/herb	URT-DIO	Stinging nettle	Urtica	dioica	avoided	Cook et al. 2016	
shrub	VAC-SCO	Grouseberry	Vaccinium	scoparium	avoided	Robatcek 2019	
forb/herb	VER-THA	Great mullein	Verbascum	thapsus	avoided	Cook et al. 2016	
forb/herb	VER-AME	American brooklime	Veronica	americana	avoided	Cook et al. 2016	

forb/herb	VER-SPP	Unknown Veronica	Veronica	spp.	avoided	Robatcek 2019	
forb/herb	ADE-BIC	American trailplant	Adenocaulon	bicolor	neutral	Cook et al. 2016	
graminoid	AEG-CYL	Jointed goat grass	Aegilops	cylindrica	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
graminoid	AGR-GIG	Black bent	Agrostis	gigantea	neutral	Cook et al. 2016	
shrub	AME-ALN	Serviceberry	Amelanchier	alnifolia	neutral	Cook et al. 2016	
forb/herb	ANG-ARG	Lyall's angelica	Angelica	arguta	neutral	Cook et al. 2016	Assume the same as Angelica genuflexa
forb/herb	ANT-NEG	Field pussytoe	Antennaria	neglecta	neutral	Cook et al. 2016	
forb/herb	ANT-SPP	Unknown pussytoe	Antennaria	spp.	neutral	Cook et al. 2016	
forb/herb	ANT-UMB	Umber pussytoes	Antennaria	umbrinella	neutral	Cook et al. 2016	
forb/herb	ART-DRA	Wild tarragon	Artemisia	dracunculus	neutral	Cook et al. 2016	Assume the same as Artemisia suksdorfii
forb/herb	ART-FRI	Prairie sagewort	Artemisia	frigida	neutral	Cook et al. 2016	Assume the same as Artemisia suksdorfii
forb/herb	ART-SPP	Unknown artemisia	Artemisia	spp.	neutral	Cook et al. 2016	Assume the same as Artemisia suksdorfii
forb/herb	ASA-CAU	Wild ginger	Asarum	caudatum	neutral	Cook et al. 2016	
forb/herb	CLI-DOU	Yerba buena	Clinopodium	douglasii	neutral	Cook et al. 2016	
shrub	COR-CAN	Canada bunchberry	Cornus	canadensis	neutral	Cook et al. 2016	
tree	COR-NUT	Mountain dogwood	Cornus	nuttalli	neutral	Cook et al. 2016	
shrub	COR-STO	Red-osier dogwood	Cornus	stolonifera	neutral	Cook et al. 2016	
forb/herb	COR-UNA	Western bunchberry	Cornus	unalaschkensis	neutral	Cook et al. 2016	Assume the same as C. spp.
forb/herb	CRE-TEC	Narrowleaf hawksbeard	Crepis	tectorum	neutral	Cook et al. 2016	
graminoid	DAC-GLO	Orchard grass	Dactylis	glomerata	neutral	Cook et al. 2016	
forb/herb	DIA-ARM	Deptford pink	Dianthus	armeria	neutral	Cook et al. 2016	

graminoid	DIS-SPI	Alkaline grass	Distichlis	spicata	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
graminoid	ELY-GLA	Blue wild-rye	Elymus	glaucus	neutral	Cook et al. 2016	
forb/herb	EQU-ARV	Common horsetail	Equisetum	arvense	neutral	Cook et al. 2016	Reported for Equisetum spp.
forb/herb	EQU-HYE	Scouringrush horsetail	Equisetum	hyemale	neutral	Cook et al. 2016	Reported for Equisetum spp.
forb/herb	EUT-OCC	Western goldenrod	Euthamia	occidentalis	neutral	Cook et al. 2016	Assume the same as Solidago canadensis
forb/herb	FRA-VES	Woodland strawberry	Fragaria	vesca	neutral	Cook et al. 2016	
forb/herb	GAL-TRI	Fragrant bedstraw	Galium	triflorum	neutral	Cook et al. 2016	
forb/herb	GEU-MAC	Large-leaved avens	Geum	macrophyllum	neutral	Cook et al. 2016	
forb/herb	HIE-ALB	White hawkweed	Hieracium	albiflorum	neutral	Cook et al. 2016	
shrub	HOL-DIS	Ocean-spray	Holodiscus	discolor	neutral	Cook et al. 2016	
graminoid	JUN-EFF	Soft rush	Juncus	effusus	neutral	Cook et al. 2016	
forb/herb	LAT-NEV	Sierra peavine	Lathyrus	nevadensis	neutral	Cook et al. 2016	
forb/herb	LAT-OCH	Cream-flowered peavine	Lathyrus	ochroleucus	neutral	Cook et al. 2016	
forb/herb	LAT-PAU	Few-flowered peavine	Lathyrus	pauciflorus	neutral	Cook et al. 2016	
forb/herb	LAT-SPP	Unknown peavine	Lathyrus	spp.	neutral	Cook et al. 2016	
forb/herb	LUP-ARG	Silvery lupine	Lupinus	argenteus	neutral	Cook et al. 2016	
forb/herb	LUP-LAT	Broadleaf lupine	Lupinus	latifolius	neutral	Cook et al. 2016	
forb/herb	LUP-SPP	Unknown lupine	Lupinus	spp.	neutral	Cook et al. 2016	
forb/herb	LYS-AME	Skunk cabbage	Lysichiton	americanus	neutral	Cook et al. 2016	
forb/herb	MOE-LAT	Bluntleaf sandwort	Moehringia	lateriflora	neutral	Cook et al. 2016	
forb/herb	PAC-MAC	Siskiyou Mountain ragwort	Packera	macounii	neutral	Cook et al. 2016	Assume the same as Senecio spp.
forb/herb	PEN-CON	Yellow penstemon	Penstemon	confertus	neutral	Cook et al. 2016	
forb/herb	PEN-SPP	Unknown penstemon	Penstemon	spp.	neutral	Cook et al. 2016	

