Human Recreation in Protected Areas Impacts Spatial Dynamics and Risk-Resource Trade-Offs Among a Wildlife Community

by

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B.S., Montana State University, 2021

A Thesis Submitted in Partial Fulfilment of the
Requirements for the Degree of

MASTER OF SCIENCE

In the Department of Geography

We acknowledge and respect the Ləkʷəŋən (Songhees and Esquimalt) Peoples on whose territory the university stands, and the Ləkʷəŋən and W̱SÁNEĆ Peoples whose historical relationships with the land continue to this day.

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Abstract

Large mammals play critical roles in maintaining ecosystem balance, but their need for expansive, undisturbed habitat makes them particularly vulnerable to human activities. Protected areas are designed to conserve biodiversity by providing refuges for wildlife. However, within these areas, large mammals remain at risk from disturbances due to the growing trend of non-consumptive outdoor recreation. Understanding the effects of human presence on mammal communities and large carnivores like cougars (*Puma concolor*) is essential for informing effective land and wildlife management. This thesis addresses this need by examining how human presence affects cougars' risk-resource trade-offs, and then broadening the scope to assess human impacts on a community of large mammals. Data were collected from an array of 48 camera traps across the public-access Sooke Hills Wilderness Area Park (SHWA) and the restricted-access Greater Victoria Water Supply Area (GVWSA) on southern Vancouver Island. In Chapter 2, cougar occurrence was evaluated through competing hypotheses related to habitat, prey, and anthropogenic risk. These results were used to predict cougar occurrence across a network of roads and trails within the study area. Cougar occurrence was best explained by habitat and risk at a 750-meter buffer, where cougars avoided human presence but were more willing to tolerate this risk when their preferred habitat was available in the same area. In Chapter 3, I assessed how a community of large mammals, including Columbian black-tailed deer (*Odocoileus hemionus columbianus*), Roosevelt elk (*Cervus canadensis roosevelti*), cougar (*Puma concolor*), black bear (*Ursus americanus*), and grey wolf (*Canis lupus*) responded to landscape heterogeneity, heterospecifics' detection frequency, and land-use restrictions. Differences in community composition between the SHWA and GVWSA revealed that all wildlife species avoided public-access sites, with a clear difference in community composition due to access restrictions. Carnivore species overlapped spatially, suggesting reduced spatial partitioning due to human activity. This thesis shows that site-level human activity can alter risk-resource trade-offs for large carnivores, which can scale upwards to shift species distributions. Given the vulnerability of large mammals to disturbance, it is crucial to consider the impacts of non-consumptive activities on both apex predators and entire wildlife communities.

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Figure 3.3: AIC weights for the global model are shown at six spatial scales for each species: black-tailed deer (a), Roosevelt elk (b), grey wolf (c), black bear (d), and cougar (e). Higher AIC weights indicate better model performance at the corresponding spatial scale. The spatial scale, ranging from 125 meters to 750 meters, represents the buffer radius around each camera site.

Figure 3.4: Responses of black bear (a), cougar (b), and grey wolf (c) to habitat, risk, and predator-prey covariates. Estimates above the red dashed line indicate positive associations, while those below indicate negative associations. Note the spatial scales used in the models: black bear (125m buffer), cougar (625m buffer), and grey wolf (500m buffer).

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Acknowledgements

First and foremost, thank you to my supervisory committee, Chris Bone and Jake Fisher. This work would not have been possible without your guidance, support, and feedback. Chris, I am especially grateful for the reassurance and opportunities you've provided throughout this process. Our meetings always leave me feeling more confident in myself and my work. Not only have you helped me stay on track with my thesis, but you've also involved me in projects that have really enriched my experience over the past two years. Jake, thank you for sharing your knowledge and providing invaluable feedback that has shaped this work. Your enthusiasm for wildlife conservation research has been truly inspiring. I feel extremely privileged to have a committee of such knowledgeable, accomplished, and helpful individuals.

I'd also like to thank everyone involved at different stages of this project--whether it was installing cameras, tagging photos, participating in fieldwork, providing feedback, or simply supporting and appreciating this work. I'm grateful to Chris Bone and Elicia Bell for kickstarting this project, and special thanks to Elicia for introducing me into the world of camera traps and RStudio analysis. Our project collaborators, including those at CRD Watershed, CRD Parks, Coexisting with Carnivores Alliance, and T'Sou-ke First Nation have been invested and supportive of this work in various contexts since its inception. And a massive thanks to the team of undergraduate students who attended weekly workshops to tag over 300,000 photos for this project. Those who lead these workshops--Connor Monk, Emerald Arthurs, Elicia Bell, and Ben Milligan--were instrumental in turning hundreds of thousands of images into something meaningful.

I'm thankful for the UVic community and the SURREAL lab members who have created such a welcoming space. You have all encouraged me, provided company during an experience that can sometimes be isolating, and generously helped with my thesis by giving me advice and helping with fieldwork. I am forever grateful to have stumbled upon such an amazing group of people. And to my UVic friends, thanks for all the weekend hikes, coffee shop dates, and fun times as we mutually supported each other through the ups and downs of grad school.

Lastly, I am incredibly grateful for my family, who has encouraged my academic journey from the very beginning. Thank you to my parents Jennifer and Keith for giving me the freedom to choose my own path and for helping me move to a new country (and for covering my ferry rides back home). Thank you to my Grandma Gayle and Grandpa Sam, who not only inspired me to pursue grad school but have also contributed to my education and consistently encouraged and celebrated my accomplishments. To my brothers Ethan and Logan, who no matter how far apart we are, we can come back together and pick up where we left off. And to my partner Shamus, who always has an incredible amount of confidence in me, thank you for all the dinners, coffee, and encouragement that kept me going.

Chapter 1: Anthropogenic Impacts to Wildlife in a Changing World

Protected areas around the world face the immense and growing pressures of human disturbance (Sarmento & Berger, 2017). Protected areas harbour important wildlife communities and serve goals of conserving rare, threatened, and keystone species. These areas provide a robust defence against biodiversity loss in a rapidly changing world. Of significant importance is the fact that protected areas are intended to provide refuge for the world’s large carnivores and large mammal species, as the aim with developing such areas is to conserve biodiversity and maintain valuable habitat free from the threats of major human disturbance (Naughton-Treves et al., 2005). Outside of protected areas, human disturbance has been shown to negatively impact large mammals, namely their population movement, species persistence, predator-prey interactions, nutrient cycling, and disease transmission (Tucker et al., 2018). This is because large mammals require sizeable areas of connected, undisturbed land (Laliberte & Ripple, 2004), and have historically faced hunting and/or persecution by people (Cardillo et al., 2005; Minin et al., 2021). These factors render large mammals especially sensitive to the growing threats of anthropogenic disturbance (Crooks, 2002).

Ecological impacts on wildlife through habitat degradation and consumptive activities have been well-studied, whereas threats from non-consumptive activities have recently surged due to rapid urbanization, growing wealth, and a thriving ecotourism industry (Shackelford et al., 2018; Winemiller et al., 2014). Numerous studies detail the impacts of consumptive activities (habitat destruction, resource extraction, and hunting) on large mammals throughout North America (Crooks, 2002; Loveridge et al., 2017). The impact of these activities is direct and tangible, manifesting in habitat loss due to infrastructure development, habitat fragmentation due to logging, and animal mortality due to hunting

(Doherty et al., 2021; Fisher & Burton, 2018). Although protected areas help mitigate these impacts, there is growing concern that the effect of recreational activities (e.g., hiking, cycling, and dog walking) necessitates updated management strategies (Larson et al., 2016). We must reevaluate how dual mandate protected areas are achieving their goals of conserving healthy wildlife communities amidst the rapid growth of nature-based tourism (Watson et al., 2016; Weaver & Lawton, 2017). Given the increasing evidence that outdoor recreation plays an influential role in wildlife's spatio-temporal habitat use, it's important for researchers to study these impacts and give them the same level of consideration that is given to consumptive activities (Taylor & Knight, 2003).

One framework that helps explain the threat of outdoor recreation is the landscape of fear theory. This theory originally described the spatial variation in risk that large prey species (typically ungulates) perceive throughout a landscape, predicated on the occurrence of potential predator species (Laundré et al., 2001). Risk is perceived by prey species in spaces where predators occur. The landscape of fear theory can also be applied to human-wildlife interactions, where humans take on the "predator" role, inducing a fear response in wildlife species (Frid & Dill, 2002). The density and distribution of predators (in this case humans) are associated with risk cues, which vary throughout a human-disturbed landscape. These cues arise not only from the presence of humans but in some cases from the physical structures associated with them (Gaynor et al., 2019). The induced fear response, also known as an anti-predator response, is defined as any action aimed at reducing predation. Some of these actions, such as selecting less disturbed sites as habitat, are employed proactively to minimize risk (Gaynor et al., 2019). Thus, species must make trade-offs between avoiding risk and acquiring resources. Individuals may tolerate human risk to access preferred resources, or they may employ flexible spatio-temporal behaviours to avoid this risk, potentially enduring physiological costs or experiencing reduced resource acquisition (Blecha et al., 2018; Laundré et al., 2001; Mills et al., 2023). Immediate impacts of risk-avoidance include increased energetic costs, reduced acquisition of food and/or prey, and reduced reproductive success (Clinchy et al., 2013; Smith et al., 2015). However, long-term impacts of human-induced fear can lead to habituated spatial or temporal avoidance of areas, and in some cases, total abandonment of previously suitable habitat (Schuette et al., 2013; Sih, 2013). Abandonment of suitable habitat can redistribute populations across the landscape (Rogala et al., 2011). Further, non-consumptive human activities can have significant, detrimental impacts to not only individual mammal species, but to wildlife communities (Suraci et al., 2019).

The human-driven landscape of fear has the potential to unbalance entire ecosystems through behaviourally mediated trophic cascades, as predators may decrease their use of spaces where prey occur (Leighton et al., 2010). The cascade of effects begins with large carnivores, North America's most common apex predators (Winemiller et al., 2014). Large carnivores control the densities of species at lower trophic levels through predation, placing them in a regulatory ecological role (Winemiller et al., 2014). This regulatory role can be altered by human disturbance (Heithaus, 2001). Carnivores' anti-predator response to human occurrence has been shown to include spatio-temporal alterations of their habitat use (Suraci et al., 2019), and has implications for predator-prey dynamics (Parsons et al., 2019). For example, prey species may exploit highly peopled areas, which are associated with a higher risk for carnivores, to buffer from their own predation risk (Berger, 2007). In this case, human presence creates a "shield" for prey species from predation. These shifts in spatial habitat use by both predator and prey species in response to human presence can lead to cascading impacts throughout wildlife communities (Kuijper et al., 2015; Muhly et al., 2011).

The spatio-temporal effects of human-induced risk may be mediated by the intensity of human activity permitted within protected spaces (Keim et al., 2019). While most protected areas in North America permit recreation through dual mandates that support both outdoor recreation and wildlife conservation, some protected areas restrict public access (Pringle, 2017). Studies suggest there are significant differences in community composition between restricted-access and public-access protected spaces, with a notable decline in carnivore density within public-access areas (Kays et al., 2017; Reed & Merenlender, 2008). Effectively, recreation may hinder the ability for dual mandate protected areas to meet their goals of wildlife conservation. These findings imply that within protected areas, public-access areas (associated with greater human use) may provide lower quality habitat than restricted-access areas (Kays et al., 2017). Herein, I examine how access may be contributing to wildlife community stressors, along with the potential for access restrictions to mitigate these impacts.

Understanding how wildlife species respond to anthropogenic risk in protected areas is a necessary step in the longer road of conserving our world's wildlife communities and protected spaces. Overall, this thesis aimed to reveal how human-induced risk and public access restrictions impact risk-resource trade-offs for apex predators and spatial dynamics within large mammal communities. To achieve this, I proposed two objectives that addressed how carnivores and wildlife communities spatially respond to risk and how public-access restrictions play a role in these responses. First, in Chapter 2, I assessed the relative influences of resources (habitat characteristics and prey occurrence) and perceived predation risk (human presence) on cougar (*Puma concolor*) detection frequency in two adjacent protected areas with mixed accessibility. Cougars are long-ranging, disturbance-sensitive species (Koehler & Hornocker, 1991). Their high densities in the study area, history of persecution, and important trophic role exemplify the need to study their responses to human disturbance (Anderson et. al., 2009). I modelled cougars' spatial responses to risk, habitat, prey, and an interaction between risk and preferred habitat through a set of competing hypotheses. Further, I depicted cougars' likely occurrence throughout the study area based on risk and habitat characteristics. Second, in Chapter 3, I took a broader approach to investigate how scale-dependent spatial partitioning among a large mammal community is influenced by human disturbance and protected area access. Species have been shown to respond divergently to humans (Suraci et al., 2021), implicating the need for species-specific management plans. I examined species-specific spatial responses to risk, habitat, and large mammal occurrence using a global model assessed at six spatial scales. I also compared similarity and dissimilarity of wildlife community composition and habitat characteristics between two adjacent protected areas. Specifically, these protected areas included a regional park that is open to the public, and an adjacent water supply area in which public-access is significantly limited. These areas are located on southern Vancouver Island in British Columbia, Canada, where a high density of wildlife and a high density of humans coexist.

This research enabled me to assess cougar's resource-risk trade-offs in the context of human presence. It also allowed me to evaluate how public access affects wildlife communities and how these disturbances change wildlife distributions on southern Vancouver Island. In this region, this study is among the first to monitor large mammals and one of the few cougar-specific studies conducted in the past twenty years. The findings are intended to inform management strategies regarding large mammal species in a landscape containing outdoor recreation. Locally, this research provides managers with insights and tools to understand where large mammal species are located and the factors that contribute to their ecological success. Globally, the findings from this thesis contribute to efforts to best manage protected areas in a rapidly changing world. This research reveals the importance of understanding how spatial partitioning among species in response to human activities and site-level disturbances can influence broader ecological communities.

References

Anderson, C. R., Lindzey, F., Knopff, K. H., Jalkotzy, M. G., & Boyce, M. S. (2009). Chapter 4. Cougar Management in North America. In *Cougar: Ecology and Conservation* (pp. 41–54). University of Chicago Press. https://doi.org/10.7208/9780226353470-009

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*(6), 620–623. https://doi.org/10.1098/rsbl.2007.0415

Blecha, K. A., Boone, R. B., & Alldredge, M. W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *Journal of Animal Ecology*, *87*(3), 609–622. https://doi.org/10.1111/1365-2656.12801

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, *309*(5738), 1239–1241. https://doi.org/10.1126/science.1116030

Clinchy, M., Sheriff, M. J., & Zanette, L. Y. (2013). Predator-induced stress and the ecology of fear. *Functional Ecology*, *27*(1), 56–65. https://doi.org/10.1111/1365-2435.12007

Crooks, K. R. (2002). Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. *Conservation Biology*, *16*(2), 488–502. https://doi.org/10.1046/j.1523-1739.2002.00386.x

Doherty, T. S., Hays, G. C., & Driscoll, D. A. (2021). Human disturbance causes widespread disruption of animal movement. *Nature Ecology & Evolution*, *5*(4), Article 4. https://doi.org/10.1038/s41559-020-01380-1

Fisher, J. T., & Burton, A. C. (2018). Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment*, *16*(6), 323–328. https://doi.org/10.1002/fee.1807

Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, *6*(1). https://www.jstor.org/stable/26271862

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution, 34*(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Heithaus, M. R. (2001). Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, *92*(3), 542–554. https://doi.org/10.1034/j.1600-0706.2001.920315.x

Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Christopher T. Rota, Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas. *Journal of Applied Ecology*, *54*(1), 242–252. https://doi.org/10.1111/1365-2664.12700

Keim, J. L., Lele, S. R., DeWitt, P. D., Fitzpatrick, J. J., & Jenni, N. S. (2019). Estimating the intensity of use by interacting predators and prey using camera traps. *Journal of Animal Ecology*, *88*(5), 690–701. https://doi.org/10.1111/1365-2656.12960

Koehler, G. M., & Hornocker, M. G. (1991). Seasonal Resource Use among Mountain Lions, Bobcats, and Coyotes. *Journal of Mammalogy*, *72*(2), 391–396. https://doi.org/10.2307/1382112

Kuijper, D. P. J., Bubnicki, J. W., Churski, M., Mols, B., & van Hooft, P. (2015). Context dependence of risk effects: Wolves and tree logs create patches of fear in an old-growth forest. *Behavioral Ecology*, *26*(6), 1558–1568. https://doi.org/10.1093/beheco/arv107

Laliberte, A. S., & Ripple, W. J. (2004). Range Contractions of North American Carnivores and Ungulates. *BioScience*, *54*(2), 123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review. *PLOS ONE, 11*(12), e0167259. https://doi.org/10.1371/journal.pone.0167259

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. https://doi.org/10.1139/z01-094

Leighton, P. A., Horrocks, J. A., & Kramer, D. L. (2010). Conservation and the scarecrow effect: Can human activity benefit threatened species by displacing predators? *Biological Conservation*, *143*(9), 2156–2163. https://doi.org/10.1016/j.biocon.2010.05.028

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: How African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825. https://doi.org/10.1111/1365-2664.12794

Mills, K. L., Belant, J. L., Beukes, M., Dröge, E., Everatt, K. T., Fyumagwa, R., Green, D. S., Hayward, M. W., Holekamp, K. E., Radloff, F. G. T., Spong, G., Suraci, J. P., Van der Weyde, L. K., Wilmers, C. C., Carter, N. H., & Sanders, N. J. (2023). Tradeoffs between resources and risks shape the responses of a large carnivore to human disturbance. *Communications Biology*, *6*(1), 1–11. https://doi.org/10.1038/s42003-023-05321-z

Minin, E. D., Clements, H. S., Correia, R. A., Cortés-Capano, G., Fink, C., Haukka, A., Hausmann, A., Kulkarni, R., & Bradshaw, C. J. A. (2021). Consequences of recreational hunting for biodiversity conservation and livelihoods. *One Earth*, *4*(2), 238–253. https://doi.org/10.1016/j.oneear.2021.01.014

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human Activity Helps Prey Win the Predator-Prey Space Race. *PLoS ONE*, *6*(3), e17050. https://doi.org/10.1371/journal.pone.0017050

Naughton-Treves, L., Holland, M. B., & Brandon, K. (2005). THE ROLE OF PROTECTED AREAS IN CONSERVING BIODIVERSITY AND SUSTAINING LOCAL LIVELIHOODS. *Annual Review of Environment and Resources*, *30*(Volume 30, 2005), 219–252. https://doi.org/10.1146/annurev.energy.30.050504.164507

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., Millspaugh, J. J., & Kays, R. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, *56*(8), 1894–1904. https://doi.org/10.1111/1365-2664.13385

Pringle, R. M. (2017). Upgrading protected areas to conserve wild biodiversity. *Nature*, *546*(7656), 91–99. https://doi.org/10.1038/nature22902

Reed, S. E., & Merenlender, A. M. (2008). Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. *Conservation Letters*, *1*(3), 146–154. https://doi.org/10.1111/j.1755-263X.2008.00019.x

Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., & Musiani, M. (2011). Human Activity Differentially Redistributes Large Mammals in the Canadian Rockies National Parks. *Ecology and Society*, *16*(3). https://www.jstor.org/stable/26268938

Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation*, *212*, 316–326. https://doi.org/10.1016/j.biocon.2017.06.032

Schuette, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, *158*, 301–312. https://doi.org/10.1016/j.biocon.2012.08.008

Shackelford, N., Standish, R. J., Ripple, W., & Starzomski, B. M. (2018). Threats to biodiversity from cumulative human impacts in one of North America’s last wildlife frontiers. *Conservation Biology*, *32*(3), 672–684. https://doi.org/10.1111/cobi.13036

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society. B, Biological Sciences*, *282*(1802), 20142711–20142711. https://doi.org/10.1098/rspb.2014.2711

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, *22*(10), 1578–1586. https://doi.org/10.1111/ele.13344

Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L. M., Forrester, T., Green, A. M., Haight, J., Harris, N. C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P. E., Lewis, J. S., McInturff, A., … Wilmers, C. C. (2021). Disturbance type and species life history predict mammal responses to humans. *Global Change Biology*, *27*(16), 3718–3731. https://doi.org/10.1111/gcb.15650

Taylor, A. R., & Knight, R. L. (2003). Wildlife Responses to Recreation and Associated Visitor Perceptions. *Ecological Applications*, *13*(4), 951–963. https://doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Zi, F. (2018). *Moving in the Anthropocene: Global reductions in terrestrial mammalian movements*. 5.

Watson, J. E. M., Shanahan, D. F., Di Marco, M., Allan, J., Laurance, W. F., Sanderson, E. W., Mackey, B., & Venter, O. (2016). Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Current Biology*, *26*(21), 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049

Weaver, D. B., & Lawton, L. J. (2017). A new visitation paradigm for protected areas. *Tourism Management*, *60*, 140–146. https://doi.org/10.1016/j.tourman.2016.11.018

Winemiller, K. O., Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Joel Berger, Berger, J., Joel Berger, Joel Berger, Elmhagen, B., Letnic, M., Nelson, M. P., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484–1241484. https://doi.org/10.1126/science.1241484

Chapter 2: Anthropogenic Risk and Habitat Best Explain Cougar Space Use in a Mixed-Access Coastal Landscape

2.0 Introduction

The extent of human presence in wild spaces is increasing across the globe, resulting in negative effects on wildlife habitat and essential ecological processes (Larson et al., 2016). The consequences of extractive disturbances such as built structures, crop lands, dense human population centers, and major travel routes are well documented (Tucker et al., 2018; Venter et al., 2016), as are the effects of consumptive activities (such as hunting; Ordiz et al., 2013). However, emerging research suggests that non-extractive, non-consumptive human activities such as hiking and cycling impact wildlife in significant ways (Nickel et al., 2020). Recreation can alter wildlife behaviour, increase stress levels, and disrupt crucial activities like movement, denning, prey acquisition, and reproduction (Procko et al., 2023; Taylor & Knight, 2003). Disturbance at fine spatio-temporal scales (at an immediate location, at one point in time) requires species to make trade-offs between resource acquisition and space use at that location versus perceived risk (Mills et al., 2023). For sensitive species such as long-ranging, low fecundity large carnivores, these trade-offs could accumulate to threaten population persistence and ecosystem function (Ripple et al., 2014; Sergio et al., 2008; Suraci et al., 2019). Cougars (*Puma concolor*) are one such species as they require vast areas of high-quality, undisturbed habitat to successfully hunt and den (Koehler & Hornocker, 1991).

Humans, who pose a tangible risk to cougars through consumptive and extractive resource use, may also create a perceived risk through non-consumptive activities (Anderson et al., 2009; Darimont et al., 2015). Human presence alone may generate fear, and the landscape of fear theory suggests that wildlife species perceive variation in predation risk across a geographic area, requiring risk-avoidance strategies as a trade-off for resource-acquisition (Laundré et al., 2001). This theory can be applied to human-carnivore relationships, with humans increasingly recognized as generators of fear across landscapes (Gaynor et al., 2019; Suraci et al., 2019). Non-consumptive human activity in an ecosystem can invoke a fear-response in wildlife, leading apex predators to alter their spatio-temporal use of "risky" areas as a protective measure against predation (Smith, 2017; Suraci, 2019). Avoidance of these “risky” areas can be energetically costly and cause carnivores to lose out on precious prey acquisition or safe access to preferred habitat (Coppes et al., 2017; Lewis et al., 2021; Naidoo & Burton, 2020; Taylor & Knight, 2003). Examining these fear responses in a heterogeneous landscape with a diversity of habitat features and a high density of human activity will help illuminate how outdoor recreation shapes a landscape of fear for cougars (Atuo & O’Connell, 2017).

While cougars are known to generally tolerate human encroachment within their home ranges (Dickson & Beier, 2002), multiple studies reveal they exhibit spatial avoidance of human presence by reducing their use of specific locations within those ranges (Dellinger et al., 2020; Kertson et al., 2011; Lewis et al., 2021; Morrison et al., 2014). They trade off using these locations against the value of preferred resources, including large prey species (deer, elk) and associated habitat characteristics that support these large prey species, while also weighing the risks these locations present (Glick, 2014; Hornocker & Negri, 2009). Cougars tend to use deer habitat (forest edge, mixed forest and shrub vegetation, proximity to water sources) more frequently than high-elevation, rocky, vegetation-sparse habitat (Morrison et al., 2014; Teichman et al., 2013); preferred prey habitat can therefore be used as a proxy for prey availability (Kertson et al., 2011). Although resources are important predictors of cougar occurrence, human presence may impact how cougars use these preferred habitat patches. For example, the sound of human voices is enough to induce anti-predator behaviours in large carnivores, causing cougars to spatially avoid areas of perceived risk, move more cautiously throughout the landscape, and reduce feeding times (Smith et al., 2017; Suraci et al., 2019).

Further, behavioural changes and spatio-temporal habitat-use alterations induced by human activity could effectively lead to habitat loss or abandonment of parts of a home range over time (Smith et al., 2015; Suraci et al., 2019). As human presence increases in cougar habitat (Kertson et al., 2011; Stoner et al., 2021), it becomes imperative for planners and wildlife managers to understand how these apex predators respond to perceived anthropogenic risk and how this risk affects their access to high-quality habitat.

Because ecological processes (such as risk avoidance or the acquisition of resources) typically occur at a characteristic scale, it is essential to assess and interpret these processes at the ecologically appropriate scale (Levin, 1992; Wiens, 1989). Therefore, we must quantify risk and resources at a range of scales, allowing us to consider those most biologically relevant to cougars (Nams et al., 2006). Cougars are known to select for home ranges in a predictable way, as they prefer low anthropogenic disturbance, a healthy prey population, and enough unoccupied territory to support male home ranges that do not overlap, and female home ranges that partially overlap (Glick, 2014; Hornocker & Negri, 2009). Cougars' home ranges vary in size across broad geographic areas and can extend upwards of 700 km^2 (Grigione et al., 2002; Spreadbury et al., 1996). However, on Vancouver Island, cougars have relatively smaller home ranges that average 61 km^2 for females and 186 km^2 (Hahn, 2001). However, within their home ranges, cougars are known to select habitat differently at different scales (Dellinger et al., 2020), and the question continues to be explored of whether there is a quantifiable "best" scale at which cougars use habitat (Gaston et al., 2024; Johnson, 1980). Examining the scale at which cougars respond to risk and resources will increase the ecological relevance of detected relationships between cougars and their environment (Fisher et al., 2011), thereby better informing conservation plans and localized habitat protections (Jordan & Ryan, 2015; Wilmers et al., 2013).

Among geographic areas harboring the highest density of cougars in North America is Vancouver Island, located in British Columbia (BC), Canada (Wilson et al., 2004). The island has experienced significant demographic and landscape restructuring over the past several decades, providing an opportunity to examine cougar responses to recreation in a changing world. In recent years, parks and protected areas governed by Capitol Regional District (CRD) have undergone improvement projects, such as the 2017 facilities improvement project for the Sooke Hills Wilderness Area (CRD, 2017). As a result of these developments, regional parks and trails experienced a 54% increase in visits between 2012 and 2021 (CRD, n.d.). Southern Vancouver Island has also experienced habitat restructuring through housing and infrastructure development, logging, and potentially consequent changes to cougar prey structure and distribution (CRD, n.d.). Despite these landscape-level changes, Vancouver Island and BC more broadly suffer from a lack of focused cougar studies over the past two decades (Hahn, 2001; Wilson et al. 2004). As outdoor recreation is a growing focus on the island, there is an urgent need to maintain spaces that permit outdoor recreation while simultaneously identifying, protecting, and supporting high-quality cougar habitat (Anderson et al., 2009; CRD, n.d.).

I explored how human recreation affects cougar space use and risk-resource trade-offs in protected areas with high densities of both cougars and human recreation. The study was conducted using an array of 48 camera traps deployed in a park and regional water supply area, covering both publicly and non-publicly accessible land. Cougar space use was assessed through a set of candidate models that examined the relative influences of habitat, prey, and anthropogenic risk on cougar occurrence across multiple spatial scales. To determine whether risk avoidance takes precedence over resource acquisition, I analyzed the interaction between perceived risk and preferred habitat. I used the results from statistical analysis to visualize areas of predicted high and low cougar occurrence across the study area. I hypothesized that risk would be an important predictor of cougar site use, with cougars favoring less-disturbed habitat--that with lower human presence--over potentially resource rich but high-risk areas. Given cougars' large range sizes (Grigione et al., 2002) and evidence showing they select habitat patches at large scales (Gaston et al., 2024), I expected them to assess risks and resources at the largest tested spatial scale.

2.1 Methods

2.1.1 Study Area

This research occurred on the traditional territory of the lək̓ʷəŋən peoples and T'Sou-ke First Nation whose relationship with the land I acknowledge and respect. The study area, marked by a hexagonal grid fitted with 48 cameras, covered approximately 36 km^2 of mixed-access terrain on a portion of southern Vancouver Island (Figure 2.1). Located 20 kilometers west of Victoria, BC, the study area covered a portion of the 40.9 km^2 Sooke Hills Wilderness Area Regional Park (SHWA) and a portion of the 205.5 km^2 Greater Victoria Water Supply Area (GVWSA) (CRD, 2001; CRD, 2023). In the park, permitted recreational activities such as hiking, cycling, and on-leash dog-walking occur on trails, rendering this a high human-use area, with some spatial variability. Managers restrict public access within the GVWSA to protect the drinking water supply for nearly 400,000 residents, making it a low human-use area. Roads and unmarked trails in the GVWSA facilitate management activities aimed at meeting water supply protection policies and other related needs.

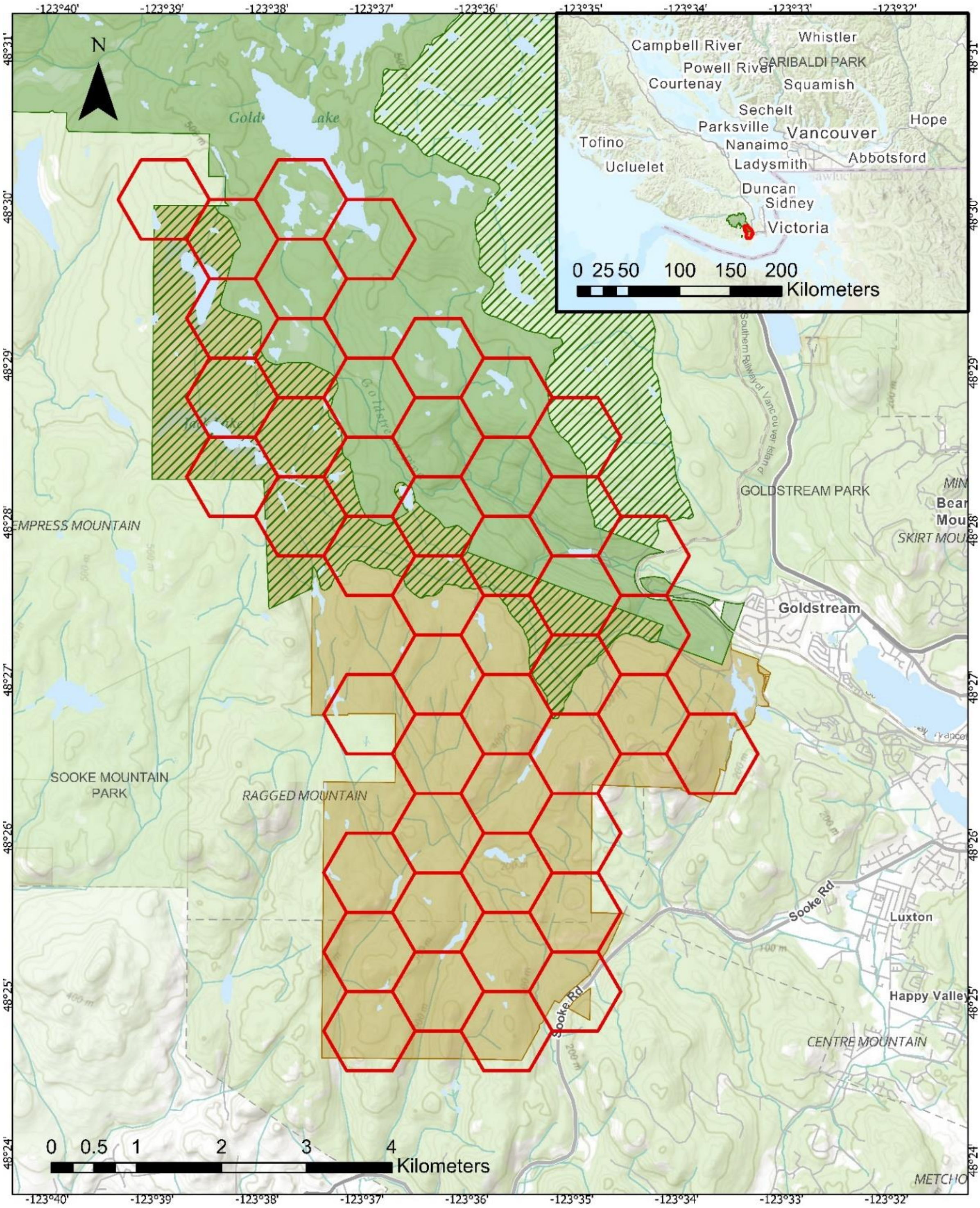


Figure 2.1: Camera trap grid (red hexagons) located in the Sooke Hills Wilderness Area (tan polygon) and Greater Victoria Water Supply Area/Drinking Water Protection Area (green polygon and green hashed lines) on Southern Vancouver Island, British Columbia, Canada. 48 infrared cameras placed along linear features near the center of each 750m^2 hexagonal grid cell.

