

MULTISPECIES MAMMAL MONITORING IN CATHEDRAL PROVINCIAL PARK

by

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Abstract

Globally, protected areas face a challenge of meeting the dual mandate of protecting biodiversity while providing recreational enjoyment for humans. Balancing these mandates is confounded by limited information on species status and insufficient recreation monitoring. Effective protected area (PA) management is critical for wildlife in this time of pervasive human impact known as the Anthropocene. Where non-consumptive human recreation is considered low impact, with growth in outdoor recreation it is important to know if recreation is impacting wildlife and how. Using camera traps, I assessed the potential for recreational impacts on mammal habitat use in space and time, in Cathedral Provincial Park, British Columbia, Canada. I also estimated population density for an at-risk mountain goat (*Oreamnos americanus*) population using two methods: spatial capture-recapture (SCR) and spatial mark-resight (SMR).

I assessed recreational impacts on habitat use at the weekly scale, while also evaluating daily activity patterns for eight mammal species. I hypothesized that coexistence with recreation would require spatial and/or temporal niche segregation, with large carnivores being most sensitive and exhibiting spatial avoidance as suggested by the predator shield hypothesis. I predicted that mesocarnivores and ungulates would exploit this “shield” spatially, while exhibiting temporal avoidance of humans. I found spatial co-occurrence between ungulates and recreation, suggesting that these species may be using people as a shield from predators or for nutritional subsidies, but did not see the predicted negative relationship between predators and humans, except for coyotes (*Canis latrans*). Temporally, all species other than cougars (*Puma concolor*) had activity patterns significantly different from that of recreationists, suggesting stronger displacement in the temporal niche, while wolves (*Canis lupus*) and mountain goats showed significantly different use of on and off-trail habitat in time.

Estimates of mountain goat density varied between methods, from a minimum 6.32 (95% CI; 2.98-13.40) to a maximum of 11.54 (6.97-19.13) goats per 100 km². I found SMR estimates to have higher precision than SCR estimates across all three years. With this study I show that camera trap surveys can be used to assess interactions between wildlife and recreation, while also providing basis for monitoring population trends in sensitive species.

Lay Summary

Many people consider protected areas as designed to conserve nature, especially for species at risk, but many of these areas also have the goal of providing enjoyment of nature for people. Human activities like hiking are often thought to have little impact on wildlife, but we don't know whether that is true. My work used motion-triggered cameras to test whether human recreation was linked to changes in wildlife use of habitat in space or time, in Cathedral Provincial Park, British Columbia, Canada. I used the same cameras to estimate the number of mountain goats in the park, which are a species of concern across the province due to their small, isolated populations and increasing threats. My thesis can be used to identify species most sensitive to recreation (coyotes, mountain goats, wolves), while informing management in Cathedral, and also giving important information on the status of this at-risk mountain goat population.

Preface

All data presented in this thesis were collected collaboratively by the University of British Columbia Wildlife Coexistence (WildCo) Lab. I led the design of the study with support and input from Dr. Cole Burton. I led the field program, as well as collection, management, and processing of all data, with the exception of data from seven camera traps used in chapter 3, which were provided by Kirk Safford/BC Parks. I conducted all analyses presented here, with the support of Dr. Burton and members of the WildCo lab. I completed all writing independently, with revision of initial drafts based on feedback from my committee (Drs. Cole Burton, Adam Ford, and Tara Martin) and other colleagues (Dr. Joanna Burgar, Dr. Catherine Sun, Jamie Clarke, and Alexia Constantinou). Ethics approval for this study was granted under UBC Animal Care Certificate #A18-0234 and UBC Behavioural Research Ethics Certificate #H21-01424. Approval for research within Cathedral Provincial Park was granted by BC Parks.

Throughout this thesis I use the word “I” to represent that the work presented within is independent research, however I strongly acknowledge the collaborative nature of this work overall, particularly the contributions and support of my collaborators, namely Drs. Cole Burton, Adam Ford, and Tara Martin.

Adaptations based on material from Chapter 2 and Chapter 3 are planned for submission to peer-reviewed journals, with myself as the primary author.

Table of Contents

Abstract	iii
Lay Summary.....	iv
Preface	v
Table of Contents.....	vi
List of Tables.....	viii
List of Figures	ix
List of Symbols.....	x
List of Abbreviations	xi
Acknowledgements	xii
Dedication.....	xiv
Chapter 1: Introduction.....	1
1.1 Wildlife under threat.....	1
1.2 Protected areas to the rescue?	2
1.2.1 Dual mandate problem	2
1.3 Tools to answer these questions	4
1.4 Thesis objectives	4
1.5 Study area description	5
Chapter 2: Using non-invasive methodology to assess the impacts of recreation on a protected area mammal community	8
2.1 Introduction	8
2.2 Methods	12
2.2.1 Camera trap survey.....	12

2.2.2	Data processing	14
2.2.3	Statistical analysis	15
2.3	Results	19
2.3.1	Spatial Effect	20
2.3.2	Temporal Partitioning.....	23
2.4	Discussion.....	27
2.5	Management Implications	32
Chapter 3: Density estimation of a partially marked mountain goat (<i>Oreamnos americanus</i>)		
population of conservation concern using camera traps		33
3.1	Introduction	33
3.2	Methods	37
3.2.1	Camera trap survey.....	37
3.2.2	Statistical analysis	39
3.3	Results	40
3.4	Discussion.....	43
Chapter 4: Synthesis and conclusions.....		46
4.1	Research strengths and limitations	47
4.2	Applications and future research	48
Works Cited		50
Appendices		66
Appendix A Chapter two supporting information.....		66
Appendix B Chapter three supporting information		73