forb/herb	PHA-HAS	Silverleaf phacelia	Phacelia	hastata	neutral	Cook et al. 2016	
forb/herb	PLA-LAN	English plantain	Plantago	lanceolata	neutral	Cook et al. 2016	Reported for Plantago spp.
forb/herb	PLA-MAJ	Common plantain	Plantago	major	neutral	Cook et al. 2016	Reported for Plantago spp.
forb/herb	PLA-PAT	Wooly plantain	Plantago	patagonica	neutral	Cook et al. 2016	Reported for Plantago spp.
forb/herb	PLA-SPP	Unknown plantain	Plantago	spp.	neutral	Cook et al. 2016	
graminoid	GRA-SPP	Unknown grass	Poaceae	spp.	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
forb/herb	PRO-HOO	Hooker's fairy-bells	Prosartes	hookeri	neutral	Cook et al. 2016	Reported for Disporum spp.
forb/herb	PRO-TRA	Roughfruit fairybells	Prosartes	trachycarpa	neutral	Cook et al. 2016	Reported for Disporum spp.
forb/herb	RAN-BUL	Bulbous buttercup	Ranunculus	bulbosus	neutral	Cook et al. 2016	
forb/herb	RAN-SPP	Unknown buttercup	Ranunculus	spp.	neutral	Cook et al. 2016	
shrub	RIB-LAC	Swamp currant	Ribes	lacustre	neutral	Cook et al. 2016	
shrub	ROS-GYM	Bald-hip rose	Rosa	gymnocarpa	neutral	Cook et al. 2016	
forb/herb	RUM-ACE	Sheep sorrel	Rumex	acetosella	neutral	Cook et al. 2016	
shrub	SAM-NIG	Black elderberry	Sambucus	nigra	neutral	Cook et al. 2016	
graminoid	SCO-FES	Common rivergrass	Scolochloa	festucacea	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
graminoid	SET-PUM	Yellow foxtail	Setaria	pumila	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
forb/herb	STA-SPP	Unknown hedge-nettle	Stachys	spp.	neutral	Cook et al. 2016	Assume the same as Stachys cooleyae
forb/herb	STE-CRI	Crisped starwort	Stellaria	crispa	neutral	Cook et al. 2016	
forb/herb	STE-MED	Common chickweed	Stellaria	media	neutral	Cook et al. 2016	
forb/herb	STR-AMP	Clasping twisted stalk	Streptopus	amplexifolius	neutral	Cook et al. 2016	Assume the same as Streptopus roseus
forb/herb	STR-STR	Small twisted stalk	Streptopus	streptopoides	neutral	Cook et al. 2016	Assume the same as Streptopus roseus
forb/herb	TAR-SPP	Unknown dandelion	Taraxacum	spp.	neutral	Cook et al. 2016	

forb/herb	THA-OCC	Western meadow rue	Thalictrum	occidentale	neutral	Cook et al. 2016	
forb/herb	TIA-TRI	Three-leaf foamflower	Tiarella	trifoliata	neutral	Cook et al. 2016	
forb/herb	TRIL-SPP	Unknown Trillium	Trillium	spp.	neutral	Cook et al. 2016	
graminoid	TRI-CAN	Tall false oat	Trisetum	canescens	neutral	Cook et al. 2016	Assume the same as T. cernuum
graminoid	TRI-AES	Common wheat	Triticum	aestivum	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
graminoid	TRI-SPP	Unknown Wheat	Triticum	spp.	neutral	Cook et al. 2016	Graminoids generally eaten in proportion to availability
shrub	VAC-MEM	Black huckleberry	Vaccinium	membranaceum	neutral	Cook et al. 2016	
shrub	VAC-OVA	Alaska blueberry	Vaccinium	ovalifolium	neutral	Cook et al. 2016	
forb/herb	VER-OFF	Common speedwell	Veronica	officinalis	neutral	Cook et al. 2016	
forb/herb	VIC-HIR	Tiny vetch	Vicia	hirsuta	neutral	Cook et al. 2016	
forb/herb	VIC-SPP	Unknown vetch	Vicia	spp.	neutral	Cook et al. 2016	
forb/herb	VIC-VIL	Wooly vetch	Vicia	villosa	neutral	Cook et al. 2016	
forb/herb	VIO-ADU	Early blue violet	Viola	adunca	neutral	Cook et al. 2016	
forb/herb	VIO-GLA	Stream violet	Viola	glabella	neutral	Cook et al. 2016	
forb/herb	VIO-ORB	Round-leaved violet	Viola	orbiculata	neutral	Cook et al. 2016	
forb/herb	VIO-SEM	Evergreen violet	Viola	sempervirens	neutral	Cook et al. 2016	
forb/herb	VIO-SPP	Unknown violet	Viola	spp.	neutral	Cook et al. 2016	
tree	ACE-GLA	Rocky mountain maple	Acer	glabrum	selected	Robatcek 2019	
tree	ACE-RUB	Red maple	Acer	rubrum	selected	Robatcek 2019	Assume the same as A. glabrum
forb/herb	ACH-MIL	Yarrow	Achillea	millefolium	selected	Robatcek 2019	
forb/herb	ACM-AME	American bird's-foot trefoil	Acmispon	americanus	selected	Cook et al. 2016	Forbs generally selected
forb/herb	ACM-DEN	Riverbar bird's-foot trefoil	Acmispon	denticulatus	selected	Cook et al. 2016	Forbs generally selected
forb/herb	ACM-NEV	Nevada deervetch	Acmispon	nevadensis	selected	Cook et al. 2016	Forbs generally selected

