Large Carnivore Behavior and Intraguild Interactions Under Anthropogenic Influence

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A dissertation

submitted in partial fulfillment of the

requirements for the degree of

Doctor of Philosophy

University of Washington

2023

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School of Environmental and Forest Sciences

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Abstract

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Among the many human activities that affect wildlife, urbanization is one of the most prominent sources of species extinction and biodiversity loss. Responses to urbanization vary across taxa, with large carnivores being particularly sensitive to this process owing to their space needs and energy requirements. Not surprisingly, therefore, large carnivore declines in the face of urbanization are well documented but changes to the behavior and ecology of species that are able to persist in built environments have received less attention. In the state of Washington, sympatric cougar (*Puma concolor*) and American black bear (*Ursus americanus*) populations overlap with wildland and residential landscapes, providing a rare opportunity to evaluate the

behavioral responses of multiple large carnivores to urbanization. Accordingly, this dissertation examines how various forms of anthropogenic disturbance linked with urbanization impact large carnivore behavior and interspecific interactions, with the broader goal of improving our understanding of the mechanisms driving changes to the ecology of large predators as they must increasingly navigate a human-dominated world. In Chapter 1, I provide justification for large carnivore research in urban environments. In Chapter 2, I explore changes to individual and population niche breadth in black bears as a function of residential development. I demonstrate using resource utilization functions (RUFs) that bear population-level use increased significantly as distance to residential mature forest, lakes, and rivers decreased. Black bears exhibited high individual variation in both residential and wildland landscapes. Nevertheless, black bear use near mature forest differed significantly between residential and wildland landscapes as bears began to enter hyperphagia and use near residential mature forest and residential rivers differed between females and males in summer. In Chapter 3, I once again employ RUFs to evaluate resource use by black bears navigating managed forests in western Washington with (Snoqualmie Forest) and without (Department of Natural Resources lands) diversionary feeding during fed and non-fed portions of the year to shed light on large carnivore responses to human subsidies in areas just beyond the urban fringe. Black bear use of young forest stands (15-30 years), as well as other landscape attributes, was similar between managed forests with and without feeding stations irrespective of whether supplemental food was supplied. Notably, individual variation was significant for nearly every covariate in both forests, with bears often demonstrating contrasting patterns of use, effectively washing out any population-level effects of diversionary feeding and harvest intensity on resource use. In Chapter 4, I explore whether residential development in the form of housing density (residences/ha), along with demographic

and environmental covariates, impact the propensity for black bears to scavenge cougar-killed prey along western Washington’s wildland-urban gradient. The summer season and housing density were significant negative predictors of black bear scavenging, and cougar handling time was a significant positive predictor of bear carcass visitation. Overall, my results reveal that residential development can modify population-wide black bear behavior in ways that may shape patterns of human-wildlife interaction even though individual bear responses to anthropogenic disturbance often vary. My results also suggest that the impact of urbanization on interspecific relationships among large carnivores can be dramatic, as even modest levels of residential development all but eliminated black bear scavenging on cougar kills. This dissertation provides novel insights into predator-predator interactions in residential landscapes and advances our understanding of the myriad ways residential development may disrupt interactions within carnivore guilds, creating avenues of further study into the mechanisms structuring urban wildlife communities.

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ACKNOWLEDGEMENTS

I wish to thank the University of Washington and the National Science Foundation (NSF GRFP) for funding my graduate education, and the Washington Department of Fish and Wildlife for generously promoting my research through funding and logistical support. Specific thanks are given to Dr. Stephanie Simek for helpful editorial feedback on Chapter 1. I also thank Ningxin Ma, Anupreet Porwal, Charlie Wolock, Victoria Knutson, Nobuaki Masaki, Peter Zuckerman, and Kenneth Rice, and University of Washington Statistical Consulting Services (Departments of Biostatistics and Statistics) for providing statistical guidance, as well as Campbell Global Timber Resources, Hancock Timber Company, the Washington Department of Natural Resources, and the myriad of private landowners for kindly providing me access to their lands.

I would like to take this opportunity to give extensive thanks to several people, all of whom were instrumental in the success of my dissertation research. First, I would like to thank my entire volunteer crew (Connor Meyer, Christine Phelan, Eric Vanderbilt-Matthews, Brooks Estes, Lars Olson, Nick Ulacia, Alex Wall, Christina Mebust-Boscolo, Nikki Love, Kyle Mabie), who put in long, tiring hours in rugged field conditions. Without their hard work, insight, and reliability, the collection of data for this research endeavor would have been severely constrained. They were not compensated nearly as well as they deserve. I would like to give special thanks to my primary research assistant, Sasha Hendricks. Her years of devoted fieldwork and emotional support provided me with a better understand of how to foster truly great working relationships in wildlife research. Sasha would lead the field crew and data collection if other responsibilities demanded my attention. For me, she was the glue that held the project together in my absence. Documenting as many cougar kill sites as we did from 2013 – 2017 was only possible because of the efforts of my crew and Sasha Hendricks. I am also grateful to Richard Beausoleil and Dr. Lindsay Welfelt for all the work they put into black bear captures, trapping, and collaring, as well as their frequent feedback and insight with Chapters 1 and 2. The amount of black bear GPS data I had at my disposal is entirely thanks to the both of them.

I would also like to take a moment to thank my academic advisors. Dr. Aaron Wirsing and Dr. John Marzluff have both been invaluable in my training as a wildlife scientist. Whether it has been advice on academic hurdles in graduate school, funding concerns, data analysis, or manuscript preparation, Dr. Marzluff, and especially Dr. Wirsing, have provided years of advice and support. I admire their patience and devotion to their students, and I am glad I had the opportunity to have them as my academic advisors. I would like to thank Dr. Sarah Converse for her insights into how to run a successful research project, as well as the statistics toolset she helped me develop. Whether it was through her class on linear and mixed models, office hours, or hours spent with me troubleshooting code for multiple dissertation chapters, Dr. Converse's assistance at critical analysis steps was key to the insights gained in this dissertation. I would also like to thank Dr. Tim Essington, my graduate student representative, who provided me with an example of the kinds of people, and scientists, I would like on my committee, and who, through multiple stories and lessons, helped me maintain perspective throughout the ups and downs of graduate school.

I would like to offer my deepest thank you to Dr. Brian Kertson. As the carnivore scientist for Washington's Department of Fish and Wildlife (WDFW) and my point of contact with WDFW, Dr. Kertson spent endless hours training me in the field, helping me with project formation, the selection of a field crew and how best to lead them, the collection of data and developing even more extensive outdoor skills, manuscript writing, and job searches. In my opinion, Dr. Kertson is the epitome of what a mentor should be. I think it is a rare opportunity to work closely with large carnivores, and I think it is even rarer to find an advisor that strives for the most rigorous science while also seeking to help those they mentor become the best versions of themselves. Without Dr. Kertson, my understanding of public perceptions on wildlife, human-wildlife issues, and how to engage with the public would be far less nuanced. Dr. Kertson's knowledge, assistance, insights, and support provided the foundation for all the work presented in this dissertation. His daily dedication to helping me complete this degree goes far beyond the support I could have expected, or asked for, from any mentor or advisor. I will be forever thankful for him.

Finally, I would like to thank my sister Elsa and her husband Billy, my mother Floriane, and my father Edward, for all their patience and love throughout this process. I am grateful my family has been there for me at every turn, even when I sacrificed time with them for my research. Reaching this level of training in wildlife science was a process, and a goal, that began long before I began graduate school. I am thankful my family had the opportunity to see this maturation process from start to finish.

DEDICATION

This dissertation is dedicated to my father, Edward A. Robins. I made him a promise many, many years ago. I'm glad I can say I've finally kept that promise.

CHAPTER 1: A BASIS FOR LARGE CARNIVORE RESEARCH IN URBAN ENVIRONMENTS

1.1 INTRODUCTION

The expansion of urban development is accelerating globally (Magle et al. 2012). Indeed, 2008 marked the first time that most of the global human population was residing in cities (Goddard et al. 2009, Gehrt 2010, Bateman and Flemming 2012), which now represent the global centers of production and consumption (Fragkias et al. 2013). Consequently, projections of future urbanization predict the loss of millions of hectares of natural habitat worldwide (Fragkias et al. 2013, Guangdong et al. 2022). Transformations of the physical environment through residential development, agricultural enterprise, and the fragmentation of habitats all functionally limit space for wildlife, and such changes to natural landscapes have been shown to reduce animal biodiversity and impact species distributions and persistence (McKinney 2006, Maxwell et al. 2016, Moll et al. 2018). Thus, as urban areas continue to expand to accommodate a growing human population, impacts on ecosystem processes and animals will continue to increase, meaning that the conservation and management of wildlife communities in human-dominated environments will require a comprehensive understanding of the changes in species' behaviors that enable them to navigate the built environment, and what such changes may mean for population dynamics and wildlife community composition (Ritzel and Gallo 2020).

Systematic research on wild animals in and near cities was pioneered by German ecologist Herbert Sukopp and began in Berlin the late 1950s (Gerht 2010, Kowarik 2020). Since then, the proliferation of wildlife research in urban systems has reinforced that urbanization, which rapidly alters natural ecosystems, can lead to the formation of unique terrestrial species assemblages that differ greatly from those in undeveloped landscapes (Shochat et al. 2010, Fischer et al. 2012). Moreover, for many wildlife species, persistence in human-dominated landscapes requires behavioral, social, and dietary plasticity as they must respond to unfamiliar circumstances in non-natural environments (Lowry et al. 2013, Evans et al. 2019). For this reason, many terrestrial mammals have experienced range contractions in the face of urbanization (Pacifici et al. 2020). This trend is particularly noticeable in large mammalian carnivores, which tend to actively avoid developed landscapes (Cardillo et al. 2004, Bateman and Flemming 2012). Large carnivores are often susceptible to persecution from people, as these species pose real and perceived threats to humans, livestock, and property (Bombieri et al. 2018, Lamb et al. 2020). However, they can also play key ecological roles in the wildland environments in which they reside.

In wildland environments, large carnivores can shape wildlife communities by inflicting mortality (Creel et al. 2017), altering prey behavior (Hebblewhite et al. 2005), subsidizing other species (Wilmers et al. 2003, Barry et al. 2019), and suppressing mesocarnivore populations (Prugh et al. 2009). These direct effects can result in trophic cascades (Wilmers and Schmitz 2016) causing increased plant diversity (Ripple and Beschta 2004), nutrient cycling (Schmitz et al. 2010), and a reduction in disease prevalence across prey populations (Packer et al. 2003). The dual role of regulating prey species through predation and limiting mesocarnivore populations through competition allows large carnivores to have the capacity to influence the flow of energy in ecosystems through multiple food web pathways (Ripple et al. 2014). Consequently, the complete loss of large carnivores from intact ecosystems can trigger shifts in the cascading controls of communities, changing entire ecosystem structure and function (Hoeks et al. 2020). If large carnivores continue to disappear, prey populations are likely to rise, and the resulting increase in herbivory is expected to be accompanied by changes in plant species diversity, biomass, and productivity (Ripple et al. 2014, Palazón 2017), alterations to the trophic foundation of all terrestrial ecosystems that will have far-reaching impacts on all species.

Large mammalian carnivores have large energy requirements and must roam widely in search of prey, which makes them vulnerable to concurrent human threats, including habitat loss, persecution (e.g., retaliatory killing), utilization, and, in particular, the depletion of prey (Ripple et al. 2014). Consequently, many large carnivore species tend to disappear as urban environments intensify (Bateman and Flemming 2012). Similar to wildland landscapes, the loss of large carnivores from urban environments will mean less top-down ecosystem regulation, leading to more robust mesocarnivore and prey populations, increased herbivory (Terborgh et al. 1997), reduced plant density (Baines et al. 1994, Ripple and Beschta 2012), and more frequent disease outbreaks in prey populations (Binkley et al. 2006, Rosenblatt et al. 2013), all of which have long-term weakening effects on ecosystem structure and stability (Miller et al. 2001, Roberson et al. 2016, Louthan et al. 2019). Urban environments tend to create new selective pressures on the large carnivores capable of navigating these environments through human-subsidized resources and anthropogenic disturbance; novel challenges that often induce behavioral changes over time in urban wildlife compared to their more rural conspecifics (Kitchen et al. 2010, Lowry et al. 2013). As intended and unintended food subsidization becomes more common and urban development continues to reduce habitat for large carnivores, there will be greater opportunity for interactions and conflict between humans and large predators. Accordingly, it will become increasingly important to understand how supplemental foods and urban development drive behavioral changes in these species in order to safely create space for these animals along urban gradients while also limiting negative interactions with people, as their presence will help maintain ecosystem resilience and complexity in degraded ecosystems (Palazón et al. 2017). Increasingly, understanding how to coexist with robust carnivore guilds in places where predators and people overlap will be crucial to biodiversity conservation at large.

Large carnivores do not generally persistent in landscapes defined by high human density, however, recent scientific research investigating large carnivore responses to urbanization has demonstrated that multiple carnivore species are recolonizing landscapes composed of cities, highways, and rural development across Western Europe (Chapron et al. 2014), Eastern Africa (Woodroffe 2011), Southeast Asia (Wikramanayake et al. 2011), and North America (LaRue et al. 2012, Lamb et al. 2020, Yovovich et al. 2023). Reasons for the successful recolonization of areas with moderate human densities by large carnivores range from changing public perception and coordinated legislation (Chapron et al. 2014) to reduced rates of urban development (Johnson et al. 2023). With climate change predictions forecasting even greater range reduction in large carnivores through declines in suitable habitat and food availability (Helman et al. 2022), finding ways to conserve these species in moderately developed landscapes where they are exhibiting range recovery will be the crucial to conserving large predators outside of protected areas. Consistently, if large carnivores are slowly recolonizing developed environs, there will be even greater pressure on researchers to understand how to promote their coexistence with humans.

In North America, most large carnivores do not occupy urban landscapes (e.g., brown bears, wolves; Bateman and Flemming 2012). However, some species such as cougars (*Puma concolor*) and American black bears (*Ursus americanus*) can successfully navigate the interface of cities and wildland landscapes (Fischer et al. 2012), providing an opportunity to explore the demographic and behavioral mechanisms facilitating large carnivore population persistence in locations where people and predators must coexistence (Lamb et al. 2020). Black bears can exhibit behavioral plasticity (Gilbert 1989, Bommel et al. 2022) which makes them more successful exploiters of anthropogenic resources in and near developed landscapes than many large carnivore species (Baruch-Mordo et al. 2014). Indeed, black bears have even demonstrated a reliance on human food subsidies and selection for developed landscapes during poor natural food production years throughout the United States (Johnson et al. 2015, Kirby et al. 2017). If habitat fragmentation and changes in climate continue to reduce natural food resources for bears, exposure to anthropogenic resources and the propensity to select for those resources among bears will continue to increase, underscoring the need to improve our understanding of the individual and population wide responses by black bears to urbanization. Cougars, which are solitary predators, have broad habitat use (Sunquist and Sunquist 2002) and dietary flexibility (Kertson et al. 2011, Robins et al. 2019) that allows them to range contiguously from Chile to British Columbia. Like black bears, cougars can display behavioral plasticity, which affords them the ability to operate in landscapes with extensive human presence (Beier et al. 2010, Kertson et al. 2022).

Throughout North America cougars and black bears have the potential to influence scavenging communities by providing carrion (Allen et al. 2014), with cougars also often losing prey biomass to black bear scavenging (Elbroch et al. 2015, Elbroch et al. 2017). Interactions at carcasses is an underappreciated mechanism by which large carnivores may affect other guild members, and ecological communities at large, by affecting the transfer of energy across trophic levels (Allen et al. 2015). Thus, the presence of large carnivores along the urban fringe may be key to promoting nutrient cycling and energy transfer in ecosystems impacted by landscape development. How urbanization impacts interspecific interactions among large carnivores, and particularly scavenging dynamics, however, remains an unexplored research horizon. In Washington State, black bears commonly scavenge cougar-killed prey, and both carnivore species frequent exurban and suburban landscapes across a well-defined urbanization gradient in the western portion of the state (Kertson et al. 2013, Welfelt et al. 2019), providing an opportunity to bridge the knowledge gap on how urban development influences predator-predator interactions.

To help shed light on how urbanization and anthropogenic disturbance impact large carnivore behavior and interactions, I first explored whether urbanization alters large carnivore population niche breadth by quantifying individual and population-level variation in resource use by black bears occupying the wildland-urban gradient of western Washington (Chapter 2). My research on changes to black bear resource use as a function of anthropogenic disturbance provide new insights into black bear individuality, and which resources bears target seasonally in residential landscapes Timber harvest and intensive forest management occur throughout Washington State and represent forms of anthropogenic disturbance and landscape modification different from those in the built environment. Accordingly, I subsequently investigated whether individual and population-level resource use among black bears remained consistent, or diverged, between two separately managed timber forests defined by differences in harvest rotation, herbicide application, and diversionary feeding practices (Chapter 3). Black bears exhibited pronounced individual variation in resource use in both managed forests, with a lack of consistency across individual bears effectively washing out population wide patterns in use. Lastly, I used cougar kill site data and evidence of black bear carcass visitation distributed across wildland and residential environments in western Washington to explore how urbanization impacted black bear proclivity to scavenge cougar-killed prey (Chapter 4). My investigation into cougar-black bear dynamics as a function of urbanization is the first research study to demonstrate that moderate levels of residential development all but eliminate black bear scavenging of cougar killed prey, providing evidence that anthropogenic development can decouple scavenging relationships within large carnivore guilds. This research provides a basis for further scientific investigation into how disrupted interspecific interactions at the top food webs resulting from urbanization impact scavenging communities and lower trophic levels. Collectively, this work highlights how multiple forms of human-induced ecosystem change can alter individual and population wide behavior in large carnivores, and the mechanisms driving interactions between carnivore guild members in developing landscapes.

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CHAPTER 2: VARIATION OF BLACK BEAR RESOURCE USE ACROSS THE WILDLAND-URBAN INTERFACE OF WESTERN WASHINGTON

2.1 ABSTRACT

Many large mammalian carnivores currently persist along wildland-urban gradients. Understanding how carnivores in such regions respond individually and at the population-level to human-driven landscape modification, particularly built structures, will be crucial to maintaining wildlife community structure and ecosystem dynamics in the face of expanding human presence. To date, few large carnivore studies have contrasted wildland and residential niches for individual members of the same population, and none have asked how urbanization impacts population niche breadth. I contrasted use of landscape features by individual black bears (*Ursus americanus*) belonging to the same population in both residential and wildland portions of western Washington to determine whether urbanization promotes intra-specific niche convergence or divergence. Washington Department of Fish and Wildlife biologists captured and collared 64 black bears from 2013 - 2017 and I used global positioning system (GPS) data to create utilization distributions (UD) for the spring, summer, and autumn seasons. Resource utilization functions (RUFs) relating the UDs to landscape features revealed that use increased significantly across all seasons as distance to residential mature forest decreased, and that use also increased significantly as distance to rivers and lakes decreased in summer and autumn during the hottest time of the year. Bear use near mature forest differed significantly between residential and wildland areas in summer and autumn and use near residential mature forest and residential rivers differed in summer between females and males. Overall, my results provide partial support to the niche convergence hypothesis, with black bears exhibiting more consistent population-level use near mature forest and rivers in residential areas compared to wildland ecosystems. By implication, residential forest patches are important landscape refugia for bears navigating urbanizing environments, and their loss could homogenize black bear movements in a

matrix of less hospitable land cover. Accordingly, wildlife managers seeking to promote bear population persistence along wildland-urban gradients can use our findings to inform public and private planners and policymakers involved in land management to consider the importance of urban forest patches connecting wildland environments.

2.2 INTRODUCTION

The global proliferation of urbanizing landscapes is a major driver of changes to species abundance, distribution, and persistence (Maxwell et al. 2016). Recent studies investigating wildlife occupying wildland-urban gradients have shown that even low-levels of human activity can change animal behavior, species interactions, and community structure (Ripple et al. 2014, Wang et al. 2017, Evans et al. 2019). Nevertheless, many species are able to adapt and can persist in urbanizing areas (Magle et al. 2012, Chapron et al. 2014, Marzluff 2016, Yue et al. 2019). Understanding how these species do so is important for biodiversity conservation and to inform policy decisions aimed at facilitating coexistence between humans and wildlife in urban areas.

Behavioral, social, and dietary plasticity enables a variety of taxa to persist in human-dominated landscapes (Bateman and Fleming 2012, Lowry et al. 2013), suggesting that urban expansion homogenizes wildlife communities toward ecologically flexible species (McKinney 2006, Evans et al. 2019). Urbanization can change individual niche characteristics within populations as well (Newsome et al. 2015, León et al. 2019). Greater use of anthropogenic food sources, for example, often accompanies the increased use of urban environments (Newsome et al. 2015, Moss et al. 2016). It is possible that access to anthropogenic resources could reduce competition and lead to individual niche convergence within populations (Lowry et. al. 2013, Santini et al. 2019), but it is also possible that niche convergence could result from homogenization of habitat characteristics in residential landscapes, where features such as forest age and complexity are often more uniform than in wildland ecosystems (Bigsby et al. 2014, Groffman et al. 2014). Alternatively, intermediate levels of disturbance that often characterize urbanizing landscapes could diversify available foraging opportunities and thus promote individual niche divergence and increased population niche breadth (Moss et al. 2016, Larson et al. 2020). As urban areas expand, it is likely that a growing number of species will come into contact with anthropogenic resources, so understanding how the behavior of individual animals change with human activity is instrumental to human-wildlife conflict mitigation (Bateman and Fleming 2012). Yet, to date few studies have compared the behavior of animal populations in developed landscapes to that of conspecifics in wildland environments to determine whether urbanization homogenizes or diversifies individual (and population) niche breadth (Bateman and Fleming 2012).

Large mammalian carnivores tend to be especially sensitive to urbanization and often come into conflict with humans (Chapron 2003, Chapron 2014, Ripple 2014). Nevertheless, many such species currently persist in human-dominated landscapes including: brown bears (*Ursus arctos,* Lamb et al. 2017), cougars (*Puma concolor,* Kertson et al. 2013, Robins et al. 2019), leopards (*Panthera pardus*, Braczkowski et al. 2018), spotted hyenas (*Crocuta crocuta*, Yirga et al. 2015), and wolves (*Canis lupus,* Kaczensky et al. 2013). The landscapes that characterize urban sprawl provide carnivore species varying levels of access to anthropogenic food resources and vegetative cover (Lanszki 2003, Contesse et al. 2004, Herr 2009, Robins et al. 2019). As a result, some carnivores occupying these landscapes have been found to subsist entirely on anthropogenic subsidies. For example, leopard diets in India consist almost exclusively of domestic prey, and waste dumps are the critical resource for hyenas in the Tigray region of Ethiopia (Yirga et al. 2015, Arthreya et al. 2016), suggesting niche contraction. By contrast, foraging (*Puma concolor*; Kertson et al. 2011, Benson et al. 2016, Moss et al. 2016, Robins et al. 2019) and establishment (*Canis lupus*; Chapron et al. 2014, *Canis latrans*; Newsome et al. 2015, Ellington and Gehrt 2019) patterns in urbanizing environments have been characterized by high levels of individual variation, tentatively supporting the niche expansion hypothesis. Few carnivore studies (Newsome et al. 2015, Scholz et al. 2020, Larson et al. 2020) have contrasted wildland and residential niches for individual members of the same population, and there are no studies investigating changes to population niche breadth in large carnivore species across wildland-urban divides.