The area sits in the Coastal Western Hemlock Very Dry Maritime Biogeoclimatic Subzone, covering a range of terrain including rocky hilltops, forests, upland meadows, wetlands, and streams (The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia, 2001). The plant community is dominated by Coastal Douglas fir (*Pseudotsuga menziesii var. menziesii*), often found with western redcedar (*Thuja plicata*), grand fir (*Abies grandis*), arbutus (*Arbutus menziesii*), Garry oak (*Quercus garryana*), and red alder (*Alnus rubra*) (CRD, 2001). The climate in this area is characterized by an average annual temperature of 9.3°C and an average annual precipitation of 1,427 mm (Chourmouzis et al., 2009). However, conditions vary throughout the study area, resulting in site-specific vegetation communities. In addition to cougars, the area supports a range of important animal species, including black bears (*Ursus americanus*), wolves (*Canis lupus*), Columbian black-tailed deer (*Odocoileus hemionus columbianus*), Roosevelt elk (*Cervus canadensis roosevelti*), and marbled murrelets (*Brachyramphus marmoratus*) (CRD, 2001).

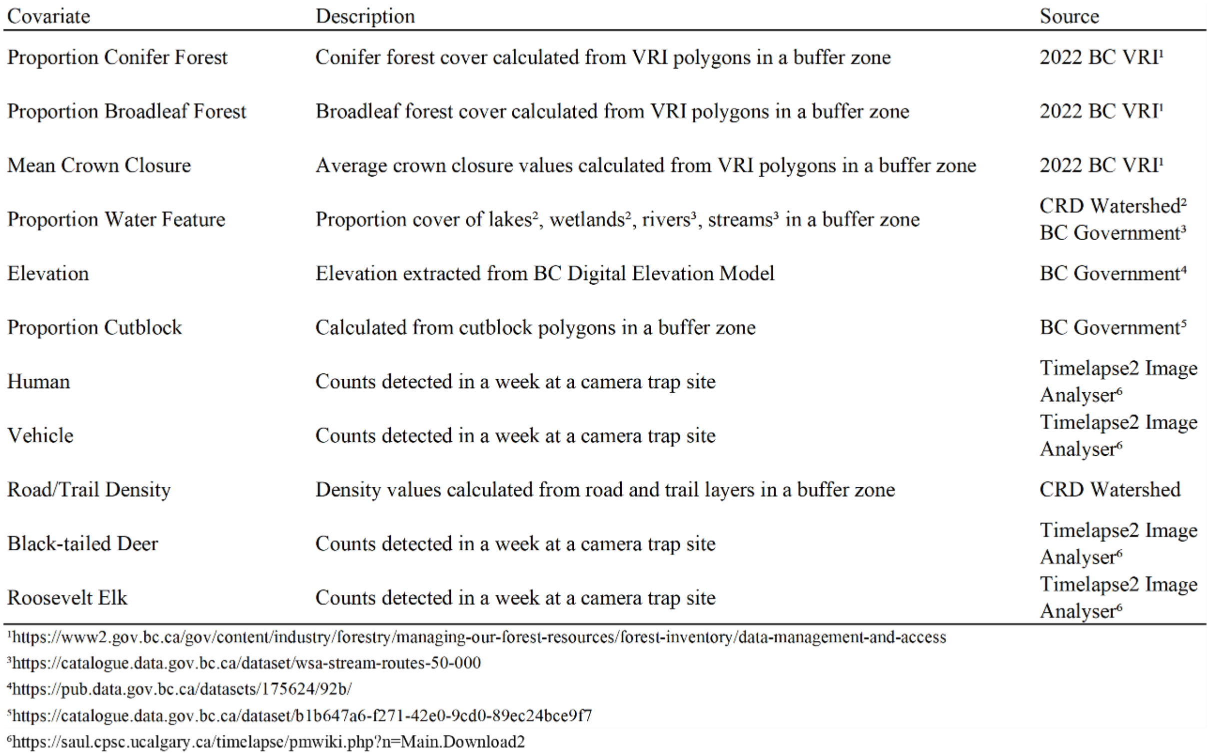
2.1.2 Sample Design

A camera trap array consisting of 50 Reconyx™ Hyperfire 2 (Reconyx, Holmen, WI) Infrared cameras were originally deployed in the SHWA and GVWSA. However, 48 sampling sites remained available for analysis due to theft and camera malfunction at two sites. Cameras were placed near the center of each 750m^2 hexagonal grid cell. The relatively small grid cell size captured the variability in elevation, climate, and vegetation communities throughout the study area. Each camera was placed at a height of about 1 meter on a tree to facilitate detection of humans and various wildlife species (Naidoo & Burton, 2020). This systematic sampling design allowed capture of these species along linear features (roads and trails) (Wearn & Glover-Kapfer, 2017). Half (24) of the available cameras were deployed in the restricted-access GVWSA, while the other 24 available cameras were deployed in the public-access SHWA.

2.1.3 Data Collection and Processing

Cameras captured images between May 1st, 2022, through September 30th, 2022. Timelapse Image Analyzer 2.0 was used to identify animal species, humans, cyclists, dogs, and vehicles present in camera trap images (Greenberg et al., 2019). Human images were blurred using Megadetector and RStudio to protect the privacy of community members (Figure 2.2) (Beery et al., 2019; R Core Team, 2023). Multiple images of an individual in close succession were considered a singular event or site visit, while repeat detections 10 minutes or greater apart were differentiated into independent events (Keim et al., 2019). This interval was chosen to accommodate sites that may have experienced multiple visitors or groups of visitors on any given day. Count data was calculated from species group size within these independent detections. Counts from independent events were aggregated into weekly counts to capture variability in the detection frequencies throughout a season, while preventing an excess of zeros commonly encountered in camera trap data for elusive, low-density species such as the cougar (Keim et al., 2019). Further, the ecological consequences of multiple individuals using a site, or individuals using a site multiple times a week, differ from simply accounting for occupancy at that site through presence or absence (Mackenzie et al., 2006). Because cougars are likely present throughout the study area, priority areas for conservation can be identified by the intensity with which different habitat patches are used (St-Pierre et al., 2022). Different forms of human presence, including cyclists, dog-walkers, and hikers, were combined into a single "Human" count for generalized linear modeling. This approach provided a measure of detection frequency that included all human activities, calculating a more accurate count of individuals visiting a site. Data were further processed and cleaned to remove any weeks when a camera was inactive. Therefore, a “0” in any species, human, or vehicle count suggests that a site was truly not used by a subject during a given week. Habitat covariates included water features, conifer and broadleaf forest cover, crown closure, logging cutblocks, and elevation, and were derived from multiple sources as described in Table 2.1.

Table 2.1: Habitat, risk, and prey covariates used in generalized linear models at six spatial scales. Proportion Conifer Forest, Proportion Broadleaf Forest, Mean Crown Closure, Proportion Cutblock, and Road/Trail Density were derived from GIS shapefiles. Elevation was derived from a GIS raster file. Human, Vehicle, Black-tailed Deer, and Roosevelt Elk counts were derived from Timelapse2 Image Analyser and RStudio. Links to data sources can be found at the bottom of the table.



Covariate	Description	Source
Proportion Conifer Forest	Conifer forest cover calculated from VRI polygons in a buffer zone	2022 BC VRI[1]
Proportion Broadleaf Forest	Broadleaf forest cover calculated from VRI polygons in a buffer zone	2022 BC VRI[1]
Mean Crown Closure	Average crown closure values calculated from VRI polygons in a buffer zone	2022 BC VRI[1]
Proportion Water Feature	Proportion cover of lakes[2], wetlands[2], rivers[3], streams[3] in a buffer zone	CRD Watershed[2] BC Government[3]
Elevation	Elevation extracted from BC Digital Elevation Model	BC Government[4]
Proportion Cutblock	Calculated from cutblock polygons in a buffer zone	BC Government[5]
Human	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Vehicle	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Road/Trail Density	Density values calculated from road and trail layers in a buffer zone	CRD Watershed
Black-tailed Deer	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Roosevelt Elk	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]

[1] https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-inventory/data-management-and-access

[3] https://catalogue.data.gov.bc.ca/dataset/wsa-stream-routes-50-000

[4] https://pub.data.gov.bc.ca/datasets/175624/92b/

[5] https://catalogue.data.gov.bc.ca/dataset/b1b647a6-f271-42e0-9cd0-89ec24bce9f7

[6] https://saul.cpsc.ucalgary.ca/timelapse/pmwiki.php?n=Main.Download2

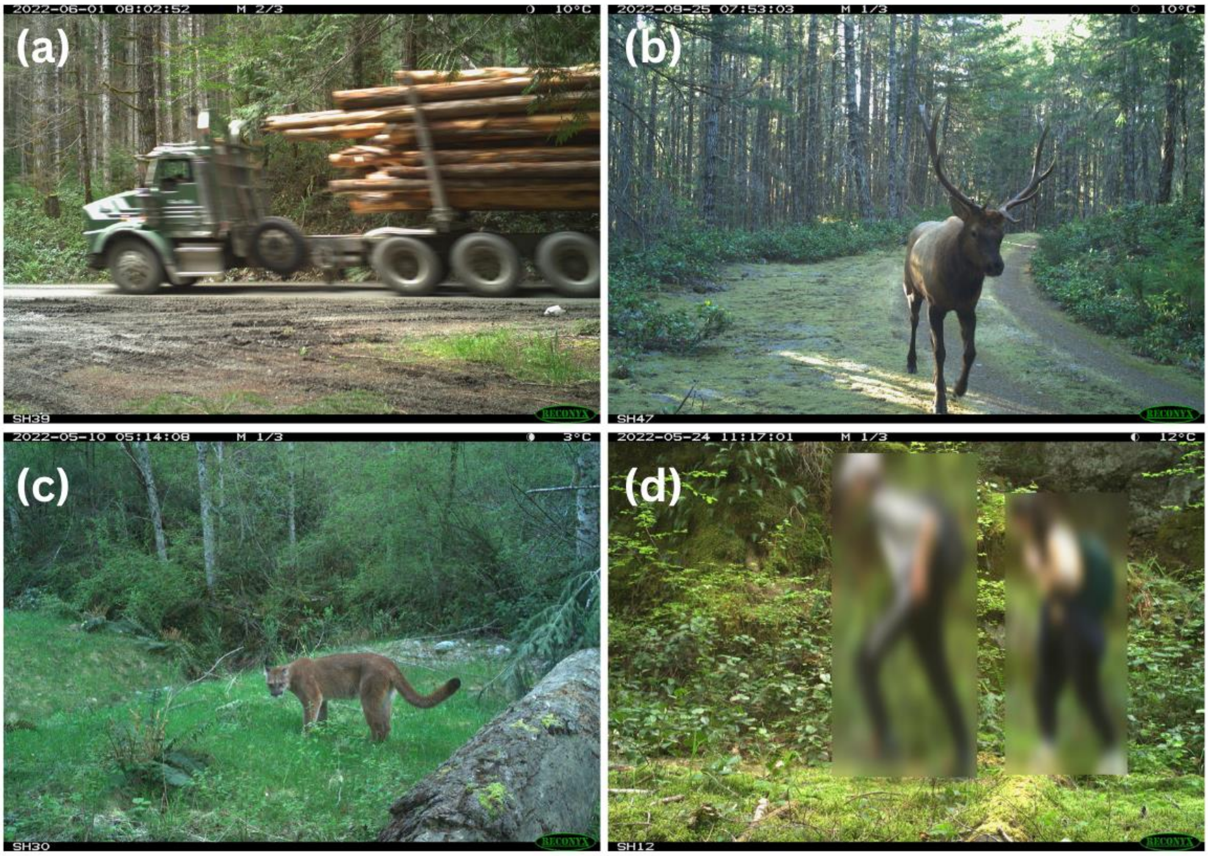


Figure 2.2: Images captured from the infrared motion-triggered cameras in our 48-camera trap array located in the SHWA and the GVWSA. Image (a) depicts a logging truck, image (b) depicts a Roosevelt elk, image (c) depicts a cougar, and image (d) depicts two hikers. Human images were blurred to protect privacy, while animal images remained unblurred. Date and timestamps are visible in the upper left-hand corner of each image, in addition to site identification in the lower left-hand corner.

2.1.4 Statistical Analyses

I applied two main approaches to address my research question: 1) I evaluated cougar space use through a candidate set of generalized linear models, and 2) I visualized top model results in a prediction surface, showing where cougars are most likely to occur throughout the landscape. This two-part approach allowed me to assess the relative impacts of risk and resources on cougar detection frequency through a statistically rigorous process, and then display how these findings contribute to a landscape of fear in a prediction map.

2.1.5 Statistical Analyses - Generalized Linear Modelling

A candidate set of generalized linear models was constructed a priori based on expected predictors of cougar space use to address the following hypotheses:

1. Perceived risk, quantified as the frequency of human activity, will act as an important predictor for cougar site use,

2. Cougars will be detected more frequently in habitat that is considered less “risky”,

3. Cougars will avoid “riskier” areas in favour of less-disturbed areas regardless of habitat characteristics, and

4. Assessment of risk-resource trade-offs will occur at the largest tested spatial scale.

These hypotheses were based on what is currently known about cougar space use in disturbed environments (Dellinger et al., 2020; LaRue & Nielson, 2011; Teichman et al., 2013), and the models for testing them are defined in Table 2.2. Model 1 (M1) was constructed as a base habitat model, and each additional hypothesis was run independently and in conjunction with the base model. The base model incorporated habitat covariates that have provided strong predictive power for cougar occurrence in past studies. The base model allowed for more rigorous testing of the competing models, so that AIC testing did not consistently default to the most parameterized model. Model 2 (M2) was constructed to independently assess the impacts of anthropogenic risk, while Model 3 (M3) assessed the combined effects of risk and habitat. Model 4 (M4) was built to assess the impact of deer on cougars’ site use independently, while Model 5 (M5) assessed its impact with habitat covariates. Similarly, Model 6 (M6) assessed the impact of elk on cougars’ site use independently, while Model 7 (M7) assessed its impact with habitat covariates. Model 8 (M8) and Model 9 (M9) assessed the combined effects of prey species both independently (M8) and in conjunction with habitat covariates (M9). Model 10 (M10), the habitat and risk interaction model, assessed the interacting influences of risk and habitat covariates on cougar site use. M10 was developed by adding an interaction term to the base habitat model. The interaction term was comprised of the habitat covariate and the risk covariate with the largest effect size.

Cougars have reportedly selected habitat covariates differently at varying spatial scales, and I suspected the explanatory power of the habitat and risk covariates would change with scale (Dellinger et al., 2020). To examine scale dependency in cougars' relationship with their environment, I developed the described set of candidate models at six buffered distances around each camera trap site. Relevant habitat and risk covariates were measured at a series of spatial buffers (125 meters, 250 meters, 375 meters, 500 meters, 625 meters, and 750 meters) around each camera using the "sf" package in R (Table 2.2) (Pebesma & Bivand, 2023; Pebesma, 2018; R Core Team, 2023). The largest buffer was limited to 750 meters to prevent substantial overlap. Before model construction, Pearson's correlation coefficient was used to calculate the correlation between covariates available for analysis with the "cor" function in R (base (version 3.6.2)) (Zuur et al., 2010). No high correlation (with a correlation coefficient greater than ±0.7) was detected between covariate pairs as seen in Appendix A (Zuur et al., 2010). All covariates were standardized using the "scale" function (mean = 0, sd = 1) in R (base (version 3.6.2)) to ensure coefficient estimates were calculated on a comparable scale (R Core Team, 2023; Zuur et al., 2007).

Table 2.2: Candidate models constructed using a base habitat model (M1) hypothesized to predict cougar space use. Spatially buffered covariates are indicated with an asterisk.

Model	Number of Covariates	Covariates
Null (M0)	0	
Habitat (M1)	6	Proportion Conifer Forest* Proportion Broadleaf Forest* Mean Crown Closure* Proportion Water Feature* Elevation Proportion Cutblock*
Risk (M2)	3	Human Vehicle Road/Trail Density*
Habitat + Risk (M3)	9	Proportion Conifer Forest* Proportion Broadleaf Forest* Mean Crown Closure* Proportion Water Feature* Elevation Proportion Cutblock* Human Vehicle Road/Trail Density*
Black-tailed Deer (M4)	1	Black-tailed Deer
Habitat + Black-tailed Deer (M5)	7	Proportion Conifer Forest* Proportion Broadleaf Forest* Mean Crown Closure* Proportion Water Feature* Elevation Proportion Cutblock* Black-tailed Deer
Roosevelt Elk (M6)	1	Roosevelt Elk
Habitat + Roosevelt Elk (M7)	7	Proportion Conifer Forest* Proportion Broadleaf Forest* Mean Crown Closure* Proportion Water Feature* Elevation Proportion Cutblock* Roosevelt Elk
Total Prey (M8)	2	Black-tailed Deer Roosevelt Elk
Habitat + Total Prey (M9)	8	Proportion Conifer Forest* Proportion Broadleaf Forest* Mean Crown Closure* Proportion Water Feature* Elevation Proportion Cutblock* Black-tailed Deer Roosevelt Elk
Habitat × Risk (M10)	7	Proportion Conifer Forest* Proportion Broadleaf Forest* Mean Crown Closure* Proportion Water Feature* Elevation Proportion Cutblock* Proportion Broadleaf Forest*: Human

* Buffered covariates

Generalized linear models (GLMs) were employed due to their ability to handle count data through Poisson or binomial distributions and their ability to further parameterize the data without overfitting (Zuur et al., 2009). Overdispersion was detected in the cougar-count data, so a negative binomial distribution with a log link was assumed (Hilbe, 2014). This distribution maintained the likelihood function and the production of Akaike's Information Criterion (AIC) values while handling the detected overdispersion (Hilbe, 2014). Models were constructed within an information-theoretic framework (Anderson & Burnham, 2002). AIC scores were calculated for each candidate set at every spatial scale using the "MASS" package in R (R Core Team, 2023; Venables & Ripley, 2002), yielding 11 models and AIC scores per set, including the null model. Effect sizes (β coefficients) were calculated for covariates within the models. ΔAIC and AIC weights were calculated to evaluate the top-performing model within each candidate set. The AIC values for the top-performing model at each spatial scale were subsequently compared to select the overall top-performing model. To further parse apart the mechanisms influencing cougar space use, I modelled the occurrence of large prey based on habitat covariates at the top-performing scale. Since prey habitat can be used as a proxy for prey availability, these prey models provided a fuller understanding of why cougars prefer certain habitat characteristics. Models were evaluated through goodness-of-fit tests, including diagnostic graphs examining residual patterns (Zuur et al., 2009). Additionally, a 10-fold cross-validation was applied to the top model at each spatial scale using the "boot" package in R (Canty & Ripley, 2021; R Core Team, 2023).

2.1.6 Statistical Analyses - Prediction Surface

A human-induced landscape of fear was visualized from GLM results to show the variation in cougar detection frequency in response to risk. This visualization aimed to incorporate several elements from the Gaynor et al. (2019) framework for representing the landscape of fear, including the physical landscape (habitat characteristics), the spatial variation in predation risk (human occurrences), and the spatial distribution of “prey” (cougar occurrences). The prediction surface bridged the gap between statistical model findings and an empirical understanding of wildlife occurrence throughout the area, offering local managers a clear and accessible view of cougar detection frequency (Willems & Hill, 2009). The prediction surface was also created to support management goals by identifying habitat patches critical for protection. The top-performing generalized linear model was selected to predict cougar detection frequency along the network of roads and trails within the study area (Eliuk, 2023). A 30-meter buffer was established around the linear features to accommodate for variations in road width, trail width, and visibility distance throughout the study area. A set of points spaced 50 meters apart from each other was created within the 30-meter buffer using the “sf” package in R (Pebesma & Bivand, 2023; Pebesma, 2018; R Core Team, 2023). In ArcGIS Pro, grid points were clipped to a 750m buffer around the camera trap grid displayed in Figure 2.1 (Esri, 2023). The coefficients from the best-supported model were extracted to each generated point from the nearest camera trap site. Using the “predict” function in R (base version 3.6.2), cougar occurrences were predicted for each grid point using the top model (R Core Team, 2023). Predicted cougar occurrence was rescaled from 0 to 1, signifying low to high likelihood of occurrence. Predicted occurrence was simply labeled as “Low” and “High” for improved interpretability. Then, predicted occurrence values were interpolated in ArcGIS Pro using ordinary Gaussian kriging masked to the 30-meter dissolved buffer of roads and trails (Esri, 2023). This interpolation was clipped to the roads/trails buffer in ArcGIS Pro (Esri, 2023). Finally, the prediction surface was symbolized using a “Histogram Equalize” stretch for easier distinction between values (Esri, 2023).

2.2 Results

2.2.1 Data Summary

The total length of camera deployment was 153 days, spanning from May 1st, 2022, to September 30th, 2022. The average number of active days for the cameras was 147.2, with a minimum of 32 days and a maximum of 153 days. A total of 2002 raw detections and 289 independent detections of cougars were captured throughout the deployment period. Capture rates were averaged across camera trap sites in the study area to account for any inactive periods in deployment. At the monthly scale, cougar capture rate peaked in May (Figure 2.3). Cougars were detected throughout the study area and were observed at 46 sites, or 96% of the sites. A total of 152,568 raw detections and 14,529 independent detections of humans occurred throughout the deployment period. At the monthly scale, human capture rate remained steady, peaking in June (Figure 2.3). Humans were observed at 100% of the sites.

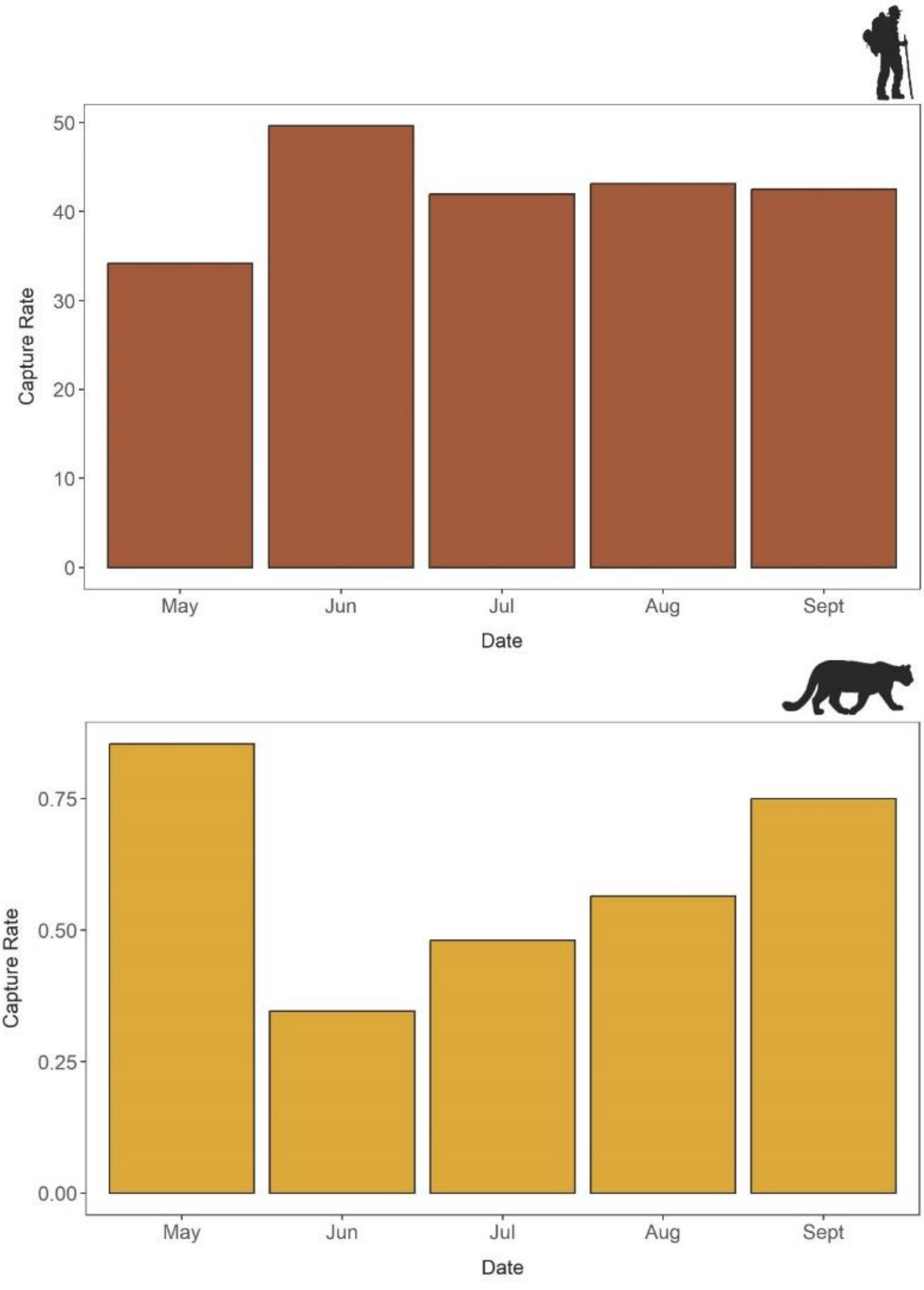


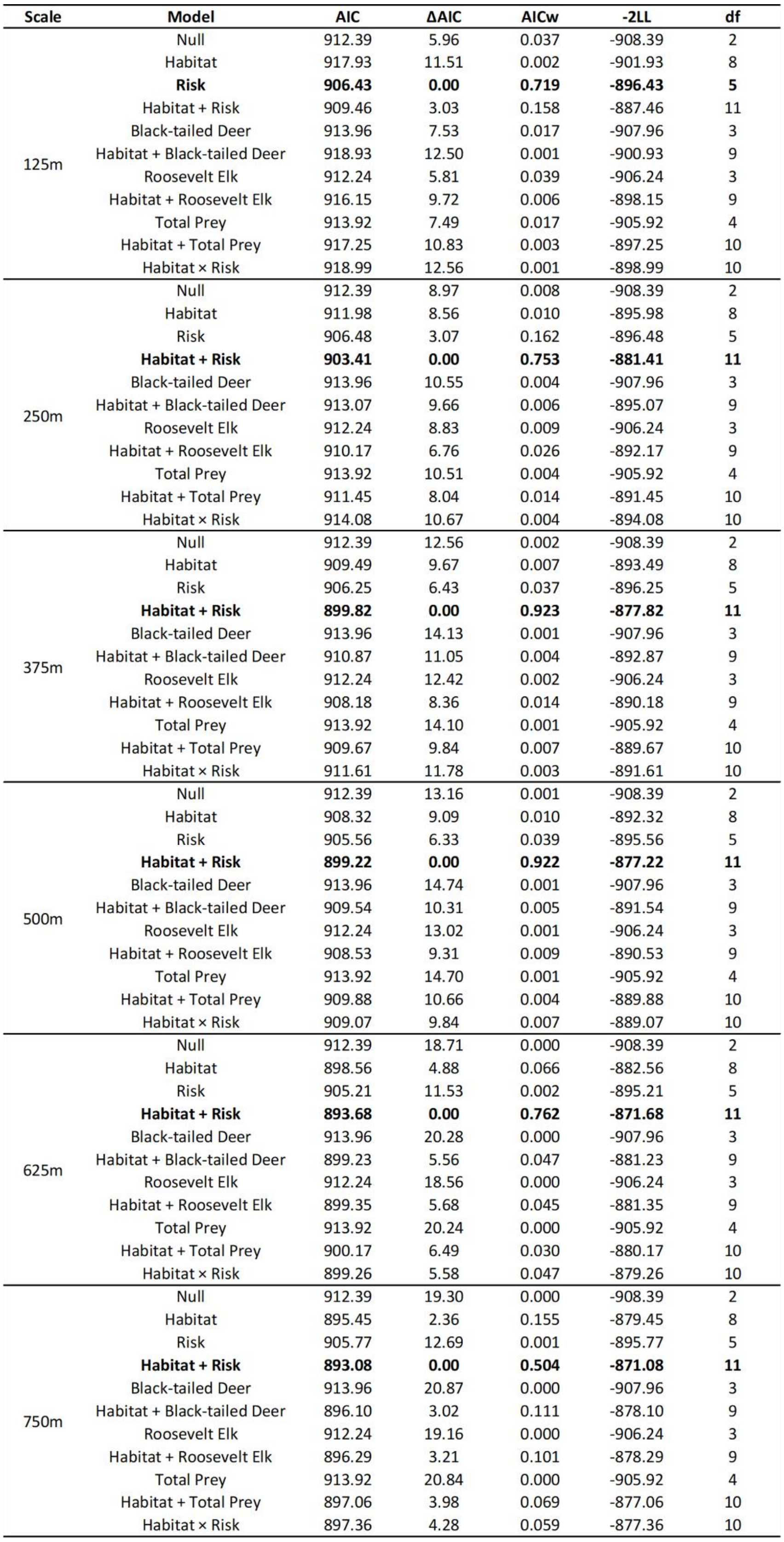
Figure 2.3: Human (top) and cougar (bottom) monthly capture rates in the SHWA and GVWSA from May 2022 to September 2022. Capture rates were derived from camera active days and the counts of species/humans for each month.

Note: Silhouette of a hiker (Silhouette of Hiker, n.d.); silhouette of a cougar (Taylor, 2019).

2.2.2 Statistical Analyses – Generalized Linear Modelling

The baseline Habitat model (M1) (AICw = 0.002 – 0.155) and Risk model (M2) (AICw = 0.001 – 0.719) performed moderately at all spatial scales (Table 2.3); however, the models performed considerably better when variables were combined in M3 (AICw = 0.505 – 0.923) (Table 2.3). This aligned with previous research demonstrating the important influence of both human disturbance and risk on cougar space use (Burdett et al., 2010; Morrison et al., 2014). Across all six spatial scales, models containing risk covariates performed best, with Habitat + Risk model (M3) outperforming other candidate models at five spatial scales (Table 2.3). Furthermore, all models containing buffered habitat covariates performed consistently better at larger spatial scales, as seen in Table 2.3. These results are also depicted in Figure 2.4 and Appendix B, as the Habitat + Risk model (M3) was assessed at six spatial scales. Out of the six candidate sets, the Habitat + Risk model (M3) at 750m best predicted cougar occurrence (AIC = 893.08, AICw = 0.504), with the Habitat + Risk model (M3) at 625m exhibiting a similar performance (AIC = 893.68, AICw = 0.762) (Table 2.3). Both M3 (Habitat + Risk) and M10 (Habitat x Risk) performed best at the largest tested spatial scale of 750m (Table 2.3).

Table 2.3: Model selection outcomes for cougar occurrence ranked using AIC at six spatial scales. The best-fit model in each candidate set is bolded. AIC = Akaike's Information Criteria, ΔAIC = Delta AIC, AICw = AIC Weight, -2LL = Negative Two Log-Likelihood, df = Degrees of freedom.