tree	ALN-INC	Mountain alder	Alnus	incana	selected	Cook et al. 2016	
tree	ALN-RUB	Red Alder	Alnus	rubra	selected	Cook et al. 2016	
tree	ALN-SPP	Unknown Alder	Alnus	spp.	selected	Cook et al. 2016	Based on A. incana and A. rubra
tree	ALN-VIR	Green alder	Alnus	viridis	selected	Cook et al. 2016	Assume same as A. incana and A. rubra
forb/herb	ANA-MAR	Pearly everlasting	Anaphalis	margaritacea	selected	Cook et al. 2016	
forb/herb	ANC-ARV	Small bugloss	Anchusa	arvensis	selected	Cook et al. 2016	Forbs generally selected
forb/herb	ANT-COT	Stinking chamomile	Anthemis	cotula	selected	Cook et al. 2016	Forbs generally selected
forb/herb	APO-AND	Spreading dogbane	Apocynum	androsaemifolium	selected	Robatcek 2019	
forb/herb	APO-CAN	Cemp dogbane	Apocynum	cannabinum	selected	Robatcek 2019	Assume the same as A. androsaemifolium
forb/herb	APO-SPP	Unknown dogbane	Apocynum	spp.	selected	Robatcek 2019	Assume the same as A. androsaemifolium
forb/herb	APO-FLO	Western dogbane	Apocynum	xfloribundum	selected	Robatcek 2019	Assume the same as A. androsaemifolium
forb/herb	AQU-FOR	Red columbine	Aquilegia	formosa	selected	Robatcek 2019	
shrub	ARC-UVA	Kinnikinnick	Arctostaphylos	uva-ursi	selected	Robatcek 2019	
forb/herb	ARN-COR	Heartleaf arnica	Arnica	cordifolia	selected	Robatcek 2019	
forb/herb	AST-CAN	Canada milk-vetch	Astragalus	canadensis	selected	Robatcek 2019	
forb/herb	BAL-SAG	Arrowleaf balsalm root	Balsamorhiza	sagittata	selected	Robatcek 2019	
forb/herb	BAS-SCO	Summer cypress	Bassia	scoparia	selected	Cook et al. 2016	Forbs generally selected
forb/herb	BIS-VIV	Alpine bistort	Bistorta	vivipara	selected	Robatcek 2019	
graminoid	BRO-CIL	Fringed brome	Bromus	ciliatus	selected	Robatcek 2019	
graminoid	BRO-COM	Meadow brome	Bromus	commutatus	selected	Robatcek 2019	Bromus generally selected
graminoid	BRO-HOR	Soft brome	Bromus	hordeaceus	selected	Robatcek 2019	Bromus generally selected
graminoid	BRO-INE	Smooth brome	Bromus	inermis	selected	Robatcek 2019	
graminoid	BRO-JAP	Japanese brome	Bromus	japonicus	selected	Robatcek 2019	Bromus generally selected
graminoid	BRO-SIT	Alaska brome	Bromus	sitchensis	selected	Robatcek 2019	Bromus generally selected
graminoid	BRO-SPP	Unknown brome	Bromus	spp.	selected	Robatcek 2019	

graminoid	BRO-SQU	Corn brome	Bromus	squarrosus	selected	Robatcek 2019	Bromus generally selected
graminoid	BRO-STE	Poverty brome	Bromus	sterilis	selected	Robatcek 2019	Bromus generally selected
graminoid	CAL-RUB	Pinegrass	Calamagrostis	rubescens	selected	Robatcek 2019	
forb/herb	CAM-ROT	Harebell	Campanula	rotundifolia	selected	Robatcek 2019	
graminoid	CAR-CUS	Cusick's sedge	Carex	cusickii	selected	Cook et al. 2016	For Carex spp.
graminoid	CAR-PRA	Meadow sedge	Carex	praticola	selected	Cook et al. 2016	For Carex spp.
graminoid	CAR-SPP	Unknown sedge	Carex	spp.	selected	Cook et al. 2016	For Carex spp.
forb/herb	CEN-ERY	Common centaury	Centaurium	erythraea	selected	Cook et al. 2016	Forbs generally selected
forb/herb	CHA-ANG	Fireweed	Chamerion	angustifolium	selected	Robatcek 2019	Assume the same as C. latifolium
forb/herb	CHE-ALB	Lambsquarters	Chenopodium	album	selected	Cook et al. 2016	Forbs generally selected
graminoid	CIN-LAT	Slender wood-reed	Cinna	latifolia	selected	Cook et al. 2016	
forb/herb	CLA-LAN	Lanceleaf springbeauty	Claytonia	lanceolata	selected	Robatcek 2019	
forb/herb	CLE-OCC	Rock clematis	Clematis	occidentalis	selected	Robatcek 2019	
forb/herb	CLI-UNI	Queen's cup	Clintonia	uniflora	selected	Cook et al. 2016	
forb/herb	COP-TRI	Threeleaf goldthread	Coptis	trifolia	selected	Robatcek 2019	Assume the same as C. occidentalis
shrub	COR-COR	Beaked hazelnut	Corylus	cornuta	selected	Cook et al. 2016	
shrub	CRA-DOU	Black hawthorn	Crataegus	douglasii	selected	Robatcek 2019	
forb/herb	DRY-ARG	Tall cinquefoil	Drymocallis	arguta	selected	Robatcek 2019	
forb/herb	DRY-GLA	Sticky cinquefoil	Drymocallis	glandulosa	selected	Robatcek 2019	
forb/herb	ERI-FIL	Threadleaf fleabane	Erigeron	filifolius	selected	Robatcek 2019	
forb/herb	ERI-SPE	Showy daisy	Erigeron	speciosus	selected	Robatcek 2019	
forb/herb	ERI-SPP	Unknown daisy	Erigeron	spp.	selected	Robatcek 2019	
forb/herb	ERI-HER	Parsnipflower buckwheat	Eriogonum	heracleoides	selected	Robatcek 2019	
forb/herb	EUR-CON	Western showy aster	Eurybia	conspicua	selected	Robatcek 2019	
forb/herb	FAL-CON	Black bindweed	Fallopia	convolvulus	selected	Cook et al. 2016	Forbs generally selected
graminoid	FES-CAM	Prairie fescue	Festuca	campestris	selected	Robatcek 2019	
graminoid	FES-IDA	Idaho fescue	Festuca	idahoensis	selected	Robatcek 2019	

graminoid	FES-OCC	Western fescue	Festuca	occidentalis	selected	Cook et al. 2016	
graminoid	FES-RUB	Red fescue	Festuca	rubra	selected	Robatcek 2019	
graminoid	FES-SPP	Unknown fescue	Festuca	spp.	selected	Robatcek 2019	
forb/herb	FRA-VIR	Mountain strawberry	Fragaria	virginiana	selected	Robatcek 2019	
shrub	FRA-PUR	Buckthorn	Frangula	purshiana	selected	Cook et al. 2016	Deciduous shrubs generally acceptable
forb/herb	GER-BIC	Northern crane's-bill	Geranium	bicknelli	selected	Robatcek 2019	
forb/herb	GER-ROB	Stinky-Bob	Geranium	robertianum	selected	Robatcek 2019	
forb/herb	GER-VIS	Sticky purple geranium	Geranium	viscosissimum	selected	Robatcek 2019	
forb/herb	GEU-RIV	Water avens	Geum	rivale	selected	Robatcek 2019	
forb/herb	GEU-TRI	Prairie smoke	Geum	triflorum	selected	Robatcek 2019	
forb/herb	GOO-OBL	Western rattlesnake-plantain	Goodyera	oblongifolia	selected	Robatcek 2019	
forb/herb	HED-SUL	Yellow sweet-vetch	Hedysarum	sulphurescens	selected	Robatcek 2019	
forb/herb	HER-SPP	Unknown herb/forb	Herb	spp.	selected	Cook et al. 2016	Forbs generally selected
forb/herb	HEU-CYL	Roundleaf alumroot	Heuchera	cylindrica	selected	Robatcek 2019	
forb/herb	HIE-AUR	Orange hawkweed	Hieracium	aurantiacum	selected	Robatcek 2019	
forb/herb	HIE-CAE	Meadow hawkweed	Hieracium	caespitosum	selected	Robatcek 2019	
forb/herb	HIE-SCO	Scouler's hawkweed	Hieracium	scouleri	selected	Robatcek 2019	
forb/herb	HIE-SPP	Unknown hawkweed	Hieracium	spp.	selected	Robatcek 2019	
forb/herb	HIE-TRI	Slender hawkweed	Hieracium	triste	selected	Robatcek 2019	
forb/herb	HIE-UMB	Narrowleaf hawkweed	Hieracium	umbellatum	selected	Robatcek 2019	
forb/herb	HYD-CAP	Ballhead waterleaf	Hydrophyllum	capitatum	selected	Robatcek 2019	