To address this knowledge gap and determine whether urbanization alters population niche breadth, I investigated individual variation in resource use for an American black bear (*Ursus americanus*) population occupying a wildland-urban gradient in western Washington state, USA. Across western Washington, black bear populations occupy wildland and urbanized systems and subsist on native vegetation, a diversity of terrestrial and aquatic prey, highly caloric anthropogenic food resources, and cougar-killed prey through facultative scavenging (Partridge et al. 2001, Welfelt et al. 2019). Thus, these populations offer the opportunity to evaluate how residential areas impact individual and population resource niche breadth in a large carnivore. Taking advantage of this opportunity, I quantified resource use for individual black bears belonging to the same population in both residential and wildland portions of a western Washington landscape to test competing hypotheses about the impact of urbanization on individual niche variation and population niche breadth. Namely, the niche convergence hypothesis (NCH), under which excess anthropogenic subsidies or habitat homogenization leads to a reduction in competition and a decrease in individual niche diversity relative to populations in wildland environments (Lowry et al. 2013, Santini et al. 2019), predicts that individuals in urbanizing areas should be more likely to share a common set of resources, leading to greater overlap and consistent space use patterns throughout the population. Human-food-conditioning has been shown to increase black bear tolerance for human activity (Hopkins et al 2012, Garshelis et al. 2017, Braunstein et al. 2020), so, the NCH additionally predicts that human-occupied buildings and other sources of anthropogenic foods should be among the resources that are used heavily by bears in residential landscapes. Conversely, the niche divergence hypothesis (NDH), under which expanded foraging and ranging opportunities in urbanizing environments promote niche diversification (Moss et al. 2016), predicts that individuals should focus on a broader array of available resources in urbanizing systems, leading to greater individual variability and less consistent space use patterns within the population. Under the NCH, I expected that fewer covariates would be associated with significant use at the population level in wildland areas compared to residential environments, and that bear presence near buildings would increase as bears entered hyperphagia. Under the NDH, I predicted black bears to exhibit more individual variation in residential landscapes, resulting in fewer population-level covariates being associated with significant use compared to wildland areas.

2.3 METHODS

2.3.1 Study Area

I examined black bear use of land cover in a 5,017 km^2 study site located in western Washington, USA (596 000 E, 5 246 000 N; Figure 2.1). The research site was topographically complex and characterized by a gradual east-west gradient spanning wildland (0 residences/ha), exurban (< 2.5 residences/ha), suburban (2.5-10 residences/ha), and urban (> 10 residences/ha) environments (Robinson et al. 2005, Kertson et al. 2011), with most wildland spaces within the study area consisting of temperate coniferous forests typical of the North Cascades ecoregion (Franklin and Dyrness 1973). We consider wildland portions of the study area “frontcountry” landscapes that remain near development, are highly accessible by vehicle, and include an amalgamation of state, federal and private property, with major landowners including

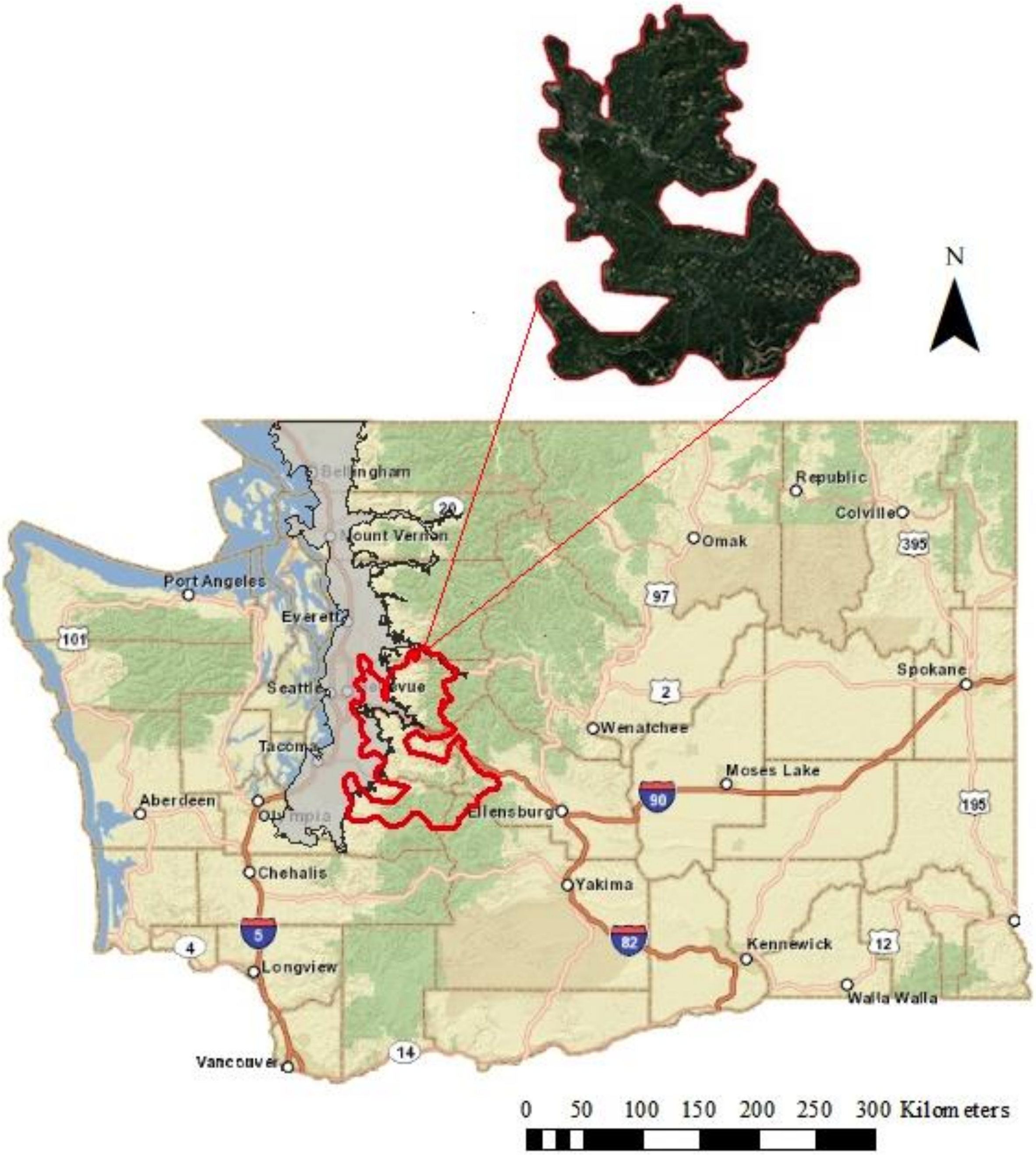

Figure 2.1. Location of the 5,017 Km^2 black bear study area in western Washington (red polygon), 2013-2017. The research site can be considered primarily “frontcountry,” and encompasses portions of King, Snohomish, and Pierce counties, with the wildland-urban interface, along with development west of the interface, indicated in gray. Wildland portions of the study were deemed undeveloped if there were 0 residences/ha.

Washington Department of Natural Resources, United States Forest Service, City of Seattle, King County, Campbell Global Forest and Natural Resource Investments, and Fruit Growers Supply Incorporated (Robins et al. 2019).

Black bears in western Washington forage on native vegetation (hard and soft masts as well as fruit producing species), with common natural foods including Himalayan blackberry (*Rubus discolor*), huckleberry (*Vaccinium spp.*), salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), skunk cabbage (*Lysichiton americanum*), and thimbleberry (*Rubus parviflorus*; Partridge et al. 2001). Black bears in western Washington also subsist on foods in unsecured human garbage, and occasionally black-tail deer (*Odocoileus hemionus columbianus*) fawns, elk (*Cervus canadensis*) calves, and fish when available (Partridge et al. 2001). Supplemental feeding of bears on commercial timberlands within the study area can occur March through mid-June with the intention of reducing tree damage caused by cambium feeding (Ziegltrum 2004).

2.3.2 Capture, Collaring, and Mapping

Washington Department of Fish and Wildlife (WDFW) biologists used spring-activated foothold snares, culvert traps, and trained dogs to capture black bears (n=64) throughout the study site from 2013 to 2017, with bear immobilization and radio-tagging occurring after capture. Bakery goods and fruit extract (Mother Murphy’s, Greensboro, NC, USA) were used as lures to attract bears. Black bears were immobilized with a 4:3 mixture of ketamine hydrochloride (200mg/kg; Ketaset, Burns Veterinary Supply, Farmers Branch, TX, USA) and xylazine hydrochloride (100mg/kg; Rompun, Haver-Lockhart, Shawnee, KS, USA). Captured bears > 1 year old were outfitted with a Global Positioning System (GPS) radio collar with the Globalstar satellite uplink (Models Vertex Lite or GPS Plus, Vectronic Aerospace, Berlin, Germany) that was programmed to record a location every 6 hours. GPS collars were equipped with a cotton spacer to ensure the collar falling off after approximately 36 months in case bears were unable to be recaptured, or collar failure occurred prematurely (Hellgren et al. 1988). All capture-related activities were conducted solely by WDFW biologists and in accordance with American Society of Mammalogists' guidelines for the use of wild mammals in research (Sikes et al. 2016).

I used the GIS layer produced by Kertson et al. (2011, 2013) delineating wildland and residential portions of the landscape, to define residential and wildland portions of utilization distributions (UDs) for individual bears (see Statistical Analysis). The wildland-urban interface represents the transition between undeveloped and developed landscapes (Moss et al. 2016); the western ⅓ of the study area contains residential development in densities from 2.5 (exurban) to >10 (urban) residences/ha (Kertson et al. 2011), and the interface marks the beginning of the undeveloped wildland landscapes that characterize the eastern ⅔ of the study area. I created landscape metrics in ArcMap 10.3 at a 30x30 meter resolution using United States Geological Survey (USGS) landcover data (https://www.usgs.gov), King County and Snohomish County parcel data, and forest data from the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) team, as well as the National Hydrography Database (http://www.nhd.usgs.gov). County parcel data have been used previously to define building density within the study site (Robins et al. 2019), and regression models used by Alberti et al. (2007) indicated that land-use and housing density data along Washington’s wildland-urban gradient are good predictors of land cover composition and configuration.

2.3.3 Statistical Analysis

I modeled individual black bear space use as a continuous variable represented by a utilization distributions (UD) - a probability distribution of an individual animal's use based on the density of its GPS locations across the landscape (Marzluff et al. 2004, Kertson and Marzluff 2010), and related use to landscape features using resource utilization functions (RUF; Marzluff et al. 2004, Millspaugh et al. 2006, Kertson et al. 2011). I constructed UDs using fixed-kernel techniques and the bivariate plug-in bandwidth in the Geospatial Modeling Environment, an ESRI ArcGIS add-on with R software integration (Beyer 2012). The bivariate plug-in bandwidth was chosen based on the dispersion pattern of black bear GPS points (Gitzen et al. 2006 and Kertson et al. 2011). I defined use for each black bear as its 99% fixed kernel boundary, and defined intensity of use by the volume (height) of the UD: the height of the UD represents the amount of use at that location relative to other locations in the layer (Silverman 1986, Marzluff et al. 2004). All UD values were multiplied by a constant of 10,000 to scale values into interpretable metrics. Black bear space use was also parsed by season (spring – March through May; summer – June through August; autumn – September through November) to account for behavioral changes in bears as they transition from den emergence to mating and then to hyperphagia, and to account for possible short-term supplemental feeding of black bears on private timberland portions of the study site in spring. I did not consider data collected during torpor (December through February) for this analysis. For individuals with >1 year of data (i.e., more than one spring, summer, or fall season), I used average values and considered the individual to be the sampling unit (Hiller et al 2015). For black bears with >1% use in residential portions of their home range, I created separate residential and wildland RUFs to test for statistical differences in use patterns between the two landscape types (Kertson et al. 2011). Under this framework, I generated landscape-specific RUFs in all seasons for which there was adequate GPS data, with a single bear producing as many as six individual RUFs. For each season and landscape type combination, I defined an animal as “adequately sampled” if there were >30 GPS locations available for UD generation (Seaman et al. 1999, Marzluff et al. 2004).

Landscape features were consistent across both landscape types and across seasons to allow for direct comparisons among RUF covariates. Important landscape attributes for black bears occupying the foothills of the west Cascades in Washington are largely unknown, so I chose landscape features that I hypothesized would be good predictors of black bear space use in both wildland and residential portions of the study area based on our observations of black bear ecology, scientific literature (Lewis et al. 2015, Zeller et al. 2019), and knowledge of management practices within the study site (Table 2.1).

All landscape metrics were constructed as continuous distance variables to associate intensity of use with proximity to specific resources for black bears, with use either increasing or decreasing as distance increases (in meters) from that landscape feature. Accordingly, negative beta estimates reflect high use proximal to a resource, whereas positive estimates reflect low use proximal to a resource use. Separate population-based residential and wildland RUFs were created from individual black bear RUFs to determine how the effects of the same covariates differed between these landscape types at the population level. I used the Pearson correlation coefficient to test for covariance among all covariates, with all r_{xy} values falling below 0.47, indicating small to moderate correlation across our predictor variables.

I used the Ruf.fit package available for R (see Marzluff et al. 2004, Kertson et al. 2011) to generate RUFs for all black bears to determine the importance of the selected landscape features to bears in residential and wildland landscapes in western Washington. The RUF

Table 2.1. Definitions of landscape features that were related to black bear (*Ursus americanus*) utilization distributions using resource utilization functions in western Washington, 2013-2017.

Landscape Term	**Definition**
Distance to Regeneration Forest	Euclidean distance in meters from pixels where most forest cover is defined by trees age 1 – 20 years.
Distance to Young Forest	Euclidean distance in meters from pixels where most forest cover is defined by trees age 21 – 40 years.
Distance to Mature Forest	Euclidean distance in meters from pixels where most forest cover is defined by trees age 41 – 149 years.
Distance to Old Growth Forest	Euclidean distance in meters from pixels where most forest cover is defined by tree age over 150 years.
Distance to Road	Euclidean distance in meters from pixels containing a paved road of 1 lane or greater. Road is defined as any local street, route, state or interstate highway, or railroad as available in the National Transportation Dataset (USGS).
Distance to Rivers	Euclidean distance in meters from pixels containing a path through which water flows as outlined by features in the National Hydrography Dataset. This includes streams, ditches, and rivers of various sizes; USGS).
Distance to Channels and Reservoirs	Euclidean distance in meters from pixels containing surface water defined as either a reservoir, or channel.
Distance to Lakes	Euclidean distance in meters from pixels containing surface water defined as a lake.
Distance to Buildings	Euclidean distance in meters from a pixel containing at least one human-occupied built structure. We considered buildings to be human-occupied if they were residences, office spaces, stores, or industrial buildings, and characterized these features using 2015 King County parcel data.

framework allowed for standardization of model coefficients, which were then averaged to test for seasonal and landscape-specific population-wide consistency in resource selection (Marzluff et al. 2004). Paired *t*-tests were used to test for statistical differences between landscape types, seasons, and black bear sexes. I did not stratify bears by age, and all age classes >1 were considered for this analysis to account for natal dispersal by young black bears.

2.4 RESULTS

2.4.1 Wildland and Residential Space Use

I evaluated space use for 59 collared black bears (M=33, F=26; 319 days average operational time) to determine whether residential development drives black bear spatial niche breadth to converge or diverge, of which 34 individuals (M=20, F=14) overlapped >1% with residential development. The wildland population RUFs revealed that use increased as distance to rivers and old growth forest decreased in spring and summer but use away from rivers in autumn increased when black bears decreased their proximity to housing (Tables 2.2 - 2.4). Across wildland population RUFs for all seasons, black bear use increased significantly only as distance to rivers in summer decreased. Residential population RUFs revealed use increased significantly in all seasons as distance to mature forest decreased, and the relative importance of lakes in these landscapes was greatest in summer during the warmest part of the year. Use increased from spring to summer and peaked in autumn as distance to rivers decreased in residential portions of the landscape. Proximity to buildings also increased from spring to autumn for both wildland and residential population RUFs, but confidence intervals for the distance to buildings covariate in both landscape types slightly overlapped 0. Comparison of wildland and residential standardized RUF coefficients supported the NCH hypothesis, with individual bears exhibiting greater inter-bear variability (Tables 2.2 - 2.4) in wildland landscapes

Table 2.2. Mean standardized RUF coefficients for black bears in residential and wildland portions of their home ranges in spring (March - May) in western Washington, 2013 - 2017. Bold font indicates significant resource use (i.e., confidence interval does not include 0). Use increases with each unit increase (+) or decrease (-) in distance from that resource attribute. Coefficients are relative values and can be ranked.

Spring Season						
	Wildland (n=28)			**Residential (n=11)**		
Landscape Attribute	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**
Regeneration Forest	-0.001 (0.046)	-0.090, 0.089	7/4	0.000 (0.015)	-0.030, 0.030	2/2
Young Forest	-0.042 (0.038)	-0.117, 0.032	4/5	-0.004 (0.012)	-0.027, 0.019	1/1
Mature Forest	-0.002 (0.021)	-0.042, 0.039	4/5	**-0.033 (0.010)**	**-0.053, -0.013**	**0/3**
Old Growth	-0.057 (0.049)	-0.154, 0.039	6/7	0.013 (0.020)	-0.026, 0.051	2/1
Roads	0.039 (0.028)	-0.016, 0.093	7/2	0.018 (0.023)	-0.026, 0.062	1/0
Rivers	-0.099 (0.055)	-0.206, 0.008	4/11	-0.019 (0.015)	-0.047, 0.010	0/2
Reservoirs & Channels	0.162 (0.097)	-0.028, 0.352	9/8	0.029 (0.040)	-0.049, 0.107	1/3
Lakes	0.072 (0.089)	-0.102, 0.247	10/6	-0.014 (0.027)	-0.067, 0.039	1/2
Buildings	-0.004 (0.065)	-0.131, 0.124	8/9	0.039 (0.050)	-0.058, 0.137	1/1

Table 2.3. Mean standardized RUF coefficients for black bears in residential and wildland portions of their home ranges in summer (June - August) in western Washington, 2013 - 2017. Bold font indicates significant resource use (i.e., confidence interval does not include 0). Use increases with each unit increase (+) or decrease (-) in distance from that resource attribute. Coefficients are relative values and can be ranked.

Summer Season						
	Wildland (n=39)			**Residential (n=23)**		
Landscape Attribute	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**
Regeneration Forest	-0.007 (0.011)	-0.029, 0.015	3/5	0.007 (0.011)	-0.015, 0.028	1/1
Young Forest	-0.005 (0.006)	-0.016, 0.007	1/2	-0.005 (0.006)	-0.018, 0.007	1/1
Mature Forest	-0.002 (0.005)	-0.012, 0.008	0/2	**-0.024 (0.007)**	**-0.038, -0.009**	**0/3**
Old Growth	-0.014 (0.014)	-0.041, 0.013	3/8	-0.007 (0.007)	-0.021, 0.007	1/2
Roads	-0.001 (0.008)	-0.017, 0.015	5/4	0.028 (0.018)	-0.007, 0.064	4/0
Rivers	**-0.014 (0.006)**	**-0.025, -0.003**	**1/5**	**-0.029 (0.009)**	**-0.047, -0.011**	**0/4**
Reservoirs & Channels	0.005 (0.023)	-0.039, 0.049	11/6	-0.001 (0.026)	-0.051, 0.050	6/1
Lakes	-0.005 (0.021)	-0.046, 0.035	12/10	**-0.033 (0.014)**	**-0.062, -0.005**	**0/6**
Buildings	-0.003 (0.027)	-0.057, 0.051	9/8	0.004 (0.014)	-0.023, 0.032	3/1

Table 2.4. Mean standardized RUF coefficients for black bears in residential and wildland portions of their home ranges in autumn (September - November) in western Washington, 2013 - 2017. Bold font indicates significant resource use (i.e., confidence interval does not include 0). Use increases with each unit increase (+) or decrease (-) in distance from that resource attribute. Coefficients are relative values and can be ranked.

Autumn Season						
	Wildland (n=36)			**Residential (n=24)**		
Landscape Attribute	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**
Regeneration Forest	-0.013 (0.016)	-0.044, 0.018	4/6	0.016 (0.014)	-0.011, 0.044	3/2
Young Forest	-0.003 (0.007)	-0.016, 0.010	5/4	0.007 (0.012)	-0.017, 0.031	3/2
Mature Forest	0.009 (0.006)	-0.003, 0.020	3/0	**-0.037 (0.011)**	**-0.058, -0.015**	**0/7**
Old Growth	-0.036 (0.027)	-0.088, 0.016	1/12	-0.006 (0.029)	-0.063, 0.051	4/5
Roads	-0.011 (0.022)	-0.054, 0.032	4/5	-0.006 (0.015)	-0.035, 0.024	3/3
Rivers	0.006 (0.025)	-0.043, 0.055	4/6	**-0.063 (0.025)**	**-0.113, -0.014**	**2/8**
Reservoirs & Channels	0.034 (0.068)	-0.010, 0.169	10/10	0.022 (0.032)	-0.042, 0.085	7/7
Lakes	0.004 (0.029)	-0.054, 0.062	8/9	-0.000 (0.037)	-0.072, 0.072	4/7
Buildings	-0.062 (0.041)	-0.142, 0.018	6/13	-0.052 (0.030)	-0.110, 0.007	3/9

than residential portions of their home ranges, indicated by the number of bears that aligned with the population trend for that covariate. Despite significant population-level use of mature forest and rivers by black bears in residential areas across all seasons, the difference in use between landscape types was only statistically significant for mature forest in summer ($P(\beta_R = \beta_W) = 0.022$) and autumn ($P(\beta_R = \beta_W) = 0.002$; Figure 2, panel A). Differences in the use of rivers between each landscape type approached significance in autumn ($P(\beta_R = \beta_W) = 0.058$) and can be attributed to a sharp increase in the use of this resource during that season (Fig. 2.2; panel B). I failed to detect a difference in use with proximity to built structures and residences when comparing residential and wildland population-level space use (Fig. 2.2, panel C), as black bears in western Washington exhibited intense use of the wildland-urban interface and less intense use of truly urban or remote wildland environments. Although bears in residential landscapes increased their proximity to buildings in autumn, differences in use near buildings between spring and autumn ($P(\beta_R = \beta_W) = 0.081$), and between summer and autumn ($P(\beta_R = \beta_W) = 0.125$), were marginally non-significant.