Scale	Model	AIC	ΔAIC	AICw	-2LL	df
125m	Null	912.39	5.96	0.037	-908.39	2
	Habitat	917.93	11.51	0.002	-901.93	8
	Risk	**906.43**	**0.00**	**0.719**	**-896.43**	**5**
	Habitat + Risk	909.46	3.03	0.158	-887.46	11
	Black-tailed Deer	913.96	7.53	0.017	-907.96	3
	Habitat + Black-tailed Deer	918.93	12.50	0.001	-900.93	9
	Roosevelt Elk	912.24	5.81	0.039	-906.24	3
	Habitat + Roosevelt Elk	916.15	9.72	0.006	-898.15	9
	Total Prey	913.92	7.49	0.017	-905.92	4
	Habitat + Total Prey	917.25	10.83	0.003	-897.25	10
	Habitat × Risk	918.99	12.56	0.001	-898.99	10
250m	Null	912.39	8.97	0.008	-908.39	2
	Habitat	911.98	8.56	0.010	-895.98	8
	Risk	906.48	3.07	0.162	-896.48	5
	Habitat + Risk	**903.41**	**0.00**	**0.753**	**-881.41**	**11**
	Black-tailed Deer	913.96	10.55	0.004	-907.96	3
	Habitat + Black-tailed Deer	913.07	9.66	0.006	-895.07	9
	Roosevelt Elk	912.24	8.83	0.009	-906.24	3
	Habitat + Roosevelt Elk	910.17	6.76	0.026	-892.17	9
	Total Prey	913.92	10.51	0.004	-905.92	4
	Habitat + Total Prey	911.45	8.04	0.014	-891.45	10
	Habitat × Risk	914.08	10.67	0.004	-894.08	10
375m	Null	912.39	12.56	0.002	-908.39	2
	Habitat	909.49	9.67	0.007	-893.49	8
	Risk	906.25	6.43	0.037	-896.25	5
	Habitat + Risk	**899.82**	**0.00**	**0.923**	**-877.82**	**11**
	Black-tailed Deer	913.96	14.13	0.001	-907.96	3
	Habitat + Black-tailed Deer	910.87	11.05	0.004	-892.87	9
	Roosevelt Elk	912.24	12.42	0.002	-906.24	3
	Habitat + Roosevelt Elk	908.18	8.36	0.014	-890.18	9
	Total Prey	913.92	14.10	0.001	-905.92	4
	Habitat + Total Prey	909.67	9.84	0.007	-889.67	10
	Habitat × Risk	911.61	11.78	0.003	-891.61	10
500m	Null	912.39	13.16	0.001	-908.39	2
	Habitat	908.32	9.09	0.010	-892.32	8
	Risk	905.56	6.33	0.039	-895.56	5
	Habitat + Risk	**899.22**	**0.00**	**0.922**	**-877.22**	**11**
	Black-tailed Deer	913.96	14.74	0.001	-907.96	3
	Habitat + Black-tailed Deer	909.54	10.31	0.005	-891.54	9
	Roosevelt Elk	912.24	13.02	0.001	-906.24	3
	Habitat + Roosevelt Elk	908.53	9.31	0.009	-890.53	9
	Total Prey	913.92	14.70	0.001	-905.92	4
	Habitat + Total Prey	909.88	10.66	0.004	-889.88	10
	Habitat × Risk	909.07	9.84	0.007	-889.07	10
625m	Null	912.39	18.71	0.000	-908.39	2
	Habitat	898.56	4.88	0.066	-882.56	8
	Risk	905.21	11.53	0.002	-895.21	5
	Habitat + Risk	**893.68**	**0.00**	**0.762**	**-871.68**	**11**
	Black-tailed Deer	913.96	20.28	0.000	-907.96	3
	Habitat + Black-tailed Deer	899.23	5.56	0.047	-881.23	9
	Roosevelt Elk	912.24	18.56	0.000	-906.24	3
	Habitat + Roosevelt Elk	899.35	5.68	0.045	-881.35	9
	Total Prey	913.92	20.24	0.000	-905.92	4
	Habitat + Total Prey	900.17	6.49	0.030	-880.17	10
	Habitat × Risk	899.26	5.58	0.047	-879.26	10
750m	Null	912.39	19.30	0.000	-908.39	2
	Habitat	895.45	2.36	0.155	-879.45	8
	Risk	905.77	12.69	0.001	-895.77	5
	Habitat + Risk	**893.08**	**0.00**	**0.504**	**-871.08**	**11**
	Black-tailed Deer	913.96	20.87	0.000	-907.96	3
	Habitat + Black-tailed Deer	896.10	3.02	0.111	-878.10	9
	Roosevelt Elk	912.24	19.16	0.000	-906.24	3
	Habitat + Roosevelt Elk	896.29	3.21	0.101	-878.29	9
	Total Prey	913.92	20.84	0.000	-905.92	4
	Habitat + Total Prey	897.06	3.98	0.069	-877.06	10
	Habitat × Risk	897.36	4.28	0.059	-877.36	10

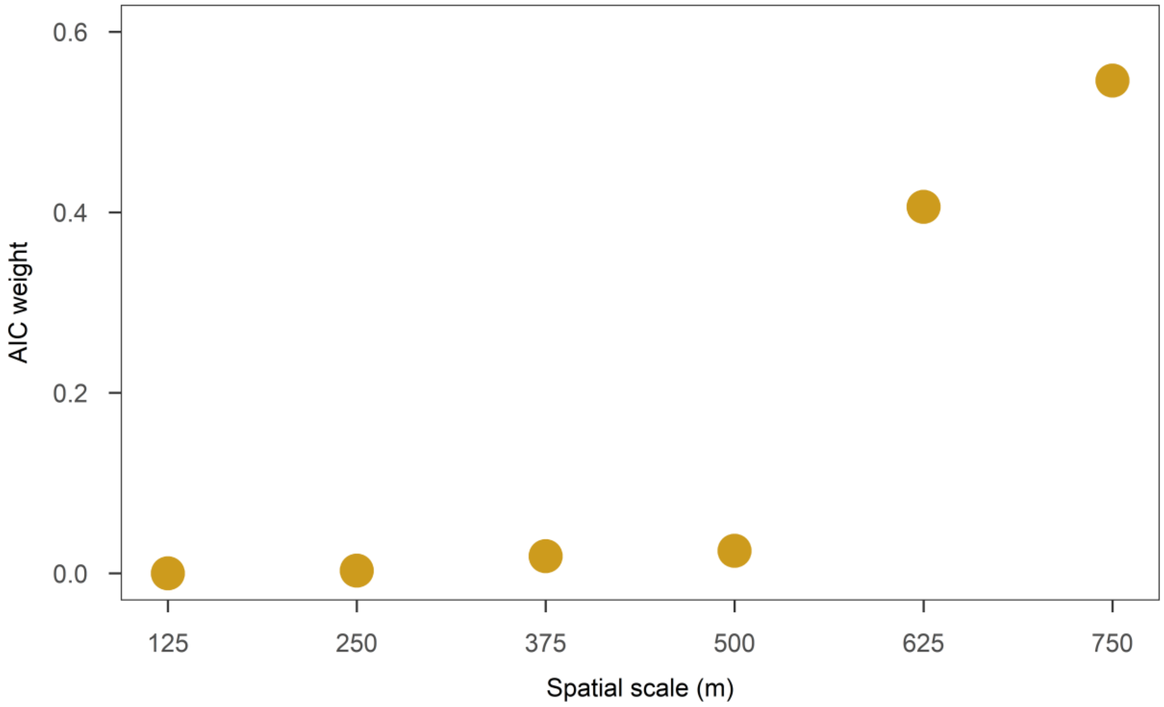


Figure 2.4: AIC weights of the Habitat + Risk model (M3) at six assessed spatial scales. The spatial scales on the x-axis represent the buffer radius around each camera trap.

While reporting and interpreting non-significant p-values has traditionally been challenged in statistics, there is a growing trend toward interpreting the magnitude and direction of all effect sizes, as these effects may hold ecological or scientific importance regardless of their statistical significance (Greenland et al., 2016). Although not interpreting significance, I still chose to report p-values to retain information about estimated effects derived from GLMs. This provided further insights into the strength and direction of the relationships between cougars and environmental characteristics, even when statistical significance was not present. M3, the Habitat + Risk model, revealed cougar responses to all risk and habitat covariates assessed in the candidate set (Figure 2.5). Risk factors within the model (humans, vehicles, and road/trail density) presented divergent directions of influence on cougar space use. Cougar occurrence was negatively associated with human presence (β = -0.14, $P = 0.37$) and road/trail density (β = -0.19, $P = 0.17$). However, cougar occurrence was positively associated with vehicle detection frequency (β = 0.23, *P* = 0.01), producing a larger effect size than habitat covariates in most cases. Among the nine covariates assessed, cougars exhibited the largest positive association with proportion broadleaf forest (β = 0.33, *P* = 0.02). Positive associations also occurred with mean crown closure (β = 0.12, P = 0.28), proportion water features (β = 5.23x10^{-4}, P = 1.00), and proportion cutblock (β = 0.14, P = 0.28). Cougars were negatively associated with remaining habitat covariates proportion conifer forest (β = -0.09, *P* = 0.59) and elevation (β = -0.29, *P* = 0.05). Although M3 (Habitat + Risk) best explained cougar occurrence, the results of M10 were explored to understand cougars' trade-offs between risk (human presence) and preferred habitat (broadleaf forest). In M10 (Figure 2.6), cougars' spatial responses to habitat variables reaffirmed the associations revealed by M3. Cougars displayed a positive association with an interaction between proportion broadleaf forest and human presence (β = 0.10, *P* = 0.50).

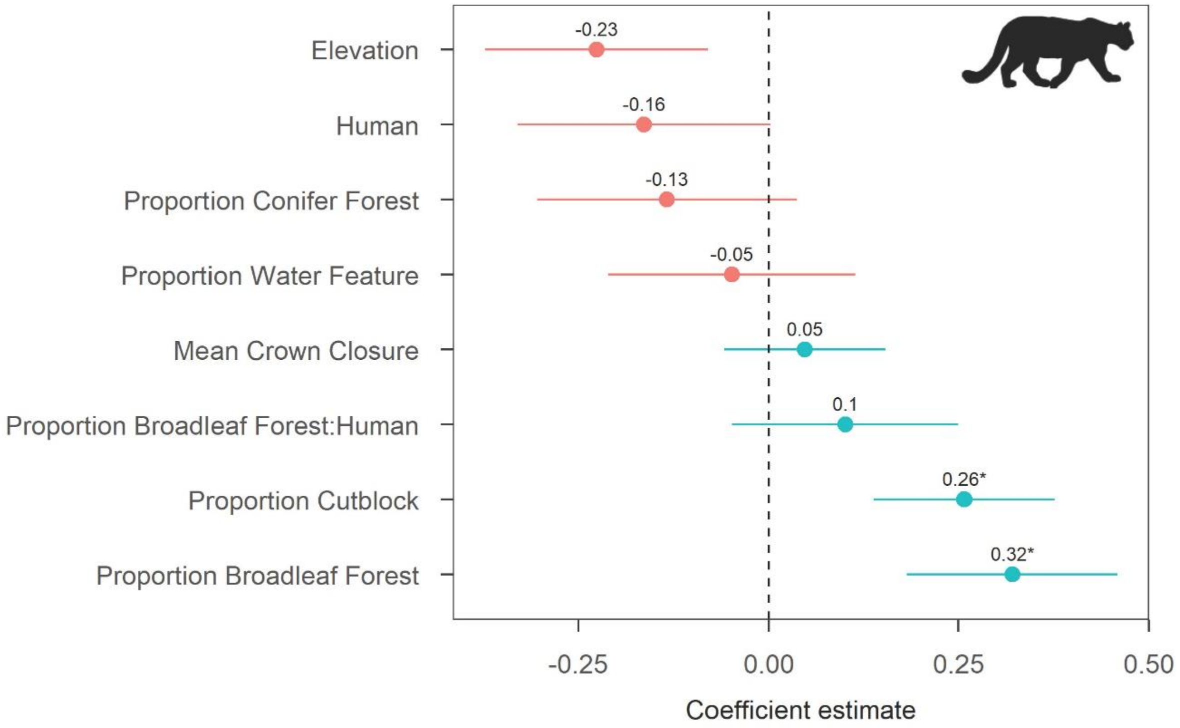


Figure 2.5: Habitat + Risk model (M3) at a 750m spatial scale. Asterisks indicate levels of significance: '*' for *P* < .05, '**' for *P* < .01, and '***' for *P* < .001. Covariates were standardized for better comparison between effect sizes.

Note: Silhouette of a cougar (Taylor, 2019).

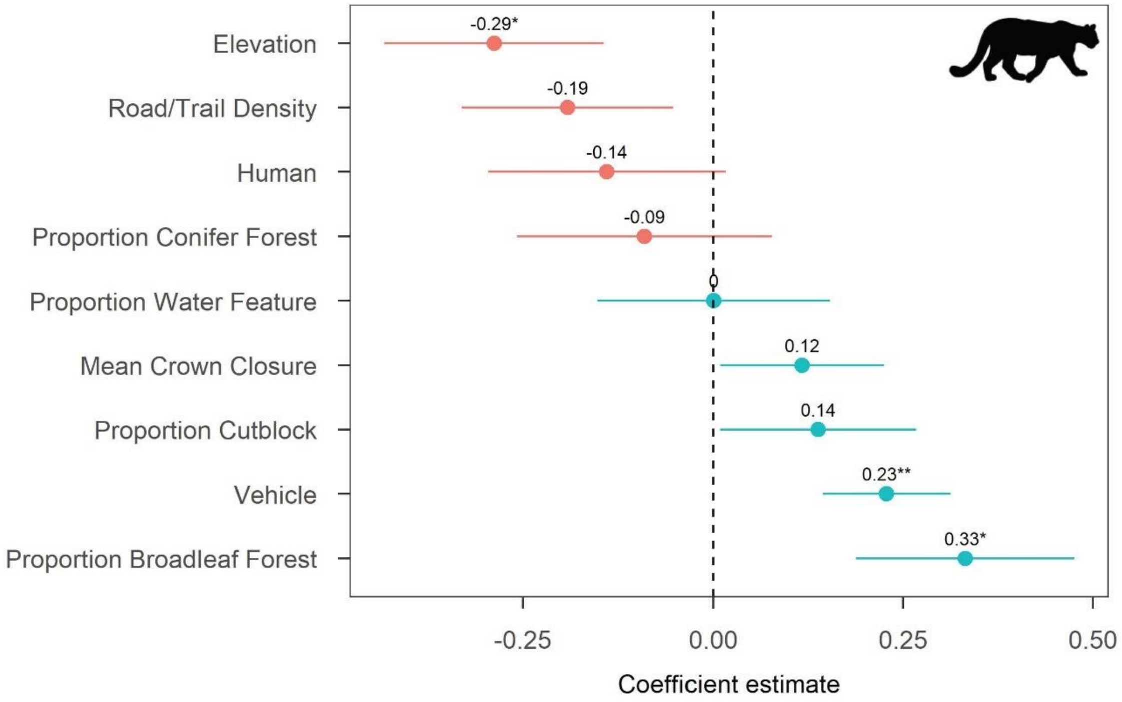


Figure 2.6: Interaction model depicting Habitat × Risk (M10) at a 750m spatial scale, using the habitat covariate with the largest effect size and the risk covariate with the largest effect size. Asterisks indicate levels of significance: '*' for $P < .05$, '**' for $P < .01$, and '***' for $P < .001$. Covariates were standardized for better comparison between effect sizes.

Note: Silhouette of a cougar (Taylor, 2019).

The occurrences of cougars' main large prey types (deer and elk) were assessed with the habitat covariates used in M3. The black-tailed deer model revealed a negative association with cougars' preferred habitat covariate of proportion broadleaf forest ($\beta = -0.21$, $P = 0.02$) and with proportion water feature ($\beta = -0.09$, $P = 0.33$) (Figure 2.7). However, deer demonstrated a positive association with proportion cutblock ($\beta = 0.30$, $P = 6.83\text{x}10^{-5}$) and mean crown closure ($\beta = 4.09\text{x}10^{-3}$, $P = 0.95$), aligning with cougars' preferences (Figure 2.7). Elk showed a positive association with cougars' preferred habitat of broadleaf forest ($\beta = 0.10$, $P = 0.67$), proportion water feature ($\beta = 0.01$, $P = 0.97$), and proportion cutblock ($\beta = 0.20$, $P = 0.24$) (Figure 2.8). Notably, both deer ($\beta = -0.16$, $P = 0.10$; Figure 2.7) and elk ($\beta = -0.57$, $P = 0.02$; Figure 2.8) spatially avoided conifer forest, aligning with cougars' negative association with higher proportions of conifer forest.

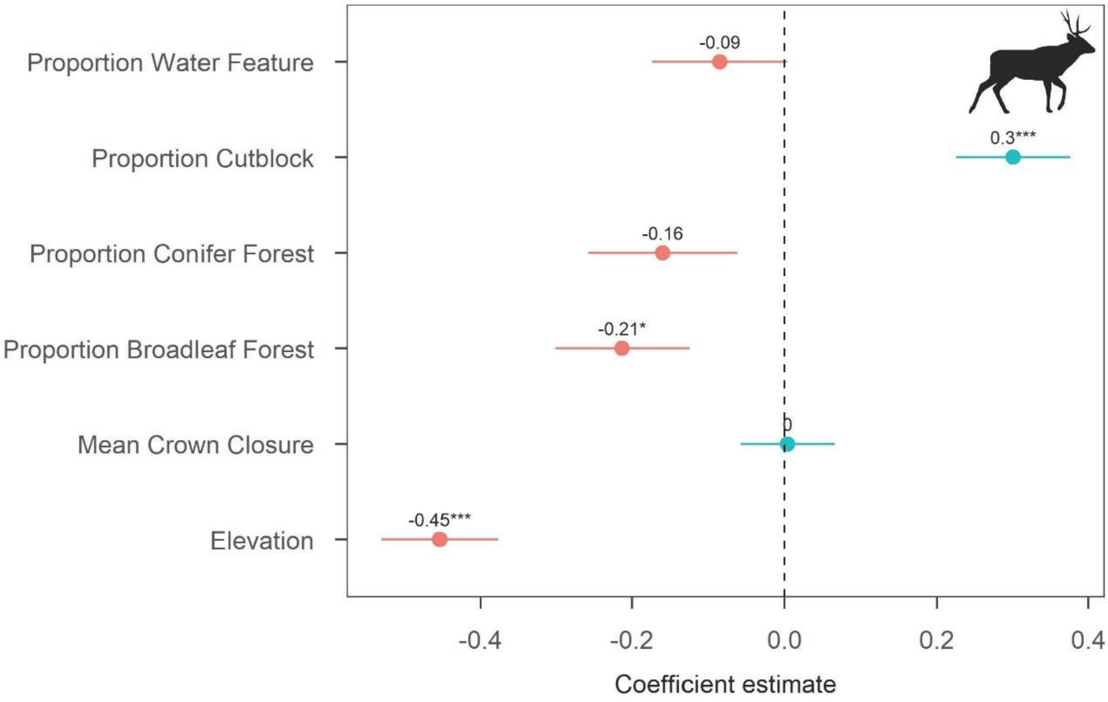


Figure 2.7: Deer occurrence modelled with habitat covariates from M3 at a 750m spatial scale. Asterisks indicate levels of significance: '*' for $P < .05$, '**' for $P < .01$, and '***' for $P < .001$. Covariates were standardized for better comparison between effect sizes.

Note: Silhouette of a deer (xgirouxb, 2019).

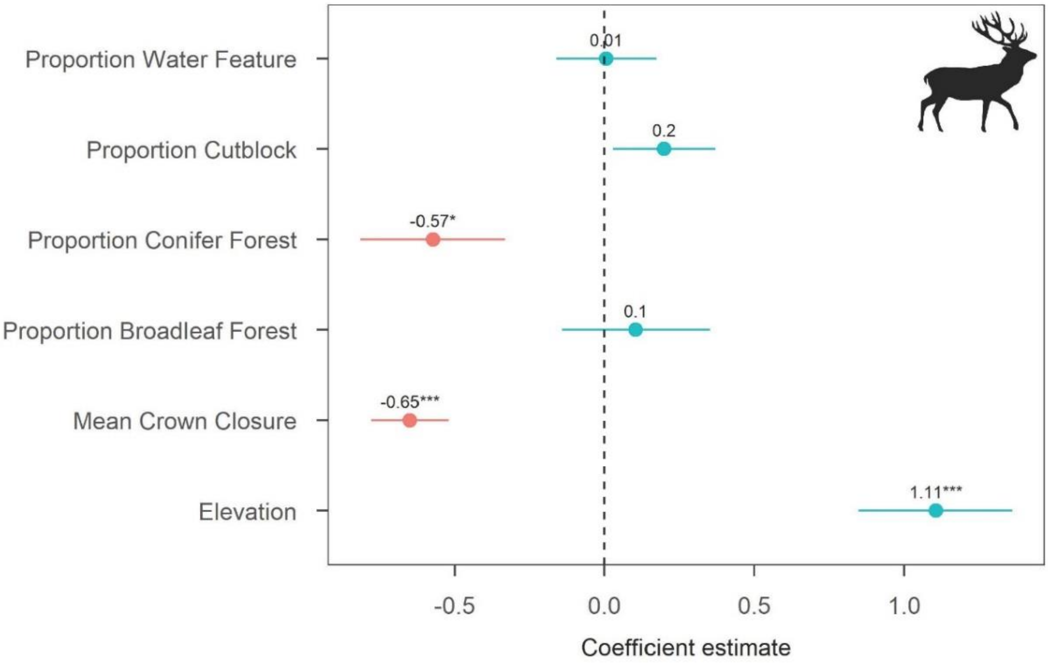


Figure 2.8: Elk occurrence modelled with habitat covariates from M3 at a 750m spatial scale. Asterisks indicate levels of significance: '*' for $P < .05$, '**' for $P < .01$, and '***' for $P < .001$. Covariates were standardized for better comparison between effect sizes.

Note: Silhouette of an elk (Sayol, 2021).

2.2.3 Statistical Analyses – Prediction Surface

The cougar occurrence prediction surface (Figure 2.9) displayed spatial variation in cougar detection frequency across the heterogeneous study area. Lower predicted occurrence values (dark purple) covered the southern portion of the buffered study area, and higher predicted occurrence values (dark green) were observed in northern and eastern portions of the buffered study area. Intermediate colours (light purple to light green) represented more neutral predictions of cougar occurrence and were seen in both the park and the water supply area. It's important to note that linear features within the GVWSA Boundary and Drinking Water Protection Zone are primarily roads, whereas linear features within the Sooke Hills Wilderness Park are mainly hiking trails. The characteristics of each protected area can help explain the trend of higher cougar likelihood observed in the northern portion of the study area.

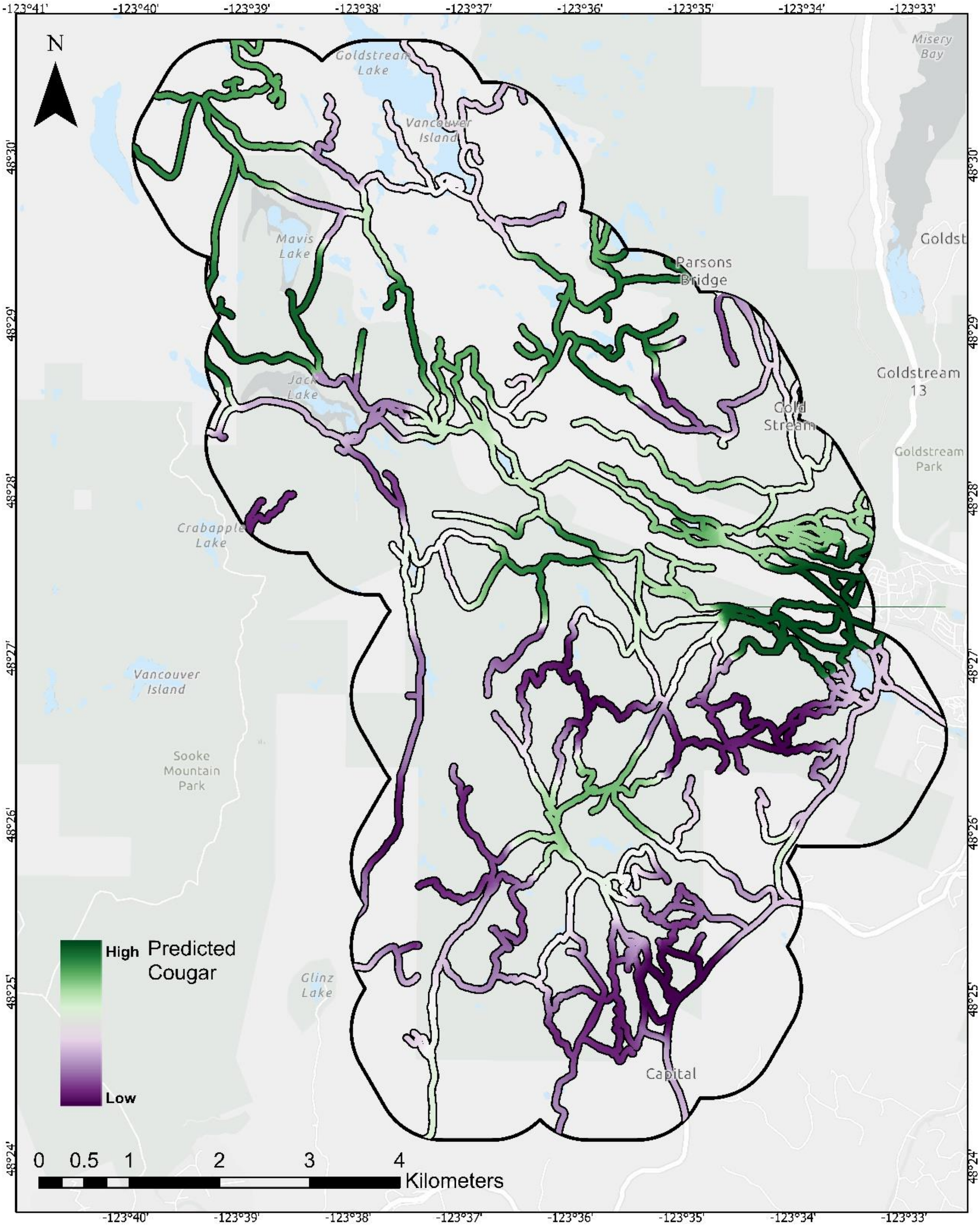


Figure 2.9: The map shows the likelihood of cougar occurrence on roads/trails within a 750-meter buffer around the camera trap grid. Areas in green indicate a higher likelihood of cougar presence, while areas in purple indicate a lower likelihood. Predictions are based on the top-performing Generalized Linear Model (GLM) using habitat and risk characteristics at each site.

2.3 Discussion

Non-consumptive human activity appears to drive cougar distributions; anthropogenic risk and habitat characteristics best explained cougar detection frequency in this mixed-accessibility coastal forest ecosystem. Risk was an important predictor for cougar occurrence, with cougars spatially avoiding areas of human activity. The people-driven landscape of fear was visualized in a prediction map, where cougar's spatial response to perceived risk and habitat characteristics varied across the landscape. Contrary to my predictions, cougars prioritized resource preferences over risk avoidance as they selected habitat. Cougars' spatial response to risks and resources occurred at the largest tested spatial scale as expected.

2.3.1 Spatial Responses to Risk

Humans shaped a landscape of fear for cougars, requiring these apex predators to employ risk-avoidance strategies in the face of human activity (Laundré et al., 2001). In response to perceived risk, cougars spatially avoided human occurrence and dense roads/trails. Human occurrence marked by direct cues (such as noise or odors), may have induced an anti-predator response, driving cougars to instead use lower-disturbance habitat patches (Suraci et al., 2019). Cougars' spatial avoidance of highly dense patches of roads and trails may have been due to indirect cues created by the patterns of human activity at trail intersections within the park (Morrison et al., 2014). Over time, cougars could have associated these physical features with perceived human risk, spatially avoiding habitat patches with many roads and trails as a habituated anti-predator response (Sih, 2013).

Cougars' different responses to human presence and vehicle activity suggested that stronger risk cues were associated with humans on foot. While cougars clearly avoided recreationalists, their positive association with vehicle detection frequency suggests that this form of human activity did not induce a strong fear response. Furthermore, vehicle activity and hiking were spatially separated throughout the study area, as vehicles almost exclusively travelled through areas closed to public access. Therefore, cougars may have been more inclined to avoid public-access areas and travel on roads rather than travel on hiking trails. This preference could be due to the easier movement through patches of thick salal understory and dense new growth, as well as the lower perceived risk associated with these roads (Reed & Merenlender, 2008). My findings align with previous research, which suggests that although cougars may avoid human activity on trails, they generally do not avoid vehicle traffic on roads within their home ranges and often use roads as movement paths (Dickson & Beier, 2002; Kertson et al., 2011). However, further research should parse apart how cougars spatially respond to public-access versus restricted-access sites to disentangle the impacts of vehicle activity. A landscape of fear created by recreationalists may have pressured cougars to seek less disturbed pathways. By using roads as movement routes, cougars may have been able to avoid habitat patches with high human activity and limited undisturbed cover.

The landscape of fear created by recreationalists was depicted in a map, where areas of high human activity in the park predicted lower occurrence of cougars, and low human activity in the closed-access watershed predicted higher occurrence of cougars. Essential elements that comprise the landscape of fear--including the physical landscape, the spatial variation in predation risk, the perception of risk, and the spatial distribution of prey--outlined a guiding framework to create visual representations (Gaynor et al., 2019). Many existing representations use only one element of this framework (Gaynor et al., 2019). My visualization attempted to capture multiple elements of the framework, including the physical landscape (habitat characteristics), the spatial variation in predation risk (human occurrences), and the spatial distribution of “prey” (cougar occurrences). This visualization of cougar occurrence confirmed the model testing results, reaffirming that cougars spatially avoided highly trafficked hiking trails in the park. This visual depiction contributes to the growing body of research aimed at better conceptualizing landscapes of fear. However, future studies should incorporate measures of fear perception, such as physiological responses associated with perceiving risks (Clinchy et al., 2013). This additional landscape of fear framework element would allow us to make stronger connections between variation in human space use and variation in carnivore space use across a landscape (Støen et al., 2015).

2.3.2 Spatial Responses to Resources

Cougars were associated with habitat characteristics in a predictable way, aligning with their specific needs for hunting and stalking cover, suitable denning sites, optimal movement corridors, and the availability of prey (Dickson & Beier, 2002; Morrison et al. 2014; Pierce et al. 1999). Cougars were detected more frequently at sites with a higher proportion of water features as these areas provide vegetation for stalking cover and prey species' forage (Kertson et al., 2011; Ripple & Beschta, 2006). Cougars' primary large prey types in this area, Roosevelt elk, and black-tailed deer, demonstrated a preference for water features and cutblocks, further explaining cougars' selection of these sites. Cougars occurred more commonly at sites with a higher proportion of broadleaf forest. Broadleaf forest offers important browse for deer and elk (Poole & Mowat, 2005); however, deer were observed avoiding patches with higher broadleaf forest proportions in the study area. This avoidance may have been due to deer selecting for broadleaf forest at a different spatial scale than cougars. Investigating the spatial scale of prey habitat selection and cougars' diet composition and could provide further insights into predator-prey dynamics in this system (Knopff et al., 2014). Additionally, exploration of the spatial scale at which cougars engage in hunting behaviours would provide a clearer picture of how available prey regulate cougar space use (Wilmers et al., 2013).