forb/herb	HYP-PER	Common St. John's-wort	Hypericum	perforatum	selected	Cook et al. 2016	
forb/herb	IPO-AGG	Scarlet gilia	Ipomopsis	aggregata	selected	Robatcek 2019	
graminoid	KOA-MAC	Prairie Junegrass	Koeleria	macrantha	selected	Robatcek 2019	
forb/herb	LAC-SER	Prickly lettuce	Lactuca	serriola	selected	Robatcek 2019	
forb/herb	LEU-VUL	Oxeye daisy	Leucanthemum	vulgare	selected	Cook et al. 2016	
forb/herb	LIG-GRA	Gray's lovage	Ligusticum	grayi	selected	Cook et al. 2016	Assume the same as Ligusticum apiifolium
forb/herb	LIG-POR	Bear root	Ligusticum	porteri	selected	Cook et al. 2016	Assume the same as Ligusticum apiifolium
forb/herb	LIN-BOR	Twinflower	Linnaea	borealis	selected	Cook et al. 2016	
forb/herb	LON-CIL	Orange honeysuckle	Lonicera	ciliosa	selected	Cook et al. 2016	
forb/herb	LON-CON	Purple-flower honeysuckle	Lonicera	conjugialis	selected	Robatcek 2019	
forb/herb	LON-SPP	Unknown honeysuckle	Lonicera	spp.	selected	Robatcek 2019	
forb/herb	LON-UTA	Utah honeysuckle	Lonicera	utahensis	selected	Robatcek 2019	
forb/herb	LUP-SER	Silky lupine	Lupinus	sericeus	selected	Robatcek 2019	
graminoid	LUZ-PAR	Small-flowered woodrush	Luzula	parviflora	selected	Cook et al. 2016	Reported for Luzula spp.
shrub	MAH-REP	Creeping Oregon-grape	Mahonia	repens	selected	Robatcek 2019	
forb/herb	MAL-NEG	Dwarf mallow	Malva	neglecta	selected	Cook et al. 2016	Forbs generally selected
forb/herb	MED-LUP	Black medic	Medicago	lupulina	selected	Robatcek 2019	Assume the same as M. sativa
forb/herb	MED-SAT	Alfalfa	Medicago	sativa	selected	Robatcek 2019	
forb/herb	MER-PAN	Tall bluebell	Mertensia	paniculata	selected	Robatcek 2019	
forb/herb	MYO-LAX	Small forget-me-not	Myosotis	laxa	selected	Robatcek 2019	
forb/herb	NEP-CAT	Catnip	Nepeta	cataria	selected	Robatcek 2019	Forbs generally selected
forb/herb	ONO-VIC	Saintfoin	Onobrychis	viciifolia	selected	Robatcek 2019	Fabaceae mostly selected
shrub	OPL-HOR	Devil's club	Oplopanax	horridus	selected	Cook et al. 2016	Deciduous shrubs generally acceptable

shrub	PAX-MYR	Oregon boxleaf	Paxistima	myrsinites	selected	Robatcek 2019	
forb/herb	PEC-BRE	Brewer's mitrewort	Pectiantia	breweri	selected	Cook et al. 2016	Forbs generally selected
forb/herb	PEN-FRU	shrubby penstemon	Penstemon	fruticosus	selected	Robatcek 2019	
forb/herb	PEN-PRO	Small-flowered penstemon	Penstemon	procerus	selected	Robatcek 2019	
forb/herb	PER-WAL	Himalayan knotweed	Persicaria	wallichii	selected	Cook et al. 2016	Forbs generally selected
forb/herb	PET-FRI	Sweet coltsfoot	Petasites	frigidus	selected	Cook et al. 2016	
forb/herb	PET-SAG	Arrow-leaved coltsfoot	Petasites	frigidus	selected	Cook et al. 2016	
graminoid	PHA-ARU	Reed canary grass	Phalaris	arundinacea	selected	Cook et al. 2016	
shrub	PHI-LEW	Lewis' mock orange	Philadelphus	lewisii	selected	Robatcek 2019	
graminoid	PHL-PRA	Timothy	Phleum	pratense	selected	Robatcek 2019	
shrub	PHY-MAL	Mallow ninebark	Physocarpus	malvaceus	selected	Robatcek 2019	
forb/herb	POL-AVI	Common knotweed	Polygonum	aviculare	selected	Robatcek 2019	
tree	POP-TRE	Quaking aspen	Populus	tremuloides	selected	Cook et al. 2016	
forb/herb	POT-ARG	Silver cinquefoil	Potentilla	argentea	selected	Robatcek 2019	
forb/herb	POT-GRA	Slender cinquefoil	Potentilla	gracilis	selected	Robatcek 2019	
forb/herb	POT-REC	Sulphur cinquefoil	Potentilla	recta	selected	Robatcek 2019	
forb/herb	POT-SPP	Unknown cinquefoil	Potentilla	spp.	selected	Robatcek 2019	
shrub	PRU-PEN	Pin cherry	Prunus	pensylvanica	selected	Robatcek 2019	
shrub	PRU-VIR	Chokecherry	Prunus	virginiana	selected	Robatcek 2019	
graminoid	PSE-SPI	Bluebunch wheatgrass	Pseudoroegneria	spicata	selected	Robatcek 2019	
shrub	RIB-ACE	Maple-leaf currant	Ribes	acerifolium	selected	Cook et al. 2016	Assume same as R. viscosissimum
shrub	RIB-AUR	Golden currant	Ribes	aureum	selected	Robatcek 2019	
shrub	RIB-CER	Wax currant	Ribes	cereum	selected	Robatcek 2019	
shrub	RIB-VIS	Mountain currant	Ribes	viscosissimum	selected	Cook et al. 2016	
forb/herb	RIG-LEP	Wireweed	Rigiopappus	leptocladus	selected	Cook et al. 2016	Forbs generally selected