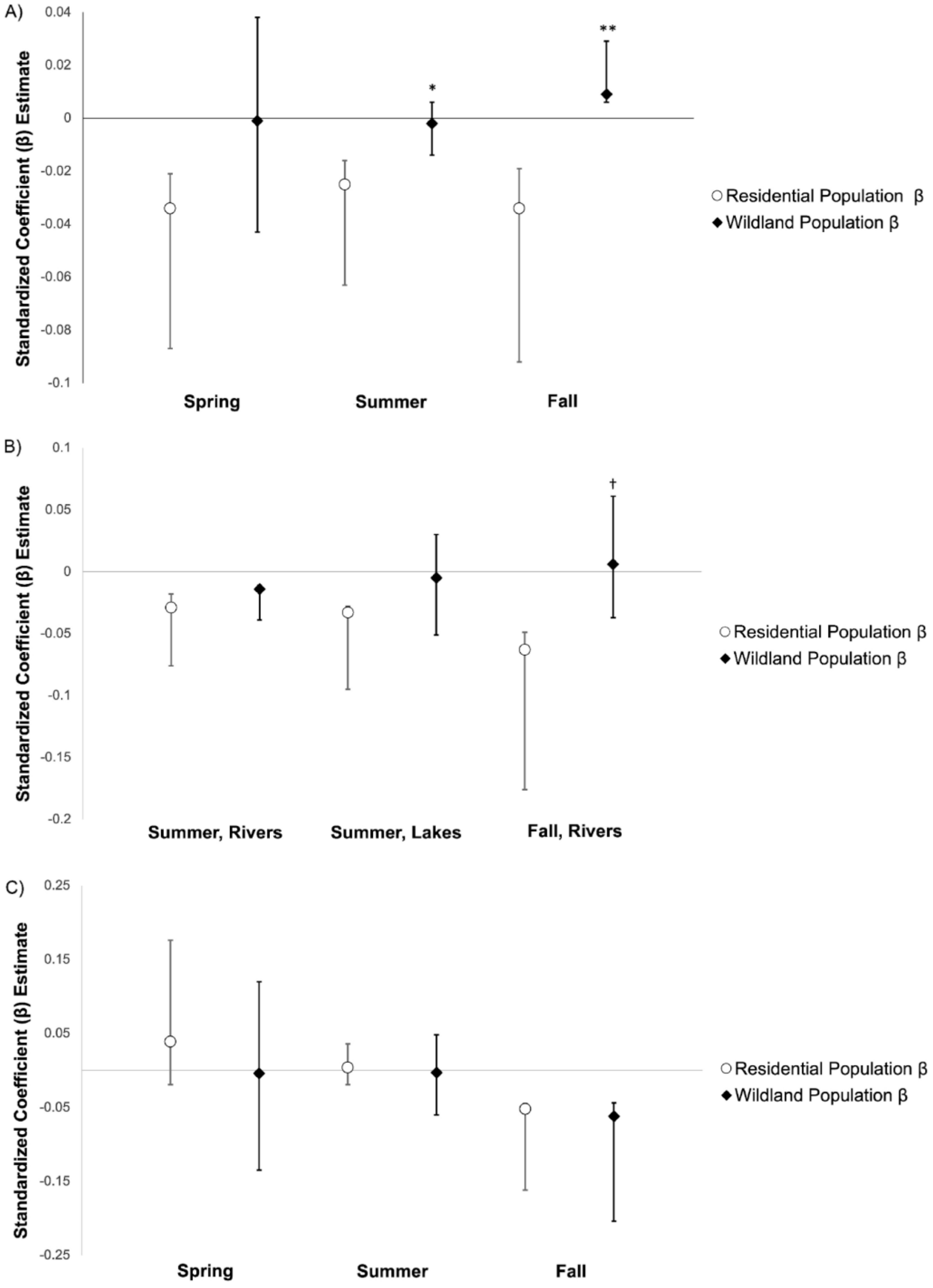

Figure 2.2. Paired t test results for residential and wildland RUF comparisons of black bears in western Washington, 2013-2017 for a) mature forests, b) significantly used water sources, and c) proximity to built structures. * Indicates a p-value <0.05, ** indicates a p-value <0.01, and † indicates a p-value <0.10.

2.4.2 Demographic Space Use Comparison

I documented different temporal and spatial use patterns between males and females including variation across landscape types. The difference in use near mature forest (P($\beta_F = \beta_M$) = 0.053) and rivers (P($\beta_F = \beta_M$) = 0.043) in residential landscapes was greatest between female and male black bears in summer (Fig. 2.3). Female use near residential mature forest was relatively consistent across seasons, whereas male bears exhibited more variable use with increasing distance from this resource (Fig. 2.3, panel A). This pattern reversed regarding use near rivers, with females exhibiting more variable seasonal use than males as distance increased from this resource (Fig. 2.3, panel B). Female bears also exhibited more intense use near residential water sources in summer than autumn. There was no significant difference in use based on proximity to buildings in autumn between male and female black bears (P($\beta_F = \beta_M$) = 0.512).

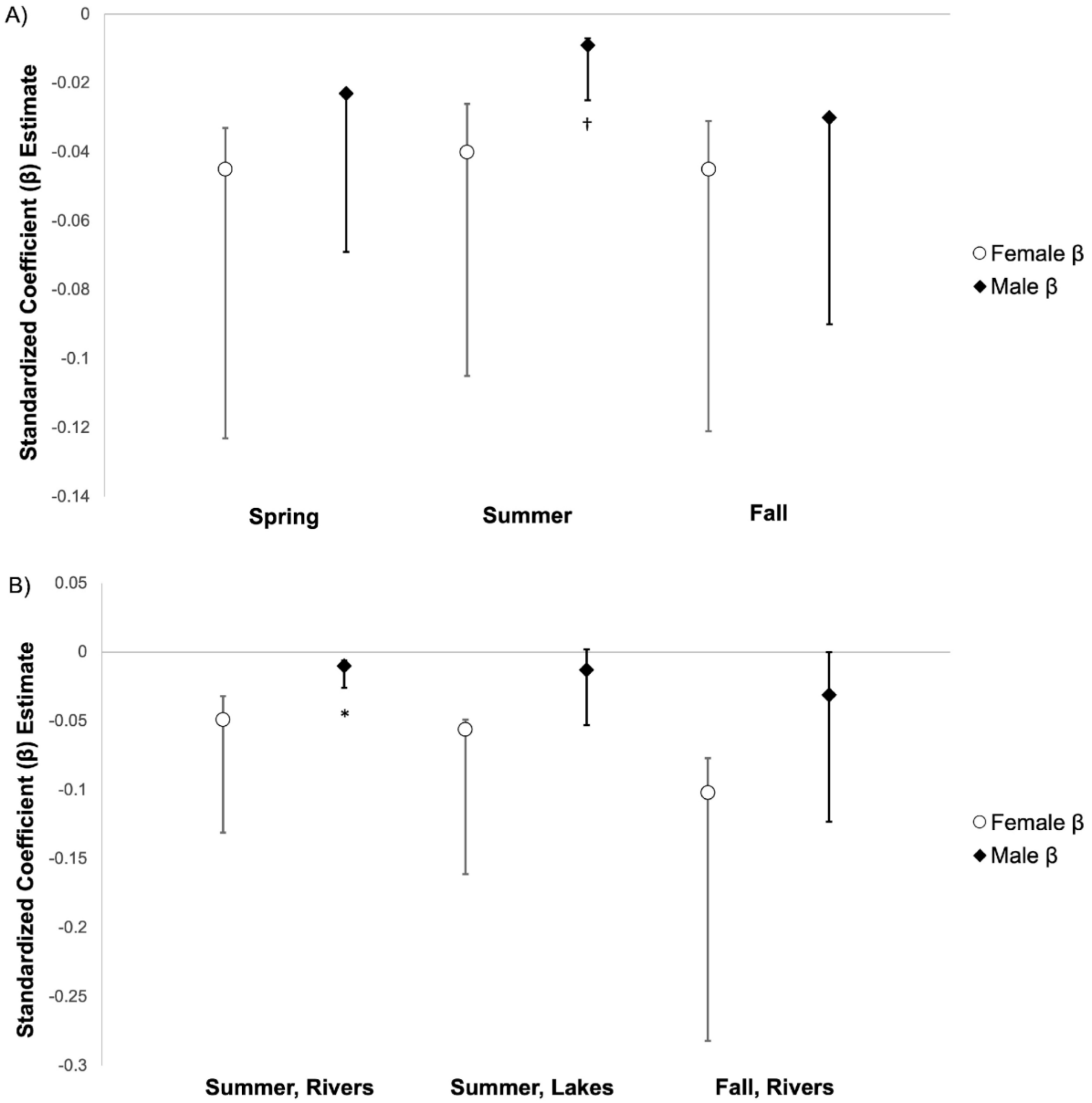

Figure 2.3. Paired t test results for female and male RUF comparisons of black bears in western Washington, 2013-2017 for a) residential mature forest, and b) significantly used residential water sources. * Indicates a p-value <0.05, ** indicates a p-value <0.01, and † indicates a p-value <0.10.

2.5 DISCUSSION

Many large mammalian carnivores currently persist along wildland-urban gradients (Bateman and Flemming 2012, Chapron et al. 2014, Lute and Carter 2020), so understanding their individual and population-level responses to landscape development is central to maintaining wildlife community structure and ecosystem dynamics as human development continues to expand. I hypothesized that a large carnivore commonly found along wildland-urban gradients, the black bear, would alter its resource use when navigating residential environments consequently exhibiting either niche divergence or niche convergence. My results provide partial support to the niche convergence hypothesis, with black bears exhibiting more consistent population-level use of mature forest and rivers in residential areas compared to wildland ecosystems. Use of mature forest, rivers, lakes, and buildings, particularly in residential developments, changed with season and as black bear energy requirements heightened prior to entering torpor. Moreover, most landscape attributes in residential areas, and nearly all landscape attributes in wildland areas, were not associated with significant use at the population-level, suggesting that there was also a high degree of individual variation in both landscape types, indicated by the number of bears with significant positive and negative coefficient estimates for each selected covariate. Alternatively, some landscape features may be poor indicators of bear space use broadly, or in certain seasons. Together, my findings reveal that residential development can modify black bear behavior in ways that may shape patterns of human-wildlife interaction and may influence potential conflict along the urban fringe.

There is a growing body of evidence demonstrating that human activity and development can alter large carnivore behavior (Newsome et al. 2015, Lewis et al. 2015, Wang et al. 2015). For black bears in residential developments, anthropogenic food resources are often clumped

(Parsons et al. 2019) and individual bears using these areas have also been previously documented with more assimilated anthropogenic foods in their diets than their more rural counterparts (Kirby et al. 2016, Braunstein et al. 2020), leading to speculation that their use of residential garbage and unsecured food attractants may promote convergent foraging behavior and space use (Beckmann and Lackey 2008; Johnson et al. 2015). I found that residential development corresponded with increased similarity in the use of certain landscape features among individual black bears. Convergence on these landscape features by black bears could either exacerbate, or reflect relaxed, intraspecific competition. Additional analyses related to home range overlap, utilization distribution overlap indices, or other metrics are needed to help tease apart these intraspecific scenarios (Robert et al. 2012, Cooper et al. 2014).

Evidence of niche convergence as a response to urbanization is by no means limited to bears, or to patterns in space use. For example, urban coyotes in southern California, USA exhibited dietary convergence compared to more rural conspecifics, with individual specialization decreasing as urbanization intensified (Larson et al. 2020). Notably, cougars, bobcats (*Lynx rufus*), and coyotes in residential developments near the Santa Cruz Mountains of California, USA collectively reduced diurnal activity and exhibited convergent nocturnal movement patterns, leading to diminished temporal partitioning and greater interspecific similarity in activity patterns (Wang et al. 2015). Similarly, habitat fragmentation from intense urban development in Washington, D.C. and North Carolina, USA has been shown to lead to higher levels of species interactions among bobcats, coyotes, red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*; Parsons et al. 2019). Although not measured in my study, black bears in our wildland-urban ecosystem may also experience decreased intraspecific diet variation and increased temporal and spatial overlap with other carnivores.

Residential development, which reduces or alters forest habitat connectivity, has been shown to concentrate carnivore activity into the limited "green space" characterizing urban and suburban environments (Parsons et al. 2019). Green spaces, such as urban parks and natural forest fragments, can provide resources for many wildlife species (Wurth et al. 2020), and black bears in residential portions of our study system displayed significant use of mature forest in these areas across all seasons at the population level. By implication, residential forest patches in western Washington are important landscape refugia for bears when navigating urbanizing environments, likely because they typically occur in riparian habitats that are protected (Forests and Fish Law RCW 76.09370) and thus retain many wildland-like habitat characteristics (e.g., closed canopies; Franklin et al. 2002) that are suitable for bears and other large carnivore species (*Puma concolor*; Kertson et al. 2013). These green space corridors have also experienced limited development, in part because of Washington's Growth Management Act (GMA; Chapter 36.70A RCW). Under the GMA (Chapter 36.70A RCW), all cities and counties are directed to designate natural resource lands to slow forest patch reduction and patch isolation. Given that residential development along wildland-urban gradients is likely to persist, continued application of this policy will be crucial to maintain or increase the size, connectivity, and quality of residential green spaces for wildlife habitat. My results also suggest that, as wildland-urban landscapes become increasingly developed, thereby leading to diminished green space (Gallo et al. 2017), a paucity of suitable habitat patches may further homogenize black bear movements in a matrix of less hospitable land cover. Moreover, forest fragmentation has proven to be the most important determinant of carnivore occupancy in metropolitan areas (Parsons et al. 2019), implying that remnant patches and corridors of wildland-like habitat may prove increasingly important for black bears seeking to exploit the resources in suburban and exurban areas (Evans et al. 2014), and that high levels of urbanization that eliminate green space are likely to exclude this and other carnivore species (Bateman and Flemming 2012, Maletzke et al. 2017). Accordingly, understanding how current and future fragmentation of forest cover affects bear use and distribution will be important for gauging the impacts of residential development to bears and other wildlife species. Future assessments of space use for black bears in residential areas should consider whether increased use of residential green space is associated with higher individual rates of human-bear conflict, bear mortality, and if utilization has impacts to black bear reproduction and dispersal.

The importance of residential lakes and rivers to bears changed seasonally. Black bear use of residential lakes peaked in summer, suggesting that large water sources are of greatest value to bears during the hottest time of the year when the landscape has dried out and ephemeral water sources are no longer available. By implication, interactions between black bears around lakes and other large water sources in urbanizing landscapes may be especially frequent in arid environments and dry times of year. However, Ochoa et al. (2021) found that residential water sources relaxed rather than aggravated spatiotemporal avoidance among carnivores in western and southwestern Utah, USA, revealing that water is not always a focal point for carnivore interaction near human settlement. Thus, the extent to which climate drives interactions among bears around large bodies of water in urbanizing environments requires further attention. Many rivers and lakes in western Washington are Pacific salmon (*Oncorhynchus* spp.) bearing waterways surrounded by berry producing riparian habitat. These food sources as well as the thick cover riparian habitats provide for bears may also influence black bear seasonal use near rivers in summer and autumn. For some bears, use may be related to the concealment these habitats provide for obtaining high calorie human-provided foods near homes.

An increase in black bear proximity to buildings in autumn approached significance for both wildland and residential portions of the population compared to the spring and summer seasons. The increase in black bear space-use near buildings in autumn can largely be attributed to bears entering hyperphagia and seeking out high-calorie food items prior to entering torpor (Lewis et al. 2015, Teunissen van Manen et al. 2019). Previous research in Minnesota (Rogers 1987) and Colorado (Baruch-Mordo et al. 2014, Lewis et al. 2015, Johnson et al. 2015) has indicated that black bears alter their foraging of anthropogenic food sources based on the availability of natural food sources, switching to the former when ripe natural mast (e.g., chokeberry, *Prunus virginiana*; serviceberry, *Amelanchier alnifolia*) was scarce. Black bears in Missoula, MT, however, have been shown to forage closer to homes, specifically consuming fruit trees, in apple season (September-October) even when wildland foods were available, suggesting that anthropogenic food sources can be more attractive than natural food resources when black bear energy requirements are elevated (Merkle et al. 2013). Collectively, these studies suggest that black bear foraging near human-occupied buildings may not only increase in autumn, reflecting rising nutritional needs as torpor approaches, but may also be influenced by attractant type and the level of natural food production. Accordingly, black bear proximity to residences in the autumn may fluctuate annually, and so quantifying changes in natural food availability (e.g., hard and soft mast) may be a useful tool for predicting bear use of human occupied areas and potentially human-black bear interactions in any given year.

I detected no difference in female and male black bear proximity to buildings in autumn, but female black bears exhibited more intense use of both residential mature forest and residential rivers compared to male black bears, thus the sharp increase in use near residential rivers in summer at the population level can be attributed to changes in female intensity of use.

My results support the findings of others and suggest that females and males balance energy budgets and safety differently when foraging in urbanizing landscapes (Merkle et al. 2013), which may ultimately drive sex-specific potential for increased bear use in human occupied areas and the subsequent potential for human-bear conflict. Notably, adult male bears in western Washington have exhibited higher proportions of assimilated anthropogenic foods in their diets than female bears (Welfelt 2018). By implication, females may spend more time in residential green space and near rivers than males resulting in a decreased reliance on anthropogenic food sources.

Whereas my study provides evidence of black bear convergence in the use of certain resources in residential areas, for many covariates in both wildland and residential landscapes black bears exhibited a high degree of individual variation, as indicated by comparable numbers of individuals with significant positive and negative associations. Individual variation has been demonstrated for cougars along the urban fringe in western Washington (Kertson et al. 2011) and west-central Colorado, USA (Moss et al. 2016), as well as for coyotes in heavily urban Chicago, Illinois, USA (Newsome et al. 2016). Cougars in Colorado exhibited greater use of exotic and invasive prey species in urbanizing landscapes, broadening their foraging niche compared to wildland conspecifics (Moss et al. 2016). For black bears, the pattern of individual variation we documented may have been a means of relaxing intra-specific competition under circumstances when natural foods were scarce and human food attractants drove individuals to converge their activity on certain resources in limited residential green space. Zeller et al. (2019) also found that black bears navigating urbanizing landscapes in Massachusetts, USA exhibited a high degree of inter-individual variation in resource use despite residential forest cover types being widely used by bears across seasons and nocturnal and diurnal activity periods. Individual specialization may therefore be a general mechanism among black bear populations whereby individuals maintain overall niche segregation even as factors such as forest fragmentation and urbanization force spatial convergence on certain key resources for bears.

Few studies have compared the behavior of individuals of large carnivore populations in developing landscapes to that of conspecifics in wildland environments to determine whether urbanization restricts or broadens space use patterns. The degree of individual variation observed among residential and wildland bears in my study area suggests that a one-size-fits-all approach is poorly suited to addressing individual or site-specific instances of bear use and presence in human occupied areas, which may influence the potential for human-bear conflict. My findings do, however, highlight attractive landscape features and seasonal changes as targets for management, as promoting forest and riparian habitat connectivity provides important habitat for wildlife. The residential green spaces in western Washington that are used by black bears can provide high-quality food resources and security from human disturbance. Based on my findings, I recommend that wildlife and land management focus on reducing the potential of human-bear overlap through promoting the presence of water sources and mature forest in residential green space, and reducing availability of anthropogenic food sources through outreach and education, and working with cities and municipalities on ordinances that address attractants and updating garbage contracts that stipulate bear-resistant container options. Such measures would prove particularly effective in autumn when western black bears utilize residential areas more intensively.

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CHAPTER 3: INDIVIDUAL VARIATION DRIVES BLACK BEAR RESOURCE USE IN TWO MANAGED FORESTS WITH DIVERGENT DIVERSIONARY FEEDING AND HARVEST PRACTICES

3.1 ABSTRACT

Forest management can have a strong impact on wildlife community assemblages and the behavior of individual animals. Diversionary feeding, whereby human-made foods are deployed to lure animals away from problem activities or locations, is a forest management practice that is often used to deter ursids from inflicting damage to timber products. The efficacy of this practice has been explored, but the degree to which it shapes ursid resource use as part of overall forest management scenarios remains unclear. To address this knowledge gap, I evaluated resource use by American black bears (*Ursus americanus*) navigating managed forests in western Washington, USA with (Snoqualmie Forest) and without (Department of Natural Resources, DNR) diversionary feeding during fed and non-fed portions of the year. Under the hypothesis that diversionary feeding alters bear use of young forest stands, we predicted that use of 16-30-year-old trees would generally be similar between our study sites but diverge when feeding stations were supplied (March -June). Resource utilization functions (RUFs) derived from positions of 24 GPS-collared bears tracked between 2013 and 2020 revealed that bear use of young forest stands, as well as other landscape attributes, was similar between landscapes with and without feeding stations irrespective of whether supplemental food was supplied. Notably, individual variation was significant for nearly every covariate, with bears often demonstrating contrasting patterns of use. Collectively, my results suggest that individual variation in black bear exploitation of young forest stands curtails consistency at the population level, and that any effects of diversionary feeding on ursid tree damage are unlikely to manifest through changes to population resource use.

3.2 INTRODUCTION

Explaining how animals respond to resource fluctuations caused by ecosystem disturbance is a principal goal in wildlife ecology (Moegenburg and Levey 2003, Wong and Candolin 2015, Rahman and Candolin 2022). With human activity acting as an increasingly pervasive source of such disturbance (Maxwell et al. 2016, Pacifici et al. 2020), the impacts of anthropogenic presence and landscape modification on faunal communities have been scrutinized intensively over the last three decades (Saunders et al. 1991, Nabe-Nielsen et al. 2010, He et al. 2021). These studies reveal that human-induced changes to resource abundance and distribution can affect the persistence and behavior of many wildlife species at the population level (Bateman and Flemming 2012, Newsome et al. 2015) as well as the composition, distribution, and richness of community assemblages (Dirzo et al. 2014, Newbold et al. 2015, Regolin et al. 2017). Accordingly, a comprehensive understanding of the ways in which various human disturbances shape consumer-resource dynamics is crucial to promoting wildlife persistence in the Anthropocene.

Forest management, and timber harvest in particular, is one of the most prominent sources of anthropogenic disturbance worldwide (Foley et al. 2005, Maxwell et al. 2016, Müller et al. 2019). Such management can modify the vegetative structure of wildland forest habitats at large spatiotemporal scales (Currylow et al. 2012, Hua and Sieving 2016, Yano et al. 2021) and, consequently, shape patterns of resource distribution for wildlife. Not surprisingly, therefore, changes to habitat structure within managed forests have been found to influence amphibians (Knapp et al. 2003, Semlitsch et al. 2009), reptiles (Renken et al. 2004), avifuana (Ribeiro et al. 2021), ungulates (Heydon and Bulloh 1997, Fisher and Wilkinson 2005), and small carnivores (Regolin et al. 2017), though not all species are affected equally (Shahabuddin and Kumar 2006, Semlitsch et al. 2009, Regolin et al. 2017). Indeed, different forms of forest management (e.g., selective logging, retention harvest, clear-cutting) have been shown to have varying degrees of impact on species richness, with more invasive methods exerting greater impact on wildlife communities (Chaudhary et al. 2016). How different management practices influence individual species, as well as the implications of more subtle forms of forest management aimed at promoting productivity (e.g., monocultures, fertilization, herbicides) or deterring herbivory or tree damage (e.g., diversionary feeding), have received less attention.