Conifer forest, which typically supports lower ungulate densities than deciduous forest (Teichman et al., 2013), was associated with fewer deer and elk, and thus fewer cougars. In contrast, Kertson et al. (2011) found a positive association between cougar occurrence and proportion conifer forest. However, in this system, conifer forest did not demonstrate strong predictive power due to its vast and consistent cover across British Columbia (Teichman et al., 2013). Cougars' preference for cutblock areas aligns with past studies, which have found that cougars use this habitat because cutblocks harbor browse for prey and adjacent patches provide cover for hunting and stalking (Kertson et al., 2011; Laing 1988; Logan & Irwin, 1985). This spatial preference may be explained by the distribution of cutblocks at varying stages in the study area due to a long history of logging. The varying stages of cutblock growth provide intermediately disturbed habitat and edge habitat that facilitate elk and deer foraging behaviour and cougar movement (Morrison et al., 2014). Other features of the studied system, including high elevations marked by rocky, open outcroppings, offered little vegetative productivity for prey forage or cougar stalking cover (Pauley et al. 1993; Teichman et al. 2013). Thus, these areas were used less frequently by cougars in favour of lower elevation, forested regions. Cougar habitat preferences were broadly consistent with findings from Dickson & Beier (2002), Kertson et al. (2011), and Morrison et al. (2014). Any dissimilarities from past findings may be due to cougars' responses to anthropogenic risk, or the scale at which habitat use was evaluated.

2.3.3 Trade-offs between Risk and Resources

A drive for resources outweighs the threat of predation for cougars, revealing the trade-offs this apex predator makes to meet its needs. While several studies have evaluated cougars' responses to risk and resources independently (Nickel et al., 2020; Sweanor et al., 2008), few have directly examined the relationship between these responses (Mills et al., 2023). In the study area, cougars were more likely to tolerate anthropogenic risk when preferential habitat patches were present. Higher proportions of broadleaf forest provide litterfall forage and habitat for prey in the spring and summer months, particularly for elk (Poole & Mowat, 2005). The potential benefits of available natural resources and preferred habitat such as broadleaf forest may outweigh the anthropogenic risk trade-offs in situations when humans are more difficult to avoid (Moss et al., 2016; Stoner et al., 2021). For example, when cougars experience periods of hunger or prey are concentrated in certain areas, cougars are more likely to use risky places as their anti-predator response becomes inhibited (Blecha et al., 2018). Alternatively, cougars may employ temporal avoidance of human presence and shift to increased nocturnality in high quality habitat patches (Gaynor et al., 2018; Lewis et al., 2021). Although cougars were willing to tolerate humans in some cases, the perceived risk of human presence can have substantial consequences, such as decreasing the efficiency of resource acquisition, increasing the energy requirements of cougar movement, and reducing feeding times (Nickel et al., 2021; Smith, 2017). This trade-off also creates a source of potential human-cougar encounters in areas where a high density of broadleaf forest and recreationalists coincide (Arundel et al., 2007). While the GVWSA provided abundant restricted-access land, wildlife in areas with reduced habitat protections and connectivity may experience a higher cost from human disturbances (Gill et al., 2001). Therefore, it is important to broaden these studies to assess how human activity impacts cougars across varying levels of landscape restriction.

2.3.4 Influences of Spatial Scale

The better performance of larger buffer sizes shows that cougars evaluate their environment at a greater scale, balancing risks and resources across large habitat patches. Cougars’ home ranges, which can vary in size across broad geographic areas (Grigione et al., 2002; Spreadbury et al., 1996), average 61 km^2 for females and 186 km^2 for males on Vancouver Island (Hahn, 2001). These relatively large home ranges suggest that the sub-1-kilometer spatial buffers used in this study have limited explanatory power for understanding cougar space use (Fisher et al., 2011; Wilson et al., 2004). However, spatial analysis was constrained by the distance between camera trap sites in my study design. Increasing the distance between camera traps would allow for larger spatial buffers, facilitating a more comprehensive exploration of habitat selection within cougars' home ranges. My findings deviate from past studies of scale selection, where Fisher et al. (2011) and Wilmers et al. (2013) assessed cougar habitat use at scales smaller than 750 meters. Heim et al. (2019) and Gaston et al. (2024) applied a range of larger-scale buffers, where Gaston et al. (2024) found a 2500-meter buffer to best explain cougar space use. Given that cougars' spatial responses to human-induced risk, habitat, and prey have been shown to vary across multiple spatial scales, future research should continue to incorporate a range of tested scales to better understand spatial responses to risk (Jordan & Ryan, 2015).

2.4 Management Implications

Conclusions about cougar responses to resources and perceived risk were constrained by the study design, particularly due to the relatively small study area (36 km^2), which is smaller than the average home range size of cougars on Vancouver Island (61 km^2 to 186 km^2) (Hahn, 2001). Additionally, the placement of camera traps along linear features, such as trails, did not account for activities occurring in off-trail habitats. Together, this limited sampling area constrained inferences about cougar habitat use in less-surveyed areas, as cougars may have been using off-road habitat and other portions of their home ranges at different frequencies. The focus on roads and trails provided a narrow view of cougar movements, potentially missing variation in their use of the broader landscape. Furthermore, the visual prediction surface for cougar occurrence was spatially restricted by the limited number of camera traps, and the interpolation of count data from these fixed points did not fully capture nuances in habitat use and the influence of risk across the study area. In this study, camera traps were placed in grid cells small enough to capture the landscape's high variability, which likely aided in accurate interpolation of estimates. However, extending the study area by adding more camera traps in diverse habitats, such as at larger water sources, could reveal emerging patterns of habitat use and risk response, especially given the large range sizes of cougars. Additionally, the inherent limitations of camera traps, such as imperfect detection, where cougars present are not captured due to camera malfunctions or being outside the field of view (Wearn & Glover-Kapfer, 2017), further emphasize the need for larger-scale studies to draw broader conclusions about cougar space use and potential risk responses.

The data were also temporally constrained to the late spring and summer months, despite expected variations in human activity, wildlife activity, and habitat conditions throughout the year. Some cougar populations, or individuals within a population, make significant seasonal movements to follow prey between winter and summer ranges (Pierce et al., 1999). These movements mirror those of prey, which respond to changing vegetation and weather conditions, such as snow, between seasons (Dellinger et al., 2018). These temporal limitations, coupled with the relatively small study area, may overlook seasonal shifts in habitat use, especially if cougars use different areas of their home ranges at certain times of the year. Additionally, seasonal fluctuations in human visitation to the public-access portion of the study area may further exacerbate these changes (Morrison et al., 2014).

Another limitation of this study involves the exclusion of community dynamics. While species-specific responses of cougars and interactions with large prey (deer and elk) were examined, the impacts of interspecific competition were not directly analyzed.

Coexistence among carnivores is driven partly by resource partitioning across spatial, temporal, and trophic dimensions, and human disturbance can disrupt this balance (Sévêque et al., 2020). Interspecific interactions, especially in an environment facing human pressures, can lead to avoidance of highly human-used areas and increased overlap among carnivores (Parsons et al., 2019). Although I found that cougars spatially avoided highly peopled areas, the omission of interactions with other carnivores limited the understanding of how cougars navigate natural and human-influenced landscapes when potential competition is present. However, this study was specifically focused on cougar responses to human activity, and the deliberate exclusion of community dynamics maintained clarity in addressing cougar-focused research questions. While broader ecological processes, including large mammal spatial partitioning, could enhance our understanding of cougars' risk-resource tradeoffs, the findings remain valid and provide insights into the impacts of outdoor recreation.

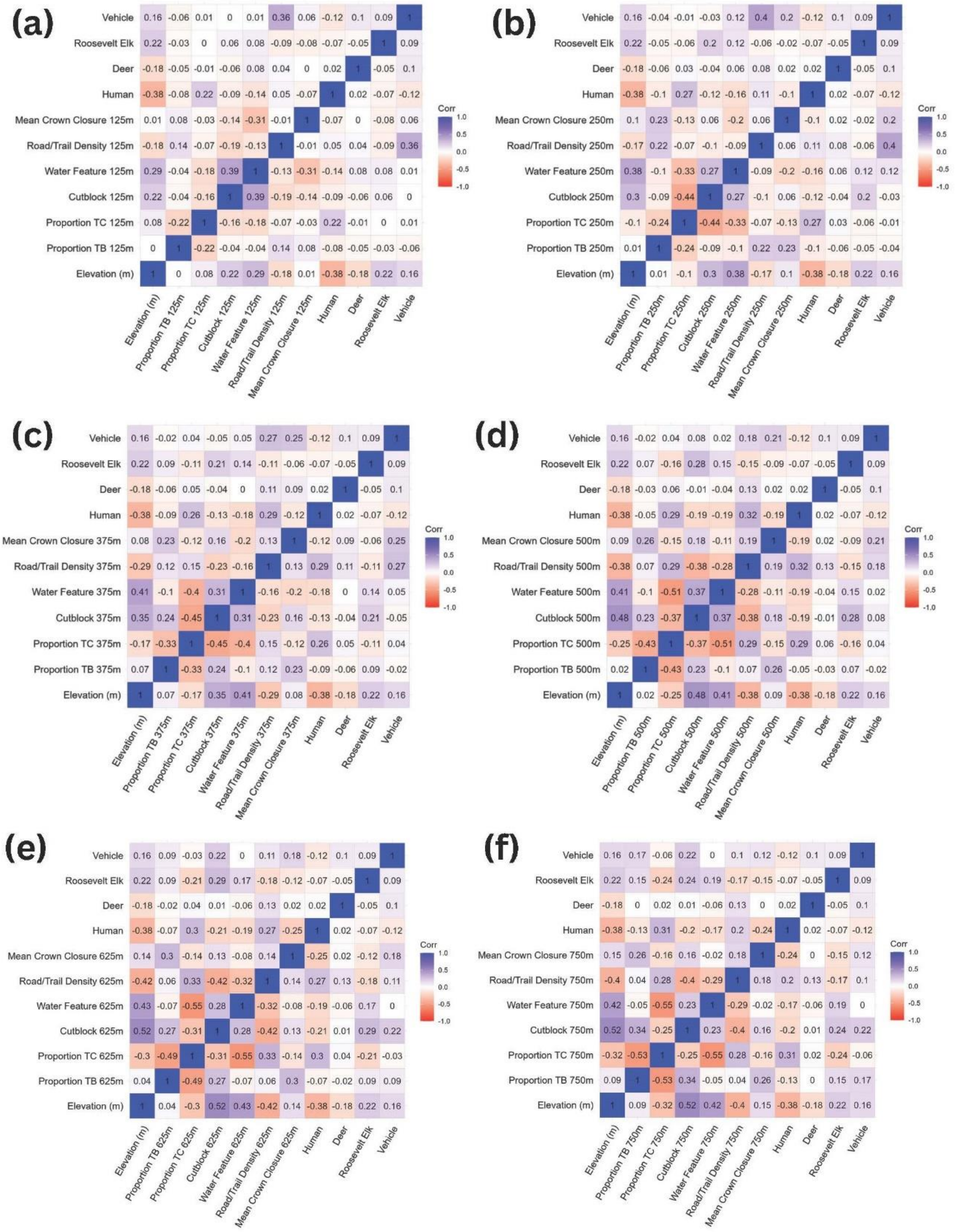
Broadly, this research adds to the growing understanding that non-consumptive human activities can alter carnivores' spatial patterns of habitat use. A fear-induced response predicates cougars' spatial avoidance of humans, pushing this apex predator into areas with a lower human presence. Potential costs to cougar's resource acquisition and energy demands must be considered in the management of outdoor recreation. Pervasive changes in wildlife behavior across an ecosystem must also be considered, as alterations in cougar space-use may trigger cascading top-down impacts (Ripple & Beschta 2006, 2008). Over time, high levels of human activity may drive cougars out of previously suitable habitat (Schuette et al., 2013; Smith et al. 2015). Further implications could ensue for predator-prey dynamics, potentially harming trophic functions. Maintaining plenty of undisturbed, high-quality habitat is important to ensure that human activities and carnivore needs remain compatible. At the landscape scale, the way cougars alter their spatial behaviour in response to predation risk reveals the importance of habitat protection. In a landscape with heterogeneous disturbances and adjacent highly protected zones, cougars have areas to retreat to when faced with perceived risk. These restricted-access patches can facilitate cougar movement, hunting, and denning, providing protection from the threats that human presence introduces to wild spaces. Without these adjacent protected zones, cougars would likely encounter risk more frequently (Schmidt & Kuijper, 2015). Highly protected habitat patches may also mitigate human-carnivore interactions, reducing the need for cougars to employ other compensatory strategies such as increasing their spatial overlap with recreationalists or with other carnivores, increasing their crepuscular activity, or moving even further into urban zones (Gaynor et al., 2018).

Locally, the prediction map will serve as a tool for park managers to identify areas where cougars are most likely to occur throughout the park and water supply area. This information supports goals to minimize human-wildlife conflict and protect areas of critical habitat (CRD, 2001; CRD, n.d.). Watershed managers may use this information to reinforce the importance of restricting public access within the water supply area. Restricting public access aligns with the goals of drinking water protection and ensures the preservation of lesser-disturbed patches of habitat for an important apex predator (CRD, 2001).

I have emphasized the need to protect valuable habitat patches for cougars, however, it is also necessary to consider the utility and effectiveness of larger protected areas. Future research should take a broad scale approach to consider how adjacent highly protected areas might influence carnivore space use in disturbed ecosystems. Within these systems, complex interspecific interactions, including spatial and temporal partitioning, may influence how cougars and other large carnivores respond to risk (Kronfeld-Schor & Dayan, 2003; Hubbard et al., 2022). Further investigation into spatial partitioning of large carnivores and their prey is needed to understand how human presence could disrupt ecological processes among the broader wildlife community. Species may respond divergently to perceived anthropogenic risk, especially across a gradient of disturbance types (Suraci et al., 2021). A look at these interactions during a longer camera trap deployment period could reveal how spatial dynamics fluctuate across seasons due to habitat changes (green-up, green-down, and snow) or seasonal variations in outdoor recreation (Morrison et al., 2014). Examining community resource partitioning in a heterogenous disturbance landscape would reveal how non-consumptive human activities scale upwards to impact entire ecosystems.

Appendix A

Pairwise Pearson correlation coefficients for all covariates used in analyses at six buffered distances: (a) 125 meters, (b) 250 meters, (c) 375 meters, (d) 500 meters, (e) 625 meters, (f) 750 meters. The correlation matrix displays the strength and direction of linear relationships between covariates. Negative correlations are indicated in red, while positive correlations are indicated in blue. The matrix helps identify how strongly variables are related to each other, with values ranging from -1 (perfect negative correlation) to +1 (perfect positive correlation).



Appendix B

Habitat + Risk (M3) model results compared across six spatial scales AIC. The model at the best-fit spatial scale is bolded. AIC = Akaike’s Information Criteria, ΔAIC = Delta AIC, AICw = AIC Weight, -2LL = Negative Two Log-Likelihood, df = Degrees of freedom.

Model	Scale	AIC	ΔAIC	AICw	-2LL	df
Null	0	912.39	19.30	0	-908.39	2
M3	125	909.46	16.38	0	-887.46	11
M3	250	903.41	10.33	0.003	-881.41	11
M3	375	899.82	6.74	0.019	-877.82	11
M3	500	899.22	6.14	0.025	-877.22	11
M3	625	893.68	0.59	0.406	-871.68	11
M3	**750**	**893.08**	**0.00**	**0.546**	**-871.08**	**11**

References

Anderson, C. R., Lindzey, F., Knopff, K. H., Jalkotzy, M. G., & Boyce, M. S. (2009). Chapter 4. Cougar Management in North America. In Chapter 4. Cougar Management in North America (pp. 41–54). University of Chicago Press. https://doi.org/10.7208/9780226353470-009

Arundel, T., Mattson, D. J., & Hart, J. (2007). *Movements and habitat selection by mountain lions in the Flagstaff uplands. In Mountain lions of the Flagstaff uplands* (Open-File Report) [Open-File Report]. US Department of the Interior, US Geological Survey.

Atuo, F. A., & O'Connell, T. J. (2017). The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. Ecology and Evolution, 7(13), 4782–4793. https://doi.org/10.1002/ece3.3021

Beery, S., Morris, D., & Yang, S. (2019). Efficient Pipeline for Camera Trap Image Review (arXiv:1907.06772). arXiv. http://arxiv.org/abs/1907.06772

Blecha, K. A., Boone, R. B., & Alldredge, M. W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. Journal of Animal Ecology, 87(3), 609–622. https://doi.org/10.1111/1365-2656.12801

Burdett, C. L., Crooks, K. R., Theobald, D. M., Wilson, K. R., Boydston, E. E., Lyren, L. M., Fisher, R. N., Vickers, T. W., Morrison, S. A., & Boyce, W. M. (2010). Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere, 1(1), art4. https://doi.org/10.1890/ES10-00005.1

Canty, A., & Ripley, B. (n.d.). Boot: Bootstrap R (S-Plus) functions (Version 1.3.28.1) [Computer software]. The R Foundation.

Chourmouzis, C., Yanchuk, A. D., Hamann, A., Smets, P., & Aitken, S. N. (2009). Forest Tree Genetic Conservation Status Report 1: In situ conservation status of all indigenous BC species [BC Technical Report]. Centre for Forest Conservation Genetics, Forest Genetics Council of BC, and BC Ministry of Forests and Range, Forest Science Program.

Clinchy, M., Sheriff, M. J., & Zanette, L. Y. (2013). Predator-induced stress and the ecology of fear. Functional Ecology, 27(1), 56–65. https://doi.org/10.1111/1365-2435.12007

Coppes, J., Ehrlacher, J., Thiel, D., Suchant, R., & Braunisch, V. (2017). Outdoor recreation causes effective habitat reduction in capercaillie Tetrao urogallus: A major threat for geographically restricted populations. Journal of Avian Biology, 48(12), 1583–1594. https://doi.org/10.1111/jav.01239

CRD. (2001). Sooke Hills Wilderness and Mount Wells Regional Parks Management Plan. https://www.crd.bc.ca/docs/default-source/parks-pdf/sooke-hills-management-plan-2001.pdf?sfvrsn=3c8d88cc_2

CRD. (2017). Regional Parks 2017 Annual Report. Capitol Regional District Parks and Environmental Services.

CRD. (2023). Greater Victoria Water Supply Area. CRD. https://www.crd.bc.ca/service/drinking-water/watershed-protection/greater-victoria-water-supply-area

CRD. (n.d.). Regional Parks and Trails Strategic Plan 2022-2023. https://www.crd.bc.ca/docs/default-source/crd-document-library/plans-reports/parks-recreation/crd-regional-parks-and-trails-strategic-plan-2022-2032-reduced.pdf

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. Science, 349(6250), 858–860. https://doi.org/10.1126/science.aac4249

Dellinger, J. A., Cristescu, B., Ewanyk, J., Gammons, D. J., Garcelon, D., Johnston, P., Martins, Q., Thompson, C., Vickers, T. W., Wilmers, C. C., Wittmer, H. U., & Torres, S. G. (2020). Using Mountain Lion Habitat Selection in Management. The Journal of Wildlife Management, 84(2), 359–371. https://doi.org/10.1002/jwmg.21798

Dellinger, J. A., Loft, E. R., Bertram, R. C., Ronald C. Bertram, Neal, D. L., Kenyon, M. W., & Torres, S. G. (2018). Seasonal Spatial Ecology of Mountain Lions (Puma concolor) in the

Central Sierra Nevada. *Western North American Naturalist*, *78*(2), 143–156. https://doi.org/10.3398/064.078.0205

Dickson, B. G., & Beier, P. (2002). Home-Range and Habitat Selection by Adult Cougars in Southern California. The Journal of Wildlife Management, 66(4), 1235–1245. https://doi.org/10.2307/3802956

Eliuk, L. (2023). The relative impacts of recreational activity and landscape protection on a Rocky Mountain mammal community. http://hdl.handle.net/1828/15150

Esri. (2023). ArcGIS Pro (Version 3.1) [Computer software]. Environmental Systems Research Institute. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecology and Evolution, 1(4), 517–528. https://doi.org/10.1002/ece3.45

Gaston, K. J., Jackson, S. F., Cantú-Salazar, L., & Cruz-Piñón, G. (2008). The Ecological Performance of Protected Areas. Annual Review of Ecology, Evolution, and Systematics, 39(1), 93–113. https://doi.org/10.1146/annurev.ecolsys.39.110707.173529

Gaston, M. V., Barnas, A. F., Smith, R. M., Murray, S., & Fisher, J. T. (2024). Native prey, not landscape change or novel prey, drive cougar (Puma concolor) distribution at a boreal forest range edge. Ecology and Evolution, 14(4), e11146. https://doi.org/10.1002/ece3.11146

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. Trends in Ecology & Evolution, 34(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. Science, 360(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Gill, J. A., Norris, K., & Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation, 97(2), 265–268. https://doi.org/10.1016/S0006-3207(00)00002-1

Glick, H. B. (2014). Modeling cougar habitat in the Northeastern United States. Ecological Modelling, 285, 78–89. https://doi.org/10.1016/j.ecolmodel.2014.02.005

Greenberg, S., Godin, T., & Whittington, J. (2019). Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution, 9(24), 13706–13730. https://doi.org/10.1002/ece3.5767

Greenland, S., Senn, S. J., Rothman, K. J., Carlin, J. B., Poole, C., Goodman, S. N., & Altman, D. G. (2016). Statistical tests, P values, confidence intervals, and power: A guide to misinterpretations. *European Journal of Epidemiology*, *31*(4), 337–350. https://doi.org/10.1007/s10654-016-0149-3

Grigione, M. M., Beier, P., Hopkins, R. A., Neal, D., Padley, W. D., Schonewald, C. M., & Johnson, M. L. (2002). Ecological and allometric determinants of home-range size for mountain lions (Puma concolor). Animal Conservation, 5(4), 317–324. https://doi.org/10.1017/S1367943002004079

Hahn, A. M. (2001). Social and spatial organization of Vancouver Island cougar (Puma concolor vancouverensis, Nelson and Goldman, 1943). https://doi.org/10.14288/1.0090208

Heim, N., Fisher, J. T., Volpe, J., Clevenger, A. P., & Paczkowski, J. (2019). Carnivore community response to anthropogenic landscape change: Species-specificity foils generalizations. Landscape Ecology, 34(11), 2493–2507. https://doi.org/10.1007/s10980-019-00882-z

Hilbe, J. M. (2014). Modeling Count Data (1st ed.). Cambridge University Press. https://doi.org/10.1017/CBO9781139236065

Hornocker, M., & Negri, S. (2009). Cougar: Ecology and Conservation. In Cougar. University of Chicago Press. https://doi.org/10.7208/9780226353470

Hubbard, T., Cove, M. V., & Diana J R Lafferty. (2022). Human recreation impacts seasonal activity and occupancy of American black bears (Ursus americanus) across the anthropogenic-wildland interface. Scientific Reports, 12(1). https://doi.org/10.1038/s41598-022-15665-x

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology, 61(1), 65–71. https://doi.org/10.2307/1937156

Jordan, L. A., & Ryan, M. J. (2015). The sensory ecology of adaptive landscapes. Biology Letters, 11(5), 20141054. https://doi.org/10.1098/rsbl.2014.1054

Keim, J. L., Lele, S. R., DeWitt, P. D., Fitzpatrick, J. J., & Jenni, N. S. (2019). Estimating the intensity of use by interacting predators and prey using camera traps. Journal of Animal Ecology, 88(5), 690–701. https://doi.org/10.1111/1365-2656.12960

Kertson, B. N., Spencer, R. D., Marzluff, J. M., Hepinstall-Cymerman, J., & Grue, C. E. (2011). Cougar space use and movements in the wildland–urban landscape of western Washington. Ecological Applications, 21(8), 2866–2881. https://doi.org/10.1890/11-0947.1

Knopff, A. A., Knopff, K. H., Boyce, M. S., & St. Clair, C. C. (2014). Flexible habitat selection by cougars in response to anthropogenic development. Biological Conservation, 178, 136–145. https://doi.org/10.1016/j.biocon.2014.07.017

Koehler, G. M., & Hornocker, M. G. (1991). Seasonal Resource Use among Mountain Lions, Bobcats, and Coyotes. Journal of Mammalogy, 72(2), 391–396. https://doi.org/10.2307/1382112

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of Time as an Ecological Resource. Annual Review of Ecology, Evolution, and Systematics, 34(1), 153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

Laing, S. P. (1988). Cougar habitat selection and spatial use patterns in southern Utah [Thesis]. University of Wyoming.

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review. PLOS ONE, 11(12), e0167259. https://doi.org/10.1371/journal.pone.0167259

LaRue, M. A., & Nielsen, C. K. (2011). Modelling potential habitat for cougars in midwestern North America. Ecological Modelling, 222(3), 897–900. https://doi.org/10.1016/j.ecolmodel.2010.11.017

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Canadian Journal of Zoology, 79(8), 1401–1409. https://doi.org/10.1139/z01-094

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology, 73(6), 1943–1967. https://doi.org/10.2307/1941447

Lewis, J., Spaulding, S., Swanson, H., Keeley, W., Gramza, A., Vandewoude, S., & Crooks, K. (2021). Human activity influences wildlife populations and activity patterns: Implications for spatial and temporal refuges. Ecosphere, 12. https://doi.org/10.1002/ecs2.3487

Logan, K. A., & Irwin, L. L. (1985). Mountain Lion Habitats in the Big Horn Mountains, Wyoming. Wildlife Society Bulletin (1973-2006), 13(3), 257–262.

MacKenzie, D. I. (2006). Modeling the Probability of Resource Use: The Effect of, and Dealing with, Detecting a Species Imperfectly. The Journal of Wildlife Management, 70(2), 367–374. https://doi.org/10.2193/0022-541X(2006)70[367:MTPORU]2.0.CO;2

Mills, K. L., Belant, J. L., Beukes, M., Dröge, E., Everatt, K. T., Fyumagwa, R., Green, D. S., Hayward, M. W., Holekamp, K. E., Radloff, F. G. T., Spong, G., Suraci, J. P., Van der Weyde, L. K., Wilmers, C. C., Carter, N. H., & Sanders, N. J. (2023). Tradeoffs between resources and risks shape the responses of a large carnivore to human disturbance. Communications Biology, 6(1), 1–11. https://doi.org/10.1038/s42003-023-05321-z

Morrison, C. D., Boyce, M. S., Nielsen, S. E., & Bacon, M. M. (2014). Habitat selection of a re-colonized cougar population in response to seasonal fluctuations of human activity. The Journal of Wildlife Management, 78(8), 1394–1403. https://doi.org/10.1002/jwmg.799

Moss, W. E., Alldredge, M. W., Pauli, J. N., & Frair, J. (2016). Quantifying risk and resource use for a large carnivore in an expanding urban–wildland interface. The Journal of Applied Ecology, 53(2), 371–378. https://doi.org/10.1111/1365-2664.12563

Naidoo, R., & Burton, A. C. (2020). Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conservation Science and Practice, 2(10), n/a. https://doi.org/10.1111/csp2.271

Nams, V. O., Mowat, G., & Panian, M. A. (2006). Determining the spatial scale for conservation purposes – an example with grizzly bears. Biological Conservation, 128(1), 109–119. https://doi.org/10.1016/j.biocon.2005.09.020

Nickel, B. A., Suraci, J. P., Allen, M. L., & Wilmers, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biological Conservation, 241, 108383. https://doi.org/10.1016/j.biocon.2019.108383

Nickel, B., Justin P. Suraci, Suraci, J. P., Anna C. Nisi, Nisi, A. C., Christopher C. Wilmers, & Wilmers, C. C. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. Proceedings of the National Academy of Sciences of the United States of America, 118(5). https://doi.org/10.1073/pnas.2004592118

Ordiz, A., Bischof, R., & Swenson, J. E. (2013). Saving large carnivores, but losing the apex predator? Biological Conservation, 168, 128–133. https://doi.org/10.1016/j.biocon.2013.09.024

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., Millspaugh, J. J., & Kays, R. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, *56*(8), 1894–1904. https://doi.org/10.1111/1365-2664.13385

Pauley, G. R., Peek, J. M., & Zager, P. (1993). Predicting White-Tailed Deer Habitat Use in Northern Idaho. The Journal of Wildlife Management, 57(4), 904–913. https://doi.org/10.2307/3809096

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal, 10(1), 439. https://doi.org/10.32614/RJ-2018-009

Pebesma, E., & Bivand, R. (2023). Spatial Data Science: With Applications in R (1st ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016

Pierce, B. M., Bleich, V. C., Wehausen, J. D., & Bowyer, R. T. (1999). Migratory Patterns of Mountain Lions: Implications for Social Regulation and Conservation. Journal of Mammalogy, 80(3), 986–992. https://doi.org/10.2307/1383269

Poole, K. G., & Mowat, G. (2005). Winter Habitat Relationships of Deer and Elk in the Temperate Interior Mountains of British Columbia. Wildlife Society Bulletin (1973-2006), 33(4), 1288–1302.

Procko, M., Naidoo, R., LeMay, V., & Burton, A. C. (2023). Human presence and infrastructure impact wildlife nocturnality differently across an assemblage of mammalian species. PLOS ONE, 18(5), e0286131. https://doi.org/10.1371/journal.pone.0286131

R Core Team (2023). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Reed, S. E., & Merenlender, A. M. (2008). Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. Conservation Letters, 1(3), 146–154. https://doi.org/10.1111/j.1755-263X.2008.00019.x

Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation, 133(4), 397–408. https://doi.org/10.1016/j.biocon.2006.07.002

Ripple, W. J., & Beschta, R. L. (2008). Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. Biological Conservation, 141(5), 1249–1256. https://doi.org/10.1016/j.biocon.2008.02.028

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. Science, 343(6167), 1241484. https://doi.org/10.1126/science.1241484

Sayol, F. (2021). Cervus elaphus by Ferran Sayol (CC0 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/cc03f5c2-933f-4c40-9c64-7f8727556fdb/cervus-elaphus

Schmidt, K., & Kuijper, D. P. J. (2015). A "death trap" in the landscape of fear. Mammal Research, 60(4), 275–284. https://doi.org/10.1007/s13364-015-0229-x

Schuette, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation, 158, 301–312. https://doi.org/10.1016/j.biocon.2012.08.008

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., & Hiraldo, F. (2008). Top Predators as Conservation Tools: Ecological Rationale, Assumptions, and Efficacy. Annual Review of Ecology, Evolution, and Systematics, 39, 1–19.

Sévêque, A., Gentle, L., López-Bao, J. V., Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biological Reviews, 95(6), 1689–1705. https://doi.org/10.1111/brv.12635

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. Animal Behaviour, 85(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences, 284(1857), 20170433. https://doi.org/10.1098/rspb.2017.0433

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. Proceedings of the Royal Society. B, Biological Sciences, 282(1802), 20142711–20142711. https://doi.org/10.1098/rspb.2014.2711

Spreadbury, B. R., Musil, R. R. K., Musil, J., Kaisner, C., & Kovak, J. (1996). Cougar Population Characteristics in Southeastern British Columbia. The Journal of Wildlife Management, 60(4), 962–969. https://doi.org/10.2307/3802398

Støen, O.-G., Ordiz, A., Evans, A. L., Laske, T. G., Kindberg, J., Fröbert, O., Swenson, J. E., & Arnemo, J. M. (2015). Physiological evidence for a human-induced landscape of fear in brown bears (Ursus arctos). Physiology & Behavior, 152(Pt A), 244–248. https://doi.org/10.1016/j.physbeh.2015.09.030

Stoner, D. C., Ditmer, M. A., Mitchell, D. L., Young, J. K., & Wolfe, M. L. (2021). Conflict, coexistence, or both? Cougar habitat selection, prey composition, and mortality in a multiple-use landscape. California Fish and Wildlife Journal, 107(3), 147–172. https://doi.org/10.51492/cfwj.hwisi.2

St-Pierre, F., Drapeau, P., & St-Laurent, M.-H. (2022). Stairway to heaven or highway to hell? How characteristics of forest roads shape their use by large mammals in the boreal forest. Forest Ecology and Management, 510, 120108. https://doi.org/10.1016/j.foreco.2022.120108

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecology Letters, 22(10), 1578–1586. https://doi.org/10.1111/ele.13344

Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L. M., Forrester, T., Green, A. M., Haight, J., Harris, N. C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P. E., Lewis, J. S., McInturff, A., … Wilmers, C. C. (2021). Disturbance type and species life history predict mammal responses to humans. Global Change Biology, 27(16), 3718–3731. https://doi.org/10.1111/gcb.15650

Sweanor, L. L., Logan, K. A., Bauer, J. W., Millsap, B., & Boyce, W. M. (2008). Puma and Human Spatial and Temporal Use of a Popular California State Park. The Journal of Wildlife Management, 72(5), 1076–1084. https://doi.org/10.2193/2007-024

Taylor, A. R., & Knight, R. L. (2003). Wildlife Responses to Recreation and Associated Visitor Perceptions. Ecological Applications, 13(4), 951–963. https://doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2

Taylor, J. (2019). Puma concolor by Jody Taylor (CC0 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/3f8eff77-2868-4121-8d7d-a55ebdd49e04/puma-concolor

Teichman, K. J., Cristescu, B., & Nielsen, S. E. (2013). Does Sex Matter? Temporal and Spatial Patterns of Cougar-Human Conflict in British Columbia. PLOS ONE, 8(9), e74663. https://doi.org/10.1371/journal.pone.0074663

The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia. (2001). *Sooke Hills Wilderness and Mount Wells Regional Parks Terrestrial Ecosystem*

Mapping. The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Zi, F. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. 5.