forb/herb	ROR-PAL	Marsh yellowcress	Rorippa	palustris	selected	Cook et al. 2016	Forbs generally selected
shrub	ROS-ACI	Prickly rose	Rosa	acicularis	selected	Robatcek 2019	
shrub	ROS-NUT	Nootka rose	Rosa	nutkana	selected	Robatcek 2019	
shrub	ROS-SPP	Unknown rose	Rosa	spp.	selected	Robatcek 2019	
shrub	ROS-WOO	Pearhip rose	Rosa	woodsii	selected	Robatcek 2019	
shrub	RUB-IDA	Red rasberry	Rubus	idaeus	selected	Robatcek 2019	
shrub	RUB-PAR	Thimbleberry	Rubus	parviflorus	selected	Cook et al. 2016	
forb/herb	RUM-CRI	Curly dock	Rumex	crispus	selected	Robatcek 2019	
tree	SAL-BAR	Barclay's willow	Salix	barclayi	selected	Cook et al. 2016	
tree	SAL-BEB	Bebb's willow	Salix	bebbiana	selected	Robatcek 2019	
tree	SAL-LAS	Pacific willow	Salix	lasiandra	selected	Cook et al. 2016	
shrub	SAL-PLA	Plane-leaf willow	Salix	planifolia	selected	Cook et al. 2016	
tree	SAL-SCO	Scouler's willow	Salix	scouleriana	selected	Robatcek 2019	
tree, shrub	SAL-SIT	Sitka willow	Salix	sitchensis	selected	Cook et al. 2016	
tree, shrub	SAL-SPP	Unknown willow	Salix	spp.	selected	Cook et al. 2016	
forb/herb	SED-LAN	Lance-leaved stonecrop	Sedum	lanceolatum	selected	Robatcek 2019	
forb/herb	SED-STE	Wormleaf stonecrop	Sedum	stenopetalum	selected	Robatcek 2019	Assume the same as S. lanceolatum
shrub	SHE-CAN	Russet buffaloberry	Shepherdia	canadensis	selected	Robatcek 2019	
shrub	SHR-SPP	Unknown shrub	Shrub	spp.	selected	Cook et al. 2016	Deciduous shrubs generally acceptable
forb/herb	SOL-SPP	Unknown goldenrod	Solidago	spp.	selected	Robatcek 2019	
forb/herb	SOR-SCO	Western mountain-ash	Sorbus	scopulina	selected	Cook et al. 2016	
forb/herb	SPE-ARV	Corn spurry	Spergula	arvensis	selected	Cook et al. 2016	Forbs generally selected
shrub	SPI-DOU	Douglas's spiraea	Spiraea	douglasii	selected	Cook et al. 2016	
shrub	SPI-LUC	Shinyleaf spiraea	Spiraea	lucida	selected	Cook et al. 2016	Assume the same as S. douglasii
shrub	SPI-PYR	Pyramid spiraea	Spiraea	pyramidata	selected	Cook et al. 2016	Assume the same as S. douglasii

forb/herb	SPI-SPL	Rosy spiraea	Spiraea	splendens	selected	Robatcek 2019	
shrub	SPI-SPP	Unknown spiraea	Spiraea	spp.	selected	Cook et al. 2016	Assume the same as S. douglasii
shrub	SYM-ALB	Common snowberry	Symphoricarpos	albus	selected	Robatcek 2019	
shrub	SYM-OCC	Western snowberry	Symphoricarpos	occidentalis	selected	Robatcek 2019	
shrub	SYM-SPP	Unknown snowberry	Symphoricarpos	spp.	selected	Cook et al. 2016	
forb/herb	SYM-FOL	Leafy aster	Symphyotrichum	foliaceum	selected	Robatcek 2019	Assume the same as S. ascendens
forb/herb	SYM-LAE	Smooth aster	Symphyotrichum	laeve	selected	Robatcek 2019	Assume the same as S. ascendens
forb/herb	TAR-OFF	Common dandelion	Taraxacum	officinale	selected	Robatcek 2019	
shrub	TOX-RAD	Poison ivy	Toxicodendron	radicans	selected	Cook et al. 2016	Deciduous shrubs generally acceptable
forb/herb	TRA-DUB	Yellow salsify	Tragopogon	dubius	selected	Robatcek 2019	
forb/herb	TRI-AUR	Large hop clover	Trifolium	aureum	selected	Cook et al. 2016	
forb/herb	TRI-CAM	Hop clover	Trifolium	campestre	selected	Cook et al. 2016	
forb/herb	TRI-PRA	Red clover	Trifolium	pratense	selected	Cook et al. 2016	
forb/herb	TRI-REP	White clover	Trifolium	repens	selected	Robatcek 2019	
forb/herb	TRI-OVA	Western trillium	Trillium	ovatum	selected	Robatcek 2019	
shrub	VAC-CES	Dwarf huckleberry	Vaccinium	cespitosum	selected	Robatcek 2019	
shrub	VAC-MYR	Velvet-leaf blueberry	Vaccinium	myrtilloides	selected	Robatcek 2019	
shrub	VAC-SPP	Unknown vaccinium	Vaccinium	spp.	selected	Robatcek 2019	
shrub	VIB-ELL	Common viburnum	Viburnum	ellipticum	selected	Cook et al. 2016	Deciduous shrubs generally acceptable
forb/herb	VIC-AME	American vetch	Vicia	americana	selected	Robatcek 2019	
forb/herb	VIO-CAN	Canadian violet	Viola	canadensis	selected	Robatcek 2019	
forb/herb	VIO-NUT	Nuttall's violet	Viola	nuttalli	selected	Robatcek 2019	

D2.2 *Results*

Biomass of suitable forage ($F_{df = 2} = 6.9$, $p = 0.001$) and horizontal cover ($F_{df = 2} = 18.0$, $p < 0.001$) varied by forest harvest history, but the differences were primarily driven by uncovered areas rather than the differences between forested and recently harvested areas (Table D2.2). Difference in biomass ($F_{df = 2} = 7.5$, $p < 0.001$) and horizontal cover ($F_{df = 2} = 20.5$, $p < 0.001$) were more pronounced between simplified landcover types, with biomass highest and horizontal cover lowest in open sites while forest and shrub sites were more similar. As a result, we relied on open landcover types to describe habitat characteristics influencing elk.