Most studies comparing effects of various forms of forest management have targeted ungulates (Heinze et al. 2011, Allen et al. 2014) or mesocarnivores (Chamberlain et al. 2002, Cheveau et al. 2013). By contrast, the impacts of forest management on large carnivore ecology have often been examined more narrowly through the lens of diversionary feeding (Notle et al. 2000, Rogers 2010, Penteriani et al. 2021). Diversionary feeding is a practice whereby supplemental food is used with the intention of deterring the activity or behavior of one or more target species that may cause negative impacts to human enterprise or recreation (Kubasiewicz et al. 2016). This approach is often used to prevent wildlife damage to forestry (e.g., red squirrels, *Tamiasciurus hudsonicus*; Sullivan and Klenner 1993) and agricultural products (e.g., voles, *Microtus montanus*, Sullivan et al. 2018) and to reduce human-wildlife conflict (Garshelis et al. 2017). However, food subsidies can alter the behavior and interactions of wildlife more broadly (Newsome et al. 2015, Goodenough et al. 2022), potentially inducing population-wide changes in habitat use (Kirby et al. 2016). Thus, there is need for studies examining how diversionary feeding affects the resource use of large carnivores in the context of mixed forest management practices and landscape patterns.

Among species targeted globally by diversionary feeding to reduce tree damage and conflict with humans, bears are among the most common (Kirby et al. 2017, Penteriani et al. 2021). To date, research on bear diversionary feeding has largely focused on the cost-effectiveness of using feeding stations to mitigate tree damage (Ziegltrum 2006, Kline et al. 2019, Taylor et al. 2019). However, food supplementation for bears may increase human-wildlife conflict (Kirby et al. 2016), so studies improving our understanding of how individuals and populations respond to diversionary feeding will inform more effective bear conservation and management policy (Kirby et al. 2017). Moreover, previous research in the Adirondack Mountains of New York, USA revealed that different forest management scenarios can influence the space use of individual bears (Costello et al. 1994), but no study to date has examined responses to diversionary feeding while also addressing impacts of other forms of management on population-wide changes to bear resource use. Here, to address these knowledge gaps, I asked whether individual and population-level resource use among American black bears (*Ursus americanus*) remained consistent or diverged between two separately managed timber forests defined by differences in harvest rotation, chemical applications, and diversionary feeding practices in western Washington, USA.

Throughout their range, black bears frequently girdle, or strip the bark from, conifers following den emergence to access the energy-rich soluble sugars available in the newly formed vascular tissues of young trees (Ziegltrum 2008, Kline et al. 2019). Black bears often target conifers that are 15-30 years old, and while complete girdling is lethal to most tree species, partial girdling often reduces growth rates and increases stand susceptibility to disease and insect infestations (Nolte et al. 1998, Nolte et al. 2002, Taylor et al. 2014). For this reason, forest management by private timber companies throughout Washington often incorporates the use of diversionary feeding to minimize economic losses from black bear damage to timber products. In western Washington, a significant segment of the black bear population overlaps with 15–30-year-old public and private Douglas-fir (*Pseudotsuga menziesii*) dominant timber forests, and these industrial stands are particularly vulnerable to bark-peeling by bears in spring because trees within managed stands are of a single species and of the same age (Nolte et al. 1998, Zielgtrum 2006). Consequently, spring diversionary feeding (March 01-June 30) began in the mid 1980's by the Washington Forest Protection Association's (WFPA) Animal Damage Control Program (ADCP) with the expectation of providing an alternate food source (Flowers 1986, Ziegltrum 2004), and the use of feeding stations is still a common practice among private timber companies in this state, where it is estimated that nearly half a million pounds of food is supplied annually (Ziegltrum 2006). Evidence for the efficacy of the diversionary feeding program in Washington comes primarily from a single study (Ziegltrum 2004) conducted by the ADCP of WFPA. Since 2004, a pair of additional articles have accompanied that publication describing the program as a non-lethal success, but the program has not contributed additional scientific evidence of damage reduction or altered bear ecology (Ziegltrum 2006, 2008). Research on black bear responses to diversionary feeding has demonstrated that food supplementation does not alter bear home range size (Fersterer et al. 2001) or prey consumption (Pugesek et al. 2021). Yet, on Washington's Olympic Peninsula, Nolte et al. (2002) found that numerous black bears including males, females with and without cubs, and yearlings used feeding stations, suggesting that widespread use of feeding stations by bears could have implications for population-level use of young timber stands as well as other landscape features. Thus, the effects of diversionary feeding on black bear movements and resource use merit further evaluation.

For this investigation, I explored black bear resource use in two study areas from 2013 - 2020. The first study site, Snoqualmie Forest, consists of private timberland in which lowland areas are dominated by stands less than 45 years old, which are currently the optimal economic harvest age for intensively managed commercial stands in western Washington (Partridge and MacGregor 2007, Ziegltrum 2006). Timber harvest in Snoqualmie Forest occurs annually and multiple clearcuts are harvested concurrently, with each stand being harvested approximately every four decades. To protect commercial Douglas-fir stands from black bear consumption, diversionary feeding was practiced in consistent locations in Snoqualmie Forest from March through June every year of this investigation. The second study area, in which diversionary feeding did not occur, comprises state trust lands including Tiger Mountain State Forest, Raging River State Forest, and Rattlesnake Mountain Scenic Area, all of which are managed by Washington’s Department of Natural Resources (WA-DNR; Partridge and MacGregor 2007). These state trust lands (hereafter ‘DNR’) are managed to achieve a blend of objectives including timber harvest for income and public infrastructure and promoting complex forest conditions (Partridge and MacGregor 2007). For this reason, timber harvest on the DNR site occurs without the use of herbicides in stands 40-120 years old (Partridge and MacGregor 2007), with fewer annual cuts compared to Snoqualmie Forest.

In Washington, diversionary feeding stations are often placed near timber stands 15-30 years old (Nolte et al. 1998, Nolte et al. 2002). It is therefore possible that use of stands of this age could either increase, because of the attractiveness of feeding stations, or decrease, because bears accessing pelletized feed may satiate quickly and then depart rather than staying to peel trees, when feeding stations are available. Accordingly, under the two-sided hypothesis that diversionary feeding alters bear use of resources associated with feeding locations, I predicted that, relative to periods of time during which diversionary feeding did not occur, bear use of 15-30-year-old stands in Snoqualmie Forest would diverge from bear use of the same-aged stands on the DNR site during months when feeding stations were regularly supplied in Snoqualmie Forest.

3.3 METHODS

3.3.1 Study Areas

I examined black bear use of landscape covariates in two separate study areas in western Washington, USA. The first study site, Snoqualmie Forest (421 km^2; 595 000 E, 5 275 000 N) was a privately-owned forest managed for commercial timber production. The second study site, the DNR study area (136 km^2; 585 000 E, 5 260 000 N), was composed of state trust lands on which timber harvest is managed by WA-DNR (Fig. 3.1). The sites varied in elevation from 10 to 2000 meters, and Douglas-fir, western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) forest associations were the dominant habitat types in both study areas. Black bears in both study areas forage on hard and soft mast, fruit-producing species, fish and ungulate neonates when available, and commonly damage young conifers in spring when multiple food sources are limited in order to access carbohydrates available beneath tree bark (Nolte et al. 2002). This behavior abates in summer, and is rare in autumn, when other natural food sources become readily available (Ziegltrum and Nolte 1996, Zielgtrum 2004). The boundaries of both Snoqualmie Forest and the DNR site come within 1 km of residential development and both study sites are characterized by an extensive network of roads with habitats largely consisting of forest age classes less than 100 years of age (Partridge and MacGregor 2007). Interstate 90 separated the two study areas.

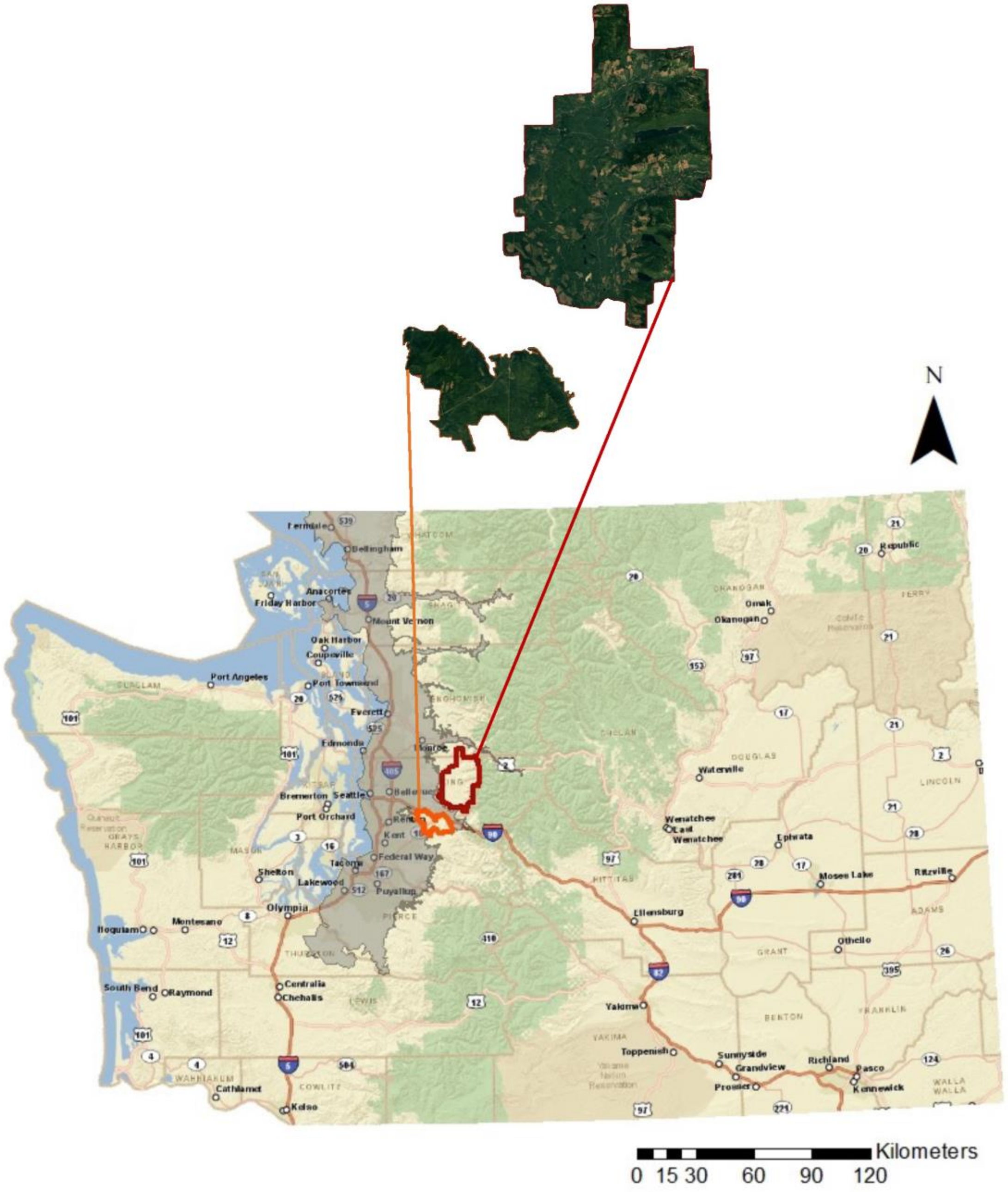

Figure 3.1. Locations of the two American black bear (*Ursus americanus*) study sites in western Washington, USA from 2013-2020. Snoqualmie Forest is outlined in red (421 km^2) and is private timber forest where diversionary feeding occurs in spring and is characterized by approximately a 40-year harvest rotation. The DNR site is outlined in orange (136 Km^2), is managed by WA-DNR, and is subject to infrequent harvest in stands 40-120 years old. Zoom-in insets provide more detailed arial imagery of both sites, with DNR to the lower left and Snoqualmie Forest to the upper right. The research sites encompass wildland portions of King and Snohomish counties, with urban development (0->10 residences/ha), indicated in gray.

The study sites differed in their forest management practices, with more frequent harvest rotations, diversionary feeding, and application of herbicides occurring in Snoqualmie Forest. Consequently, there was a greater proportion of timber stands <45 years of age on Snoqualmie Forest than on the DNR site (Appendix S1, Figures S1 – S4, Supplemental Material). While both study sites had annual timber harvest occurring on the landscape, there were far fewer annual clearcuts on DNR than the private timber forest. Recreational activity also occurred in both study areas, however, there was public access, and thus greater hiker presence, in the DNR site.

3.3.2 Capture and Collaring

Washington Department of Fish and Wildlife biologists used spring-activated foothold snares, culvert traps, and trained dogs to capture and radio-tag black bears (n=64) in western Washington from 2013 to 2017. Of those 64 bears, 23 (Snoqualmie Forest, n = 11; DNR, n = 12) provided sufficient GPS data during fed and non-fed portions of the year in either study site to allow for comparisons of resource use between times of year and landscapes with and without diversionary feeding. All bears on Snoqualmie Forest overlapped with at least one known diversionary feeding station during the months of March through June (Appendix S1, Supplemental Material).

Black bears were immobilized with a 4:3 mixture of ketamine hydrochloride (200mg/kg; Ketaset, Burns Veterinary Supply, Farmers Branch, TX, USA) and xylazine hydrochloride (100mg/kg; Rompun, Haver-Lockhart, Shawnee, KS, USA). Captured bears > 1 year old were outfitted with a Global Positioning System (GPS) radio collar with the Globalstar satellite uplink (Vertex Lite or GPS Plus models, Vectronic Aerospace, Berlin, Germany) that was programmed to record a location every 6 hours. GPS collars were equipped with a cotton spacer designed to degrade after approximately 36 months in case bears were not recaptured, or if collar failure occurred prior to recapture (Hellgren et al. 1988). All capture related activities were conducted in accordance with department protocols and American Society of Mammalogists' guidelines for the use of wild mammals in research (Sikes et al. 2016).

3.3.3 Mapping and Statistical Analysis

I related landscape metrics to black bear use by estimating individual black bear utilization distributions (UDs) using fixed-kernel techniques, and measured resource and use values throughout the UD (Marzluff et al. 2004). I constructed UDs for individual black bears using black bear GPS locations and accounted for the onset and termination of diversionary feeding in Snoqualmie Forest by creating seasonal UDs that coincided with fed (March, following den emergence, through June) and non-fed (July through October, prior to denning) months. This approach allowed for UDs in both study sites to represent resource use when diversionary feeding was present and absent on the landscape. For individuals with >1 year of data, I used average values across fed and non-fed months and considered the individual to be the sampling unit (Hiller et al. 2015). Black bear kernel density estimates (KDEs), UDs, and use (inferred from a volume contour based on the UD) were generated using the ‘ks’, ‘rgdal’, ‘maptools’, ‘gpclib’, ‘PBSmapping’, ‘raster’, ‘rgeos’, ‘adehabitat’, and the ‘adehabitatHR’ packages in R (Bates et al. 2015, R Core Team 2022). I used the bivariate plug-in bandwidth when constructing UDs as it is most appropriate for kernel density estimation based on the dispersion of black bear GPS locations (Gitzen et al. 2006, Kertson et al. 2011), and defined projections as WGS84 zone 10. I defined use for each black bear as its 99% fixed kernel boundary to account for all movements within the home range, defined intensity of use by the height of the volume contour, which allowed UD values to be converted to a 0-100 scale (Beyer et al. 2004, Kertson and Marzluff 2010). I then created resource utilization functions (RUFs) to evaluate associations between intensity of use and spatially quantifiable resources important to bears and timber management (Marzluff et al. 2004, Kertson and Marzluff 2010).

I quantified landscape metrics in ArcMap 10.3 at a 30x30 m resolution using forest data from the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) team (https://lemma.forestry.oregonstate.edu/data), hydrography data from the National Hydrography Database (http://www.nhd.usgs.gov), and topographic data from the Washington State Geospatial Data Archive (https://wagda.lib.washington.edu/). Forest data from the LEMMA team are the best available forest data for the area and were generated in 2012. For temporal accuracy, forest ages were adjusted to each individual bear to properly identify forest age classes at the time each bear was actively using the landscape. To account for clearcuts occurring after 2012, I digitized yearly clearcuts as polygons in both study sites using Google Earth Pro version 7.3 (Google Earth 7.3.6.9345, 2022) for every year of the investigation and removed LEMMA forest age classes coinciding with these polygons. All landscape metrics were structured as continuous distance variables to associate intensity of use with proximity to resources assumed to be important to bears and/or reflective of timber management, with use either increasing or decreasing as distance increases (in meters) from that specific landscape feature. Landscape metrics were identified based on tree ages targeted by bears (15–30-year-old stands; Nolte et al. 2002), harvest rotation on Snoqualmie Forest (40-50 years), key water resources for bears (Robins et al., unpublished data), and topographical features we considered may be important for bears based on their influence on natural food production. Namely, southern aspects receive more sunlight than northern aspects in western Washington, translating to vegetative biomass and forage for bears. Similarly, the start of the vegetation growing season in both study sites often occurs in landscapes characterized by low elevation and low slope. Accordingly, the landscape attributes that were included in the RUF analysis to compare black bear use were: distance to stands 0-15 years old, 16-30 years old (which we considered synonymous with 15-30-year-old-stands), 31-45 years old, >45 years old, distance to road, distance to waterbodies (e.g., lakes) and rivers, distance to creeks and streams, elevation, slope, and north-south aspect (Table 3.1). The 16-30-year-old stand covariate was used to test my prediction that bear use of highly productive timbers stands in Snoqualmie Forest would diverge from bear use of the same-aged stands in the DNR site during months when feeding stations were regularly supplied in Snoqualmie Forest.

I considered black bears navigating either forest study site during fed and non-fed months as "adequately sampled" if there were >30 GPS locations available for UD generation (Seaman et al. 1999, Marzluff et al. 2004). The same landscape metrics were sampled across all RUF files to allow for statistical comparisons between fed and non-fed months and across study sites. I used the Ruf.fit package (see Marzluff et al. 2004) in R (R Core Team 2021) to generate RUFs for all black bears to determine the importance of the selected landscape features to bears in the presence and absence of diversionary feeding. The ruf.fit package can produce both standardized and unstandardized regression coefficients, and standardized coefficients allow for comparisons of the relative use of different landscape covariates. Population-level RUFs for each forest were created from individual black bear RUFs during fed and non-fed portions of the year to determine if the presence of diversionary feeding had a population level effect within and between study areas. Significance was determined for covariate estimates in individual bear RUFs, as well as population-level RUFs, using 95% confidence intervals. Paired t-tests (significant at α = 0.05, marginally non-significant at α = 0.10) were used to test for statistical differences between bears in Snoqualmie Forest and bears within the DNR site during fed and

Table 3.1. Definitions of landscape features that were related to black bear (*Ursus americanus*) utilization distributions using resource utilization functions in Snoqualmie Forest and on the DNR site, 2013-2020.

Landscape Term	**Definition**
Distance to 0–15-Year-Old Stands	Euclidean distance in meters from pixels where most forest cover is defined by trees aged 0 to 15 years.
Distance to 16–30-Year-Old Stands	Euclidean distance in meters from pixels where most forest cover is defined by trees aged 16 to 30 years.
Distance to 31–45-Year-Old Stands	Euclidean distance in meters from pixels where most forest cover is defined by trees aged 31 to 45 years.
Distance to >45-Year-Old Stands	Euclidean distance in meters from pixels where most forest cover is defined by trees aged greater than 45 years.
Distance to Road	Euclidean distance in meters from pixels containing a dirt, gravel, or paved road of 1 lane or greater. Road is defined as any local street, route, state or interstate highway, or railroad as available in the National Transportation Dataset (USGS).
Distance to Waterbodies and Rivers	Euclidean distance in meters from pixels containing large water flows and waterbodies. This includes rivers of various sizes and surface water defined as lakes as outlined by features in the National Hydrography Dataset (USGS).
Distance to Creeks and Streams	Euclidean distance in meters from pixels containing smaller water flows, such as streams and creeks as outlined by the NDH (USGS).
Elevation	Digital elevation model, with elevation in meters; data available through the Washington State Geospatial Data Archive (WAGDA).
Slope	Layer data with slope in meters available in the WAGDA digital elevation model.
North-South Aspect	Aspect data available as a layer in the WAGDA digital elevation model. To produce a North-South aspect variable, decimal degrees were first converted to radians. The cosine function was then applied to the radian values to produce a variable ranging from - 1(due south) to 1 (due north).

non-fed seasons, as well as differences between black bear sexes. I did not stratify bears by age, and all age classes >1 were considered for this analysis.

3.4 RESULTS

I evaluated space use for 23 collared black bears in the Snoqualmie Forest (n=11) and on the DNR site (n=12). My monitoring of black bears yielded an average of 462 (*SD* = 239, n = 11) locations for black bears in Snoqualmie Forest during the months of March through June, and an average of 670 (*SD* = 354, n = 11) locations from July through October. My monitoring in the DNR site produced an average of 514 (*SD* = 391, n = 12) locations during fed months, and an average of 541 (*SD* = 363, n = 12) locations during non-fed months.

I failed to detect differences in the use of 16-30-year-old stands between the DNR site and Snoqualmie Forest study areas during fed and non-fed months at the population level (Tables 3.2 and 3.3). I failed to detect significant population-level use of any landscape covariate in Snoqualmie Forest with the notable exception of the use of low elevation areas during non-fed portions of the year. Black bears also demonstrated significant use of low elevation areas in the DNR site, but this phenomenon occurred during fed months when DNR bears also displayed significant use of >45-year-old stands. Department of Natural Resource site bears exhibited significant use away from creeks and streams and high use in low elevation areas during non-fed months. I documented significant variation in resource use among individuals in both study areas during fed and non-fed times of year (Table 2). Namely, when diversionary feeding was active in Snoqualmie Forest, nine or more bears demonstrated significant positive and negative use for every covariate, with at least five bears exhibiting significant use in opposing directions (+/-) for three covariates. At least six bears also displayed significant positive and negative use for every covariate during months when diversionary feeding stations were not supplied in Snoqualmie

Forest, with the elevation covariate being the only exception; no bears exhibited significant increases in use as elevation increased. Seven of the eleven bears in Snoqualmie Forest displayed significant use away from 16-30-year-old stands during fed and non-fed portions of the year. Similarly, multiple bears demonstrated significant positive and negative use of every covariate in the DNR study area, with at least five bears displaying significant use in opposing directions (+/-) for two covariates during fed months and five covariates during non-fed months. Eight bears in DNR had significant use further from 16-30-year-old stands in March through June when diversionary feeding stations were supplied in Snoqualmie Forest, with three DNR bears exhibited high use near this forest age class. In the DNR site, the number of bears demonstrating significant use near 16-30-year-old sands more than doubled once feeding stations were no longer active (July through October), with seven bears in the DNR study site demonstrated significant use near this forest age class when feeding stations were no longer active and five bears exhibiting significantly high use further from these stand types. I failed to detect significant differences between Snoqualmie Forest and DNR for any covariate in during both fed and non-fed times of year ($P[\beta\text{Snoqualmie} = \beta\text{DNR}]$: 0.08 – 0.72). I also failed to detect differences between male and female bears in their use of landscape covariates within ($P[\beta\text{Female} = \beta\text{Male}]$: 0.09 – 0.92) and between ($P[\beta\text{Female} = \beta\text{Male}]$: 0.37 – 0.49) study sites.