Venables WN, Ripley BD (2002). *Modern Applied Statistics with S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0, https://www.stats.ox.ac.uk/pub/MASS4/.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nature Communications, 7(1), 12558. https://doi.org/10.1038/ncomms12558

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. https://doi.org/10.13140/RG.2.2.23409.17767

Wiens, J. A. (1989). Spatial Scaling in Ecology. https://doi.org/10.2307/2389612

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. Ecology, 90(2), 546–555. https://doi.org/10.1890/08-0765.1

Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., Kermish-Wells, J., Yovovich, V., & Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. PloS One, 8(4), e60590. https://doi.org/10.1371/journal.pone.0060590

Wilson, S. F., Hahn, A., Gladders, A., Goh, K. M. L., & Shackleton, D. M. (2004). Morphology and Population Characteristics of Vancouver Island Cougars. The Canadian Field-Naturalist, 118(2), Article 2. https://doi.org/10.22621/cfn.v118i2.903

xgirouxb. (2019). Odocoileus hemionus by xgirouxb (PDM 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/f889b336-9e67-4154-bc96-db4095a55be2/odocoileus-hemionus

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution, 1(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). Analysing Ecological Data. Springer. https://doi.org/10.1007/978-0-387-45972-1

Silhouette of Hiker. (n.d.). [Graphic]. https://www.pngkey.com/detail/u2q8a9w7y3y3w7r5_hiking-silhouette-vector/

Chapter 3: Protected Area Access Impacts the Distributions and Spatial Dynamics of Large Mammals

3.0 Introduction

Protected natural areas conserve biodiversity and promote ecosystem functioning, offering essential refuges in regions affected by human development and disturbances (Reed & Merenlender, 2008). However, many of these protected areas operate under a dual mandate of supporting both conservation and outdoor recreation goals, thus allowing some human influence. Human visitation rates to protected areas vary greatly worldwide, driven by factors such as regulated access, nearby population density, and recreation infrastructure (Neuvonen et al., 2010). A growing body of research demonstrates that higher levels of human activity in protected areas have more pronounced impacts on wildlife (Naidoo & Burton, 2020; Nickel et. al., 2020; Reed & Merenlender, 2008). While it is well-established that consumptive activities such as hunting and landscape development impact wildlife habitat use (Ordiz et al., 2013; Tucker et al., 2018), non-consumptive activities such as hiking, cycling, and dog-walking also impact spatio-temporal behaviours of various species (Frid & Dill, 2002; Procko et al., 2023). As humans make approximately 8 billion visits to protected spaces each year--a number that continues to rise--the impact of non-consumptive activities on wildlife becomes an urgent issue (Balmford et al., 2015; Watson et al., 2016).

Although protected spaces across North America share the common goal of supporting wildlife and conservation, their effectiveness varies based on their level of permitted human access. Non-consumptive activities within North America’s protected spaces affect wildlife both spatially and temporally (Coppes et al., 2017; Naidoo & Burton, 2020; Taylor & Knight, 2003), and differences in ecological health have been noted between protected areas facing low and high human pressures (Jones et al., 2018). Closed-access protected spaces facing lower human pressures consistently harbor a higher diversity of species than public-access spaces (Reed & Merenlender, 2008). This suggests that wildlife in public-access areas may exhibit greater sensitivity to disturbances due to, amongst other things, a heightened perception of predation risk that leads to greater vigilance (Baker & Leberg, 2018; Frid & Dill, 2002). Despite these significant findings, few studies have directly compared spatial wildlife responses to human activity across different levels of public-access (Reed & Merenlender, 2008).

Wildlife have been shown to exhibit behaviourally mediated spatial shifts in habitat use due to human presence (Frid & Dill, 2002). Human presence imposes a perceived risk to large mammal species, inducing a fear response that drives them to seek refuge in “safer” habitats (Gaynor et al., 2019; Van Scoyoc et al., 2023). Consequently, these spatial shifts may increase sympatry between species as wildlife concentrate in remaining low-risk areas (Parsons et al. 2019). High spatial overlap can disrupt ecosystem dynamics and stability that rely on spatial partitioning and sufficient habitat for both predators and prey (Schoener, 1974; Smith, 2018). Increased spatial overlap could also exacerbate interspecific competition among a wildlife community as access to shared resources becomes constrained (Sévêque et al., 2020). Specifically, carnivores’ sensitivity to disturbance places them in a precarious position, as non-consumptive human activities can harm ecosystem balance by altering their ecological role (Baker & Leberg, 2018). For example, human-induced risk can reduce feeding times and restrict movement (Smith, 2015; Smith, 2017). Further, according to a review by Sévêque et al. (2020), a common impact of human activity was the total spatial exclusion of less disturbance-tolerant species. However, in cases where total spatial exclusion did not occur, spatial avoidance of humans was the most-reported impact, leading to increased interactions and spatial overlap among carnivores (Sévêque et al., 2020). This is significant because if carnivores experience spatial avoidance, their critical role in regulating prey populations may be disrupted (Suraci et al., 2019).

Although human recreation may induce spatial shifts across species (Naidoo & Burton, 2020), evidence suggests that carnivore and ungulate species respond variably according to their trophic role and life history (Suraci et al., 2019). Prey have been found to exploit carnivores' avoidance of human presence by overlapping their spatial and temporal habitat use with humans (Berger, 2007). This spatio-temporal overlap allows prey species to buffer against the predation risk posed by carnivores (Muhly et al., 2011). This tactic is known as the human shield hypothesis (Berger, 2007). Ungulates and small mammals may also experience benefits like increased resource acquisition, evidenced by their increased foraging intensity in response to human presence (Suraci et al., 2019). Anthropogenic impacts on wildlife spatial dynamics such as the "human shield" phenomena can cause cascading and potentially detrimental effects to large and small mammals, vegetation, and overall ecosystem health (Muhly et al., 2011). As species alter how and where they use habitat and acquire resources through trophic cascades, these shifts can disrupt ecological balance (Berger, 2007). In protected areas, access restrictions and spatial variation in human activity significantly influence these dynamics, reinforcing the importance of carefully managed human presence to maintain wildlife species' ecological roles.

Addressing non-consumptive human impacts on wildlife in protected areas requires an understanding of the role of protected areas in ecological health, specifically regarding how varying levels of activity might affect wildlife spatial behaviour, and whether access restrictions (even partial restrictions) could mitigate the impacts of human disturbance. By examining the effectiveness of protected spaces in maintaining well-supported wildlife communities, we can better evaluate the influences on wildlife at a scale relevant to management decisions; this allows us to determine the utility of access restrictions as a management tactic (Reed & Merenlender, 2008).

However, despite the growing recognition of scale as an influential and important consideration of ecological study design, it is often not given enough consideration in ecological research (McGarigal et. al. 2016; Wiens 1989). Scaling must be considered adequately, as it has the power to influence the results and interpretation of a study. The characteristic spatial scale of habitat selection varies among species (Holland et al., 2004), indicating that scale-dependent ecological mechanisms drive habitat selection differently for each species (Fisher et al., 2011). Therefore, multi-scale studies with an organism-centered approach facilitate a more ecologically accurate assessment of species' responses to habitat, risk, and the presence of other species (McGarigal et al. 2016; Wiens, 1989). By analyzing the scale at which wildlife spatially assess risks and resources, we can gain an ecologically relevant understanding of how space is partitioned and how habitat is used among species.

I aimed to investigate how scale-dependent spatial partitioning among a wildlife community (including large predator and prey species) is influenced by human disturbance and protected area access restrictions. Focusing on a high-biodiversity region on Southern Vancouver Island in British Columbia, Canada, I assessed these impacts where human population density is rapidly increasing. To do this, I used an array of 48 wildlife cameras stratified across two adjacent protected areas: the publicly accessible Sooke Hills Wilderness Area Regional Park and the restricted-access Greater Victoria Water Supply Area. I hypothesized that human activity would significantly influence wildlife community dynamics, with carnivores showing a stronger tendency to avoid human presence compared to ungulates. Additionally, I expected that access regulations in protected areas would shape species distributions and habitat use. Specifically, I anticipated that large carnivores would prefer areas with higher levels of protection, avoiding heavily trafficked public-access. Consequently, I predicted that carnivores would spatially overlap with one another due to redistribution pressures driven by human presence. In contrast, I expected ungulates to be more frequently detected in areas with human activity, using human presence as a shield against predation (Berger, 2007; Oliff et al., 1999; Taylor & Knight 2003). Finally, I anticipated that the spatial scale at which these responses occurred would vary across species (Fisher et al., 2011).

3.1 Methods

3.1.1 Study Area

This research occurred on the traditional territory of the lək̓ʷəŋən peoples and T'Sou-ke First Nation whose relationship with the land I acknowledge and respect. The study area is delineated by a 48-camera trap grid, covering 36km^2 , as illustrated in Figure 3.1. This grid encompassed approximately equal-sized portions of the 40.9 km^2 Sooke Hills Wilderness Area Regional Park (SHWA) and the 205.5 km^2 Greater Victoria Water Supply Area (GVWSA) (CRD, 2001; 2023). The SHWA is the largest park in the Capital Regional District (CRD) Regional Parks system. Characterized by its high level of protection as a "Wilderness Area", this park mandates minimal human interference with the ecosystem. The park permits recreational activities such as hiking, cycling, and dog-walking on public-access, marked trails. Adjacent to it, the GVWSA restricts public access to mitigate potential threats to the drinking water quality that supplies over 400,000 residents in the region. Active roads through the GVWSA provide access for water supply management as well as commercial logging on a relatively small portion of privately owned land that falls within the water supply area. These roads, along with decommissioned roads and unmarked trails provide movement corridors for wildlife in the area and are occasionally used by CRD employees.

The SHWA and the GVWSA sit within the Coastal Western Hemlock Very Dry Maritime Biogeoclimatic Subzone and a small portion lies within the Coastal Douglas-fir subzone (The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia, 2001). The climate in this area is characterized by an average annual temperature of 9.3°C and an average annual precipitation of 1,427 mm (Chourmouzis et al., 2009). The Goldstream watershed, beginning in the GVWSA and extending into the SHWA, provides wildlife habitat through high variable, localized vegetation communities. These protected areas support a range of important wildlife species, including Vancouver Island cougars (*Puma concolor vancouverensis*), black bears (*Ursus americanus*), grey wolves (*Canis lupus*), Columbian black-tailed deer (*Odocoileus hemionus columbianus*), Roosevelt elk (*Cervus canadensis roosevelti*), and the marbled murrelet (*Brachyramphus marmoratus*) (CRD, 2001).Though an arbitrary boundary exists between the SHWA and GVWSA, there are some differences to be noted in vegetation and landscape features. Areas around the Goldstream Lake Reservoir, Mavis Lake, and old-growth stands in the GVWSA differ from the wetlands found in the SHWA, offering different vegetation communities and landscape variables immediately surrounding these water features. Upland meadow complexes are common, especially throughout the SHWA, and the region is marked by steep grades and rocky outcroppings. Ecologically important mature and old-growth forest that is considered rare throughout the study area was once plentiful in the SHWA and GVWSA, however the cover of valuable old-growth has drastically decreased over time due to a long history of road building, forest management, and resource extraction (The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia, 2001). Despite these differences, the SHWA lacks dense young stands that might restrict large mammal movement. Both protected areas are broadly characterized by mixed age stands dominated by Douglas fir (*Pseudotsuga menziesii var. menziesii*), with a salal (*Gaultheria shallon*) understory. Water features throughout the two protected areas such as streams, wetlands, and lakes characterize this region that supports the CRD’s drinking water supply. Terrain within these protected areas is highly variable, driving more localized variability in habitat than variability between the two larger areas.

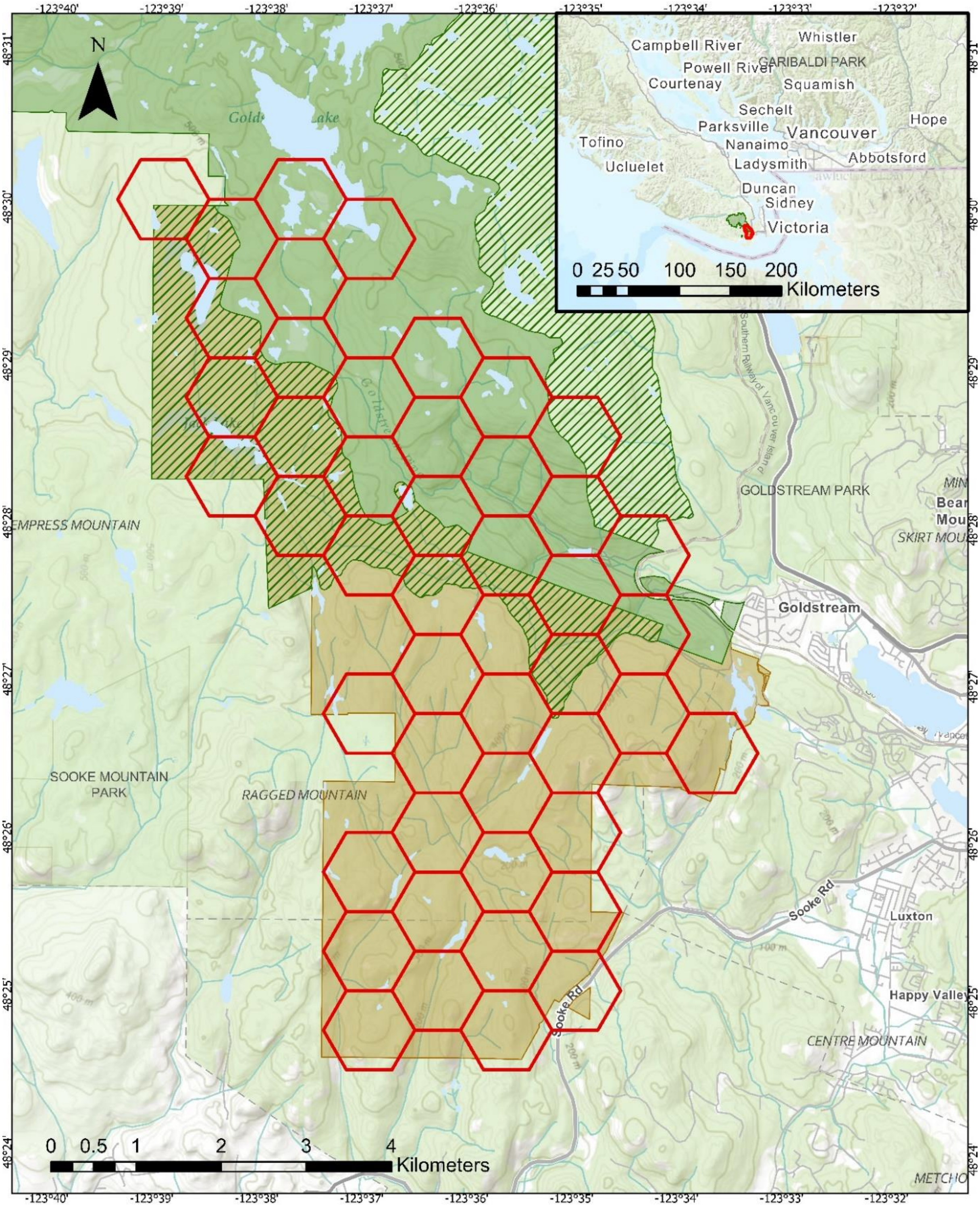


Figure 3.1: Camera trap grid (red hexagons) located in the Sooke Hills Wilderness Area (tan polygon) and Greater Victoria Water Supply Area/Drinking Water Protection Area (green polygon and green hashed lines) on Southern Vancouver Island, British Columbia, Canada. 48 infrared cameras placed along linear features near the center of each 750m^2 hexagonal grid cell.

3.1.2 Sample Design

A camera trap array of 50 Reconyx™ Hyperfire 2 (Reconyx, Holmen, WI) Infrared cameras were originally deployed in the SHWA and GVWSA, however 48 cameras remained available throughout the deployment period due to theft and camera malfunction at two sites. Cameras were deployed from May 1st, 2022, to December 31st, 2022 to monitor the study area across all four seasons. This deployment period captured most of the variation in wildlife behaviour, human visitation, and climatic conditions that tend to occur throughout the year. Cameras were placed along linear features (roads/trails) near the center of 750m^2 grid cells, as seen in Figure 3.1. This grid size allowed me to stratify cameras across habitat features while considering the small-scale landscape variability observed across the SHWA and GVWSA. Each camera was placed at a height of about 1 meter on a tree 1-20 meters from a linear feature, ensuring detectability of mammals of a variety of body sizes and ensuring detectability of vehicles (Naidoo & Burton, 2020). Half of the cameras were deployed in each protected area, enabling an even survey of both public-access and restricted-access sites.

3.1.3 Data Collection and Processing

Camera trap images were collected and analyzed over a 35-week study period. Timelapse Image Analyzer 2.0 was used to identify animal species, humans, cyclists, dogs, and vehicles present in camera trap images (Greenberg et al., 2019). As seen in Figure 3.2, human images were blurred using Megadetector and RStudio to protect community privacy (Beery et al., 2019; R Core Team, 2023). Images were processed to identify human and wildlife species counts and locations. To do this, independent events were defined as a site visit by an individual or group and were separated by 10 minute-intervals. This relatively short independence interval captured the frequency at which wildlife, humans, and vehicles used sites, where repeat visits throughout a day or week would be considered independent events (Keim et al., 2019). While measures of occupancy inform us about wildlife locations and can remain constant over long periods of time, measures of detection frequency offer insights into how often a site is used (Lele et al., 2013; MacKenzie et al., 2017). Detection frequency provides different ecological implications, as sites used repeatedly suggest underlying ecological influences at these locations (Keim et al., 2019). Different forms of human presence, including cyclists, dog-walkers, and hikers, were combined into a single "Human" count for generalized linear modeling. This approach provided a measure of detection frequency that included all human activities, calculating a more accurate count of individuals visiting a site. Species counts were calculated weekly throughout the study period, accounting for expected seasonal and monthly variations.

We measured landscape heterogeneity, heterospecifics' detection frequency, and categorized land-use restrictions to help explain wildlife detection frequency across the study area. These were derived from a variety of sources, as described in Table 3.1. "Public-Access" was incorporated as a hypothesized risk factor for wildlife species. "Public-Access" was thus modelled as a binary dummy variable to quantitatively measure wildlife responses to public-access sites. Values for covariates marked by an asterisk were calculated through a series of spatial buffers around each camera using the "sf" package in R (Pebesma & Bivand, 2023; Pebesma, 2018; R Core Team, 2023). All covariates were checked for correlation using Pearson's correlation coefficient within the "cor" function in R (base (version 3.6.2)) (Zuur et al., 2010). No strong correlation (with a correlation coefficient greater than ±0.7) was detected between covariates as seen in Appendix A.

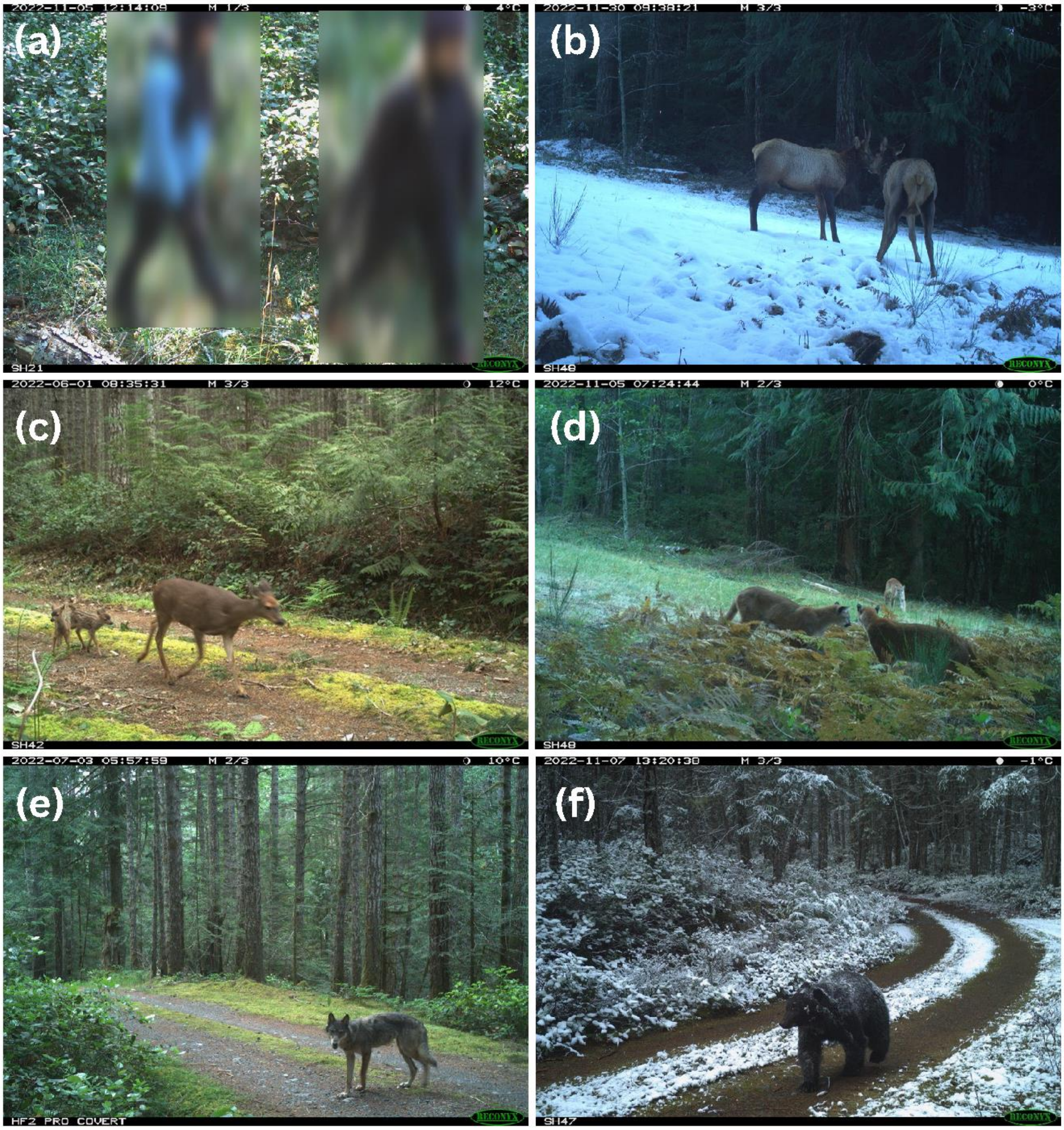


Figure 3.2: Images captured from the infrared motion-triggered cameras in the 48-camera trap array located in the SHWA and the GVWSA. Image (a) depicts two hikers, image (b) depicts a male and female Roosevelt elk, image (c) depicts a black-tailed deer with two fawns, image (d) depicts three cougars, image (e) depicts a grey wolf, and image (f) depicts a black bear. Human images were blurred to protect privacy, while animal images remained unblurred. Dates and timestamps are visible in the upper left-hand corner of each image, in addition to site identification in the lower left-hand corner.

Table 3.1: Habitat, risk, and prey covariates used in generalized linear models at six spatial scales. Proportion Conifer Forest, Proportion Broadleaf Forest, Mean Crown Closure, Proportion Cutblock, and Road/Trail Density were derived from GIS shapefiles. Elevation was derived from a GIS raster file. Public-Access was derived from RStudio. Human, Vehicle, Black-tailed Deer, and Roosevelt Elk, Cougar, Black Bear, and Grey Wolf counts were derived from group counts calculated using Timelapse2 Image Analyser and RStudio. Links to data sources can be found at the bottom of the table.

Covariate	Description	Source
Proportion Conifer Forest	Conifer forest cover calculated from VRI polygons in a buffer zone	2022 BC VRI[1]
Proportion Broadleaf Forest	Broadleaf forest cover calculated from VRI polygons in a buffer zone	2022 BC VRI[1]
Mean Crown Closure	Average crown closure values calculated from VRI polygons in a buffer zone	2022 BC VRI[1]
Proportion Water Feature	Proportion cover of lakes[2], wetlands[2], rivers[3], streams[3] in a buffer zone	CRD Watershed[2] BC Government[3]
Elevation	Elevation extracted from BC Digital Elevation Model	BC Government[4]
Proportion Cutblock	Calculated from cutblock polygons in a buffer zone	BC Government[5]
Human	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Vehicle	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Road/Trail Density	Density values calculated from road and trail layers in a buffer zone	CRD Watershed
Public-Access	Dummy variable created from site access status	R Studio[7]
Black-tailed Deer	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Roosevelt Elk	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Cougar	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Black Bear	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]
Grey Wolf	Counts detected in a week at a camera trap site	Timelapse2 Image Analyser[6]

[1] https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-inventory/data-management-and-access

[3] https://catalogue.data.gov.bc.ca/dataset/wsa-stream-routes-50-000

[4] https://pub.data.gov.bc.ca/datasets/175624/92b/

[5] https://catalogue.data.gov.bc.ca/dataset/b1b647a6-f271-42e0-9cd0-89ec24bce9f7

[6] https://saul.cpsc.ucalgary.ca/timelapse/pmwiki.php?n=Main.Download2

[7] https://cran.rstudio.com/

3.1.4 Statistical Analyses – Generalized Linear Modelling

A global model was constructed with habitat, risk, and community (heterospecifics' detection frequency) covariates relevant to protected spaces in the Southern Vancouver Island area and based on common predictors for large carnivores and their ungulate prey species (Dupke et al., 2017; Naidoo & Burton, 2020). Risk covariates were included in the model to assess how human presence and vehicles impact community- and species-specific spatial responses to anthropogenic risk. Global generalized linear models (GLMs) were constructed using appropriate distributions for each species. Count datasets were assessed for overdispersion to fit the best-suited model distribution for each species in the analysis. Overdispersion was detected in the deer-count data. To correct for overdispersion, a negative binomial distribution with a log-link was assumed (Hilbe, 2014). Cougar, elk, black bear, and wolf count data did not have overdispersion, and were therefore fit with a Poisson distribution with a log-link using the “MASS” package in R (R Core Team, 2023; Venables & Ripley, 2002; Zuur et al., 2009). Covariates within the model were standardized using the “scale” function in R (mean = 0, sd = 1) so that all estimates were calculated on a comparable scale (base (version 3.6.2) (R Core Team, 2023; Zuur et al., 2007). Landcover covariates and road/trail density within the global model were evaluated at six spatial scales for each species, using model selection within an information-theoretic framework. Akaike’s Information Criteria (AIC) was employed to select the best-fit spatial scale for each species, prioritizing the model with the lowest AIC (Anderson & Burnham, 2002). Models were assessed using spatial buffers at 125 meters, 250 meters, 375 meters, 500 meters, 625 meters, and 750 meters. To avoid substantial overlap between spatial buffers, the largest size was limited to 750m. Models were validated through a 10-fold cross validation using the “boot” package in R (v1. 3-27; Canty & Ripley, 2021).

3.1.5 Visual Analyses – NMDS

A non-metric multidimensional scaling (NMDS) ordination was used to plot the similarities in community composition and habitat features at each camera site. This ordination method displayed multidimensional spatial count data across the study area on a two-dimensional plot. Points (camera trap sites) closer together on the plot were more similar in count data, and those further away were more dissimilar. Camera site count data was plotted with respect to protected area (public-access versus restricted-access), and any clustering was denoted with an overlayed ellipse. The NMDS process was repeated for habitat covariates (proportion of broadleaf forest, proportion of conifer forest, proportion of cutblock, proportion of water features, mean crown closure, and elevation) at each tested spatial scale (125 meters, 250 meters, 375 meters, 500 meters, 625 meters, 750 meters). This was done to rule out any significant differences in habitat characteristics between the two protected areas, ensuring that observed variations in wildlife community composition were not solely due to differences in habitat structure.

3.2 Results

3.2.1 Data Summary

Human activities accounted for the majority of camera trap detections during the deployment period, with 15,423 independent detections of humans on foot, 8,866 independent detections of vehicles, and 1,061 independent detections of cyclists. As reported in Table 3.2, humans were observed at 100% of sites, vehicles were observed at 52% of sites, and cyclists were observed at 23% of sites. Deer accounted for most of the wildlife detections, with 1,560 independent detections, followed by 496 independent detections of black bears, 300 independent detections of cougars, 233 independent detections of Roosevelt elk, and 53 independent detections of grey wolves. Deer were observed at 100% of sites, while black bears and cougars were observed at nearly every site (94% and 98% respectively). Roosevelt elk and grey wolves were observed at about half of the sites (Table 3.2).

Table 3.2: Detections and capture rates for anthropogenic and wildlife covariates. Independent detections are defined as the total number of detections of each species throughout the study period, divided into 10-minute intervals. Average capture rate indicates the mean count of each species detected per site-week. The proportion of sites detected is expressed as a percentage. Average group size is calculated based on each independent event.

Common Name	Independent Detections	Average Capture Rate	Proportion Sites Detected	Average Group Size
Anthropogenic				
Human	15423	124.91	100	1.98
Vehicle	8866	73.92	52	1
Cyclist	1061	8.21	23	1.37
Wildlife				
Deer	1560	10.57	100	1.25
Black bear	496	3.46	94	1.14
Cougar	300	2.11	98	1.17
Roosevelt Elk	233	1.6	52	1.51
Grey wolf	53	0.44	52	1.04

3.2.2 Statistical Analyses – Generalized Linear Modeling

Model selection results revealed that the scale at which wildlife spatially respond to risk, habitat, and community variables differs by species (Figure 3.3; Table 3.3). The global model performed best at a 125m scale for black bear (AIC = 2265.70, AICw = 1.000) and a 250m scale for deer (AIC = 4102.18, AICw = 0.874) (Table 3.3). The model performed best at a more intermediate scale of 500m for grey wolves (AIC = 381.15, AICw = 0.471; Table 3.3). The model performed best at a larger scale of 625m for cougars (AIC = 1435.23 AICw = 0.972) and 750m for elk (AIC = 1158.27, AICw = 1.000) (Table 3.3).

Table 3.3: Model selection outcomes for each species ranked using AIC at six spatial scales. The best-fit model within each candidate set is bolded. Distribution = the GLM distribution fit to the count data, Scale = radius of buffer around camera in meters, AIC = Akaike's Information Criteria, ΔAIC = Delta AIC, AICw = AIC Weight, df = Degrees of freedom.