Table D2.2 Differences in biomass of acceptable elk forage and horizontal cover to 2m by history of timber harvest and landcover type in Northeastern Washington, USA from July – September 2019 and 2020. Standard deviation (SD) shown for each measure.

Classification scheme	Classification	n sites	mean biomass suitable forage (kg/ha)	SD suitable forage	mean horizontal cover to 2m (%)	SD horizontal cover to 2m
Timber harvest history	Uncovered 2000	61	545.2	457.2	32.4	28.8
	Forest, no harvest	73	346.8	250.3	58.5	26.2
	Harvested forest	65	469.0	185.8	54.5	24.5
Simplified landcover	Open	33	576.8	510.1	23.4	22.3
	Forest	80	349.8	253.3	57.6	26.4
	Shrub	86	488.8	260.2	51.3	27.4

D.3 STEP SELECTION FUNCTIONS

Table D3.1 Summary information on female elk captured > 1 year old in northeast Washington USA from January 2017 – January 2021, detailing capture dates, age of capture, mortality date, cause of death and the number of locations (n) in the seasonal models. Unknown abbreviated Unk. Two elk were not aged at capture, so we set their age at capture to be the median age of adult elk at capture (6 years).

ID	Capture Date	Age Captured	Mortality Date	Mortality Type	Notes	Used locations in summer model	Used locations in hunting season model
1EA17	2017-03-09	Unk.			Collar Fail 2017-11-28	347	478
3676EA17	2017-03-06	2				1594	1870
3677EA17	2017-03-06	8			Collar Fail 2020-08-21	1889	2134
3678EA17	2017-01-24	9	2017-11-01	Human		527	353
3679EA17	2017-03-06	2				2120	2833
3680EA17	2017-01-23	6			Collar Fail 2020-12-04	2127	2493
3681EA17	2017-01-23	7	2017-12-04	Human		525	542
3682EA17	2017-01-21	9	2017-02-23	Disease		0	0
3683EA17	2017-01-24	6				2061	2831
3684EA17	2017-01-23	7	2020-08-23	Unk.		1853	2075
3685EA17	2017-01-22	Unk.	2017-11-04	Human		462	318
3686EA17	2017-01-21	6			Collar Fail 2020-08-11	1825	2096
3687EA17	2017-01-22	6				1775	2648
3688EA17	2017-01-22	2				1963	2609
3689EA17	2017-01-22	1			Collar Fail 2019-03-26	1024	1423

3690EA17	2017-01-22	8				2058	2623
3691EA17	2017-01-22	14			Collar Fail 2018-03-03	494	669
3692EA17	2017-03-06	14			Collar Fail 2020-01-14	1571	2117
3693EA17	2017-01-23	7			Collar Fail 2020-04-13	1546	2097
3696EA17	2017-03-06	1			Collar Fail 2019-06-21	687	653
3697EA17	2017-01-24	2			Collar Fail 2021-05-09	986	1693
3698EA17	2017-03-06	6			Collar Fail 2021-02-26	2063	2132
3699EA17	2017-01-22	14	2017-12-27	Human		492	624
3700EA17	2017-01-21	4	2018-11-04	Vehicle		977	1026
3701EA17	2017-03-08	2				1937	2742
3702EA17	2017-03-07	4	2021-02-16	Disease		2037	2808
3703EA17	2017-03-07	5				1783	2209
3704EA17	2017-03-08	3				1873	2211
3705EA17	2017-03-08	6	2019-12-30	Human		1550	2087
3709ELK18	2018-01-07	3				1533	2138
3712ELK18	2018-01-05	2				1556	2108
3726ELK18	2018-01-04	5	2019-12-20	Human		954	1276
3783EA17	2017-03-08	9	2017-12-16	Human		509	606
3784EA17	2017-03-08	4				2063	2767
3785EA17	2017-03-08	4	2018-10-12	Human		1022	919
3786EA17	2017-03-07	4				2102	2704
3787EA17	2017-03-08	2				1605	2027
3930ELK18	2018-01-06	13			Collar Fail 2020-09-03	1081	1362
3936ELK18	2018-01-03	7			Collar Fail 2020-09-01	1569	1418
3962ELK18	2018-01-05	3			Collar Fail 2021-04-26	1526	2117
3965ELK18	2018-01-04	5	2020-10-03	Vehicle		1550	1578
3970ELK18	2018-01-07	10				1495	1832
3974ELK18	2018-01-05	5				1476	2088
3975ELK18	2018-01-04	6				1470	1966

3978ELK18	2018-01-07	3				1539	2075
3992ELK18	2018-01-06	9				1593	1464
3999ELK18	2018-01-06	6				1602	2125
4391ELK18	2018-01-03	3				1493	2100
4394ELK18	2018-01-03	7				1264	1960
4395ELK18	2018-01-04	8				1248	1876
4396ELK18	2018-01-04	12			Collar Fail 2019-06-25	572	689
4397ELK18	2018-01-03	4	2019-04-17	Vehicle		519	670
4398ELK18	2018-01-04	6			Collar Fail 2020-12-16	1251	1262
4399ELK18	2018-01-05	5				1571	1914
4408ELK18	2018-01-07	7			Collar Fail 2018-05-21	0	0
4430ELK18	2018-01-05	3			Collar Fail 2018-06-27	0	0
4829ELK20	2020-01-08	3			Collar Fail 2020-12-31	520	702
4830ELK20	2020-01-08	3				494	612
4831ELK20	2020-01-07	8				541	726
4832ELK20	2020-01-07	3				505	725
4833ELK20	2020-01-07	10				537	719
4835ELK20	2020-01-07	2				533	710
4838ELK20	2020-01-07	8				549	728

Table D3.2 Covariate estimates for summer (June – August) step selection functions separately modeled for elk with calves (*n* = 15) and elk without calves (*n* = 12) from summer (June – August) 2018 - 2020 for northeastern, WA, USA. The interactive effect of night is additive to the daytime effect for that covariate.