Table 3.2. Mean standardized RUF coefficients for black bears in both study areas during diversionary feeding months (March through June) in western Washington, 2013 - 2020. Bold font indicates significant resource use (i.e., confidence interval does not include 0). Use increases with each unit increase (+) or decrease (-) in distance from that resource attribute.

	Snoqualmie Forest (n=11)			**DNR Site (n=12)**		
Landscape Attribute	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (-/+)**	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (-/+)**
Distance to 0–15-Year-Old Stands	-13.545 (11.223)	-35.542, 8.453	7/4	-3.628 (2.962)	-9.434, 2.177	7/5
Distance to 16–30-Year-Old Stands	14.999 (12.299)	-9.107, 39.105	4/7	4.296 (2.415)	-0.437, 9.030	3/8
Distance to 31–45-Year-Old Stands	2.507 (3.328)	-4.015, 9.029	5/6	3.061 (1.783)	-0.435, 2.210	3/7
Distance to >45-Year-Old Stands	0.843 (0.724)	-0.575, 2.262	3/6	**-0.725 (0.337)**	**-1.385, -0.064**	**7/4**
Distance to Roads	-0.461 (0.444)	-1.331, 0.410	6/5	-0.231 (0.682)	-1.569, 1.106	5/7
Distance to Waterbodies and Rivers	-0.984 (1.072)	-3.085, 1.117	7/4	-3.640 (2.390)	-8.323, 1.044	6/3
Distance to Creeks and Streams	-0.622 (0.817)	-2.222, 0.978	6/5	2.884 (1.047)	0.833, 4.935	2/10
Elevation	-1.759 (1.457)	-4.616, 1.097	7/4	**-3.292 (2.017)**	**-7.245, 0.660**	**9/3**
Slope	0.083 (0.617)	-1.126, 1.292	4/7	0.974 (0.558)	-0.120, 2.067	4/8
North-South Aspect	-0.145 (0.135)	-0.410, 0.120	8/2	0.056 (0.071)	-0.083, 0.195	4/5
Intercept	**23.205 (1.349)**	**20.562, 25.849**	**0/11**	**20.138 (2.027)**	**16.164, 24.111**	**0/12**

Table 3.3. Mean standardized RUF coefficients for black bears in both study areas during months when diversionary feeding did not occur (July through October) in western Washington, 2013 - 2020. Bold font indicates significant resource use (i.e., confidence interval does not include 0). Use increases with each unit increase (+) or decrease (-) in distance from that resource attribute.

	Snoqualmie Forest (n=11)			**DNR Site (n=12)**		
Landscape Attribute	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (-/+)**	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (-/+)**
Distance to 0–15-Year-Old Stands	-5.950 (5.144)	-16.032, 4.133	6/4	-0.087 (1.799)	-4.392, 2.661	9/3
Distance to 16–30-Year-Old Stands	7.653 (5.392)	-2.915, 18.221	3/7	-0.923 (1.409)	-3.685, 1.840	7/5
Distance to 31–45-Year-Old Stands	2.757 (1.968)	-1.010, 6.614	3/7	0.964 (1.688)	-2.343, 4.272	7/5
Distance to >45-Year-Old Stands	-0.337 (0.437)	-1.193, 0.520	6/4	-0.281 (0.294)	-0.857, 0.296	7/5
Distance to Roads	-0.302 (0.699)	-1.672, 1.067	6/4	0.165 (0.430)	-0.677, 1.007	5/5
Distance to Waterbodies and Rivers	-1.386 (0.809)	-2.972, 0.200	7/3	-2.217 (1.436)	-5.031, 0.597	9/3
Distance to Creeks and Streams	-0.046 (0.644)	-1.309, 1.216	4/4	**1.293 (0.591)**	**0.135, 2.451**	**3/9**
Elevation	**-2.312 (0.936)**	**-4.146, -0.478**	**6/0**	**-5.798 (1.854)**	**-9.432, -2.164**	**10/2**
Slope	-0481 (0.684)	-1.823, 0.860	6/4	-0.599 (0.881)	-2.326, 1.129	5/6
North-South Aspect	0.076 (0.098)	-0.115, 0.267	4/6	0.003 (0.154)	-0.299, 0.305	3/9
Intercept	**20.159 (2.408)**	**15.438, 24.879**	**0/11**	**19.836 (2.294)**	**15.339, 24.333**	**0/12**

3.5 DISCUSSION

There is growing evidence that human-provided foods can alter the behavior and ecology of large terrestrial predators (Newsome et al. 2015). Accordingly, the diversionary feeding of black bears to reduce damage to managed timber resources in western Washington, irrespective of its effectiveness, elicits concerns over potential impacts to at least some segments of bear populations (Witmer et al. 2000). However, contrary to my expectations, I failed to detect differences in bears use of 16-30-year-old forest stands between Snoqualmie Forest and the DNR site across fed and non-fed portions of the year. Population-level use by bears was non-significant for all covariates from March through June in Snoqualmie Forest, with bears only exhibiting significant population wide use of low elevation areas in this study site when diversionary feeding stations were no longer supplied. Use of mature forest (>45-year-old stands) and low elevation areas was significant at the population level in the DNR site when diversionary feeding was active in Snoqualmie Forest and bears in the DNR site continued to use low elevation areas, and displayed high use away from creeks and streams, after diversionary feeding in Snoqualmie Forest ceased. I did not detect any differences between the sexes in use of any covariates in either study area, but individual variation was significant across bears within each study site, during fed and non-fed times of year, and for nearly every covariate considered in this analysis. Collectively, my findings support previous research on the impacts of diversionary feeding on ursid behavior (Fersterer et al. 2001, Ziegltrum 2008, Steyaert et al. 2014) and indicate that this forest management practice has minimal influence on use of 16-30-year-old stands by black bear populations as a whole. They also highlight the importance of individual patterns of behavior in black bear populations and how bears may respond to different forest management techniques.

The lack of any population-level consistency in changes to black bear use of forest stands between 16 and 30 years old, and indeed the other covariates I examined, in response to the presence of diversionary feeding is generally consistent with previous bear behavior research. Namely, diversionary feeding has been shown to increase black bear density around feeding stations in spring yet have minimal effect on average home range size near Olympia, Washington (Fersterer et al. 2001, Ziegltrum 2008), and supplementally pellet-fed and non-fed bears in the same system exhibited similar body composition despite individuals exposed to diversionary feeding manifesting faster growth rates during food supplementation periods (Partridge et al. 2001). Diversionary feeding has also been shown to have minimal effect on overall black bear travel patterns and subadult dispersal in Ely, Minnesota (Rogers 2010). A reduction in daily movement patterns, however, has been documented for brown bears (*Ursus arctos*) with access to feeding stations in south and central Finland as well as parts of Russian Karelia (Penteriani et al. 2021), implying that anthropogenic foods can impact individual movement patterns, at least in other bear species. Nevertheless, in conjunction with prior work on American black bears, my findings indicate that the presence of diversionary feeding has minimal impact on population-wide patterns in use of forest stands. By implication, any effects of diversionary feeding on tree damage caused by black bears are unlikely to manifest through changes to population-level use of forest age classes.

In my two study areas, individual black bears exhibited significant but contrasting use of nearly every covariate during both fed and unfed intervals, revealing considerable variation in resource use among individuals. The number of individuals displaying high use near 16-30-year-old stands stayed consistent in Snoqualmie Forest, but more individuals demonstrated high use away from, rather than near, this stand type during both fed and non-fed months. By contrast, the number of individual bears displaying significant use near young productive stands doubled in the DNR site from fed to non-fed times of year, suggesting there are other, unknown factors beyond feeding stations driving changes in habitat use among individual black bears. Variation in individual bear habitat selection has been documented previously in Michigan's northern Lower Peninsula, USA, with multiple bears demonstrating extreme, yet contrasting parameter estimates for habitat selection of various vegetative and topographic landscape features (Carter et al. 2010). Collectively, these findings support the growing body of evidence that variation among individual animals drives behavioral heterogeneity at the population-level. By implication, understanding patterns of resource use across bear populations will require increased scrutiny of individual behavior. Notably, I also documented individual variation in use of feeding stations by black bears in Snoqualmie Forest (Appendix S1, Supplemental Material). Namely, while black bears demonstrated significant population-wide use of feeding stations when they were supplied, three bears demonstrated significant use away from these locations during the months of March through June, underscoring the strong contrasting patterns in resource use I observed across landscape covariates. Similarly, research on black bear use of anthropogenic food sources in Colorado and Nevada showed that unintended food provisioning does not entice all bears (Johnson et al. 2015, Lewis et al. 2015, Garshelis et al. 2017), and individual variation in brown bears, rather than physiological state, best explained the strength and direction of selection for feeding stations in south-Central Sweden and south-central Slovenia (Kavčič et al. 2013, Stayaert et al. 2014, Kavčič et al. 2015), indicating that individual bear responses to anthropogenic disturbance can also vary and that diversionary feeding efforts are unlikely to entice all bears. Thus, our understanding of the causes of human-bear conflict, including the damage caused by tree peeling, may benefit from targeting the drivers of individual variability rather than assuming that there is population uniformity.

Although individual variation largely precluded consistent population trends in resource use in my two study areas, I did detect significant population use of a few resources. Namely, bears on the DNR site manifested significant population use of mature forest (>45 years of age), however, there were no significant differences between the study areas in black bear use near these stand ages. I also documented significant use of low elevation areas by the bear populations in both study areas, which may be tied to a general trend of higher use near large waterbodies and rivers by bears as seasons change and daily temperatures begin to increase from spring to summer (Sawaya et al. 2016). The use of low elevation areas July through October suggests that black bears venture into lowland areas during warmer months in Washington where they can access perennial water sources and opportunities to forage on natural food sources (e.g., salmonberry) become more plentiful.

I failed to detect differences between male and female bears in the use of various forest age classes. In the DNR study area from March through June, however, only females bears exhibited significant use near the 16–30-year stand age class, whereas on Snoqualmie Forest an equal number of male and female bears displayed significant use near this stand age. This pattern is consistent with previous research in the Pacific Northwest demonstrating that female bears are associated with higher tree peeling frequency and conifer damage than their male counterparts (Collins et al. 2002), which requires greater time allocation in highly productive forest stands, yielding more intense resource use of these forest types. Fersterer et al. (2001) found some bears, particularly females with cubs, avoided feeding locations where antagonistic encounters with male bears heightened, suggesting additional research investigating differences between bear sexes in tree peeling behavior and the use of diversionary feed is needed. Patterns of interspecific competition around feeding stations and how they influence individual black bear resource use also warrants further investigation.

The proportion of 16-30-year-old stands was slightly different between the two study sites prior to and during the study (Appendix S1, Supplemental Material), with greater amounts of young forest stands present in Snoqualmie Forest, presumably because harvest occurs much more frequently and with greater intensity in this forest than on the DNR site. Nevertheless, there were no differences between study sites in bear use near this forest age class despite all bears in both study areas having access to 16-30-year-old stands, and all bears in Snoqualmie Forest having access to at least one known feeding station within their home range. Thus, my study design allowed for robust comparison of bears with broadly similar environments but exposure to divergent forest management systems. I do acknowledge, however, that differences in herbicide application, human recreational activity, and other unmeasured factors may have impacted black bear use of young forest stands in the two study sites, but addressing these possibilities was beyond the scope of my investigation. Accordingly, there remains a need for additional work, and in particular, experiments that specifically address the direct impacts of diversionary feeding on bear behavior and ecology.

Despite diversionary feeding of American black bears being a component of private forestry management for decades, both the effects of diversionary feeding and harvest rotation on bear behavior and population dynamics remain largely unknown. In this study, I attempted to bridge this knowledge gap by investigating whether divergent management practices and the presence or absence of diversionary feeding altered black bear use of productive young timber stands. Use by black bears did not differ between forested land with and without diversionary feeding stations, when they were and were not supplied. Some individual bears, though, spent less time in young forest stands, a possible consequence of diversionary feeding. Thus, the effects of diversionary feeding on bear resource use may not manifest at the population level yet still intensify competition and alter behavior for individual animals at specific locations around feed sites. Future investigations of diversionary feeding should explore direct use of, and foraging patterns by, individual animals at feeding stations to identify the mechanism driving the efficacy of this management practice. Such inquiry would help to explain why feeding stations appear to reduce tree damage (Ziegltrum 2004, Ziegltrum 2008) even though they apparently do not diminish use of land cover associated with tree peeling. From a forest management perspective, the individual variation exhibited by black bears in this study suggests that supplemental feeding programs will not entirely obviate bear-induced tree damage (Nolte et al. 2002). Accordingly, forest management entities seeking to minimize economic losses to timber products should consider other non-lethal deterrents, especially for individual bears not attracted to feeding stations. Overall, the diversionary feeding program in western Washington has been ongoing for more than 3 decades, yet timber damage complaints have not been reduced (R. Beausoleil, Washington Department of Fish and Wildlife, unpublished data). Other studies have found that predictable artificial foods may attract bears from other areas (Massé et al. 2014), and also cause earlier den emergence. Artificially fed bears may grow faster, be larger, reproduce at an earlier age, and have increased litter sizes. Given the amount of food being provided in private timberland across Washington State, it is therefore likely that den emergence, reproduction, dispersal, survival, and density are all affected in areas with feeding stations, so it remains unclear whether pellet feed has a net positive or negative effect on bear populations, or the amount of damage to timber products. Accordingly, there is need for further research exploring both the demographic and economic consequences of this management activity.

3.6 LITERATURE CITED

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3.7 APPENDIX S1: SUPPLEMENTAL MATERIAL

3.7.1 Study Site Differences in Forest Stand Composition

I assessed the proportion and distribution of 0-15, 16-30, 31-45, and >45-year-old forest stands in the Snoqualmie Forest and Department of Natural Resources (DNR) study sites using the *R* package *Landscapemetrics* to quantify habitat differences between these managed landscapes in 2013 and 2018. Functions within Landscapemetrics use raster data as input and FRAGSTATS-style metrics (Kupfer 2012, McGarigal et al. 2012) to conduct analyses of patch-based discrete landcover classes (Hesselbarth et al. 2019). In both 2013 and 2018, there was a greater proportion of mature forest (>45-year-old stands) in the DNR site than in Snoqualmie Forest (Figures S1-S4). By contrast, the proportion of forest stands <45 years of age was greater in 2013 and 2018 in Snoqualmie Forest than in DNR. The proportion of 16-30-year-old stands, which was the age distribution targeted by our prediction that the presence of diversionary feeding would translate to divergent population wide patterns in bear resource use between our study sites, was different between Snoqualmie Forest and DNR at the beginning and end of the investigation.

In 2013, 16-30-year-old stands comprised 18% of the forest cover in Snoqualmie Forest at an average patch distance of 119 (sd = 57) m, whereas the same-aged timber stands in 2013 comprised 12% of DNR land at an average patch distance of 127 (sd = 67) m (Fig. 2). The proportion of 16-30-year-old stands on Snoqualmie Forest decreased to 13% in 2018, likely a consequence of timber harvest. Mean patch distance decreased slightly as well to 76 (sd = 39.9) m, suggesting these stands occurred in closer proximity toward the end of the study despite fewer overall stands of this age. The amount of 16-30-year-old stands on state trust lands also decreased over time, with the proportion of this age class on the DNR site in 2018 being 8%, with a mean patch distance of 79.5 (sd = 52) m. Thus, there was approximately an additional 60 km^2 of 16-30-year-old stands in Snoqualmie Forest compared to the DNR site at the beginning of the study, which was reduced to a difference of 44 km^2 in 2018.

3.7.2 Use of Diversionary Feeding Stations

In Snoqualmie Forest, Washington Department of Fish and Wildlife biologists identified and recorded coordinates for 55 feeding stations, providing an opportunity for me to test how attractive these locations were for individual bears overlapping at least one feed site. I used the Ruf.fit package (Marzluff et al. 2004) in R (R Core Team 2021) using only distance to known feeding locations as a covariate for only bears navigating Snoqualmie Forest during fed (March 01 - June 30) and non-fed (July 01 – October 30) times of year. Diversionary feeding RUFs revealed significant use near diversionary feeding stations for seven (64%) black bears occupying Snoqualmie forest during times when feeding stations were supplied (a diversionary feeding RUF for a single bear failed to converge), suggesting that feeding stations represent an attractive landscape attribute for most black bears. The consistency across bears translated to significant population-level use of feeding stations (-2.813, CI: -5.059, -0.567) when diversionary feeding was active in Snoqualmie Forest (Table S1). The same RUF analysis was run for non-fed times of year (July – October), and only five (45%) bears exhibited high use near diversionary feeding locations. Population level use near feeding stations was non-significant for bears from July – October, providing further evidence that diversionary feeding is a food source that is widely used across bears.

3.7.3 LITERATURE CITED

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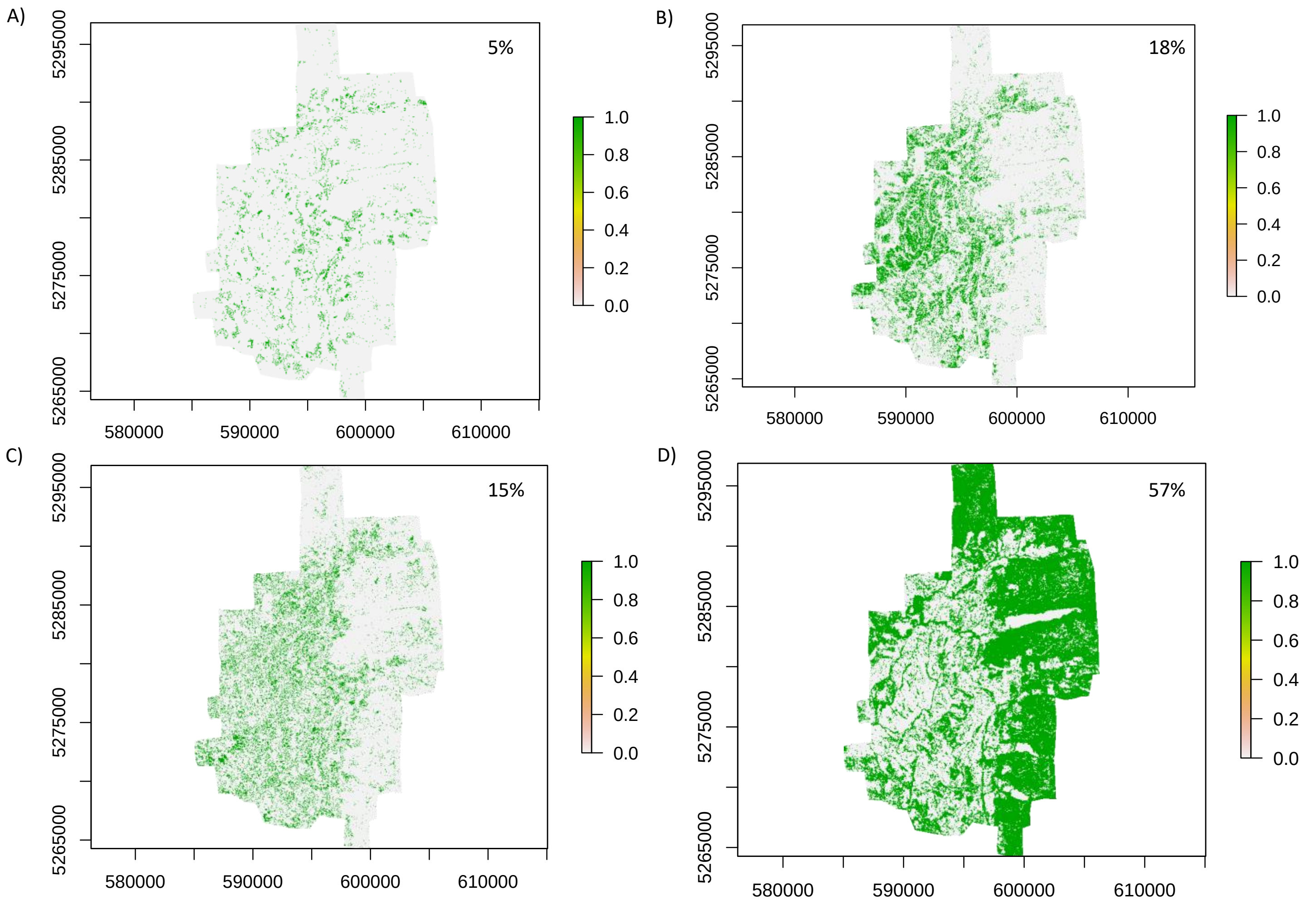

Figure S1. Location and distribution of forest stands in 2013 in Snoqualmie Forest across a) 0-15, b) 16-30, c) 31-45, and d) >45 (and <1000) year-old age classes. Proportions of each stand type are indicated by percent forest in the upper right corner of each panel. Diversionary feeding occurred in consistent locations in Snoqualmie Forest every year of the study March through June. UTM coordinates are represented by the x and y axes and the map legend indicates pixel values, with each panel containing only pixels of that selected age class.