Species	Distribution	Scale	AIC	ΔAIC	AICw	df
Deer	Negative Binomial	Null	4175.55	73.36	0.000	1415
		125	4113.11	10.92	0.004	1401
		250	**4102.18**	**0.00**	**0.874**	**1401**
		375	4113.24	11.05	0.003	1401
		500	4106.29	4.10	0.112	1401
		625	4113.01	10.82	0.004	1401
		750	4113.61	11.43	0.003	1401
Roosevelt Elk	Poisson	Null	1768.18	609.92	0.000	1415
		125	1281.43	123.16	0.000	1401
		250	1286.36	128.09	0.000	1401
		375	1231.34	73.08	0.000	1401
		500	1200.45	42.18	0.000	1401
		625	1174.62	16.36	0.000	1401
		750	**1158.27**	**0.00**	**1.000**	**1401**
Grey Wolf	Poisson	Null	447.91	66.76	0.000	1415
		125	393.69	12.54	0.001	1401
		250	385.65	4.50	0.050	1401
		375	381.25	0.10	0.447	1401
		500	**381.15**	**0.00**	**0.471**	**1401**
		625	386.75	5.60	0.029	1401
		750	391.82	10.67	0.002	1401
Black Bear	Poisson	Null	2473.77	208.07	0.000	1415
		125	**2265.70**	**0.00**	**1.000**	**1401**
		250	2322.07	56.37	0.000	1401
		375	2337.54	71.84	0.000	1401
		500	2326.91	61.20	0.000	1401
		625	2319.09	53.39	0.000	1401
		750	2326.51	60.81	0.000	1401
Cougar	Poisson	Null	1550.06	114.83	0.000	1415
		125	1480.65	45.42	0.000	1401
		250	1476.27	41.04	0.000	1401
		375	1452.60	17.37	0.000	1401
		500	1449.88	14.65	0.001	1401
		625	**1435.23**	**0.00**	**0.972**	**1401**
		750	1442.37	7.14	0.027	1401

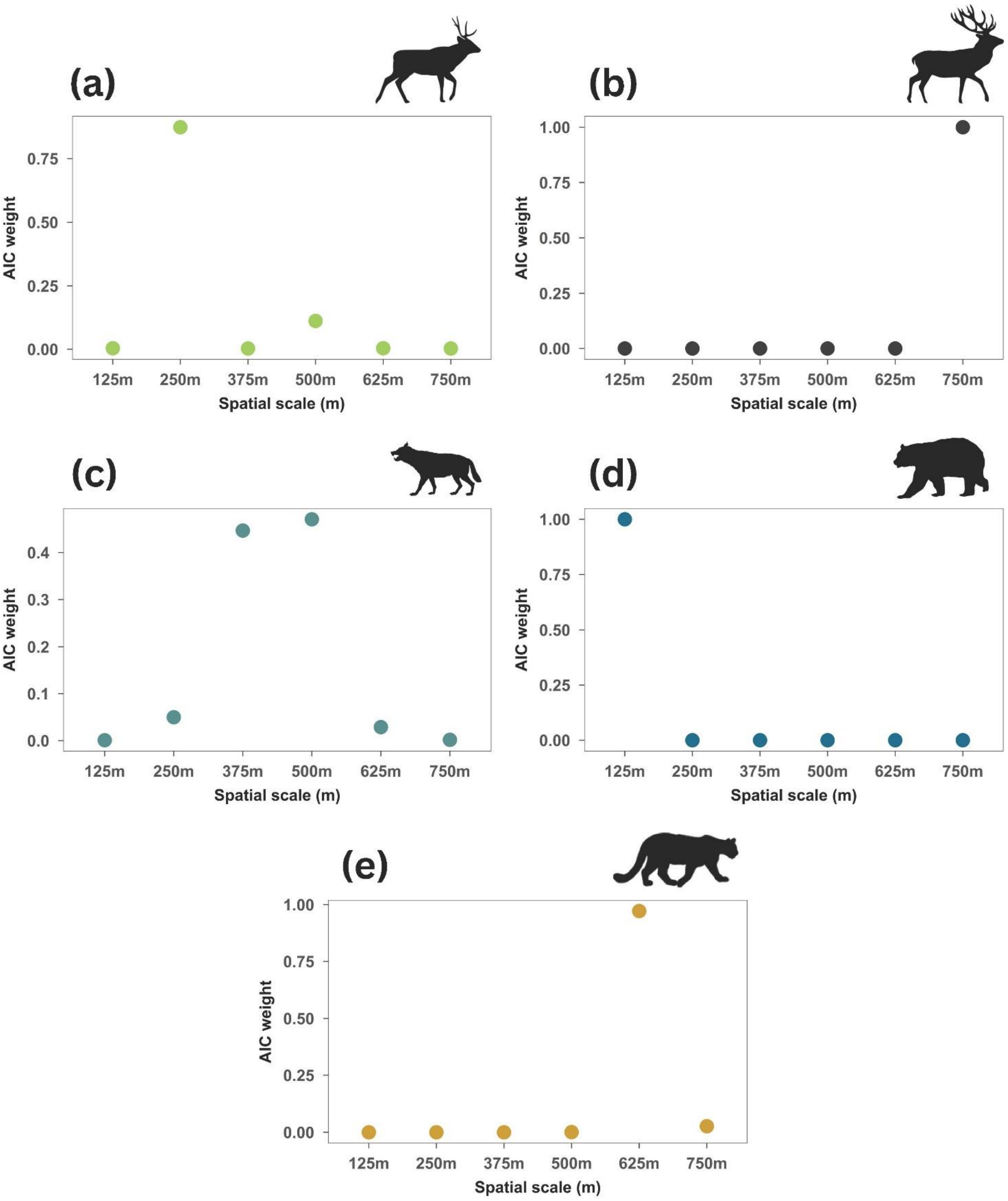


Figure 3.3: AIC weights for the global model are shown at six spatial scales for each species: black-tailed deer (a), Roosevelt elk (b), grey wolf (c), black bear (d), and cougar (e). Higher AIC weights indicate better model performance at the corresponding spatial scale. The spatial scale, ranging from 125 meters to 750 meters, represents the buffer radius around each camera site.

Note: Silhouette of a deer (xgirouxb, 2019); silhouette of an elk (Sayol, 2021); silhouette of a wolf (Traver, 2012); silhouette of a black bear (Heath, 2013); silhouette of a cougar (Taylor, 2019).

While reporting and interpreting non-significant p-values has traditionally been challenged in statistics, there is a growing trend toward interpreting the magnitude and direction of all effect sizes, as these effects may hold ecological or scientific importance regardless of their statistical significance (Greenland et al., 2016). Although not interpreting significance, I still chose to report p-values to retain information about estimated effects derived from GLMs. This provided further insights into the strength and direction of the relationships between large mammals and their habitat, humans, and each other, even when statistical significance was not present. Carnivores (Figure 3.4) and ungulates (Figure 3.5) responded very differently to both human activity and landscape features. Although cougars (β = -0.05, *P* = 0.64), deer (β = -0.14, *P* = 0.01), and black bears (β = -0.39, *P* = 2.35x10^{3}) spatially avoided highly peopled sites, elk (β = 0.50, *P* = 9.07x10^{-4}) and wolves (β = 0.11, *P* = 0.21) were positively associated with these sites. Conversely, cougars (β = 0.13, *P* = 0.02), black bears (β = 0.05, *P* = 0.27), and deer (β = 0.05, *P* = 0.29) were positively associated with vehicle detection frequency, while elk (β = -0.22, *P* = 7.02x10^{-3}) and wolves (β = -0.66, *P* = 0.08) were negatively associated with vehicle detection frequency. Deer (β = 0.14, *P* = 0.01), elk (β = 0.20, *P* = 0.14), and wolves (β = 0.41, *P* = 0.05) were associated with areas of high road/trail density, while cougars (β = -0.20, *P* = 0.01) and black bears (β = -0.13, *P* = 0.03) avoided these areas. Although both carnivores and ungulates diverged in their responses to human activity, all species were detected less frequently in the public-access landscape, and more frequently in the restricted-access landscape. Grey wolves (β = -2.60, *P* = 0.23) and elk (β = -1.63, *P* = 4.3x10^{-11}) showed the largest spatial avoidance of public-access sites, followed by cougars (β = -0.38, *P* = 7.97x10^{-5}), black bears (β = -0.40 *P* = 2.14x10^{-7}), and deer (β = -0.12, *P* = 0.08).

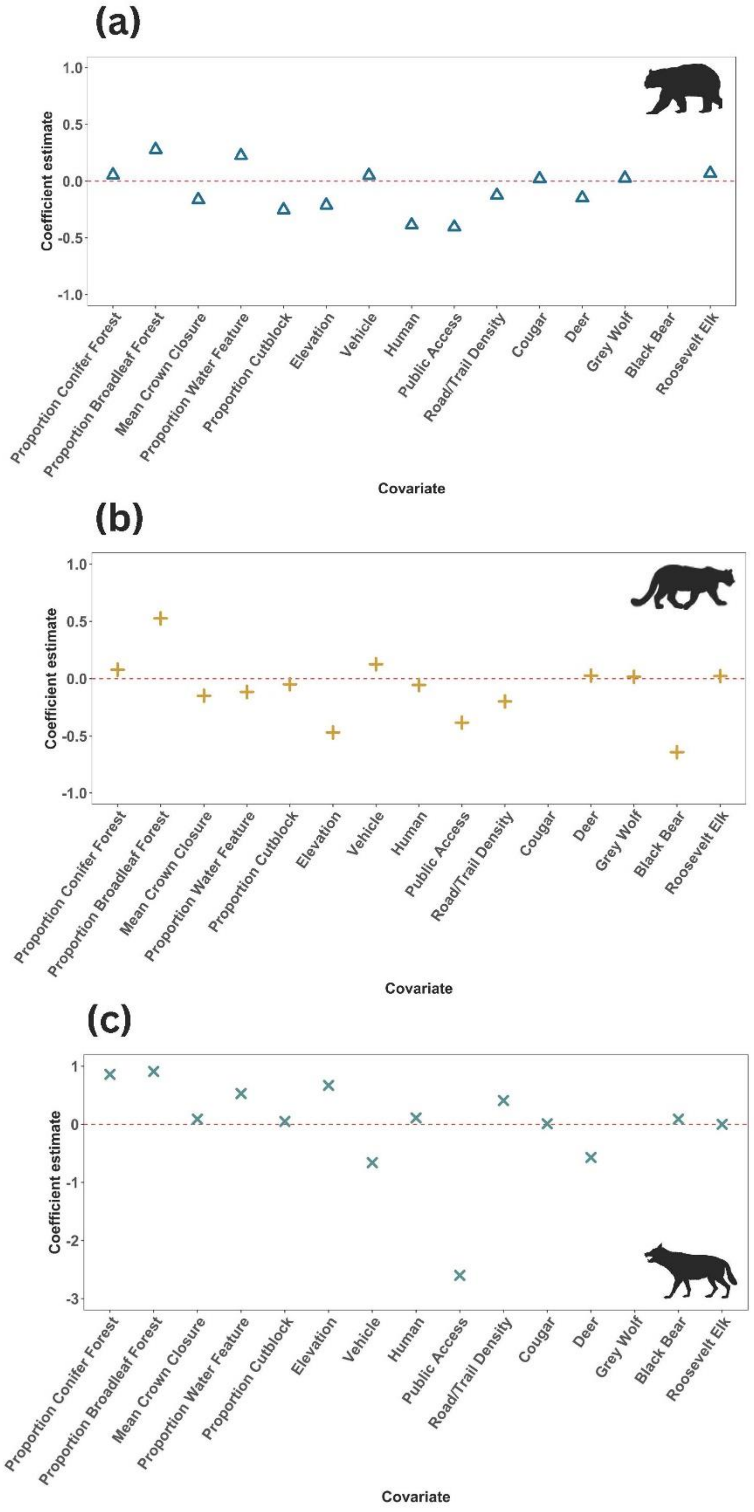


Figure 3.4: Responses of black bear (a), cougar (b), and grey wolf (c) to habitat, risk, and predator-prey covariates. Estimates above the red dashed line indicate positive associations, while those below indicate negative associations. Note the spatial scales used in the models: black bear (125m buffer), cougar (625m buffer), and grey wolf (500m buffer).

Note: Silhouette of a black bear (Heath, 2013); silhouette of a cougar (Taylor, 2019); silhouette of a wolf (Traver, 2012).

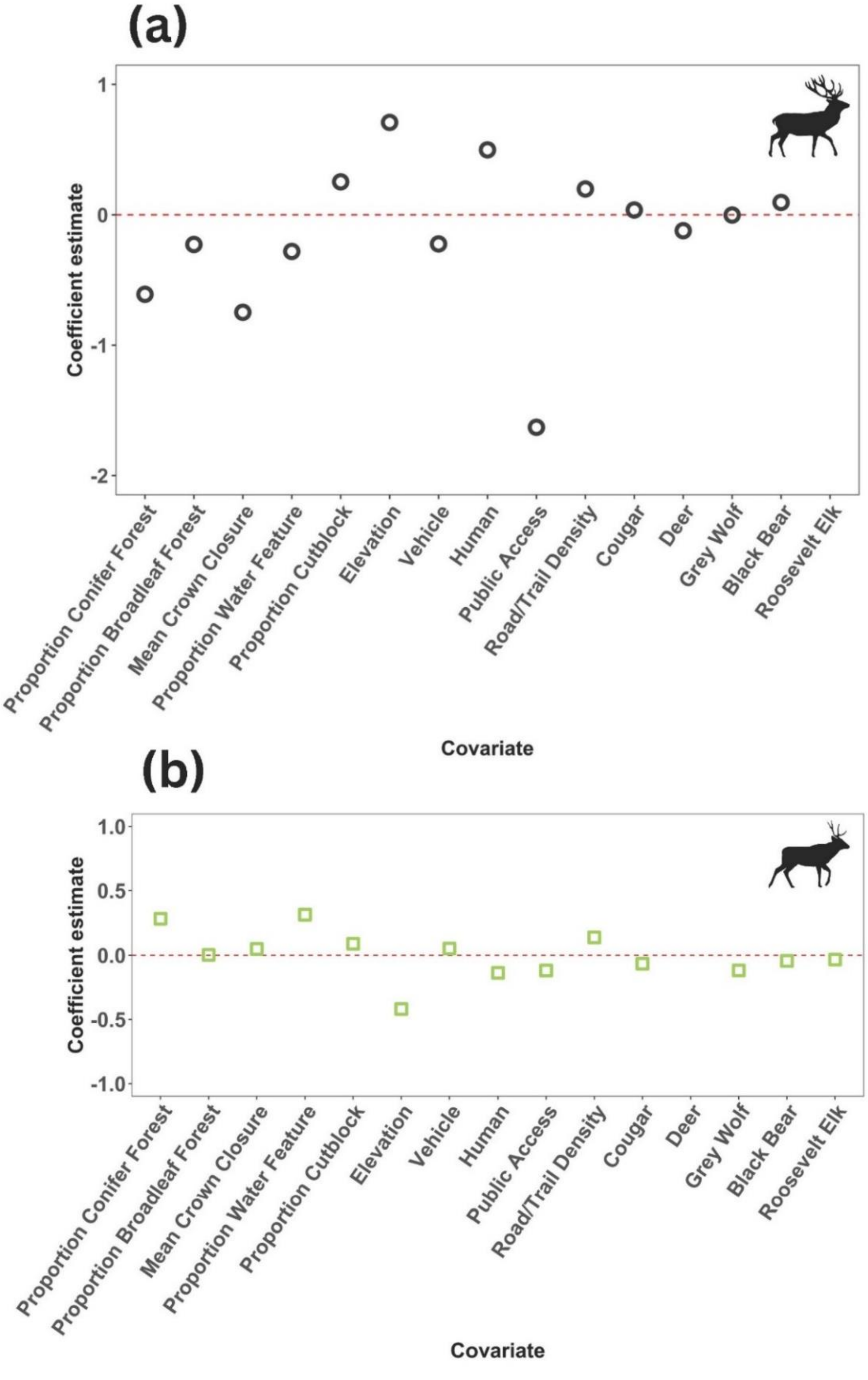


Figure 3.5: Roosevelt elk (a) and Columbian black-tailed deer (b) responses to habitat, risk, and heterospecifics' detection frequency covariates. Estimates above the red dashed line indicate positive associations, while estimates below the red dashed line indicate negative associations. Note the spatial scales used in the models: elk (750m buffer) and deer (250m buffer).

Note: Silhouette of an elk (Sayol, 2021); silhouette of a deer (xgirouxb, 2019).

Carnivore species demonstrated moderately positive associations with each other (Figure 3.4). Carnivores utilize some shared resources, as black bears (Conifer forest: $\beta = 0.05$, $P = 0.31$; Broadleaf forest: $\beta = 0.28$, $P = 6.35\text{x}10^{-16}$), cougars (Conifer forest: $\beta = 0.08$, $P = 0.46$; Broadleaf forest: $\beta = 0.53$, $P = 1.12\text{x}10^{-8}$), and wolves (Conifer forest: $\beta = 0.86$, $P = 0.01$; Broadleaf forest: $\beta = 0.91$, $P = 2.57\text{x}10^{-4}$) shared preferences for forested sites (higher proportions of conifer and broadleaf forest). Cougars ($\beta = 0.02$, $P = 0.65$) and black bears ($\beta = 0.07$, $P = 0.02$) exhibited positive associations with the prey species elk; however, wolves exhibited slightly negative associations ($\beta = -4.22\text{x}10^{-4}$, $P = 1.00$). Black bears ($\beta = -0.15$, $P = 0.01$) and grey wolves ($\beta = -0.57$, $P = 0.05$) were negatively associated with deer. Conversely, cougars ($\beta = 0.03$, $P = 0.57$) were slightly positively associated with deer. Despite these shared spatial associations, some habitat preferences varied among carnivores. Cougars were negatively associated with the proportion of water features ($\beta = -0.12$, $P = .31$), while wolves ($\beta = 0.53$, $P = 0.03$) and black bears ($\beta = 0.23$, $P = 4.81\text{x}10^{-9}$) were positively associated. Furthermore, cougars ($\beta = -0.05$, $P = 0.58$) and black bears ($\beta = -0.25$, $P = 5.17\text{x}10^{-6}$) were negatively associated with proportion of cutblock, while wolves were slightly positively associated ($\beta = 0.05$, $P = 0.78$).

3.2.3 Visual Analyses - NMDS

Large mammals steered clear of busy recreational areas, seeking refuge in quieter, restricted areas. This trend was evident across species, as NMDS findings backed up statistical results that showed large mammals' clear preference for low-disturbance habitat. In Figure 3.6, we saw that each type of protected area (SHWA and GVWSA) displayed a unique community composition as shown by the clustering of similar points. Black bears, Roosevelt elk, and grey wolves were mostly found in the restricted-access (water supply) sites, while humans and cyclists were more common at sites in the park, indicating high dissimilarity between the two protected areas. Further NMDS analysis of habitat characteristics revealed overlap between public-access and restricted-access sites at all six spatial scales (Appendix B). Plots displayed strong similarities between the two protected areas when it came to their vegetation characteristics (crown closure and proportion conifer forest) and their elevation, as seen in Figure 3.7. These findings suggest that other factors, beyond habitat characteristics, drove the differences in observed species.

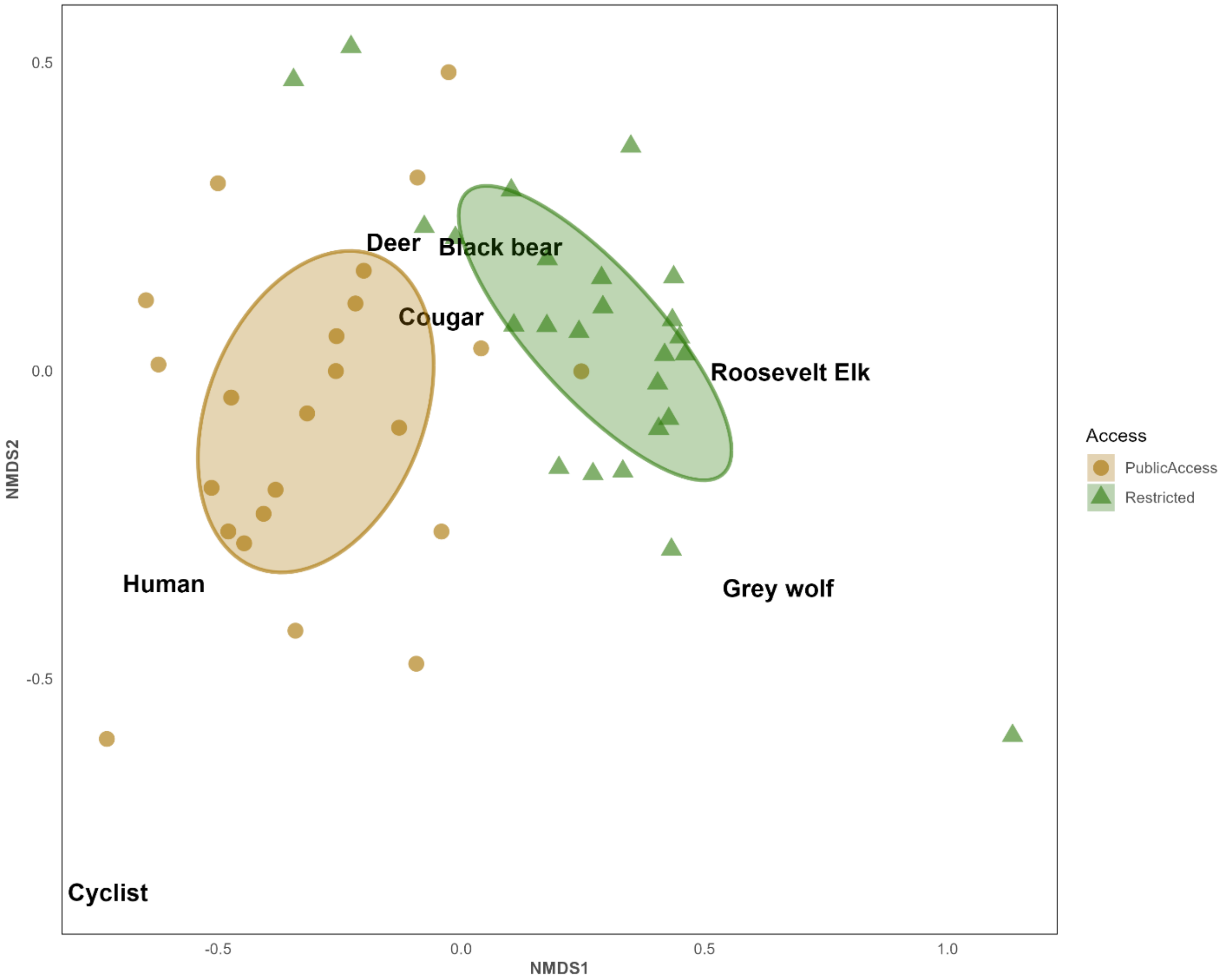


Figure 3.6: Non-metric multidimensional scaling (NMDS) plot illustrating site similarities and differences based on species counts. Clustering of points reflects similarity between sites, while separation indicates dissimilarity.

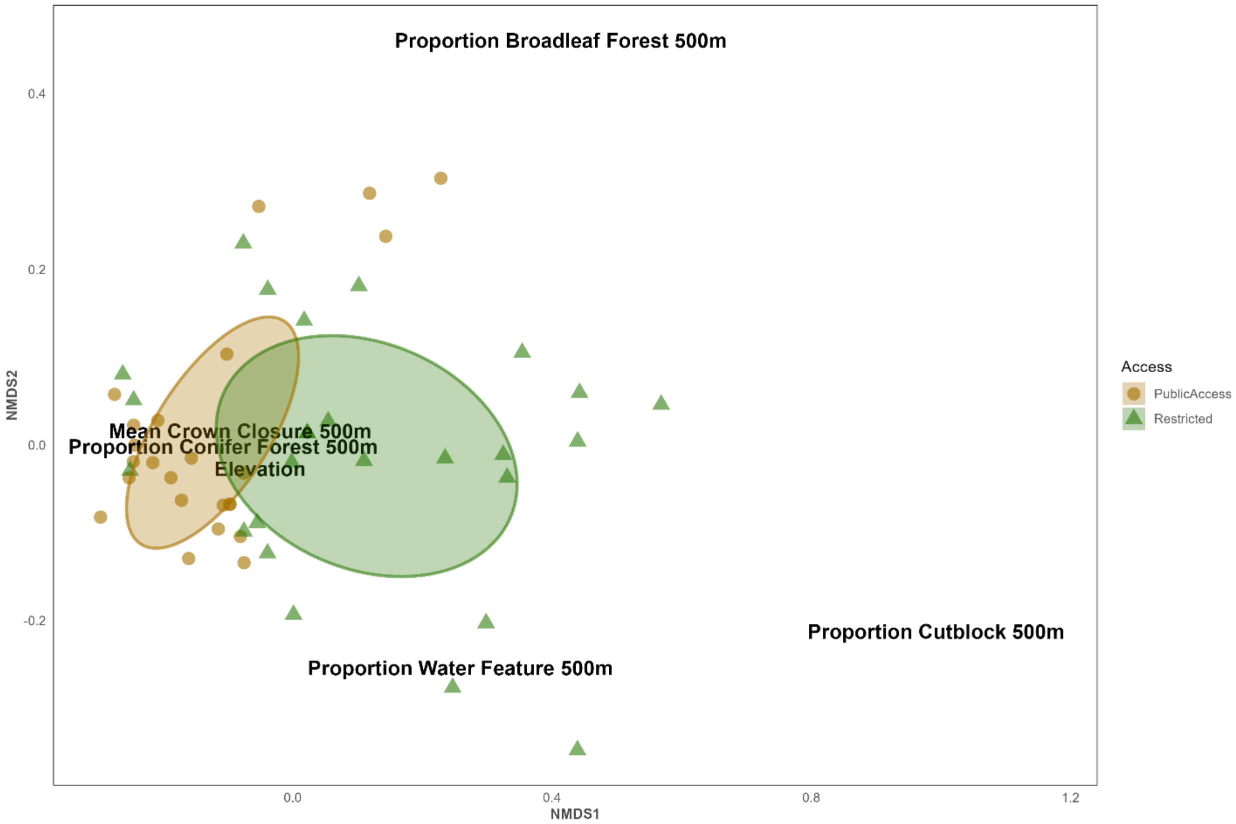


Figure 3.7: Non-metric multidimensional scaling (NMDS) plot showing site similarity and dissimilarity regarding habitat covariates within a 500-meter buffer radius. Clustering of points reflects similarity between sites, while separation indicates dissimilarity.

3.3 Discussion

Mammal species throughout the lower Vancouver-Island Douglas-fir complex spatially avoided areas of high human use, likely due to fear responses. Whereas past studies have shown declining wildlife use on a site-by-site basis, this study demonstrated that wildlife doesn’t just avoid humans at specific sites -- they actually change their overall distribution patterns across landscapes to escape human presence. Contrary to my hypothesis that carnivores would show the greatest avoidance of humans, trophic level did not appear to play a large role in the degree of spatial avoidance. However, my initial prediction that carnivores would use similar sites was supported, as they exhibited positive spatial associations with one another. Carnivores likely shared space due to similar habitat and resource requirements, but their overlap may also have been driven by human disturbance.

All species strongly avoided public-access sites in favour of restricted-access sites, supporting my predictions that carnivores would prefer habitat free from frequent human activity. However, these findings did not provide strong evidence for the human shield hypothesis. Furthermore, the spatial scale at which wildlife responded to habitat, risk, and the presence of other species varied among the five species studied.

3.3.1 Community Responses to Risk

Ungulate species and top predators were not uniform in their responses to anthropogenic risk, reflecting complex and species-specific risk avoidance (Suraci et al., 2021). Cougars, black bears, and black-tailed deer avoided humans at the weekly scale, in contrast to elk and wolves, which were positively associated with humans. Most of the wildlife community avoided areas with humans present, likely due to a heightened perception of risk (Gaynor et al., 2019; Laundré et al., 2001). However, elk and wolves may have demonstrated a more habituated avoidance of sites frequented by humans over a longer temporal scale than was measured in this study. A possible habituated avoidance was evidenced by their negative associations with public-access sites (Schuette et al., 2013; Smith et al. 2015). My findings here align with those of Sytsma et al. (2022), who found wolves were totally excluded from sites experiencing human activity in a protected area. Cougars and black bears also avoided public-access areas, reinforcing previous findings that these species use spatial avoidance in the face of human-induced fear (Hubbard et al., 2022; Suraci et al., 2019). Notably, deer demonstrated the least avoidance of these sites, indicating that they perceive a lower risk from humans than sensitive large carnivores. This finding aligns with previous research that found deer do not significantly avoid human recreation (Naidoo & Burton, 2020). The differential use of areas with high road and trail density further demonstrates species-specific responses to human-induced risk. While deer, elk, and wolves were present in areas of high road and trail density, black bears and cougars avoided these areas. Black bears and cougars, both large-bodied carnivores, may be more sensitive to human-induced risk. Due to their long-ranging, low reproductive rate life histories, they likely avoid these areas to reduce potential encounters with humans (Suraci et al., 2021). Although elk and deer were present in these disturbed sites, their avoidance of public-access sites and their inconsistent response to human presence indicate weak support for the human shield hypothesis (Granados et al., 2023). In fact, this broad-scale avoidance of human presence could increase predator (carnivore species) and prey (ungulate species) overlap, proving energetically costly for deer and elk as they employ anti-predator responses (Frid & Dill, 2002).

The wildlife community's responses to vehicle activity offer additional insights into spatial partitioning. Elk and wolves' avoidance of vehicle activity contrasts with the positive associations that cougars, black bears, and deer exhibited with vehicle activity, suggesting different strategies in managing risks associated with various types of human disturbance. Although wolves were observed in areas with high road/trail density, their avoidance of vehicle activity and public-access sites suggests they may have used low-traffic roads as travel routes, as found by Whittington et al. (2005). While cougars have demonstrated avoidance of human activity (Dellinger et al., 2020), they have not demonstrated avoidance of vehicle routes within their home ranges and instead use these as travel paths (Dickson & Beier, 2009; Kertson et al., 2011). Additionally, Keim et al. (2019) found that some species tolerated low levels of vehicle traffic, especially during winter when vehicle routes provided snow-packed corridors for easier movement. Overall, the results supported my prediction that carnivores would consistently avoid risks of human presence, public-access, and road and trail density, aligning with past studies that found carnivores spatially avoid anthropogenic risk (Gaynor et al., 2019; Nickel et al., 2021; Smith et al., 2017; Suraci et al., 2019).

Although species exhibited positive spatial associations with some anthropogenic site characteristics, the consistent avoidance of public-access sites, coupled with the avoidance of at least one additional risk factor, provides valuable insights into the effects of outdoor recreation. These findings demonstrate the need for parks and conservation managers to consider implementing access restrictions and managing levels of human activity in protected areas.

3.3.2 Carnivore Spatial Partitioning

Carnivores showed positive spatial association with each other, supported by the theory that spatial overlap occurs when carnivores are accessing shared resources, especially in the face of human disturbance (Sévêque et al., 2020). This spatial sympatry can be attributed to several underlying ecological processes, such as shared access to resources, mutual risk-aversion, and resource partitioning across different niche dimensions (temporal or trophic) (Schoener, 1974). Carnivores showed a preference for forested sites with higher proportions of conifer and broadleaf forests, consistent with Kays et al. (2017), who found that large, unfragmented forest habitats were important predictors of carnivore occurrence. The observed spatial avoidance of humans, public-access sites, high road/trail density, and vehicles may force these top predators into the limited remaining undisturbed habitats, increasing the likelihood of spatial overlap and interspecific competition (Farris et al., 2017; Sévêque et al., 2020). Greater spatial overlap among carnivores could decrease resource acquisition for the “losing” species due to heightened competition (Fisher & Burton, 2018; Smith et al., 2018). For instance, Engebretsen et al. (2021) observed reduced feeding times in cougars in areas with higher bear densities, revealing the pressure of interspecific competition that arises when multiple carnivore species share the same space.