	Calf				No calf			
covariate	$\hat{\beta}$	SE	z-score	*P*	$\hat{\beta}$	SE	z-score	*P*
elevation	0.34	0.03	10.7	0.000	0.39	0.04	9.3	0.000
slope	-0.19	0.02	-12.1	0.000	-0.11	0.02	-5.6	0.000
cougar - day	-0.53	0.14	-3.9	0.000	0.35	0.14	2.5	0.013
cougar x night	-3.02	0.22	-13.8	0.000	-3.26	0.22	-14.6	0.000
wolf - day	-10.39	4.56	-2.3	0.023	-7.55	0.99	-7.6	0.000
wolf x night	4.41	6.38	0.7	0.489	6.39	1.60	4.0	0.000
human - day	-20.96	2.09	-10.0	0.000	-2.04	0.85	-2.4	0.016
human x night	18.16	2.45	7.4	0.000	1.65	1.05	1.6	0.118
open - day	-2.78	0.18	-15.3	0.000	-4.20	0.22	-19.2	0.000
open x night	3.16	0.18	17.9	0.000	5.26	0.23	23.3	0.000
open x cougar	3.44	0.40	8.7	0.000	3.22	0.38	8.4	0.000
open x wolf	-21.91	14.93	-1.5	0.142	1.41	2.34	0.6	0.547

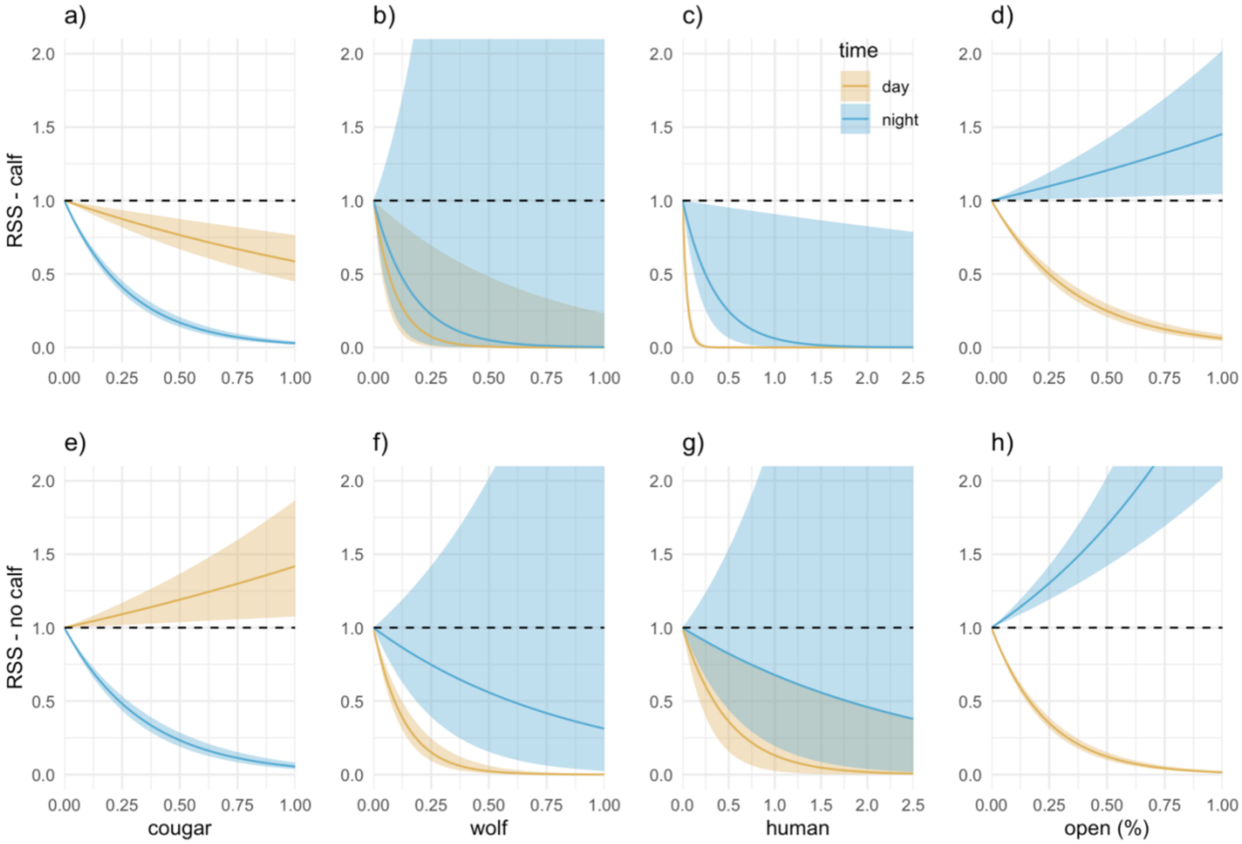

Figure D3.1 Relative strength of selection (RSS; Avgar et al. 2017) by time of day in the summer for elk with a calf (top row) and elk without a calf (bottom row) for elk in response to cougars (a, e), wolves (b, f), humans (c, g) and open habitat (d, h). Values were computed relative to selection if covariates were 0. Relative selection occurs when the RSS is > 1 (above the dashed horizontal line) while relative avoidance occurs when the RSS is < 1 (below the dashed horizontal line).