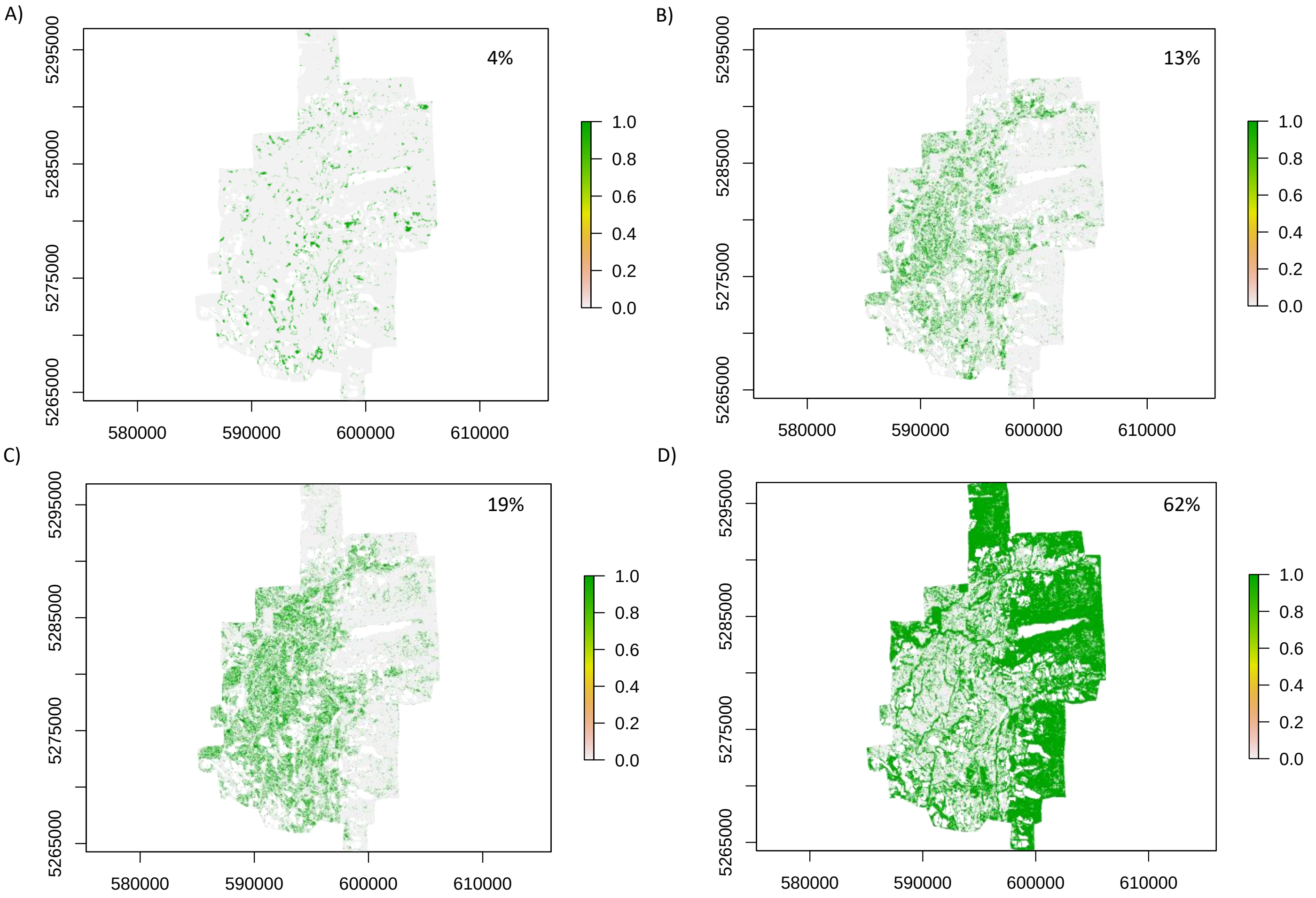

Figure S2. Location and distribution of forest stands in 2018 in Snoqualmie Forest across a) 0-15, b) 16-30, c) 31-45, and d) >45 (and <1000) year-old age classes. All clearcuts that occurred during the study are included in this analysis of landscape configuration, and proportions of each stand type are indicated by percent forest in the upper right corner of each panel. Diversionary feeding occurred in consistent locations in Snoqualmie Forest every year of the study March through June. UTM coordinates are represented by the x and y axes and the map legend indicates pixel values, with each panel containing only pixels of that selected age class.

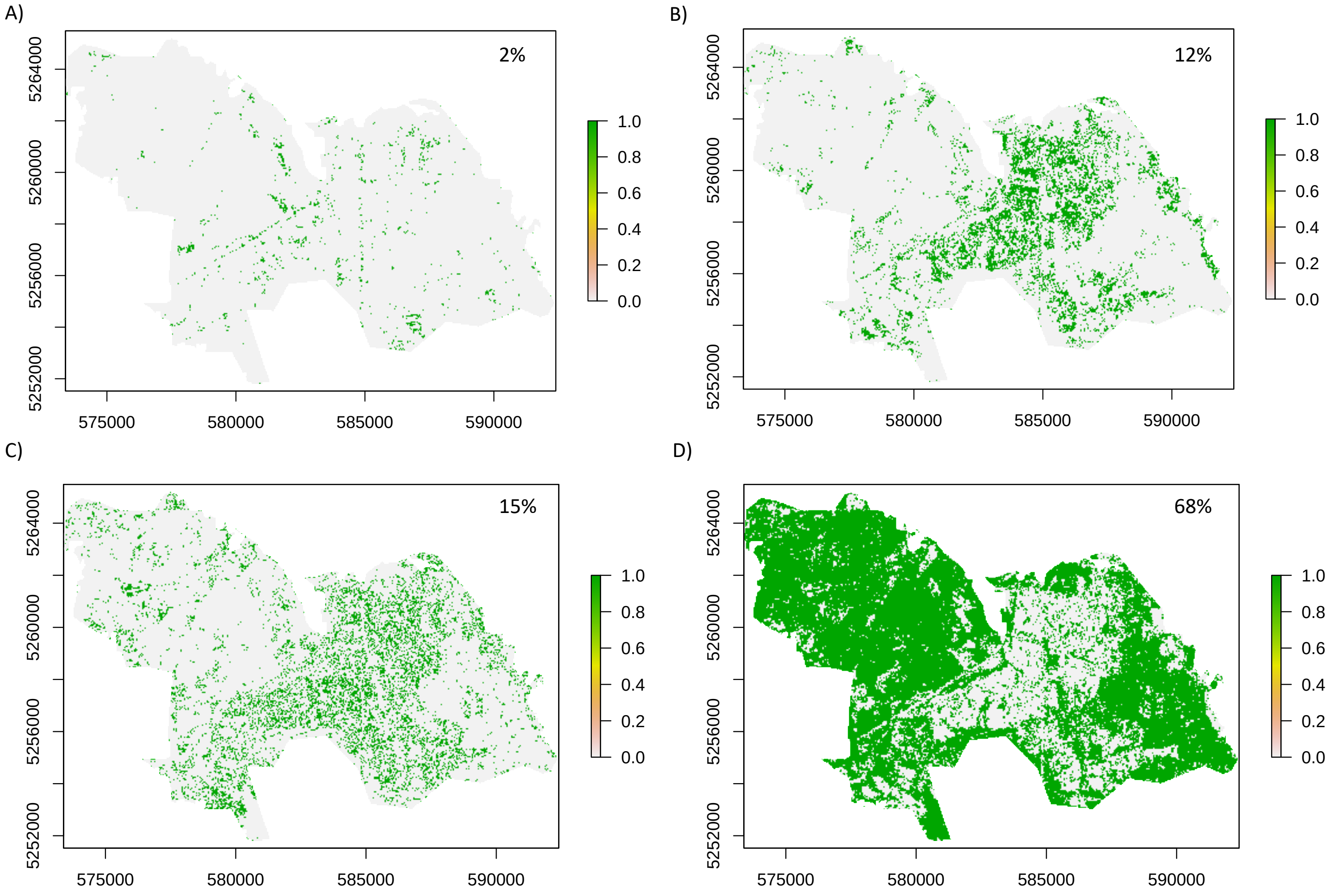

Figure S3. Location and distribution of forest stands in 2013 in the DNR study area (Tiger Mountain State Forest, Raging River State Forest, and Rattlesnake Scenic Area) across a) 0-15, b) 16-30, c) 31-45, and d) >45 (and <1000) year-old age classes. The proportion of each stand type is indicated by percent forest in the upper right corner of each panel. Diversionary feeding never occurred on the DNR site. UTM coordinates are represented by the x and y axes and the map legend indicates pixel values, with each panel containing only pixels of that selected age class.

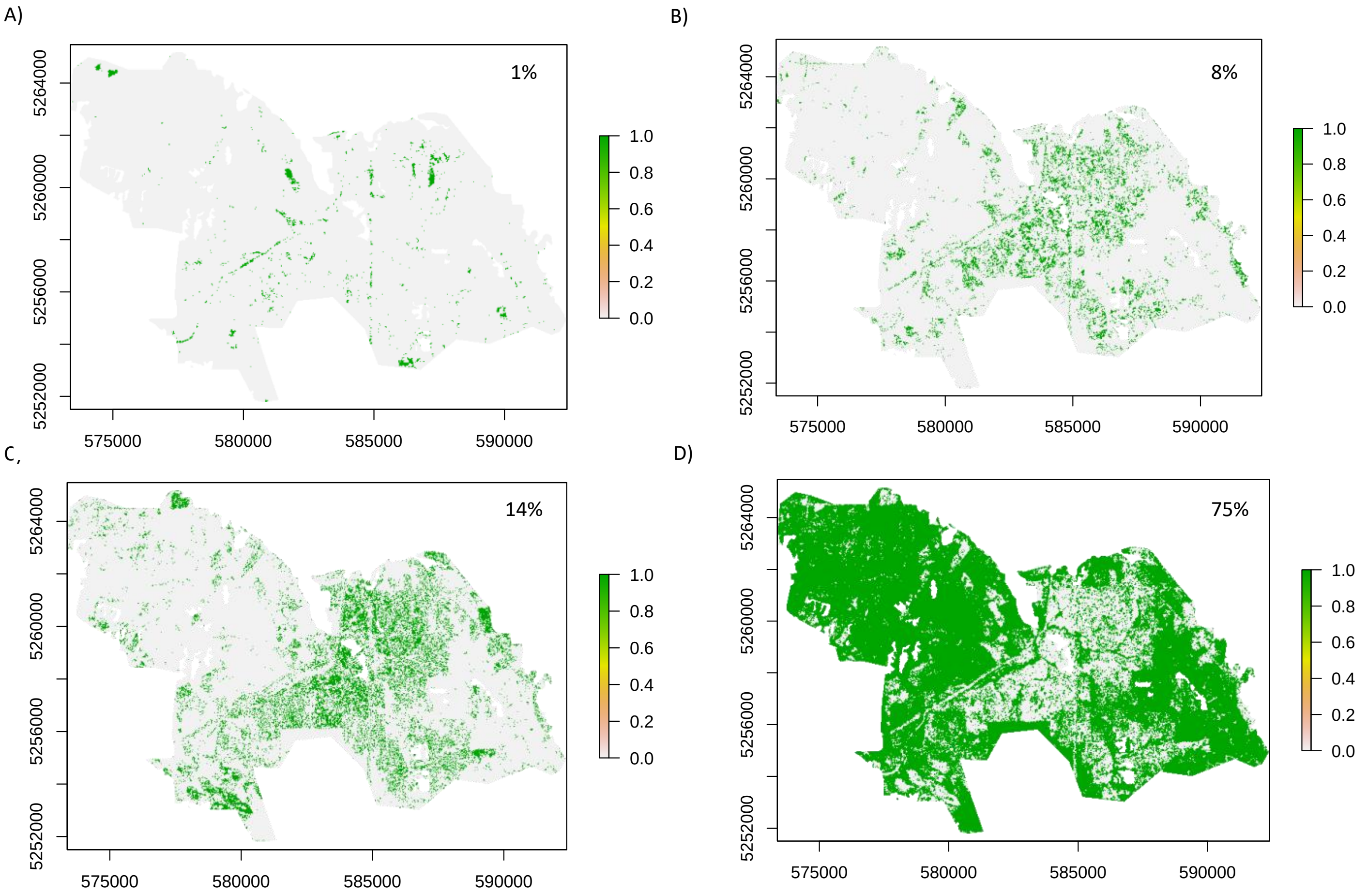

Figure S4. Location and distribution of forest stands in 2018 in the DNR study area (Tiger Mountain State Forest, Raging River State Forest, and Rattlesnake Scenic Area) across a) 0-15, b) 16-30, c) 31-45, and d) >45 (and <1000) year-old age classes. All clearcuts that occurred during the study are included in this analysis of landscape configuration, and proportions of each stand type are indicated by percent forest in the upper right corner of each panel. Diversionary feeding never occurred on the DNR site. UTM coordinates are represented by the x and y axes and the map legend indicates pixel values, with each panel containing only pixels of that selected age class.

Table 1S. Diversionary feeding mean standardized RUF coefficients for black bears (*Ursus americanus*) in Snoqualmie Forest during months when feeding stations were supplied (March through June) and non-supplied (July through October) in western Washington, USA 2013 - 2020. Diversionary foods were pellet-based feed and were placed in consistent locations throughout the course of this investigation. We were able to locate and GPS 55 feeding station locations, which we consider a conservative estimate of the number of feeding stations in Snoqualmie Forest. Bold font indicates significant resource use (i.e., confidence interval does not include 0). Use increases with each unit increase (+) or decrease (-) in distance from feeding stations. The furthest right column indicates number of individual bears with significant positive (+) or negative (-) coefficient estimates.

		Snoqualmie Forest (n = 11)		
Attribute	**Season**	**Mean standardized $\hat{\beta}$ (SE)**	**95% Confidence Interval**	**No. Bears with significant Coefficient (+/-)**
Feeding Stations	Feeding Months	**-2.813**	**-5.059, -0.567**	3/7
Feeding Stations	Non-Feeding Months	-1.633	-6.282, 3.015	5/5

CHAPTER 4: RESIDENTIAL DEVELOPMENT REDUCES BLACK BEAR SCAVENGING ON COUGAR KILLED PREY

4.1 ABSTRACT

Large carnivores commonly scavenge on kills made by fellow guild members, but the degree to which this type of intraguild interaction is influenced by urbanization remains unclear. To address this knowledge gap, I investigated whether residential development, measured as housing density, along with demographic and environmental covariates, impacted the propensity for American black bears (*Ursus americanus*) to scavenge cougar (*Puma concolor*) killed prey along the wildland-urban gradient of western Washington, USA. Under the refuge hypothesis, whereby residential development increases foraging on small-bodied prey by cougars and/or draws black bears to anthropogenic subsidies, I expected scavenging events to decrease as housing density increased. Alternatively, under the pile-up hypothesis whereby reduced green space drives greater overlap and thus interactions among carnivores, I predicted that bear scavenging events would increase with housing density. Generalized linear models (GLMs) derived from kill site data from 12 GPS-collared cougars and forensic evidence of bear carcass visitation demonstrated that cougar prey handling time was a significant positive predictor of bear scavenging probability, whereas the summer season and housing density were significant negative predictors of black bear scavenging events. The odds of a black bear scavenging a cougar kill under the top scavenging GLM indicated a multiplicative decrease of 1000 in the odds of black bear carcass visitation for every additional house/ha on the landscape, supporting the refuge hypothesis. These results suggest that residential development has the potential to alter intraguild relationships among large carnivores, even at modest levels where robust carnivore populations persist on the landscape and may promote provisioning of carrion for non-bear scavengers by virtually eliminating black bear scavenging.

4.2 INTRODUCTION

Large mammalian carnivores can exert top-down control of ecosystems by suppressing ungulate herbivory (e.g., Hebblewhite et al. 2005), modifying intraguild competition (e.g., Vanak et al. 2013, Pringle et al. 2019), reducing prey abundance through direct predation (e.g., Holt et al. 2008), altering prey behavior (e.g., Preisser et al. 2005, Creel and Christianson 2008, Say-Sallaz et al. 2019), and subsidizing other species (e.g., Elbroch et al. 2017, Barry et al. 2019). Consequently, these species often play pivotal ecological roles from their positions at the top of food webs (Estes et al. 2011, Ripple et al. 2014, Stier et al. 2016). By implication, interspecific interactions among large carnivores have the potential to alter spatiotemporal patterns of top-down forcing and, ultimately, ecosystem properties (Grassel et al. 2015, Hubbard et al. 2022). Accordingly, studies of factors that shape intraguild relationships among large carnivores can improve our capacity to predict how ecosystem dynamics are likely to respond to perturbation.

Large carnivores commonly interact by competing indirectly (via resource exploitation) or directly (via interference) for food (Creel 2001) and through interspecific killing (Kerry et al. 2004, Donadio and Burskirk 2006). These species may also scavenge on kills made by other guild members (Pereira et al. 2014, Walker et al. 2021). In so doing, they may affect the amount of carcass tissue available for cycling through the rest of the food web (Allen et al. 2014) and, in the case of kleptoparasitism (i.e., parasitism by theft; Allen et al. 2021), resource acquisition and potentially fitness of the carnivore that made the kill (Elbroch et al. 2015, Balme et al. 2017). Thus, studies of scavenging interactions among large carnivores are key to a comprehensive understanding of their ecological effects.

Research on scavenging interactions at carcasses among large carnivores has thus far occurred predominantly in wildland landscapes or protected areas. In the Dinaric Mountain Range of Slovenia and the Gorski Kotar region of Croatia, for example, brown bears (*Ursus arctos*) are among a group of carnivores that kleptoparasitizes Eurasian lynx (*Lynx lynx*) prey remains, leading to reduced carcass biomass for lynx (Krofel et a. 2019, Krofel et al. 2022). Similarly, ursids and avian scavengers have been observed visiting grey wolf (*Canis lupus*) prey remains in Yellowstone National Park, Wyoming, USA, and south-central Scandinavia (Ballard et al. 2003, Tallian et al. 2021), with small wolf packs losing large amounts of carcass biomass to scavengers (MacNulty et al. 2001, Smith et al. 2003). Yet, many landscapes occupied by or being recolonized by large carnivores are subject to at least some form of anthropogenic disturbance, which can modify the ecological relationships of these species (Kuijper et al. 2016, Gaynor et al. 2019, Ordiz et al. 2021). Hence, there remains need for a better understanding of patterns of kleptoparasitism in anthropogenic landscapes and how human-driven landscape modification may shape this kind of predator-predator interaction. To address this knowledge gap, I explored how residential development impacts scavenging of cougar (*Puma concolor*) prey remains by a sympatric large carnivore, the American black bear (*Ursus americanus*), in western Washington, USA.

Cougars are solitary, far-ranging predators that often subsist on ungulate species (Kertson et al. 2011a, Robins et al. 2019) and occupy a broad range of habitat types in both temperate and tropical environments of the Americas (Sunquist and Sunquist 2002). Cougars, like many solitary predators, suffer energetic loss due to kelptoparasitism when foraging on large ungulate prey (Krofel et al. 2012, Allen et al. 2021), and this resource subsidization has been shown to support high vertebrate scavenger diversity, including several carnivore species (Elbroch et al. 2017). The black bear is a generalist, opportunistic omnivore, and although meat usually accounts for a small proportion of this carnivore’s diet (Maser 1998), it is known to scavenge large-bodied cougar-killed prey. In wildland environments, black bears have been documented visiting carcasses of cougar-killed ungulates in California (Allen et al. 2014, Elbroch et al. 2021), Washington (Kertson et al. 2011a), and the Greater Yellowstone Ecosystem (GYE; Elbroch et al. 2017). Prior research on black bear use of cougar kills in California and Colorado (Elbroch et al. 2015) demonstrated that partial prey consumption by cougars is more strongly explained by bear visitation than the tenets of optimal foraging, suggesting scavenging events often involve instances of kleptoparasitism. Consequently, cougars often adjust their foraging rate in response to bear kleptoparasitism. For example, cougars spent 22% less time at ungulate carcasses when black bear (*Ursus americanus*) scavenging occurred in Mendocino National Forest, California (Allen et al. 2021). Thus, bear scavenging of cougar-killed prey can be important to the foraging behavior of both species, but how urbanization impacts this interaction has yet to elucidated.

In western Washington at the foothills of the Cascade Mountains, cougars and black bears occur throughout a well-defined wildland-urban gradient (0 - >10 residences/ha; Robinson et al. 2005, Kertson et al. 2011b, Kertson et al. 2013). Prior research in this region indicates that black bears scavenge cougar kills, and that both species use exurban and suburban landscapes (Kertson et al. 2013, Welfelt 2019). Accordingly, I leveraged this system to evaluate two hypotheses about how increasing residential development could alter the propensity for black bears to scavenge cougar kills. The refuge hypothesis, whereby residential development reduces the incentive for black bears to scavenge carrion by increasing cougar use of small-bodied (<40 kg; Smith et al. 2016), non-ungulate prey and providing anthropogenic food resources for bears (Elbroch et al. 2015, Robins et al. 2019), predicts black bear occurrence at cougar kill sites to decrease with increasing housing density. Alternatively, the pile-up hypothesis, whereby the intensity of carnivore competition peaks at moderate levels of anthropogenic disturbance because top predators are still capable of persisting, but habitat and resource limitations heighten antagonistic encounters (Riley et al. 2006, Gehrt et al. 2010), predicts black bear visitation to cougar kills to increase with increasing housing density. I also expected under both hypotheses that bear scavenging of cougar killed prey would be correlated with warmer daily temperatures and the summer season, which is consistently the warmest season in Washington State, as hotter weather may contribute to carcass spoilage, increasing carcass detection by bears. Lastly, I tested for differences in cougar handling time as a function of housing density to determine whether cougars decreased time spent at kills as urbanization intensified, functionally reducing scavenging opportunities for bears. Under the refuge hypothesis, where cougar diets in urbanizing landscapes include more alternative, small-bodied prey, I expected handling time to decrease as housing density increases. I also expected handling time to decease as housing density increases under the pile-up hypothesis, as cougars have previously demonstrated reduced handling times as a response to kleptoparasitism (Elbroch et al. 2015).

4.3 METHODS

4.3.1 Study area

I visited cougar kill site locations and documented scavenging behavior by black bears in a 993 km^2 research site encompassing portions of King and Snohomish Counties in Washington, USA (590 000 E, 5 260 000 N; Fig. 4.1). The study site is an amalgamation of state, federal, municipal, and private property, with major landowners including the Washington Department of Natural Resources, the United States Forest Service, City of Seattle, King County, and Campbell Global, (King County GIS Center, 2016). Cities and towns within the study area include Bellevue (population 139,820), Redmond (60,598), Issaquah (36,081), Snoqualmie (13,169), Duvall (7,674), and North Bend (6,679) (US Census Bureau 2015).

The study site is topographically complex and is characterized by a gradual east-west gradient spanning wildland (0 residences/ha), exurban (< 2.5 residences/ha), suburban (2.5-10 residences/ha), and urban (> 10 residences/ha) environments (Robinson et al. 2005, Kertson et al. 2011b). Private timberland, Washington Department of Natural Resources forestland, and United

Figure 4.1. Location of the 993 km^2 research site encompassing portions of King County, Snohomish County, and a small section of wildland in Pierce County (<75 km^2). The study site is characterized by a gradual east-west gradient of residential development (gray polygon) spanning wildland (0 residences/ha), exurban (<2.5 residences/ha), suburban (2.5-10 residences/ha), and urban (>10 residences/ha) environments.

States Forest Service holdings comprise much of the eastern portion of the study site. Most wildland spaces within the study area consist of temperate coniferous forests typical of the North Cascades eco- region (Franklin and Dyrness 1973). Cougars within the study area primarily prey on black- tailed deer (*Odocoileus hemionus columbianus*), elk (*Cervus elaphus*), beaver (*Castor canadensis*), raccoon (*Procyon lotor*), and mountain beaver (*Aplodontia rufa*; Kertson et al. 2011b, Robins et al. 2019), but their diet can also include mountain goats (*Oreamnos americanus*), coyotes (*Canis latrans*), opossums (*Didelphis virginiana*), river otters (*Lontra canadensis*), mink (*Neovison vison*), black bears (*Ursus americanus*), and domestic species. Black bears in western Washington are a dominant scavenger, but may also prey upon deer fawns, elk calves, and fish when available. The topographic, physiographic, and developmental characteristics of the study site are described at greater length in Kertson et al. (2011b, 2013).