Long-term research could better support the theory that human activity drives spatial overlap among carnivores in protected spaces, particularly if visitor numbers continue to rise. Species-specific responses to site characteristics like water features and elevation may be explained by one of two phenomena: species exhibited different habitat preferences, or species employed resource partitioning of preferred habitat through mechanisms other than spatial separation. My research focused on one of the three main niche dimensions described by Schoener (1974) -- the spatial niche. While we have advanced our understanding of how wildlife partition space, species may also use temporal or trophic partitioning to access shared resources. Temporal partitioning might involve wildlife altering their habitat use to avoid "risky" times of day when predators or perceived threats (humans) are more active (Lewis et al., 2021; Procko et al., 2023). Some studies have revealed consistent shifts to increased nocturnality in response to human disturbance regardless of spatial impacts (Gaynor et al., 2018). Other studies have found weak evidence that human presence induces shifts towards nocturnality in carnivores (Frey et al., 2020), or they have found correlational impacts to both spatial and temporal behaviours (Suraci et al., 2019; Wang et al., 2015). In trophic partitioning, we might observe shifts in wildlife diet or hunting and foraging behaviour due to an external force, such as human presence (Sévêque et al., 2020). Examining these dimensions would provide a fuller picture of how wildlife partition space in a human-used, mixed-accessibility habitat. In addition to studying niche partitioning within wildlife communities, future research should consider landscape-level impacts on protected areas. For example, outside influences, such as urban development, high population densities, housing, infrastructure, and major roads can impede wildlife movement in and out of ecologically important areas. Past studies have shown that carnivores tend to avoid densely populated housing areas, while ungulates may be more inclined to use these spaces (Kays et al., 2017). Examining connectivity between protected areas in the broader geographic region would contribute to a fuller understanding of how humans alter the ecological dynamics occurring within these areas.

3.3.3 Protected Area Effectiveness

Increasing human encroachment suggests that protected areas may no longer provide the pristine, ecological baselines for the world's remaining biodiversity that they once did (Arcese & Sinclair, 1997). Growing per capita wealth and increasing tourism across the world bring more people into these protected spaces (Wijesekara et al., 2022). High rates of human visitation--especially in parks close to urban centres, as in this study--have affected the spatial distribution of wildlife. Research increasingly suggests that even low levels of human activity can cause spatio-temporal avoidance behaviour, raising concern about how we visit and appreciate these spaces without harming the wildlife communities that inhabit them (Sytsma et al., 2022). The NMDS analysis of community composition revealed distinct groupings between public-access sites and restricted-access sites based on the species observed and their counts. The SHWA, consisting of public-access sites, predominantly supported a human-centric community of recreationalists and cyclists. In contrast, the GVWSA, characterized by restricted-access sites, harbored a wildlife-centric community of Roosevelt elk, grey wolves, and black bears. Although cougars and deer appeared in both protected areas, their measured spatial avoidance of public-access sites suggests a preference for less-disturbed habitat. The spatial impact of human disturbance is further evidenced by most wildlife species avoiding various forms of human risk. The measurable spatial impacts on wildlife support the theory that varying levels of disturbance can fundamentally alter community composition in protected areas, pushing disturbance-sensitive species into less-impacted areas (Reed & Merenlender, 2008; Schuette et al., 2013). As these impacts accumulate, they create greater differences in community composition and ecological health between low- and high-disturbance landscapes (Heim et al., 2019; Jones et al., 2018)

3.4 Management Implications

Wildlife consistently choosing quiet, low-disturbance areas over busy sites shows just how important it is to manage protected areas and limit access to natural spaces. However, this study's design constraints must be considered, as study design created some spatial limitations. While it is known that wildlife use roads and trails for movement, cameras were exclusively placed on linear features and did not capture activity in off-trail areas. These areas likely provide valuable habitat for activities such as foraging, hunting, and denning (Kertson et al., 2011). Camera traps as a monitoring tool inherently introduce imperfect detection; wildlife could have been present nearby but not captured due to camera error, or because they remained outside the detection zone (Burton et al., 2015). Although imperfect detection remains a limitation of camera trap studies, the relatively small size of the study area (36 km^2) may have further constrained inferences about spatial partitioning across these large mammals' home ranges, particularly considering their seasonal movements that may have extended beyond the study area (Pierce et al., 1999). Surveying off-trail habitat and expanding the study area to include a larger and potentially more diverse landscape could reveal different spatial patterns or characteristic scales of selection due to other ecological processes at play (Wiens, 1989). While spatial buffers helped identify the scale at which wildlife select sites based on habitat preferences, the location of the cameras limited the ability to make definitive conclusions about wildlife activity in off-road and off-trail habitat (Parsons et al., 2016). Despite these limitations, the relatively close spacing of cameras across the study area captured the variability in habitat, as well as the variability in human and wildlife occurrence throughout two protected areas. This provided strong evidence for the impacts of human visitation and protected area access on wildlife spatial dynamics.

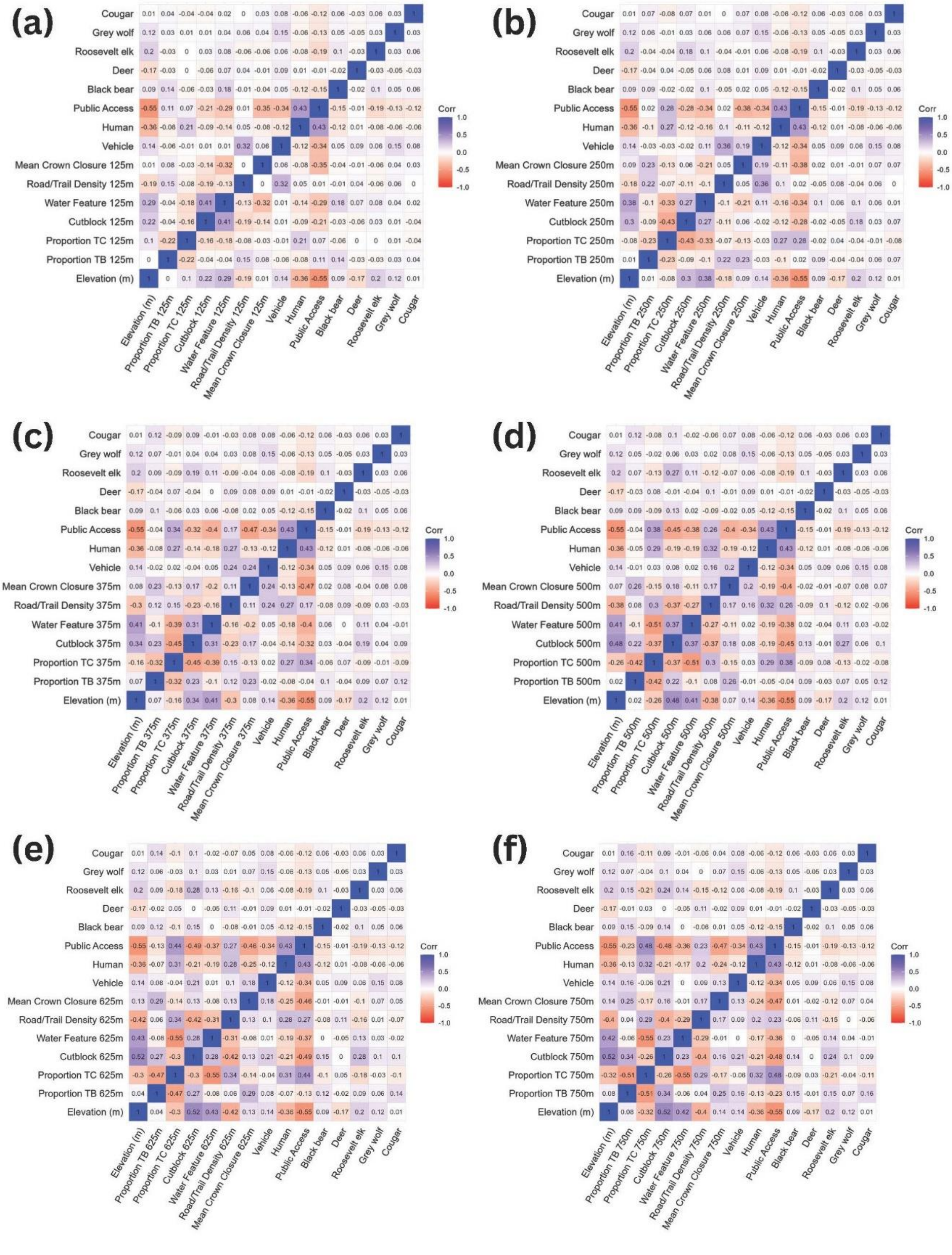
Although cameras were deployed across all four seasons, the deployment mainly occurred in the late spring, summer, and fall months, introducing a potential limitation. Many species, including cougars and ungulates, exhibit seasonal movements influenced by weather conditions, vegetation availability, and prey availability (Pierce et al., 1999; Dellinger et al., 2018). By focusing solely on eight months out of the year, this study may not have fully captured the variation in habitat preferences, human visitation, or seasonal space use that occurs throughout a year. Further, long-term monitoring could provide evidence that increasing human visitation impacts wildlife, particularly as local and global trends suggest a notable rise in outdoor recreation in recent years (Balmford et al., 2015; CRD, n.d.). This long-term increase could drive a broader-scale exclusion of large mammals from highly used areas (Schuette et al., 2013). Continuous monitoring of human and wildlife space use in this mixed-access system would support more informed, long-term management plans.

Additionally, my analyses grouped various human activities (hiking, cycling, dog-walking) into a single “Human” count, generalizing the nuances of different types of human disturbance. This generalization could be a limitation, as different types of human activities likely have varying levels of disturbance to wildlife. For example, dog-walking may introduce a greater fear response by large mammals due the presence of a potential predator (dogs) (Parsons et al., 2016). Hiking or cycling may create different levels of disturbance due to speed or noise (Naidoo & Burton, 2020). Furthermore, varying types of vehicle activity were grouped together, introducing a similar limitation. For example, vehicle activity related to logging likely creates a greater disturbance then pickup trucks or small cars. Future research should focus on how different types of recreation affect wildlife spatio-temporal behaviour. Although this study found impacts to wildlife spatial dynamics from human and vehicle activity, future studies might disentangle the specific effects of different types of recreation and vehicles.

By refining methods to include off-trail surveys and more detailed categorization human activities, we can acquire a better understanding of wildlife habitat use and the influence of human presence. In the meantime, to effectively mitigate human disturbance and support the needs of both wildlife and recreationalists, we must enhance the connectivity and protection of wildlife habitat. By doing so, we can create more resilient ecosystems that accommodate the spatial and behavioural needs of wildlife species, ensuring long-term conservation of biodiversity in an increasingly urbanized world. To achieve this overarching goal, careful local management of outdoor recreation in protected areas is required, ensuring minimal human disturbance while addressing wildlife and recreationalists' needs.

Appendix A

Pairwise Pearson correlation coefficients for all covariates used in analyses at six buffered distances: (a) 125 meters, (b) 250 meters, (c) 375 meters, (d) 500 meters, (e) 625 meters, (f) 750 meters. The correlation matrix displays the strength and direction of linear relationships between covariates. Negative correlations are indicated in red, while positive correlations are indicated in blue. The matrix helps identify how strongly variables are related to each other, with values ranging from -1 (perfect negative correlation) to +1 (perfect positive correlation).



(a)

	Elevation (m)	Proportion TB 125m	Proportion TC 125m	Cutblock 125m	Water Feature 125m	Road/Trail Density 125m	Mean Crown Closure 125m	Vehicle	Human	Public Access	Black bear	Deer	Roosevelt elk	Grey wolf	Cougar
Cougar	0.01	0.04	-0.04	-0.04	0.02	0	0.03	0.08	-0.06	-0.12	0.06	-0.03	0.06	0.03	1
Grey wolf	0.12	0.03	0.01	0.01	0.04	0.06	0.04	0.15	-0.06	-0.13	0.05	-0.05	0.03	1	0.03
Roosevelt elk	0.2	-0.03	0	0.03	0.08	-0.06	-0.06	0.06	-0.08	-0.19	0.1	-0.03	1	0.03	0.06
Deer	-0.17	-0.03	0	-0.06	0.07	0.04	-0.01	0.09	0.01	-0.01	-0.02	1	-0.03	-0.05	-0.03
Black bear	0.09	0.14	-0.06	-0.03	0.18	-0.01	-0.04	0.05	-0.12	-0.15	1	-0.02	0.1	0.05	0.06
Public Access	-0.55	0.11	0.07	-0.21	-0.29	0.01	-0.35	-0.34	0.43	1	-0.15	-0.01	-0.19	-0.13	-0.12
Human	-0.36	-0.08	0.21	-0.09	-0.14	0.05	-0.08	-0.12	1	0.43	-0.12	0.01	-0.08	-0.06	-0.06
Vehicle	0.14	-0.06	-0.01	0.01	0.01	0.32	0.06	1	-0.12	-0.34	0.05	0.09	0.06	0.15	0.08
Mean Crown Closure 125m	0.01	0.08	-0.03	-0.14	-0.32	0	1	0.06	-0.08	-0.35	-0.04	-0.01	-0.06	0.04	0.03
Road/Trail Density 125m	-0.19	0.15	-0.08	-0.19	-0.13	1	0	0.32	0.05	0.01	-0.01	0.04	-0.06	0.06	0
Water Feature 125m	0.29	-0.04	-0.18	0.41	1	-0.13	-0.32	0.01	-0.14	-0.29	0.18	0.07	0.08	0.04	0.02
Cutblock 125m	0.22	-0.04	-0.16	1	0.41	-0.19	-0.14	0.01	-0.09	-0.21	-0.03	-0.06	0.03	0.01	-0.04
Proportion TC 125m	0.1	-0.22	1	-0.16	-0.18	-0.08	-0.03	-0.01	0.21	0.07	-0.06	0	0	0.01	-0.04
Proportion TB 125m	0	1	-0.22	-0.04	-0.04	0.15	0.08	-0.06	-0.08	0.11	0.14	-0.03	-0.03	0.03	0.04
Elevation (m)	1	0	0.1	0.22	0.29	-0.19	0.01	0.14	-0.36	-0.55	0.09	-0.17	0.2	0.12	0.01

(b)

	Elevation (m)	Proportion TB 250m	Proportion TC 250m	Cutblock 250m	Water Feature 250m	Road/Trail Density 250m	Mean Crown Closure 250m	Vehicle	Human	Public Access	Black bear	Deer	Roosevelt elk	Grey wolf	Cougar
Cougar	0.01	0.07	-0.08	0.07	0.01	0	0.07	0.08	-0.06	-0.12	0.06	-0.03	0.06	0.03	1
Grey wolf	0.12	0.06	-0.01	0.03	0.06	0.06	0.07	0.15	-0.06	-0.13	0.05	-0.05	0.03	1	0.03
Roosevelt elk	0.2	-0.04	-0.04	0.18	0.1	-0.04	-0.01	0.06	-0.08	-0.19	0.1	-0.03	1	0.03	0.06
Deer	-0.17	-0.04	0.04	-0.05	0.06	0.08	0.01	0.09	0.01	-0.01	-0.02	1	-0.03	-0.05	-0.03
Black bear	0.09	0.09	-0.02	-0.02	0.1	-0.05	0.02	0.05	-0.12	-0.15	1	-0.02	0.1	0.05	0.06
Public Access	-0.55	0.02	0.28	-0.28	-0.34	0.02	-0.38	-0.34	0.43	1	-0.15	-0.01	-0.19	-0.13	-0.12
Human	-0.36	-0.1	0.27	-0.12	-0.16	0.1	-0.11	-0.12	1	0.43	-0.12	0.01	-0.08	-0.06	-0.06
Vehicle	0.14	-0.03	-0.03	-0.02	0.11	0.36	0.19	1	-0.12	-0.34	0.05	0.09	0.06	0.15	0.08
Mean Crown Closure 250m	0.09	0.23	-0.13	0.06	-0.21	0.05	1	0.19	-0.11	-0.38	0.02	0.01	-0.01	0.07	0.07
Road/Trail Density 250m	-0.18	0.22	-0.07	-0.11	-0.1	1	0.05	0.36	0.1	0.02	-0.05	0.08	-0.04	0.06	0
Water Feature 250m	0.38	-0.1	-0.33	0.27	1	-0.1	-0.21	0.11	-0.16	-0.34	0.1	0.06	0.1	0.06	0.01
Cutblock 250m	0.3	-0.09	-0.43	1	0.27	-0.11	0.06	-0.02	-0.12	-0.28	-0.02	-0.05	0.18	0.03	0.07
Proportion TC 250m	-0.08	-0.23	1	-0.43	-0.33	-0.07	-0.13	-0.03	0.27	0.28	-0.02	0.04	-0.04	-0.01	-0.08
Proportion TB 250m	0.01	1	-0.23	-0.09	-0.1	0.22	0.23	-0.03	-0.1	0.02	0.09	-0.04	-0.04	0.06	0.07
Elevation (m)	1	0.01	-0.08	0.3	0.38	-0.18	0.09	0.14	-0.36	-0.55	0.09	-0.17	0.2	0.12	0.01

(c)

	Elevation (m)	Proportion TB 375m	Proportion TC 375m	Cutblock 375m	Water Feature 375m	Road/Trail Density 375m	Mean Crown Closure 375m	Vehicle	Human	Public Access	Black bear	Deer	Roosevelt elk	Grey wolf	Cougar
Cougar	0.01	0.12	-0.09	0.09	-0.01	-0.03	0.08	0.08	-0.06	-0.12	0.06	-0.03	0.06	0.03	1
Grey wolf	0.12	0.07	-0.01	0.04	0.04	0.03	0.08	0.15	-0.06	-0.13	0.05	-0.05	0.03	1	0.03
Roosevelt elk	0.2	0.09	-0.09	0.19	0.11	-0.09	-0.04	0.06	-0.08	-0.19	0.1	-0.03	1	0.03	0.06
Deer	-0.17	-0.04	0.07	-0.04	0	0.09	0.08	0.09	0.01	-0.01	-0.02	1	-0.03	-0.05	-0.03
Black bear	0.09	0.1	-0.06	0.03	0.06	-0.08	0.02	0.05	-0.12	-0.15	1	-0.02	0.1	0.05	0.06
Public Access	-0.55	-0.04	0.34	-0.32	-0.4	0.17	-0.47	-0.34	0.43	1	-0.15	-0.01	-0.19	-0.13	-0.12
Human	-0.36	-0.08	0.27	-0.14	-0.18	0.27	-0.13	-0.12	1	0.43	-0.12	0.01	-0.08	-0.06	-0.06
Vehicle	0.14	-0.02	0.02	-0.04	0.05	0.24	0.24	1	-0.12	-0.34	0.05	0.09	0.06	0.15	0.08
Mean Crown Closure 375m	0.08	0.23	-0.13	0.17	-0.2	0.11	1	0.24	-0.13	-0.47	0.02	0.08	-0.04	0.08	0.08
Road/Trail Density 375m	-0.3	0.12	0.15	-0.23	-0.16	1	0.11	0.24	0.27	0.17	-0.08	0.09	-0.09	0.03	-0.03
Water Feature 375m	0.41	-0.1	-0.39	0.31	1	-0.16	-0.2	0.05	-0.18	-0.4	0.06	0	0.11	0.04	-0.01
Cutblock 375m	0.34	0.23	-0.45	1	0.31	-0.23	0.17	-0.04	-0.14	-0.32	0.03	-0.04	0.19	0.04	0.09
Proportion TC 375m	-0.16	-0.32	1	-0.45	-0.39	0.15	-0.13	0.02	0.27	0.34	-0.06	0.07	-0.09	-0.01	-0.09
Proportion TB 375m	0.07	1	-0.32	0.23	-0.1	0.12	0.23	-0.02	-0.08	-0.04	0.1	-0.04	0.09	0.07	0.12
Elevation (m)	1	0.07	-0.16	0.34	0.41	-0.3	0.08	0.14	-0.36	-0.55	0.09	-0.17	0.2	0.12	0.01

(d)

	Elevation (m)	Proportion TB 500m	Proportion TC 500m	Cutblock 500m	Water Feature 500m	Road/Trail Density 500m	Mean Crown Closure 500m	Vehicle	Human	Public Access	Black bear	Deer	Roosevelt elk	Grey wolf	Cougar
Cougar	0.01	0.12	-0.08	0.1	-0.02	-0.06	0.07	0.08	-0.06	-0.12	0.06	-0.03	0.06	0.03	1
Grey wolf	0.12	0.05	-0.02	0.06	0.03	0.02	0.08	0.15	-0.06	-0.13	0.05	-0.05	0.03	1	0.03
Roosevelt elk	0.2	0.07	-0.13	0.27	0.11	-0.12	-0.07	0.06	-0.08	-0.19	0.1	-0.03	1	0.03	0.06
Deer	-0.17	-0.03	0.08	-0.01	-0.04	0.1	-0.01	0.09	0.01	-0.01	-0.02	1	-0.03	-0.05	-0.03
Black bear	0.09	0.09	-0.09	0.13	0.02	-0.09	-0.02	0.05	-0.12	-0.15	1	-0.02	0.1	0.05	0.06
Public Access	-0.55	-0.04	0.38	-0.45	-0.38	0.26	-0.4	-0.34	0.43	1	-0.15	-0.01	-0.19	-0.13	-0.12
Human	-0.36	-0.05	0.29	-0.19	-0.19	0.32	-0.19	-0.12	1	0.43	-0.12	0.01	-0.08	-0.06	-0.06
Vehicle	0.14	-0.01	0.03	0.08	0.02	0.16	0.2	1	-0.12	-0.34	0.05	0.09	0.06	0.15	0.08
Mean Crown Closure 500m	0.07	0.26	-0.15	0.18	-0.11	0.17	1	0.2	-0.19	-0.4	-0.02	-0.01	-0.07	0.08	0.07
Road/Trail Density 500m	-0.38	0.08	0.3	-0.37	-0.27	1	0.17	0.16	0.32	0.26	-0.09	0.1	-0.12	0.02	-0.06
Water Feature 500m	0.41	-0.1	-0.51	0.37	1	-0.27	-0.11	0.02	-0.19	-0.38	0.02	-0.04	0.11	0.03	-0.02
Cutblock 500m	0.48	0.22	-0.37	1	0.37	-0.37	0.18	0.08	-0.19	-0.45	0.13	-0.01	0.27	0.06	0.1
Proportion TC 500m	-0.26	-0.42	1	-0.37	-0.51	0.3	-0.15	0.03	0.29	0.38	-0.09	0.08	-0.13	-0.02	-0.08
Proportion TB 500m	0.02	1	-0.42	0.22	-0.1	0.08	0.26	-0.01	-0.05	-0.04	0.09	-0.03	0.07	0.05	0.12
Elevation (m)	1	0.02	-0.26	0.48	0.41	-0.38	0.07	0.14	-0.36	-0.55	0.09	-0.17	0.2	0.12	0.01

(e)

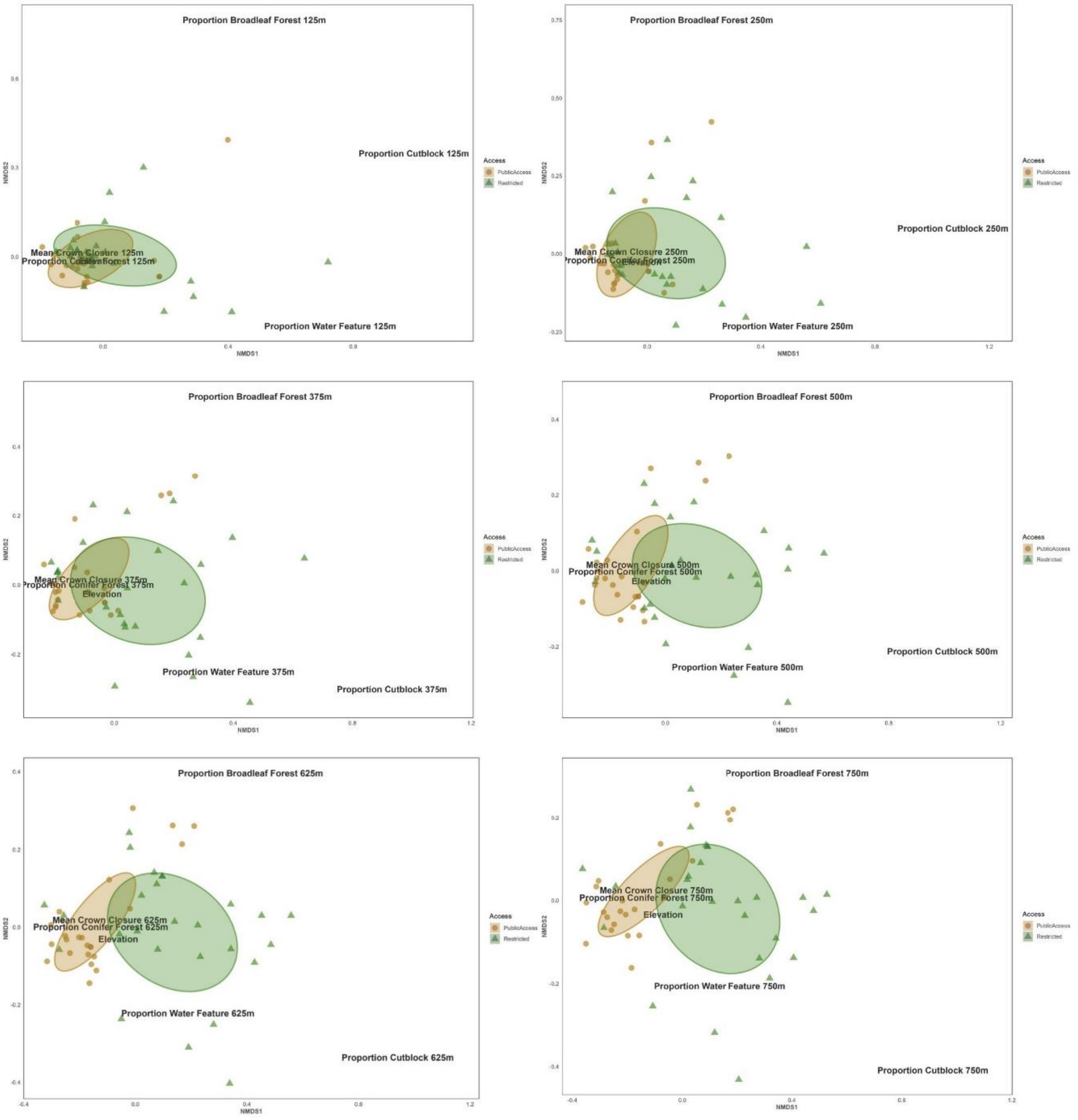
	Elevation (m)	Proportion TB 625m	Proportion TC 625m	Cutblock 625m	Water Feature 625m	Road/Trail Density 625m	Mean Crown Closure 625m	Vehicle	Human	Public Access	Black bear	Deer	Roosevelt elk	Grey wolf	Cougar
Cougar	0.01	0.14	-0.1	0.1	-0.02	-0.07	0.05	0.08	-0.06	-0.12	0.06	-0.03	0.06	0.03	1
Grey wolf	0.12	0.06	-0.03	0.1	0.03	0.01	0.07	0.15	-0.06	-0.13	0.05	-0.05	0.03	1	0.03
Roosevelt elk	0.2	0.09	-0.18	0.28	0.13	-0.16	-0.1	0.06	-0.08	-0.19	0.1	-0.03	1	0.03	0.06
Deer	-0.17	-0.02	0.05	0	-0.05	0.11	-0.01	0.09	0.01	-0.01	-0.02	1	-0.03	-0.05	-0.03
Black bear	0.09	0.12	-0.1	0.15	0	-0.08	-0.01	0.05	-0.12	-0.15	1	-0.02	0.1	0.05	0.06
Public Access	-0.55	-0.13	0.44	-0.49	-0.37	0.27	-0.46	-0.34	0.43	1	-0.15	-0.01	-0.19	-0.13	-0.12
Human	-0.36	-0.07	0.31	-0.21	-0.19	0.28	-0.25	-0.12	1	0.43	-0.12	0.01	-0.08	-0.06	-0.06
Vehicle	0.14	0.08	-0.04	0.21	0.01	0.1	0.18	1	-0.12	-0.34	0.05	0.09	0.06	0.15	0.08
Mean Crown Closure 625m	0.13	0.29	-0.14	0.13	-0.08	0.13	1	0.18	-0.25	-0.46	-0.01	-0.01	-0.1	0.07	0.05
Road/Trail Density 625m	-0.42	0.06	0.34	-0.42	-0.31	1	0.13	0.1	0.28	0.27	-0.08	0.11	-0.16	0.01	-0.07
Water Feature 625m	0.43	-0.08	-0.55	0.28	1	-0.31	-0.08	0.01	-0.19	-0.37	0	-0.05	0.13	0.03	-0.02
Cutblock 625m	0.52	0.27	-0.3	1	0.28	-0.42	0.13	0.21	-0.21	-0.49	0.15	0	0.28	0.1	0.1
Proportion TC 625m	-0.3	-0.47	1	-0.3	-0.55	0.34	-0.14	-0.04	0.31	0.44	-0.1	0.05	-0.18	-0.03	-0.1
Proportion TB 625m	0.04	1	-0.47	0.27	-0.08	0.06	0.29	0.08	-0.07	-0.13	0.12	-0.02	0.09	0.06	0.14
Elevation (m)	1	0.04	-0.3	0.52	0.43	-0.42	0.13	0.14	-0.36	-0.55	0.09	-0.17	0.2	0.12	0.01

(f)

	Elevation (m)	Proportion TB 750m	Proportion TC 750m	Cutblock 750m	Water Feature 750m	Road/Trail Density 750m	Mean Crown Closure 750m	Vehicle	Human	Public Access	Black bear	Deer	Roosevelt elk	Grey wolf	Cougar
Cougar	0.01	0.16	-0.11	0.09	-0.01	-0.06	0.04	0.08	-0.06	-0.12	0.06	-0.03	0.06	0.03	1
Grey wolf	0.12	0.07	-0.04	0.1	0.04	0	0.07	0.15	-0.06	-0.13	0.05	-0.05	0.03	1	0.03
Roosevelt elk	0.2	0.15	-0.21	0.24	0.14	-0.15	-0.12	0.06	-0.08	-0.19	0.1	-0.03	1	0.03	0.06
Deer	-0.17	-0.01	0.03	0	-0.05	0.11	-0.02	0.09	0.01	-0.01	-0.02	1	-0.03	-0.05	-0.03
Black bear	0.09	0.15	-0.09	0.14	0	-0.06	0.01	0.05	-0.12	-0.15	1	-0.02	0.1	0.05	0.06
Public Access	-0.55	-0.23	0.48	-0.48	-0.36	0.23	-0.47	-0.34	0.43	1	-0.15	-0.01	-0.19	-0.13	-0.12
Human	-0.36	-0.13	0.32	-0.21	-0.17	0.2	-0.24	-0.12	1	0.43	-0.12	0.01	-0.08	-0.06	-0.06
Vehicle	0.14	0.16	-0.06	0.21	0	0.09	0.13	1	-0.12	-0.34	0.05	0.09	0.06	0.15	0.08
Mean Crown Closure 750m	0.14	0.25	-0.17	0.16	-0.01	0.17	1	0.13	-0.24	-0.47	0.01	-0.02	-0.12	0.07	0.04
Road/Trail Density 750m	-0.4	0.04	0.29	-0.4	-0.29	1	0.17	0.09	0.2	0.23	-0.06	0.11	-0.15	0	-0.06
Water Feature 750m	0.42	-0.06	-0.55	0.23	1	-0.29	-0.01	0	-0.17	-0.36	0	-0.05	0.14	0.04	-0.01
Cutblock 750m	0.52	0.34	-0.26	1	0.23	-0.4	0.16	0.21	-0.21	-0.48	0.14	0	0.24	0.1	0.09
Proportion TC 750m	-0.32	-0.51	1	-0.26	-0.55	0.29	-0.17	-0.06	0.32	0.48	-0.09	0.03	-0.21	-0.04	-0.11
Proportion TB 750m	0.08	1	-0.51	0.34	-0.06	0.04	0.25	0.16	-0.13	-0.23	0.15	-0.01	0.15	0.07	0.16
Elevation (m)	1	0.08	-0.32	0.52	0.42	-0.4	0.14	0.14	-0.36	-0.55	0.09	-0.17	0.2	0.12	0.01

Appendix B

Non-metric multidimensional scaling (NMDS) plot showing the similarity and dissimilarity of sites based on spatially buffered habitat covariates at six buffer radii. Clustering reflects the level of similarity between the sites.