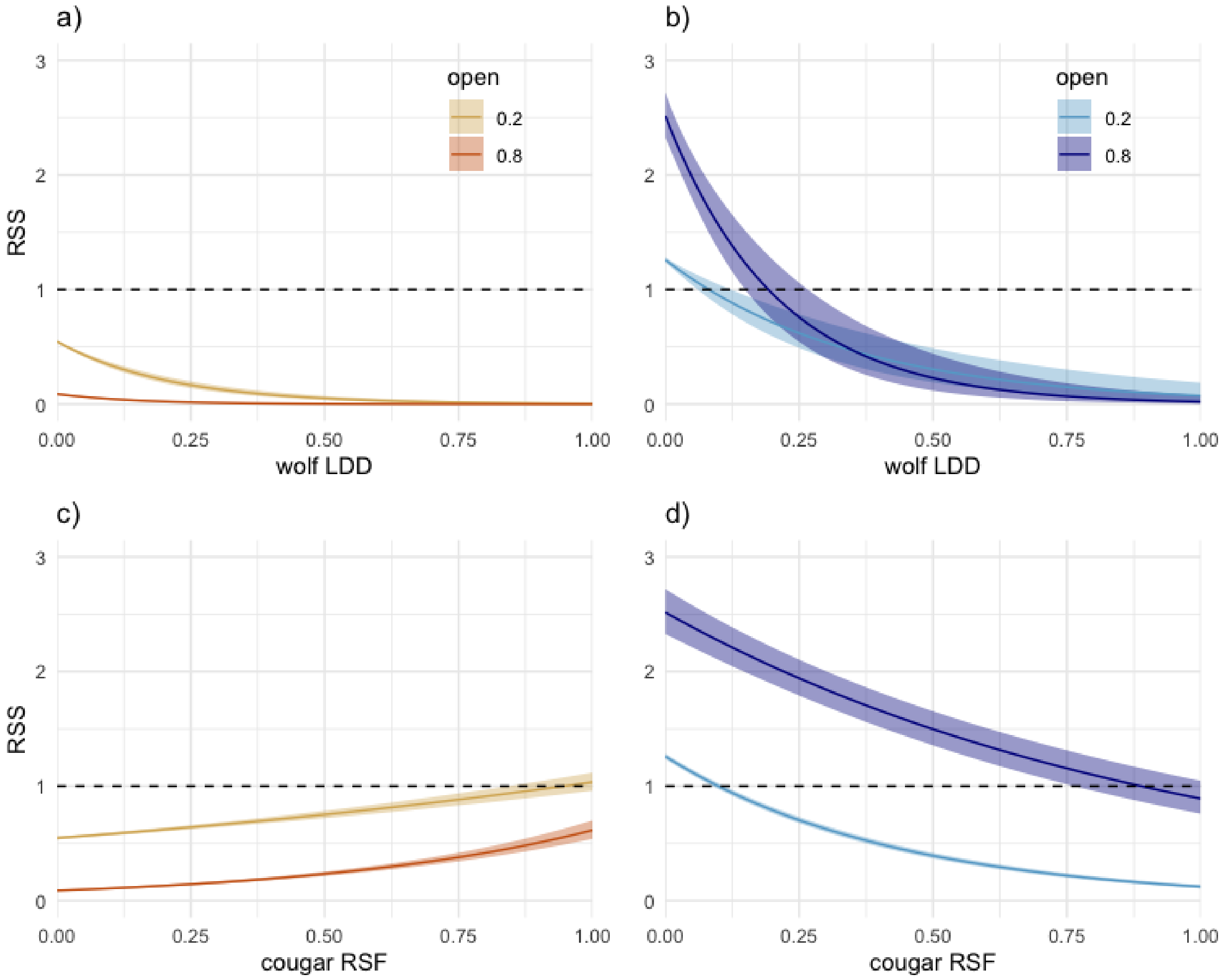

Figure D3.2 Interactive effects of predator exposure and % open habitat (within a 250m radius) for wolves in the day (a) and at night (b) and cougars in the day (c) and at night in the summer. Relative strength of selection (RSS; Avgar et al. 2017) is relative to selection if all covariates were 0. Relative selection occurs when the RSS is > 1 while relative avoidance occurs when the RSS is < 1.

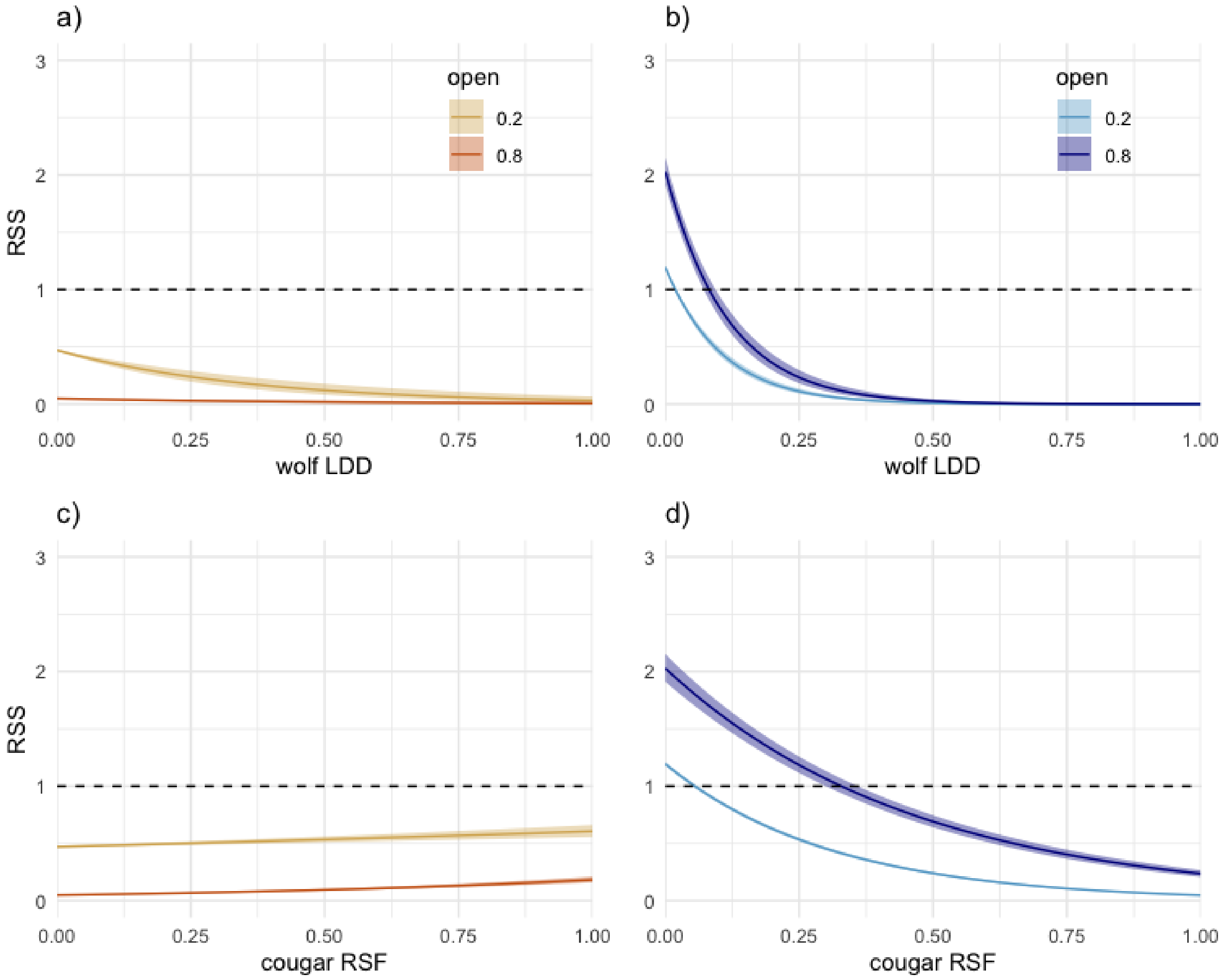

Figure D3.3 Interactive effects of predator exposure and % open habitat (within a 250m radius) for wolves in the day (a) and at night (b) and cougars in the day (c) and at night in the fall. Relative strength of selection (RSS; Avgar et al. 2017) is relative to selection if all covariates were 0. Relative selection occurs when the RSS is > 1 while relative avoidance occurs when the RSS is < 1.

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