4.3.2 Capture, Collaring, and GPS Cluster Analysis

Washington Department of Fish and Wildlife biologists and I used trained dogs to tree cougars, and cage traps to capture cougars, allowing us to radio-tag adult cats (n=37) throughout the study site from 2013 to 2017. Once captured, cougars were immobilized, given a physical examination, and outfitted with a global positioning system (GPS) radio-collar equipped with Globalstar satellite uplinks (GPS Plus-2, Vectronic Aerospace, Berlin, Germany). All captured cougars were anesthetized using a 10:1 mixture of Ketamine hydrochloride and Xylazine hydrochloride (Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) at a dosage of 8.8 mg/kg ketamine and 0.88 mg/kg xylazine and handled in accordance with University of Washington Institutional Animal Care and Use Committee (IACUC) protocol No. 3077-07 and American Society of Mammalogists' guidelines for the use of wild mammals in research (Sikes et al. 2016).

All cougar capture methods have been vetted previously and described in detail elsewhere (Kertson et al. 2011a, Kertson et al. 2011b, Robins et al. 2019).

Cougar global positioning system radio-collars were programmed to attempt a satellite fix for 180 seconds every 4 hours at 2:00, 6:00, 10:00, 14:00, 18:00, and 22:00 hours. The 4-hour fix interval was chosen to maximize data acquisition and battery life (Cain et al. 2005, Kertson et al. 2011b). I identified potential cougar kill site locations in accordance with the methodology used by Robins et al. (2019). Namely, I first plotted cougar relocations in ArcMap 10.3 and 10.4 (Environmental Systems Research Institute 2016) and Google Earth (Google Inc., Mountain View, California, USA) and then defined location clusters as ≥3 GPS fixes occurring within an area ≤100m^2 (methods by Anderson and Lindzey 2003 adapted slightly to account for small prey items). After identifying potential predation sites, I used a handheld GPS receiver (Model Etrex 20, Garmin Ltd., Schaffhausen, Switzerland) to navigate to the geometric center of the cluster and then searched in concentric circles varying between 5m and 10m apart (depending on visibility) out to the extent of the cluster radius (up to 100m) or until prey remains were discovered. I recorded a GPS location at the kill site if prey remains were found that closely matched the dates during which the cluster was created and if I also found definitive evidence of cougar feeding behavior (e.g., carcass caching behavior, drag marks, hemorrhaging, skeletal remains, and cougar scat; Knopff et al. 2009, White et al. 2011, Kertson et al. 2011a, Wilckens et al. 2016). I attempted to visit potential cougar kill sites after the animal ceased foraging, but within 2-4 weeks of the final GPS fix recorded at the cluster location in order to obtain as much data on each prey item as possible (e.g., sex, age, and relative condition, Cheatum 1949, Ballard 1995).

4.3.3 Kill Site Assessment and Scavenging Behavior Documentation

Kill site assessment followed the same methodology as Kertson et al. (2011a) and is described in detail in Robins et al. (2019). Briefly, after confirming each kill site location based on the presence of prey remains, hair, drag marks, and caching behavior (Beier et al. 1995; Knopff et al. 2009, Wilckens et al. 2016), I adjusted kill site coordinates on-site to correspond to the location of the rumen. Cougars may cache a carcass 0-80 meters from the initial kill location during subsequent feeding bouts (Beier et al. 1995), so designating the position of the rumen as the kill location allowed for more consistent assessment of kill site features. If the prey item was a non-ungulate species, I used the presence of intestines and internal organs to record the location of the kill site. Whenever possible, I documented prey species, sex, age, condition, and relative carcass consumption. I determined prey sex in ungulates based on antler presence or absence, and prey age using dentition and patterns of tooth wear and replacement (Severinghaus 1949). Similar to other studies, I documented black bear scavenging behavior at cougar kill sites using forensic evidence of bear visitation on the ground determined by the presence of black bear footprints, hair, and scat near carcasses (Murphy et al. 1998, Elbroch et al. 2015). Forensic evidence is effective at documenting bear visitation, with cameras often used to quantify carcass consumption or scavenger diversity (Allen et al. 2014, Allen et al. 2021). Twelve cougars wore GPS collars long enough to produce adequate kill data for this investigation; I documented 306 non-winter (November – February) kills by these individuals when bears were largely active on the landscape. Of those 306 predation events, 58 were visited by black bears based on forensic evidence.

4.3.4 Assessing Housing Density

To create a housing density predictor variable, I identified residences throughout the study area using ArcMap 10.3 and 10.4 (Silverman 1986, Robins et al. 2019) and 2015 GIS county parcel data from King and Snohomish counties, Washington, USA. All portions of Pierce country in the study site were considered wildland. available county parcel data and their associated assessor's tables containing parcel attribute information were acquired through the university of Washington libraries media archive. county parcel data have been used previously to assess large carnivore responses to urbanization in western Washington (Robins et al. 2019) and housing density data have been shown to be a good predictor of land cover composition and configuration (Alberti et al. 2007).

4.3.5 Statistical Analysis

I tested for differences in bear scavenging of cougar killed prey as a function of housing density and several other covariates using generalized linear models (GLMs) with a binomial distribution and logit link function using the 'glm' function in the 'lmer4' package in R (Bates et al. 2015, R Core Team 2022). I initially tested for the need to use generalized linear mixed models (GLMMs), as multiple observations for individual animals often warrant the inclusion of random effects. A likelihood ratio test comparing null GLM and GLMM models demonstrated random effects were not necessary, however, as cougars exhibited little variation in propensity to have their kills scavenged by black bears (Appendix S2, Figure S5, Supplemental Material). GLM covariates other than housing density included cougar sex, the seven-day temperature high and low following the first cougar GPS location at the kill site, season (spring: March – May, Summer: June – August, Autumn: September – November), time until investigation in days, and handling time in hours. I included time until kill site investigation to account for the influence of temporal variation in data collection on detecting black bear scavenging events. I considered the refuge hypothesis supported if housing density was a significant negative predictor of scavenging events, and the pile-up hypothesis supported if housing density was a significant positive predictor of black bear carcass visitation. Under the refuge hypothesis, as well as the pile-up hypothesis, I expected higher daily temperature, the summer season, and handling time to be significant positive predictors of kleptoparasitism. I ran all combinations of predictor variables and ranked GLM models according to differences in Akaike's Information Criterion (ΔAIC) and considered models within < 2 AIC_c units of the top model to be equally supported (Burnham and Anderson 2002). The top model was used to make inferences on the effect of housing density on black bear scavenging behavior.

I separately tested for differences in cougar handling time as a function of housing density, including cougar sex, season, and prey type using a GLM with a negative binomial distribution and log link function through the 'glm.nb' function in the 'MASS' package in R (Venables and Ripley 2002, R Core Team 2022). Handling time in this analysis was treated as the number of 4-hour fix intervals, with the number of GPS fixes determined according to the first and last cougar GPS location at a given kill site (Elbroch et al. 2015). A likelihood ratio test comparing null negative binomial GLM and GLMM models demonstrated random effects were not a significant model predictor and therefore did not need to be included in model structure (Appendix S2, Figure S6, Supplemental Material). I considered the refuge hypothesis supported with significant a negative predictor for the summer season, decreasing handling time, and significant negative predictors for prey type and housing density. I again made inferences based on the top handling time model and used (ΔAIC) for model ranking, considering models within < 2 AIC_c units of the top model to be equally valid (Burnham and Anderson 2002). Significance for all covariates in scavenging GLMs and handling time GLMs were determined using 95% confidence intervals.

4.4 RESULTS

I documented 306 cougar (*n* = 2 males, *n* = 10 females) kill site locations in spring (*n* = 100), summer (*n* = 142), and autumn (*n* =64) from 2013-2017, and 58 black bear scavenging events. Only one cougar, F34, had zero kills scavenged during this investigation (Table 4.1). Under the top scavenging model (Table 4.2), which included all predictor variables, black bear scavenging of cougar-killed prey decreased significantly as housing density increased (β = -7.135, CI = -14.644, -2.339; Table 4.3). I found that the odds of a black bear scavenging cougar prey remains were 0.001 (CI = 0.000, 0.313) as housing density increased, which translates to a multiplicative decrease of 1000 in the odds of black bear kleptoparasitism for every additional house per ha on the landscape (Figure 4.2). Thus, the probability of a kill being scavenged by a black bear decreased to greater than 99% in landscapes characterized by 1 or more residences/ha (Figure 4.3). The summer season (β = 1.130, CI = 0.066, 2.314) and cougar handling time (β = 0.010923, CI = 0.003, 0.019) were also significant positive predictors of black bear visitation in the top model. The odds of black bear scavenging were 3.096 (CI = 2.769, 3.461) times greater in summer than the fall season. The odds of scavenging events exhibited a multiplicative increase of 1.011 (CI = 1.003, 1.019) as handling time increased, translating to a 14% increase in the chances of a black bear scavenging a cougar prey remains for each additional 4-hour GPS interval a cougar was present at a kill (figure 4.4).

The top handling time GLM model included season and prey type (Table 4.4). A statistically competitive model included housing density as an independent variable, but this covariate was dropped during model fit due to rank deficiency (e.g., insufficient variable data to estimate the model). In this model (Table 4.5), the spring season was a significant positive predictor (β = 0.357, CI = 0.124, 0.588), and small-bodied prey was a significant negative predictor (β = -0.473, CI = -0.832, -0.094), of cougar handling time. The incidence rate ratio for the spring season was 1.43 (CI = 1.13, 1.80), indicating greater handling times occurred at approximately a 1.5 times greater rate in spring than in fall (Figure 4.5). The incidence rate ratio for cougars foraging on small-bodied prey was 0.62 (CI = 0.44, 0.91), demonstrating that handling time approximately doubles for cougars foraging on large-bodied prey relative to small-bodied prey.

Table 4.1. Cougars (*Puma concolor*) used in this analysis (n = 12) with associated identification numbers, sexes, numbers of kills found through field investigations, as well numbers of kills scavenged by black bears (*Ursus americanus*).

Cougar ID	Cougar Sex	Total Kills	Kills Scavenged
4	Female	27	3
5	Male	10	3
6	Female	29	7
8	Female	25	5
12	Female	20	2
14	Female	33	6
17	Female	64	11
30	Female	9	1
34	Female	21	0
35	Female	25	6
37	Male	14	2
41	Female	29	12

Table 4.2. Generalized linear models (GLM) of black bear scavenging on cougar killed prey, with all models within 10 ΔAIC_c of the top model included, as well as the null model.

Response Variable	**Predictor Variables**	**AIC_c**	**ΔAIC_c**	**Model likelihood**	**AIC_c Weight**
Scavenged	Cougar Sex, Season, Temperature (High/Low), Time Until Investigation, Handling Time, Prey Type, Housing Density	279.77	0	1	0.551
Scavenged	Season, Handling Time, Housing Density		1.67	0.434	0.239
Scavenged	Handling Time, Housing Density		2.15	0.341	0.188
Scavenged	Season, Housing Density		7.04	0.030	0.027
Scavenged	Cougar Sex, Housing Density		9.02	0.011	0.006
Scavenged	Null Model		16.46	0.000	0.000

Table 4.3. Covariate estimates for the best fit binomial scavenging GLM model. Bold fonts indicate significant covariates, defined by a 95% confidence interval not overlapping zero.

Generalized Linear Model		
Predictor	**Estimate (SE)**	**95% Confidence Interval**
Cougar Sex (Male)	0.443 (0.580)	-0.772, 1.541
Season (Spring)	0.740 (0.525)	-0.257, 1.826
Season (Summer)	**1.130 (0.569)**	**0.066, 2.314**
Temperature (High)	-0.042 (0.022)	-0.087, 0.001
Temperature (Low)	0.004 (0.035)	-0.023, 0.116
Time until Investigation	0.001 (0.003)	-0.006, 0.007
Handling Time	**0.011 (0.004)**	**0.003, 0.019**
Prey Type (small-bodied)	-15.720 (703.599)	-257.327, 12.559
Housing Density	**-7.135 (3.071)**	**-14.644, -2.339**
Intercept	-1.827 (1.456)	-4.801, 0.928

Table 4.4. All negative binomial generalized linear models (GLM) of cougar handling time, with models within 10 ΔAICc of the top model shown, as well as the null model.

Response Variable	**Predictor Variables**	**AICc**	**ΔAICc**	**Model likelihood**	**AICc Weight**
Handling time	Season, Prey Type	1572.4	0	1	0.303
Handling time	Season, Prey Type, Housing Density		0	1	0.303
Handling time	Cougar Sex, Season, Prey Type		1.0	0.607	0.184
Handling time	Cougar Sex, Season, Prey Type, Housing Density		1.0	0.607	0.184
Handling time	Cougar Sex, Season		5.0	0.082	0.025
Handling time	Null Model		22.5	0.000	0.000

Table 4.5. Covariate estimates for the best fit handling time GLMM model of cougar handling time. Bold fonts indicate significant covariates, defined by a 95% confidence interval not overlapping zero.

Predictor	Estimate (SE)	95% Confidence Interval
Season (Spring)	**0.357 (0.118)**	**0.124, 0.588**
Season (Summer)	-0.116 (0.112)	-0.339, 0.104
Prey Type (small-bodied)	**-0.473 (0.186)**	**-0.832, -0.094**
Intercept	2.630 (0.092)	2.450, 2.815

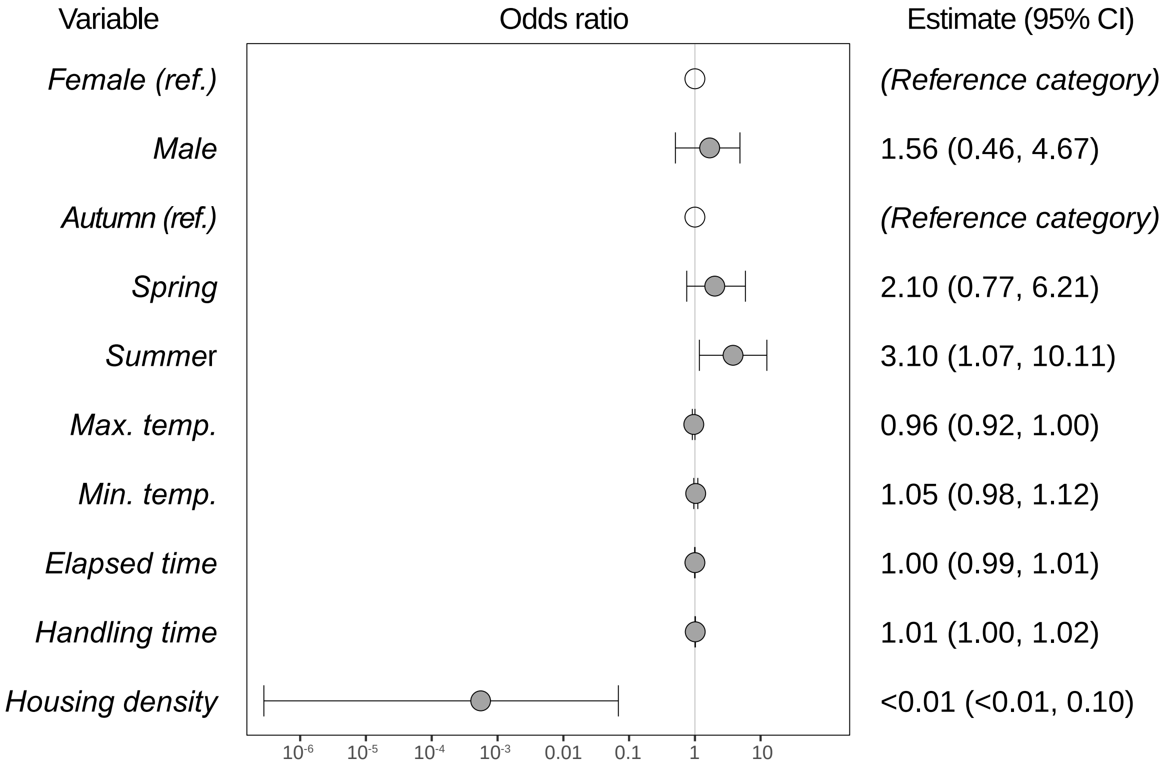

Figure 4.2. Odds ratios and 95% confidence intervals for all covariates included in the top scavenging binomial GLM model. Odds ratios are relative to 1, with values greater than 1 signifying increased chances of kleptoparasitism and values less than 1 indicating decreasing chances of kleptoparasitism. Parentheses indicate reference categories used in the GLM.

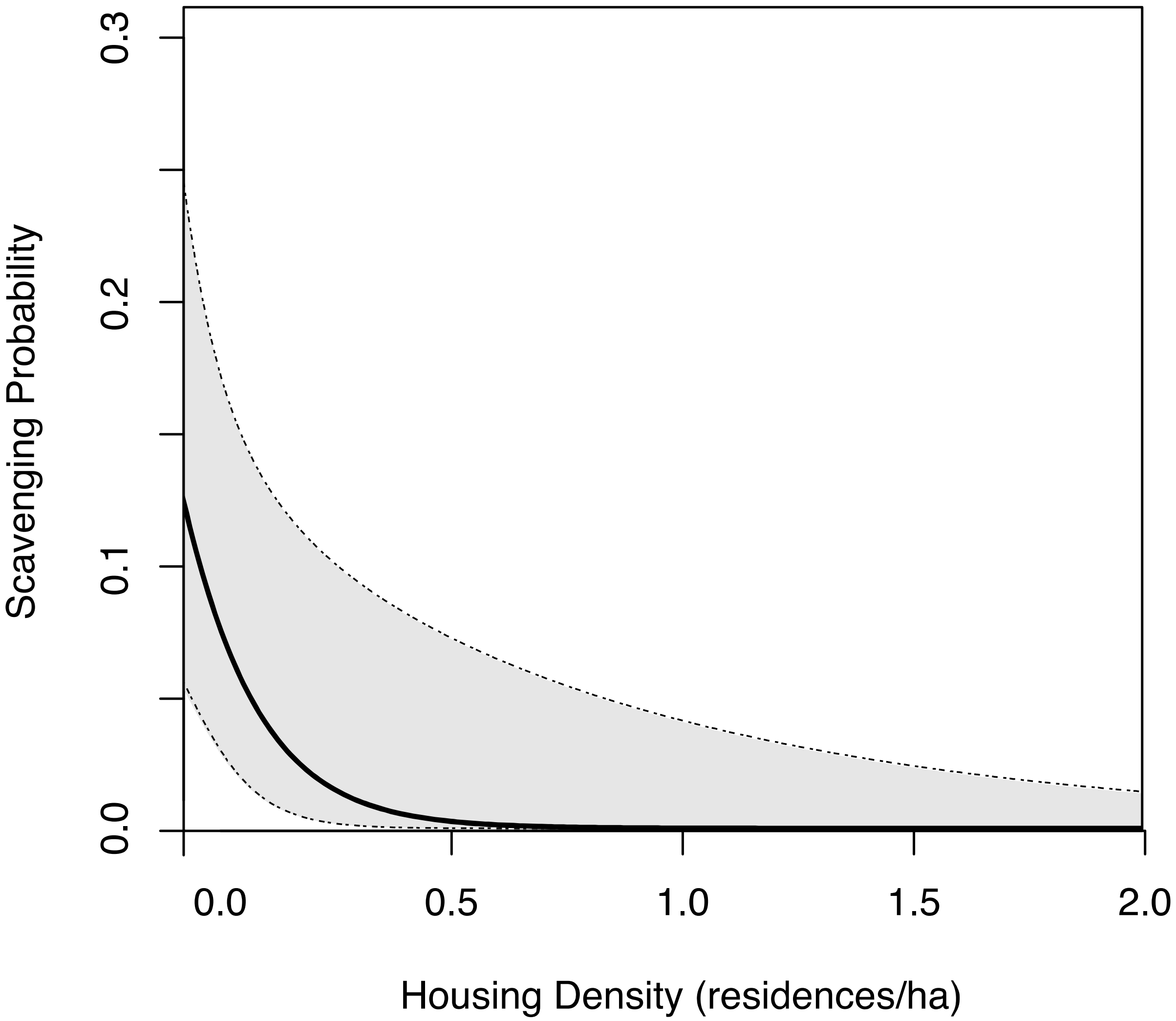

Figure 4.3. Probability of black bear kelptoparasitism as housing density increases (residences/ha) based on the top scavenging GLM model. All other model covariates are held constant at their means, with the black line indicating probability and the boundaries of the gray polygon indicating the 95% confidence band.

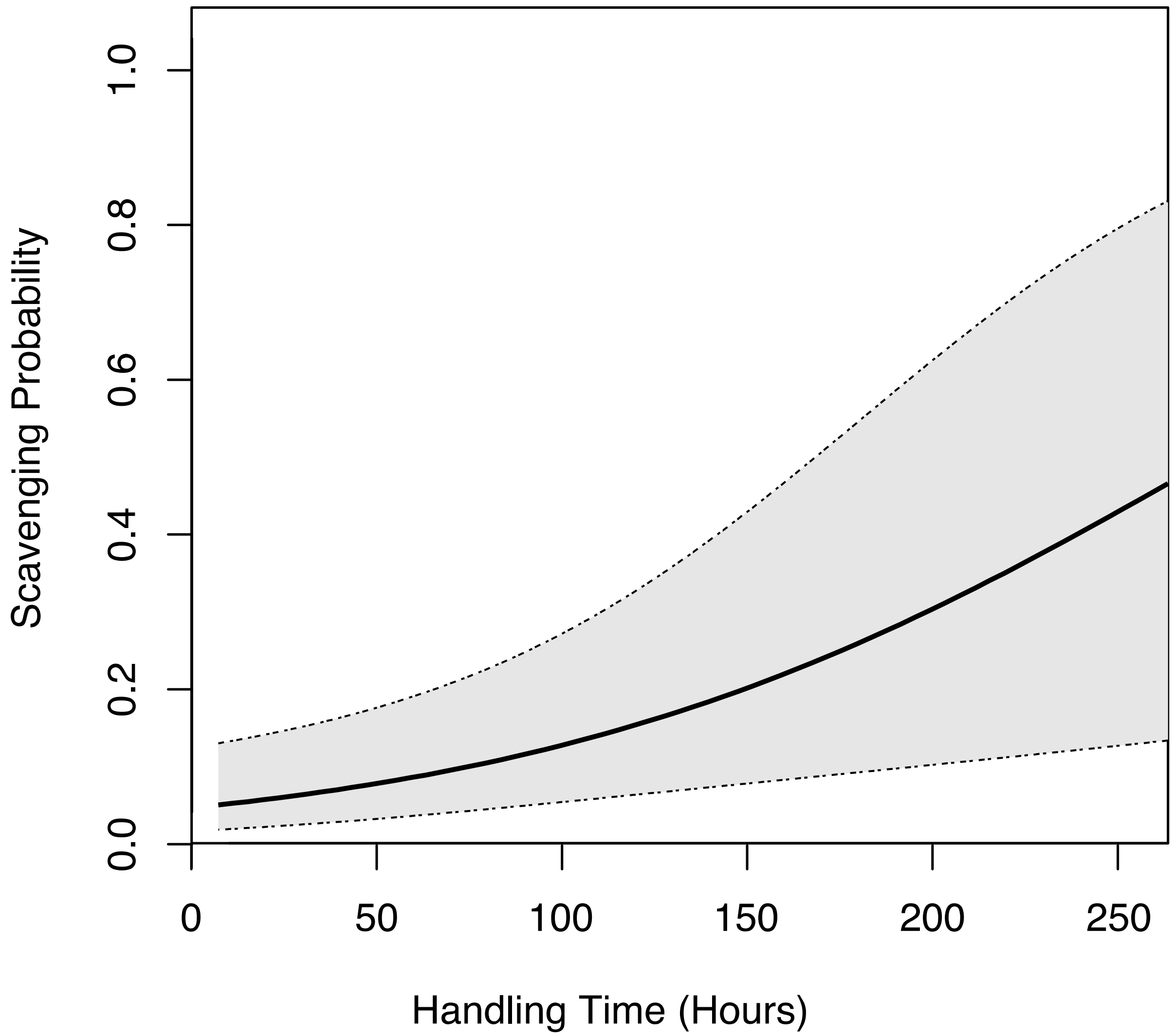

Figure 4.4. Predicted probability of black bear scavenging as carcass handling time (hours) by cougars increases under the top scavenging GLM model. All other model covariates are held constant at their means, with the black line indicating probability and the boundaries of the gray polygon indicating the 95% confidence band.