References

Anderson, D. R., & Burnham, K. P. (2002). Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management*, *66*(3), 912–918. https://doi.org/10.2307/3803155

Arcese, P., & Sinclair, A. R. E. (1997). The Role of Protected Areas as Ecological Baselines. *The Journal of Wildlife Management*, *61*(3), 587–602. https://doi.org/10.2307/3802167

Baker, A., & Leberg, P. (2018). Impacts of human recreation on carnivores in protected areas. *PLOS ONE*, *13*, e0195436. https://doi.org/10.1371/journal.pone.0195436

Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M., & Manica, A. (2015). Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas. *PLOS Biology*, *13*(2), e1002074. https://doi.org/10.1371/journal.pbio.1002074

Beery, S., Morris, D., & Yang, S. (2019). *Efficient Pipeline for Camera Trap Image Review* (arXiv:1907.06772). arXiv. http://arxiv.org/abs/1907.06772

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*(6), 620–623. https://doi.org/10.1098/rsbl.2007.0415

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685. https://doi.org/10.1111/1365-2664.12432

Canty, A., & Ripley, B. (n.d.). *Boot: Bootstrap R (S-Plus) functions* (Version 1.3.28.1) [Computer software]. The R Foundation.

Chourmouzis, C., Yanchuk, A. D., Hamann, A., Smets, P., & Aitken, S. N. (2009). *Forest Tree Genetic Conservation Status Report 1: In situ conservation status of all indigenous BC* *species* [BC Technical Report]. Centre for Forest Conservation Genetics, Forest Genetics Council of BC, and BC Ministry of Forests and Range, Forest Science Program.

Coppes, J., Burghardt, F., Hagen, R., Suchant, R., & Braunisch, V. (2017). Human recreation affects spatio-temporal habitat use patterns in red deer (Cervus elaphus). *PLOS ONE*, *12*(5), e0175134. https://doi.org/10.1371/journal.pone.0175134

CRD. (2001). *Sooke Hills Wilderness and Mount Wells Regional Parks Management Plan*. https://www.crd.bc.ca/docs/default-source/parks-pdf/sooke-hills-management-plan-2001.pdf?sfvrsn=3c8d88cc_2

CRD. (2023). *Greater Victoria Water Supply Area*. CRD. https://www.crd.bc.ca/service/drinking-water/watershed-protection/greater-victoria-water-supply-area

Dellinger, J. A., Cristescu, B., Ewanyk, J., Gammons, D. J., Garcelon, D., Johnston, P., Martins, Q., Thompson, C., Vickers, T. W., Wilmers, C. C., Wittmer, H. U., & Torres, S. G. (2020). Using Mountain Lion Habitat Selection in Management. *The Journal of Wildlife Management*, *84*(2), 359–371. https://doi.org/10.1002/jwmg.21798

Dickson, B. G., & Beier, P. (2002). Home-Range and Habitat Selection by Adult Cougars in Southern California. *The Journal of Wildlife Management*, *66*(4), 1235–1245. https://doi.org/10.2307/3802956

Dupke, C., Bonenfant, C., Reineking, B., Hable, R., Zeppenfeld, T., Ewald, M., & Heurich, M. (2017). Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. *Ecography*, *40*(8), 1014–1027. https://doi.org/10.1111/ecog.02152

Engebretsen, K. N., Beckmann, J. P., Lackey, C. W., Andreasen, A., Schroeder, C., Jackson, P., & Young, J. K. (2021). Recolonizing carnivores: Is cougar predation behaviorally mediated by bears? *Ecology and Evolution*, *11*(10), 5331–5343. https://doi.org/10.1002/ece3.7424

Farris, Z. J., Gerber, B. D., Valenta, K., Rafaliarison, R., Razafimahaimodison, J. C., Larney, E., Rajaonarivelo, T., Randriana, Z., Wright, P. C., & Chapman, C. A. (2017). Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. *Biological Conservation*, *210*, 116–124. https://doi.org/10.1016/j.biocon.2017.04.010

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution*, *1*(4), 517–528. https://doi.org/10.1002/ece3.45

Fisher, J. T., & Burton, A. C. (2018). Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment*, *16*(6), 323–328. https://doi.org/10.1002/fee.1807

Frey, S., Volpe, J. P., Heim, N. A., Paczkowski, J., & Fisher, J. T. (2020). Move to nocturnality not a universal trend in carnivore species on disturbed landscapes. *Oikos*, *129*(8), 1128–1140. https://doi.org/10.1111/oik.07251

Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, *6*(1). https://www.jstor.org/stable/26271862

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, *34*(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Granados, A., Sun, C., Fisher, J. T., Ladle, A., Dawe, K., Beirne, C., Boyce, M. S., Chow, E., Heim, N., Fennell, M., Klees van Bommel, J., Naidoo, R., Procko, M., Stewart, F. E. C., & Burton, A. C. (2023). Mammalian predator and prey responses to recreation and land use across multiple scales provide limited support for the human shield hypothesis. *Ecology and Evolution*, *13*(9), e10464. https://doi.org/10.1002/ece3.10464

Greenberg, S., Godin, T., & Whittington, J. (2019). Design patterns for wildlife-related camera trap image analysis. *Ecology and Evolution*, *9*(24), 13706–13730. https://doi.org/10.1002/ece3.5767

Greenland, S., Senn, S. J., Rothman, K. J., Carlin, J. B., Poole, C., Goodman, S. N., & Altman, D. G. (2016). Statistical tests, P values, confidence intervals, and power: A guide to misinterpretations. *European Journal of Epidemiology*, *31*(4), 337–350. https://doi.org/10.1007/s10654-016-0149-3

Heath, T. A. (2013). Ursus americanus ssp. Emmonsii by Tracy A. Heath (CC0 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/5a5dafa2-6388-43b8-a15a-4fd21cd17594/ursus-americanus-ssp-emmonsii

Heim, N., Fisher, J. T., Volpe, J., Clevenger, A. P., & Paczkowski, J. (2019). Carnivore community response to anthropogenic landscape change: Species-specificity foils generalizations. *Landscape Ecology*, *34*(11), 2493–2507. https://doi.org/10.1007/s10980-019-00882-z

Hilbe, J. M. (2014). *Modeling Count Data*. Cambridge University Press. https://doi.org/10.1017/CBO9781139236065

Holland, J. D., Bert, D. G., & Fahrig, L. (2004). Determining the Spatial Scale of Species' Response to Habitat. *BioScience*, *54*(3), 227–233. https://doi.org/10.1641/0006-3568(2004)054[0227:DTSSOS]2.0.CO;2

Hubbard, T., Cove, M. V., & Diana J R Lafferty. (2022). Human recreation impacts seasonal activity and occupancy of American black bears (Ursus americanus) across the anthropogenic-wildland interface. *Scientific Reports*, *12*(1). https://doi.org/10.1038/s41598-022-15665-x

Jones, K. R., Venter, O., Fuller, R. A., Allan, J. R., Maxwell, S. L., Negret, P. J., & Watson, J. E. M. (2018). One-third of global protected land is under intense human pressure. *Science*, *360*(6390), 788–791. https://doi.org/10.1126/science.aap9565

Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Christopher T. Rota, Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas. *Journal of Applied Ecology*, *54*(1), 242–252. https://doi.org/10.1111/1365-2664.12700

Keim, J. L., Lele, S. R., DeWitt, P. D., Fitzpatrick, J. J., & Jenni, N. S. (2019). Estimating the intensity of use by interacting predators and prey using camera traps. *Journal of Animal Ecology*, *88*(5), 690–701. https://doi.org/10.1111/1365-2656.12960

Kertson, B. N., Spencer, R. D., Marzluff, J. M., Hepinstall-Cymerman, J., & Grue, C. E. (2011). Cougar space use and movements in the wildland–urban landscape of western Washington. *Ecological Applications*, *21*(8), 2866–2881. https://doi.org/10.1890/11-0947.1

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. https://doi.org/10.1139/z01-094

Lele, S. R., Merrill, E. H., Keim, J., & Boyce, M. S. (2013). Selection, use, choice and occupancy: Clarifying concepts in resource selection studies. *Journal of Animal Ecology*, *82*(6), 1183–1191. https://doi.org/10.1111/1365-2656.12141

Lewis, J. S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A. R., VandeWoude, S., & Crooks, K. R. (2021). Human activity influences wildlife populations and activity patterns: Implications for spatial and temporal refuges. *Ecosphere*, *12*(5), e03487. https://doi.org/10.1002/ecs2.3487

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2017). *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier.

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: A review and outlook. *Landscape Ecology*, *31*(6), 1161–1175. https://doi.org/10.1007/s10980-016-0374-x

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human Activity Helps Prey Win the Predator-Prey Space Race. *PLoS ONE*, *6*(3), e17050. https://doi.org/10.1371/journal.pone.0017050

Naidoo, R., & Burton, A. C. (2020). Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. *Conservation Science and Practice*, *2*(10), e271. https://doi.org/10.1111/csp2.271

Neuvonen, M., Pouta, E., Puustinen, J., & Sievänen, T. (2010). Visits to National Parks: Effects of Park Characteristics and Spatial Demand. *Journal for Nature Conservation*, *18*(3), 224–229. https://doi.org/10.1016/j.jnc.2009.10.003

Nickel, B. A., Suraci, J. P., Allen, M. L., & Wilmers, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*, *241*, 108383. https://doi.org/10.1016/j.biocon.2019.108383

Nickel, B. A., Suraci, J. P., Nisi, A. C., & Wilmers, C. C. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. *Proceedings of the National Academy of Sciences*, *118*(5), e2004592118. https://doi.org/10.1073/pnas.2004592118

Olliff, T., Legg, K., & Kaeding, B. (1999). *Effects of Winter Recreation on Wildlife of the Greater Yellowstone Area: A Literature Review and Assessment*. Greater Yellowstone Winter Wildlife Working Group.

Ordiz, A., Bischof, R., & Swenson, J. E. (2013). Saving large carnivores, but losing the apex predator? *Biological Conservation*, *168*, 128–133. https://doi.org/10.1016/j.biocon.2013.09.024

Parsons, A. W., Bland, C., Forrester, T., Baker-Whatton, M. C., Schuttler, S. G., McShea, W. J., Costello, R., & Kays, R. (2016). The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. *Biological Conservation*, *203*, 75–88. https://doi.org/10.1016/j.biocon.2016.09.001

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., Millspaugh, J. J., & Kays, R. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, *56*(8), 1894–1904. https://doi.org/10.1111/1365-2664.13385

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, *10*(1), 439. https://doi.org/10.32614/RJ-2018-009

Pebesma, E., & Bivand, R. (2023). *Spatial Data Science: With Applications in R* (1st ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016

Pierce, B. M., Bleich, V. C., Wehausen, J. D., & Bowyer, R. T. (1999). Migratory Patterns of Mountain Lions: Implications for Social Regulation and Conservation. *Journal of Mammalogy*, *80*(3), 986–992. https://doi.org/10.2307/1383269

Procko, M., Naidoo, R., LeMay, V., & Burton, A. C. (2023). Human presence and infrastructure impact wildlife nocturnality differently across an assemblage of mammalian species. *PLOS ONE*, *18*(5), e0286131. https://doi.org/10.1371/journal.pone.0286131

R Core Team (2023). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Reed, S. E., & Merenlender, A. M. (2008). Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. *Conservation Letters*, *1*(3), 146–154. https://doi.org/10.1111/j.1755-263X.2008.00019.x

Sayol, F. (2021). Cervus elaphus by Ferran Sayol (CC0 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/cc03f5c2-933f-4c40-9c64-7f8727556fdb/cervus-elaphus

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities. *Science, 185*(4145), 27–39.

Schuette, P., Creel, S., & Christianson, D. (2013). Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. *Biological Conservation*, *157*, 148–154. https://doi.org/10.1016/j.biocon.2012.09.011

Sévêque, A., Gentle, L., López-Bao, J. V., Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, *95*(6), 1689–1705. https://doi.org/10.1111/brv.12635

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1857), 20170433. https://doi.org/10.1098/rspb.2017.0433

Smith, J. A., Thomas, A. C., Levi, T., Wang, Y., & Wilmers, C. C. (2018). Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos, 127*(6), 890–901. https://doi.org/10.1111/oik.04592

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society. B, Biological Sciences*, *282*(1802), 20142711–20142711. https://doi.org/10.1098/rspb.2014.2711

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, *22*(10), 1578–1586. https://doi.org/10.1111/ele.13344

Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L. M., Forrester, T., Green, A. M., Haight, J., Harris, N. C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P. E., Lewis, J. S., McInturff, A., … Wilmers, C. C. (2021). Disturbance type and species life history predict mammal responses to humans. *Global Change Biology*, *27*(16), 3718–3731. https://doi.org/10.1111/gcb.15650

Sytsma, M. L. T., Lewis, T., Gardner, B., & Prugh, L. R. (2022). Low levels of outdoor recreation alter wildlife behaviour. *People and Nature*, *4*(6), 1547–1559. https://doi.org/10.1002/pan3.10402

Taylor, A. R., & Knight, R. L. (2003). Wildlife Responses to Recreation and Associated Visitor Perceptions. *Ecological Applications*, *13*(4), 951–963. https://doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2

Taylor, J. (2019). Puma concolor by Jody Taylor (CC0 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/3f8eff77-2868-4121-8d7d-a55ebdd49e04/puma-concolor

The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia. (2001). *Sooke Hills Wilderness and Mount Wells Regional Parks Terrestrial Ecosystem Mapping*. The Ministry of Environment, Lands and Parks Resources Inventory Branch of British Columbia.

Traver, S. (2012). Canis lupus by Steven Traver (CC0 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/5036f260-5a0d-42c5-a0bd-9eb0729e54e0/canis-lupus

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant,

J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Zi, F. (2018). *Moving in the Anthropocene: Global reductions in terrestrial mammalian movements*. 5.

Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K., & Brashares, J. S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, *92*(6), 1124–1134. https://doi.org/10.1111/1365-2656.13892

Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation, 190*, 23–33. https://doi.org/10.1016/j.biocon.2015.05.007

Watson, J. E. M., Shanahan, D. F., Di Marco, M., Allan, J., Laurance, W. F., Sanderson, E. W., Mackey, B., & Venter, O. (2016). Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Current Biology*, *26*(21), 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049

Whittington, J., St. Clair, C. C., & Mercer, G. (2005). Spatial Responses of Wolves to Roads and Trails in Mountain Valleys. *Ecological Applications*, *15*(2), 543–553. https://doi.org/10.1890/03-5317

Wiens, J. A. (1989). *Spatial Scaling in Ecology*. https://doi.org/10.2307/2389612

Wijesekara, C., Tittagalla, C., Jayathilaka, A., Ilukpotha, U., Jayathilaka, R., & Jayasinghe, P. (2022). Tourism and economic growth: A global study on Granger causality and wavelet coherence. *PLOS ONE*, *17*(9), e0274386. https://doi.org/10.1371/journal.pone.0274386

Winnie, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, *12*, 88–94. https://doi.org/10.1016/j.fooweb.2016.09.002

xgirouxb. (2019). Odocoileus hemionus by xgirouxb (PDM 1.0)—PhyloPic [Graphic]. https://www.phylopic.org/images/f889b336-9e67-4154-bc96-db4095a55be2/odocoileus-hemionus

Zuur, A. F. (2009). Chapter 9. GLM and GAM for count data. In *Mixed effects models and extensions in ecology with R*.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). *Analysing Ecological Data*. Springer. https://doi.org/10.1007/978-0-387-45972-1

Chapter 4: Conclusion

Researching how human activity impacts wildlife has become a critical area of study due to increasing outdoor recreation in protected or previously undisturbed places (Jones et al., 2018). Protected areas across the world provide large refuges for important species from major infrastructure development and habitat fragmentation. These protected areas buffer from the threats of connectivity loss to wildlife populations (Crooks et al., 2011). However, non-consumptive activities within these “pristine” areas have been shown to alter wildlife spatial behaviours, thereby bringing into question the effectiveness of protected areas (Reed & Merenlender, 2008). To preserve the ability for protected areas to serve their goals of promoting biodiversity and maintaining healthy functioning wildlife communities, the potential negative effects of human visitation must be thoroughly examined (Jones et al., 2018; Sarmento & Berger, 2017). This thesis aimed to expand our understanding of recreational impacts by assessing how human-induced risk and public access restrictions affect the risk-resource trade-offs of an apex predator and the spatial partitioning among a community of large mammals.

4.0 Summary of Findings

The effects of recreation on mammal space use show that species don’t simply “move aside” for humans at a site but actually adjust their distributions to accommodate for human activity. In Chapter 2, I examined the relative influences of habitat quality, perceived risk, and prey availability on cougar detection frequency across a landscape with varying public-access. The results revealed that cougar presence was best explained by both habitat features and human activity, with a clear pattern of risk-avoidance emerging at fine and broad scales. Cougars were more willing to tolerate risk at sites with a higher proportion of their preferred habitat, forcing them to make a trade-off in areas containing quality habitat and human activity. Despite the risk posed by activity in recreation areas, cougars may need to face the threat of human encounters to access essential resources (Sévêque et al., 2020). Cougars' risk aversion, coupled with high levels of human activity, could affect their ecological role and the broader wildlife community (Ripple & Beschta, 2006). As apex predators, cougars regulate ecosystems by controlling herbivore behaviour through predation (Beier, 2009). However, when cougars do not avoid human activity, facing risk can be physiologically costly (Nickel et al., 2021; Smith, 2017), and may pose safety concerns for recreationalists (Beier, 2009). The increased likelihood of cougar-human encounters in areas of preferred habitat necessitates careful management of recreation and public education (Inskip & Zimmermann, 2009; Sweanor et al., 2008). This research improves our understanding of the factors that contribute to human-wildlife conflict and provides opportunities to mitigate risk (Sweanor & Logan, 2009). From this work, cougars emerge as a focal species for recreation impact studies due to their regulatory role in ecosystems (Ripple & Beschta, 2006, 2008), their status as an indicator species (Beier, 1993), and their charismatic ability to garner support for broader conservation efforts (Beier, 2009).

In Chapter 3, I took a community-centric approach to assess how human presence and public-access influenced large mammal space use and partitioning among five ecologically important species. I found that large mammal species responded varyingly to habitat characteristics, types of human disturbance, and the presence of other wildlife species. However, access restrictions had a notable impact on the spatial partitioning of the broader wildlife community. Specifically, spatial overlap among the community of large carnivores was detected, likely due to their shared avoidance of public-access sites and partial exclusion from the regional park. This decrease in adequate spatial partitioning among large carnivores can lead to increased competition, impaired hunting success, and potential trophic cascades that affect smaller mammals and local vegetation communities (Estes et al., 2011; Haswell et al., 2017; Winemiller et al., 2014; Winnie & Creel, 2017). For example, black bears, cougars, and wolves preferred highly forested sites, creating the potential for competition where these species spatially overlapped. In addition to more frequent interspecific-interactions, carnivores' avoidance of human-used habitats can alter predator-prey relationships. Findings showed that ungulate prey species also avoided human activity and/or public-access sites, rejecting the human-shield hypothesis (Granados et al., 2023). Mutual avoidance of humans at the landscape scale could result in increased spatial overlap among predators and prey distributions, leading to more frequent predation and thus an increase in ungulates' energetically costly anti-predator behaviours (Van Scoyoc et al., 2023). Highly protected areas free from outdoor recreation provide essential refuges to mitigate impacts to spatial partitioning, as even low levels of recreation can alter wildlife behaviour (Sytsma et al., 2022). These protected areas can alleviate the anthropogenic pressures imposed by widespread human encroachment (Jones et al., 2018).

The findings from Chapter 3 also showed that species exhibited varying responses to different types of human disturbance and habitat characteristics; yet their consistent avoidance of public-access areas indicated landscape-level effects. Study results confirmed that wildlife community composition differed notably between protected areas, even though these areas shared similar landscape characteristics. Human presence may have driven species to adjust their site use at fine scales, but differences in land-use restrictions drove distinct wildlife communities between two otherwise similar landscapes. Further, the negative responses of wolves, black bears, and elk to public-access areas suggest that human presence may drive exclusion from otherwise suitable habitat. Although some anthropogenic activities can consistently impact wildlife species at the landscape level (Reed & Merenlender, 2008), others can have different impacts at the site level (Rogala et al., 2011). Therefore, it's important to examine wildlife communities, in addition to indicator species (such as the cougar), to understand the full spectrum of human impacts.

This thesis contributes to a growing body of literature examining the impacts of non-consumptive human activity on wildlife. While numerous studies have explored these impacts at the site level, I went a step further by assessing impacts at the landscape level. These findings provide strong evidence that the effects of human presence can scale upwards to redistribute wildlife in ways that have been less thoroughly considered. Further, I modelled cougar occurrence across a visual prediction surface, providing an accessible visualization of how risk impacts cougar distributions (Gaynor et al., 2019). Additional findings improved our knowledge of how wildlife respond to their surroundings, more specifically revealing how cougars spatially assess human-induced risk and habitat in a heterogenous landscape. Cougars' willingness to tolerate risk in certain areas, especially where preferred habitat was present, indicated a trade-off between resource acquisition and risk avoidance. This behaviour revealed factors that may contribute to human-wildlife encounters in disturbed landscapes. Proactive insights into the conditions that could foster encounters add to a field of study that often makes management decisions only after encounters have occurred (Arundel et al., 2007). This work also contributes to the literature focused on the role of spatial scale in ecological processes (Fisher et al., 2011; Gaston et al., 2024; Heim et al., 2017; Heim et al., 2019). My results confirmed long-established theory that ecological processes occur at characteristic scales (Wiens, 1989), especially for different species (Levin, 1992), as spatial selection of habitat was observed at varying scales for five species within a community of large mammals. It’s important to take a spatial approach and continue to assess ecological processes at multiple scales (Crooks, 2002; Wilmers et al., 2013), especially because landscapes are often managed spatially (i.e., closing off portions to protect critical habitat) (Reed & Merenlender, 2008).

4.1 Caveats and Management Implications

Although this study derived well-supported conclusions regarding anthropogenic impacts on wildlife within protected areas, these inferences were spatially and temporally limited. Assessing spatial partitioning within protected areas provides valuable insights, but broad geographic features may regulate these processes. External influences such as proximity to urban centres and local population densities (Winkel et al., 2023), habitat connectivity (Crooks, 2002), and the presence of established wildlife corridors (LaRue & Nielsen, 2008) can influence where we find species throughout a large-scale patchwork of protected and developed land. Future studies might consider including broad-scale covariates that quantify external influences, such as distance to protected area edge, distance to major roads/highways, or distance to urban centres (Kays et al., 2017). My inferences were based on less than one year's worth of data, temporally limiting the scope of analyses. Multi-year studies can effectively identify trends in protected area visitation, revealing long-term impacts of anthropogenic activity on wildlife. Findings could provide additional evidence of the total exclusion of species from recreation areas, or at least exclusion from high activity sites (Coppes et al., 2017).

While human recreation affects wildlife spatial distributions, potential solutions exist to mitigate these impacts and strengthen the ecological benefits of protected areas. Numerous studies on human-wildlife interactions have identified spatial restrictions on recreation as a common management tactic to mitigate negative impacts (Larson et al., 2016). Restricting access to quality habitat can help reduce spatial overlap among carnivores, promote healthy competition, maintain predator-prey relationships, and minimize the effects of human-induced fear (Baker & Leberg, 2018; Reed & Merenlender, 2008). Limiting development in highly cougar-trafficked areas and expanding undisturbed habitat can decrease negative encounters, thus increasing peaceful coexistence between humans and wildlife (Arundel et al., 2007). Minimizing the density of roads and trails throughout natural areas may be one mode of ensuring sufficient undisturbed habitat for a variety of species (Whittington et al., 2005). Establishing connectivity between quality habitat is essential for safe wildlife movement and dispersal. Further research and efforts to establish wildlife corridors between protected areas, especially in rapidly urbanizing regions, are recommended. Movement towards the coexistence of carnivores and people is possible, especially with public support and locally focused legislation and management practices (Chapron et al., 2014). Understanding human impacts and garnering public support are crucial for conserving large mammals, especially in the face of contentious public perceptions, range contractions in North America (Laliberte & Ripple, 2004), and threats to habitat through development and increasing population density (Woodroffe, 2000).

4.2 Summary

Overall, this research supports the hypothesis that human activities affect cougar spatial dynamics and reduce spatial partitioning among a broader wildlife community. My findings call for action from managers and research scientists to mitigate human disturbance amidst the rapid expansion of outdoor recreation. This thesis' evidence that humans induce a fear response in cougars builds on a growing body of research and emphasizes the urgent need to address human influence on natural landscapes. Effective management of protected areas must ensure enough undisturbed habitat is available to maintain the ecological roles of cougars and other large mammals. Human activity in protected natural areas must be monitored and managed accordingly so that species do not face habitat degradation or exclusion from portions of their home ranges. Identifying these high use areas by both wildlife and humans can mitigate potential conflict, supporting public interest in local conservation efforts. An approach that adaptively manages both wildlife needs, and human needs is essential for the long-term protection of biodiversity in shared spaces.

References

Arundel, T., Mattson, D. J., & Hart, J. (2007). *Movements and habitat selection by mountain lions in the Flagstaff uplands. In Mountain lions of the Flagstaff uplands* (Open-File Report) [Open-File Report]. US Department of the Interior, US Geological Survey.

Baker, A., & Leberg, P. (2018). Impacts of human recreation on carnivores in protected areas. *PLOS ONE*, *13*, e0195436. https://doi.org/10.1371/journal.pone.0195436

Beier, P. (1993). Determining Minimum Habitat Areas and Habitat Corridors for Cougars. *Conservation Biology*, *7*(1), 94–108. https://doi.org/10.1046/j.1523-1739.1993.07010094.x

Beier, P. (2009). Chapter 12. A Focal Species for Conservation Planning. In *Chapter 12. A Focal Species for Conservation Planning* (pp. 177–189). University of Chicago Press. https://doi.org/10.7208/9780226353470-020

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216), 1517–1519. https://doi.org/10.1126/science.1257553

Coppes, J., Ehrlacher, J., Thiel, D., Suchant, R., & Braunisch, V. (2017). Outdoor recreation causes effective habitat reduction in capercaillie Tetrao urogallus: A major threat for geographically restricted populations. *Journal of Avian Biology*, *48*(12), 1583–1594. https://doi.org/10.1111/jav.01239

Crooks, K. R. (2002). Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. *Conservation Biology*, *16*(2), 488–502. https://doi.org/10.1046/j.1523-1739.2002.00386.x

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical*

Transactions of the Royal Society B: Biological Sciences, *366*(1578), 2642–2651. https://doi.org/10.1098/rstb.2011.0120

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science (New York, N.Y.)*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution*, *1*(4), 517–528. https://doi.org/10.1002/ece3.45

Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, *6*(1). https://www.jstor.org/stable/26271862

Gaston, M. V., Barnas, A. F., Smith, R. M., Murray, S., & Fisher, J. T. (2024). Native prey, not landscape change or novel prey, drive cougar (Puma concolor) distribution at a boreal forest range edge. *Ecology and Evolution*, *14*(4), e11146. https://doi.org/10.1002/ece3.11146

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, *34*(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Haswell, P. M., Kusak, J., & Hayward, M. W. (2017). Large carnivore impacts are context-dependent. *Food Webs*, *12*, 3–13. https://doi.org/10.1016/j.fooweb.2016.02.005

Heim, N., Fisher, J. T., Clevenger, A., Paczkowski, J., & Volpe, J. (2017). Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine (Gulo gulo L.). *Ecology and Evolution*, *7*(21), 8903–8914. https://doi.org/10.1002/ece3.3337

Heim, N., Fisher, J. T., Volpe, J., Clevenger, A. P., & Paczkowski, J. (2019). Carnivore community response to anthropogenic landscape change: Species-specificity foils generalizations. *Landscape Ecology*, *34*(11), 2493–2507. https://doi.org/10.1007/s10980-019-00882-z

Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities worldwide. *Oryx*, *43*(1), 18–34. https://doi.org/10.1017/S003060530899030X

Jones, K. R., Venter, O., Fuller, R. A., Allan, J. R., Maxwell, S. L., Negret, P. J., & Watson, J. E. M. (2018). One-third of global protected land is under intense human pressure. *Science*, *360*(6390), 788–791. https://doi.org/10.1126/science.aap9565

Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Christopher T. Rota, Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas. *Journal of Applied Ecology*, *54*(1), 242–252. https://doi.org/10.1111/1365-2664.12700

Laliberte, A. S., & Ripple, W. J. (2004). Range Contractions of North American Carnivores and Ungulates. *BioScience*, *54*(2), 123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review. *PLOS ONE*, *11*(12), e0167259. https://doi.org/10.1371/journal.pone.0167259

LaRue, M. A., & Nielsen, C. K. (2008). Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. *Ecological Modelling*, *212*(3), 372–381. https://doi.org/10.1016/j.ecolmodel.2007.10.036

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology*, *73*(6), 1943–1967. https://doi.org/10.2307/1941447

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human Activity Helps Prey Win the Predator-Prey Space Race. *PLoS ONE*, *6*(3), e17050. https://doi.org/10.1371/journal.pone.0017050

Nickel, B., Justin P. Suraci, Suraci, J. P., Anna C. Nisi, Nisi, A. C., Christopher C. Wilmers, & Wilmers, C. C. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(5). https://doi.org/10.1073/pnas.2004592118

Reed, S. E., & Merenlender, A. M. (2008). Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. *Conservation Letters*, *1*(3), 146–154. https://doi.org/10.1111/j.1755-263X.2008.00019.x

Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation*, *133*(4), 397–408. https://doi.org/10.1016/j.biocon.2006.07.002

Ripple, W. J., & Beschta, R. L. (2008). Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation*, *141*(5), 1249–1256. https://doi.org/10.1016/j.biocon.2008.02.028

Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., & Musiani, M. (2011). Human Activity Differentially Redistributes Large Mammals in the Canadian Rockies National Parks. *Ecology and Society*, *16*(3). https://www.jstor.org/stable/26268938

Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation*, *212*, 316–326. https://doi.org/10.1016/j.biocon.2017.06.032

Sévêque, A., Gentle, L., López-Bao, J. V., Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, *95*(6), 1689–1705. https://doi.org/10.1111/brv.12635

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores.

Proceedings of the Royal Society B: Biological Sciences, *284*(1857), 20170433. https://doi.org/10.1098/rspb.2017.0433

Sweanor, L. L., & Logan, K. A. (2009). Chapter 13. Cougar-Human Interactions. In *Chapter 13. Cougar-Human Interactions* (pp. 190–205). University of Chicago Press. https://doi.org/10.7208/9780226353470-021

Sweanor, L. L., Logan, K. A., Bauer, J. W., Millsap, B., & Boyce, W. M. (2008). Puma and Human Spatial and Temporal Use of a Popular California State Park. *The Journal of Wildlife Management*, *72*(5), 1076–1084. https://doi.org/10.2193/2007-024

Sytsma, M. L. T., Lewis, T., Gardner, B., & Prugh, L. R. (2022). Low levels of outdoor recreation alter wildlife behaviour. *People and Nature*, *4*(6), 1547–1559. https://doi.org/10.1002/pan3.10402

Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K., & Brashares, J. S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, *92*(6), 1124–1134. https://doi.org/10.1111/1365-2656.13892

Whittington, J., St. Clair, C. C., & Mercer, G. (2005). Spatial Responses of Wolves to Roads and Trails in Mountain Valleys. *Ecological Applications*, *15*(2), 543–553. https://doi.org/10.1890/03-5317

Wiens, J. A. (1989). *Spatial Scaling in Ecology*. https://doi.org/10.2307/2389612

Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., Kermish-Wells, J., Yovovich, V., & Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. *PloS One*, *8*(4), e60590. https://doi.org/10.1371/journal.pone.0060590

Winemiller, K. O., Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Joel Berger, Berger, J., Joel Berger, Joel Berger, Elmhagen, B., Letnic, M., Nelson, M. P., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J.

(2014). Status and ecological effects of the world’s largest carnivores. *Science*, *343*(6167), 1241484–1241484. https://doi.org/10.1126/science.1241484

Winkel, B. M., Nielsen, C. K., Hillard, E. M., Sutherland, R. W., & LaRue, M. A. (2023). Potential cougar habitats and dispersal corridors in Eastern North America. *Landscape Ecology*, *38*(1), 59–75. https://doi.org/10.1007/s10980-022-01538-1

Winnie, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs, 12*, 88–94. https://doi.org/10.1016/j.fooweb.2016.09.002

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation Forum*, *3*(2), 165–173. https://doi.org/10.1111/j.1469-1795.2000.tb00241.x