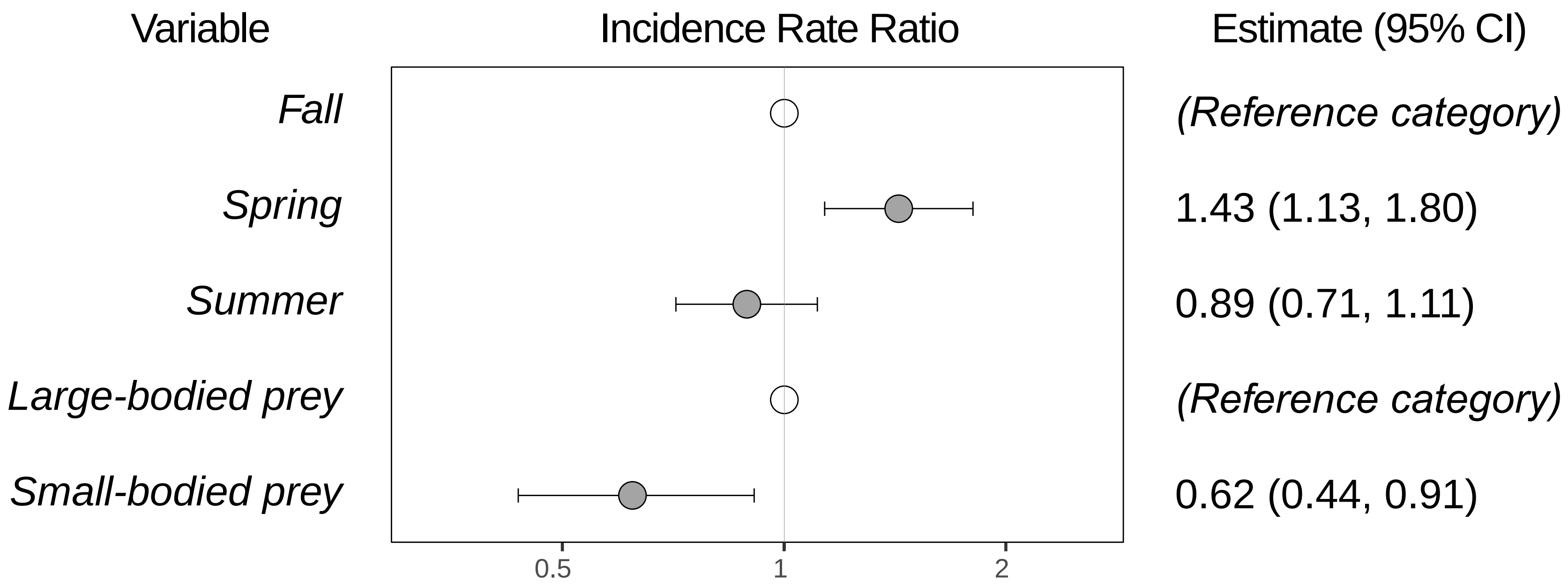

Figure 4.5. Incidence rate ratios and associated confidence intervals for all covariates in the top negative binomial handling time GLM. Rate ratios can be interpreted as relative risk related to 1, with values greater than 1 signifying increasing probability of longer handling times by cougars and values less than 1 indicating reduced handling time. Parentheses indicate reference categories used in the GLM.

4.5 DISCUSSION

Urbanization is a pervasive driver of large carnivore presence and behavior globally (Woodroffe 2000, Cadillo et al. 2004, Bateman and Flemming 2012). However, previous research on large carnivore responses to urbanization have largely focused on individual species and less so on changes to interspecific relationships (Lewis et al. 2017), including scavenging interactions (Luna et al. 2021). To address this knowledge gap, I asked whether black bear scavenging of cougar-killed prey would either decrease (refuge hypothesis) or increase (pile-up hypothesis) as urbanization intensifies. I found that black bear scavenging events increased in frequency during the summer season and with the time it took cougars to handle prey, but decreased significantly as housing density increased, supporting the refuge hypothesis. Furthermore, cougar prey handling time increased significantly during the spring season and decreased significantly when cougars were foraging on small-bodied prey (<40 kg), partially supporting the refuge hypothesis as I expected handling times to decrease when cougars were foraging on synanthropic prey and in the summer season during the hottest portion of the year. To my knowledge, this is the first study to demonstrate that anthropogenic development can decouple scavenging relationships within large carnivore guilds. My results also shed new light on the cougar-black bear relationship, particularly by suggesting that residential development may shape cougar foraging behavior through reduced costs imposed by black bear kleptoparasitism.

There is growing recognition that anthropogenic landscape modification and presence can alter interactions involving predators (Newsome et al. 2015, Kuijper et al. 2016, Gaynor et al. 2019, Ordiz et al. 2021). Most research to date has addressed the possibility of humans modifying large predator effects on smaller predators and prey species. In Croatia, for example, shifts to increased nocturnality by red foxes (*Vulpes vulpes*) to reduce detection by larger carnivores (grey wolf, *Canis lupus*; Eurasian lynx, *Lynx lynx*) were moderated in areas with increased human activity (Haswell et al. 2020), and anthropogenic resource subsidies (livestock carcasses) reduced wolf predation on wild prey in Italy (Ciucci et al. 2020). My results add a new pathway by which human activity can influence predator ecology: disruption of scavenging relationships between large carnivores. Notably, the effect of residential development on black bear scavenging was immediate and marked. Namely, the odds of a black bear scavenging on cougar-killed prey decreased by greater than 1000 times for every additional residence per ha on the landscape, resulting in the chances of a bear scavenging event being less than 1% at residential densities greater than 1 house/ha. Moreover, this effect was not solely a function of reduced black bear presence or density. Although Welfelt et al. (2019) estimated that black bear density in my study area decreased with human development (from 27.8 bears/100 km^2 in wildland areas to 13.5 bears/100 km^2 in developed areas), the odds of bear scavenging at cougar kills decreased by multiple orders of magnitude across the landscape – a far greater effect size than differences in bear density alone can explain. Cougar have also demonstrated a consistent, albeit nuanced, response to human development in both eastern and western portions of Washington state (Maletzke et al. 2017). By implication, residential development has the potential to alter intraguild relationships among large carnivores even at levels that allow for the affected carnivores to persist on the landscape. The extents to which this effect of residential development on large carnivore scavenging relationships triggers population responses and is mirrored by other forms of anthropogenic disturbance are beyond the scope of the present study and remain as important research frontiers.

Previous research on carnivore-carnivore interactions in urbanizing environments has largely focused on competition involving mesocarnivores (Lewis et al. 2015, Malhotra et al.

2022) and often indicated that urbanization increases opportunity for interspecific interactions by limiting useable greenspace for wildlife, supporting the pile-up hypothesis. For example, forest fragmentation was the most important determinant of interspecific interactions between foxes, bobcats (*Lynx rufus*), and coyotes in Washington, D.C., USA and Raleigh, N.C., USA, especially as urbanization increased (Parsons et al. 2019). My results demonstrate, by contrast, that residential development reduces black bear scavenging of cougar prey remains, supporting the refuge hypothesis. Thus, the impacts of urbanization on interspecific relationships in carnivore communities appear to differ as a function of the species involved and the type of interaction in question. Similarly, temporal avoidance of humans and dominant competitors by subordinate carnivores in anthropogenic ecosystems does not follow a consistent pattern (Seveque et al. 2021), suggesting more broadly that human mediation of intraguild interactions involving carnivores is context dependent. Accordingly, there is need for studies aimed at identifying the factors that determine whether and how anthropogenic perturbation shapes carnivore interactions and coexistence.

Why did the incidence of black bear scavenging on cougar-killed prey decrease with increasing residential development? Previous research on cougar foraging behavior along the wildland-urban gradient of western Washington revealed increased usage of synanthropic prey as urbanization intensified (Kertson et al. 2011a, Robins et al. 2019), suggesting that cougars adjust their diets when exposed to more opportunities to exploit urban prey (Moss et al. 2016, Smith et al. 2016). Consistently, all cougar kills in this study that occurred at housing densities greater than 0.5 residences/ha were of either alternative prey (e.g., raccoon) or young ungulates, ultimately translating to a significant reduction in handling time compared to wildland kills in the handling GLM model. Similarly, cougar research in the central coast region of California and the northern Front Range of Colorado showed that housing density contributed to increased use of alternative or small-bodied (<20kg) prey species, which were often synanthropic species common in urbanization environments owing to a commensal relationship with humans (Smith et al. 2016, Moss et al. 2016). Increased use of smaller, synanthropic prey taxa by cougars may therefore be at least partly responsible for limiting scavenging opportunities for black bears near residential development.

A second and non-mutually exclusive reason for reduced scavenging of cougar kills as urbanization intensifies is that black bears in developed landscapes have greater access to alternative, calorie-rich food sources than their wildland counterparts. Indeed, black bears in western Washington occupying the urban fringe have been shown to be larger and rely more heavily on anthropogenic food sources than conspecifics navigating much less developed eastern portions of the state (Welfelt et al. 2019). Furthermore, black bears have been shown to forage on anthropogenic foods near residences even when natural, wildland foods were available in and around Missoula, Montana, USA (Merkle et al. 2013), suggesting that human foods provide greater nutritional value than carrion and natural food sources. Answering whether black bears in our study system were drawn away from cougar kills in areas with higher residential density by more attractive anthropogenic food sources was beyond the scope of the present analysis and thus fodder for future research. Anecdotally, however, I would note that, in support of this hypothesis, all focal cougars provided carrion to black bears with the exception of F34, a female that spent relatively little time in wildland environments compared to other study animals.

Black bear scavenging of cougar-killed prey peaked during the summer season, with 50% of all scavenging events occurring during the months of June through August, partially supporting my carcass spoilage prediction. My covariate for high daily temperature during the kill period was marginally non-significant in our scavenging GLM model. It is therefore possible that warmer ambient temperatures translate to more rapid carcass decomposition and greater olfactory cues for black bears, but this phenomenon may be more strongly tied to seasonal shifts in western Washington than to more granular changes in daily temperatures. Increased carcass visitation by black bears in summer was also documented in Rocky Mountain National Park, Colorado, where bears increased their use of animals, and particularly ungulates, following the spring season (Baldwin and Bender 2009). A relationship between scavenging and warm weather was also found for black bears in the Mendocino National Forest of northern California (Allen et al. 2021), though in this study bears had a greater propensity for carcass visitation when there were higher daily temperatures. In conjunction with the results of these other investigations, my findings suggest that carcass biomass may be an especially important source of animal protein for black bears during the summer, at least in wildland landscapes. Furthermore, the fact that past studies have documented effects of seasonal and daily temperature fluctuations suggests that both variables should be considered in future explorations of bear scavenging in urbanizing landscapes.

Previous research has demonstrated significant individual variation in cougar diets across western Washington’s wildland-urban gradient (Robins et al. 2019). The focal cougars in the present study, however, did not differ significantly with respect to prey handling time, with disparities among cougars in time spent at carcasses predominantly being tied to prey size. Collectively, these patterns suggest that susceptibility to black bear carcass visitation may be relatively consistent across individual cougars in wildland landscapes. The random effect variable for cougar identity was also not retained in the top model of black bear scavenging. My analysis did not discriminate between cases where black bears kleptoparasitized cougar kills from those where bears merely visited carcasses after the cougar had departed. Therefore, it remains possible that rates of kleptoparasitism, rather than scavenging overall, vary among cougars. Accordingly, future research should isolate cases of carcass usurpation by bears and then test for individual variability and demographic differences in the frequency with which cougars experience this phenomenon.

It is possible that some bear scavenging events were not detected in this study. However, my kill site investigations were conducted thoroughly and with a standardized protocol that has also been employed by prior studies investigating cougar kill sites and the bear-cougar relationship (Kertson et al. 2011a, Elbroch et al. 2015, Allen et al. 2021). Thus, given the strength of the negative relationship between residential development and black bear scavenging that was detected, the addition of what was probably a small number of missed scavenging events would have been unlikely to alter the outcome of our analysis. It is also possible that housing density has an impact on cougar handling time, and the inclusion of this covariate during handling time model fitting may have altered the strength of small-bodied prey effect. The prey type covariate, however, was significant in all viable handling models, suggesting it is an important predictor of handling time. Nevertheless, other aspects of urban development that I did not address (e.g., roads and trails, time of day, human presence) may have affected both cougar handling time and bear foraging behavior and thus should be the focus of further investigation.

There is ample evidence that human landscape development and associated food resources can alter the behavior and ecology of large terrestrial predators (Newsome et al. 2014), but this is the first study to show that residential development can shape scavenging relationships between large carnivores. My findings also reveal that the impacts of urbanization on interspecific relationships among large carnivores can be dramatic: even relatively modest levels of residential development associated with the transition from wildland to exurban environments (1 house/ha) all but eliminated black bear scavenging, effectively disassociating this aspect of the bear-cougar relationship. Kleptoparasitism is a common outcome when black bears make use of cougar kills, with 38% of scavenging events in Colorado and California, USA resulting in kelptoparasitism (Elbroch et al. 2015). Thus, my results imply that the negative effects of bears on cougars may relax in residential landscapes despite reduced green space and natural food sources compared to wildland environments. If so, then cougar kill rates, which have been shown to increase in wildland landscapes in response to black bear kleptoparasitism (Elbroch et al. 2015), may actually decline in urban environments that also include bears. Accordingly, there is need for research examining how urbanization gradients shape cougar predation patterns, particularly on ungulates. In wildland environments, cougars have been found to support a greater diversity of scavenging species by providing carrion than either wolves or human hunters (Elbroch et al. 2017). My findings suggest that residential development may promote this provisioning effect for non-bear scavengers by virtually eliminating bear scavenging events, both before and after the cougar has departed. On the other hand, urbanization appears to correspond with cougars using smaller, synanthropic prey species, which may provide less tissue to scavengers. Thus, future studies also should explore use of cougar-provided carcasses by the wider scavenging community along wildland-urban gradients.

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4.7 APPENDIX S2: SUPPLEMENTAL MATERIAL

4.7.1 Random Effect Estimates

I tested for the inclusion of random effects in both the scavenging binomial models and handling time negative binomial models. Random effect estimates for a scavenging GLMM with all covariates revealed minimal variance across cougars (Figure S5). A Likelihood ratio test (LRT) was used to test for the importance of random effects in scavenging models and demonstrated random effects did not improve model fit ($\chi^2(1) = 0.610$, $p = 0.435$), signifying only GLMs were necessary to model scavenging behavior. Similarly, an LRT for handling time models indicated random effects did not significantly improved model fit ($\chi^2(1) = 0.898$, $p = 0.343$), warranting the use of only GLMs. Random effect estimates for a handling time GLMM including all covariates demonstrated that only one female cougar, F14, exhibited significantly less handling time than the average study animal (Figure S6).

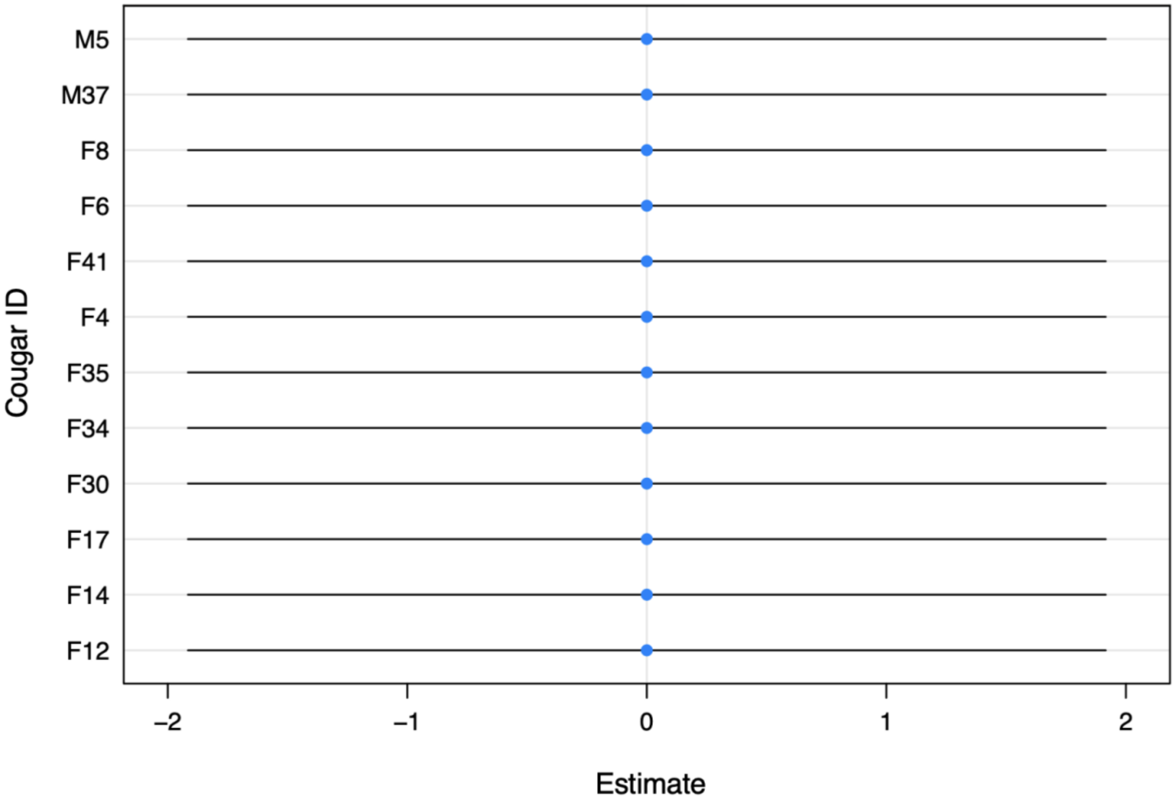

Figure S5. Random effects estimates for the full scavenging binomial GLMM. Blue dots indicate random effect estimates and grey bars indicate confidence intervals, with any confidence interval overlapping 0 indicating scavenging risk similar to the average cougar in this study.

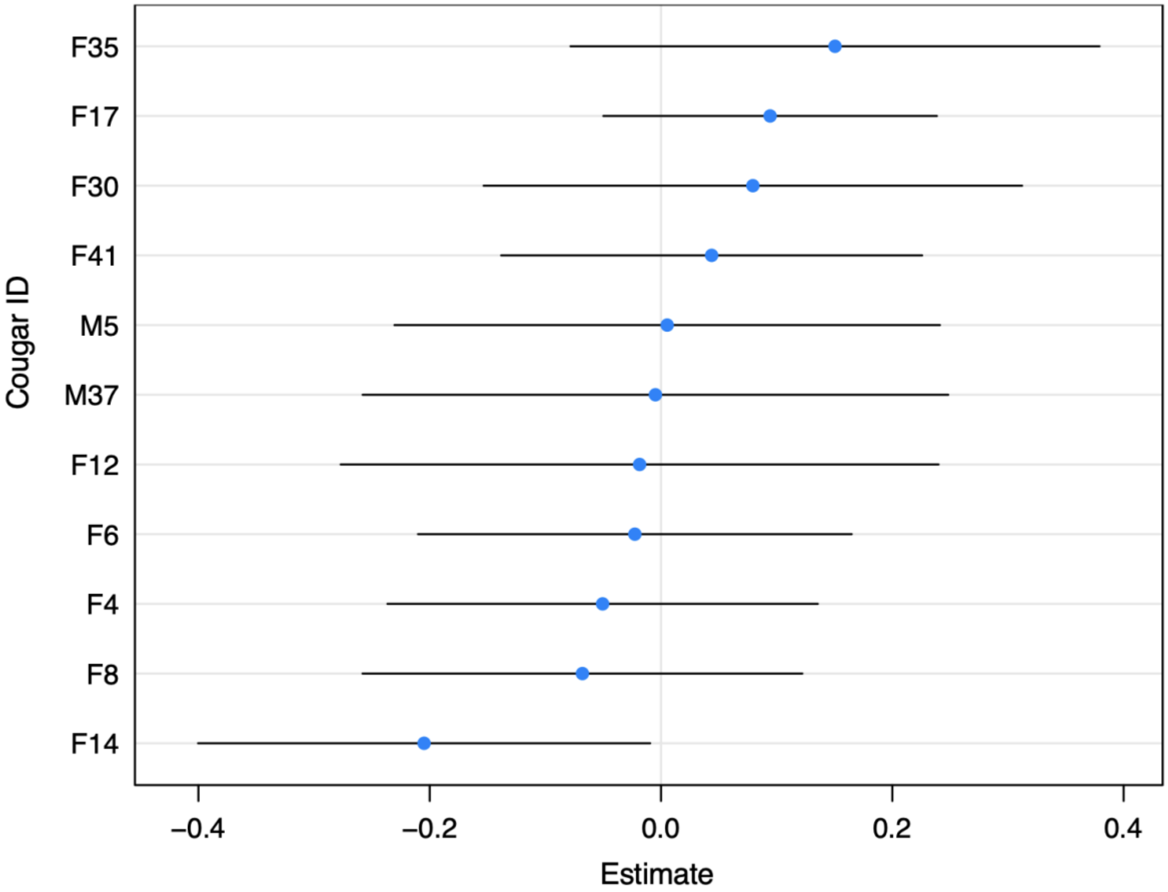

Figure S6. Random effects estimates for the full cougar handling time negative binomial GLMM. Grey bars indicate confidence intervals, with any confidence interval overlapping 0 indicating scavenging risk similar to the average cougar in this study.