List of Tables

Table 2.1. Predicted response to human recreation, for commonly encountered medium and large-bodied mammal species in Cathedral Provincial Park. Predicted responses spatially and temporally are listed for each species, with + representing a positive response to human recreation, - a negative, and +/- a neutral response. Also included is the hypothesis supporting the prediction and key associated references. _____ 11

Table 2.2. Predictor variables used in Bayesian regression models of wildlife detections at 45 sites in Cathedral Provincial Park. I also provide the mean and range for each predictor at on and off-trail sites. _____ 18

Table 2.3. Number of independent detection events, as well as on- and off-trail detections and the ratio of on- to off-trail detections for each species of interest in Cathedral Provincial Park. Off-trail detections include the study team. _____ 20

Table 2.4. Overlap coefficient (with 95% confidence interval as generated by 10,000 bootstrap samples), Wald statistic, and Wald test *p*-value for activity patterns of single species on- versus off-trail and human versus each species. Statistically significant differences between activity patterns are denoted in bold. _____ 26

Table 3.1. Mountain goat detection summary from 17,15, and 10 camera traps sampled for 98, 98, and 63 camera-days in summer 2019, 2020 and 2021 respectively in Cathedral Provincial Park. The total number of detections are provided for identifiable marked individuals (Marked-ID), unidentifiable marked individuals (Marked-noID) and unmarked individuals. The number of marked and recaptured individuals are also provided. _____ 41

Table 3.2. Results for SCR and SMR models of mountain goats in Cathedral Provincial Park, from 2019 to 2021. Estimates of density (D , goats/100km²), abundance (N), σ (in meters), and g_0 with 95% CIs in parentheses. RSE is relative standard error, a measure of the precision of the density estimate. _____ 42

List of Figures

Figure 2.1. Map of camera trap deployments in Cathedral Provincial Park. The outer green polygon is the park boundary, while the inner is the park core area boundary where recreation is highest. Solid black lines are roads, and dashed lines are trails. Orange pentagons represent off-trail camera traps, and purple pentagons represent on-trail camera traps. _____ 14

Figure 2.2. Effect of human detections on species habitat use. Shown are parameter estimates and credible intervals from Bayesian GLMMs at sampling sites at a weekly scale (see Table 2.2 for the full set of parameters included in models). Thick lines represent 80% credible intervals, and thin lines represent 95% credible intervals. _____ 21

Figure 2.3. Parameter estimates for predictors strong predictors of wildlife habitat use. Shown are parameter estimates from Bayesian GLMMs. Strong predictors are defined as 95% credible interval not overlapping zero. Species are (top to bottom): mountain goats, mule deer, black bears, Canada lynx, cougars, wolves, and coyotes. Thick lines represent 80% credible intervals, and thin lines represent 95% credible intervals. Credible intervals are not visible for some estimates at this scale. All predictors were standardized to have a mean of 0 and standard deviation of 1. Moose are not shown due to no significant predictors. _____ 22

Figure 2.4. Human (solid line) and animal (dashed line) comparisons of activity for eight focal species, with overlap coefficient (Δ) estimates (generated with 10 000 bootstraps). _____ 24

Figure 2.5. Comparisons of diel activity for each species between camera trap sites on (solid line) vs. off (dashed line) of recreation trails, with overlap coefficient (Δ) estimates (generated with 10 000 bootstraps). Note the varied Y-axis scale between each plot, which represents the kernel density estimate. _____ 25

Figure 3.1 Example camera trap images of A) unmarked, B) marked and identifiable, C) marked and unidentifiable mountain goats. _____ 38

Figure 3.2 Map of camera trap deployments in Cathedral Provincial Park used for mountain goat density estimation, and the years each camera was active. The orange polygon is the state space (322 km²) and the green polygon is the park boundary. Solid black lines are roads, and dashed lines are recreation trails. _____ 38

Figure 3.3 Mean (point) and 95% CI (bars) estimates of adult mountain goat population density from spatial capture-recapture (SCR) and spatial mark-resight (SMR) models in Cathedral Provincial Park from 2019 to 2021. _____ 42

List of Symbols

Δ : Coefficient of overlap between kernel density estimates of temporal activity

σ : Spatial scale parameter

g_0 : Baseline encounter rate

List of Abbreviations

CT: Camera trap

PA: Protected area

SCR: Spatial capture-recapture

SMR: Spatial mark-resight

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I first wish to gratefully, sincerely, and respectfully acknowledge that this work takes place on the unceded and traditional territory of the Syilx (Okanagan) Nation, particularly on the lands of the Smelqmix (Similkameen) Peoples who have inhabited these territories since time immemorial, and will continue to steward them into the future. While my work has focussed on protected areas established under a colonial framework, I look forward to witnessing the prosperity and further protection of these and surrounding lands via an Indigenous Protected and Conserved Area moving forward.

I would like to extend my sincere gratitude to my committee members Dr. Adam Ford, Dr. Tara Martin, and particularly my supervisor Dr. Cole Burton, for their support, mentorship, and kind guidance through this process. Your encouragement has made this all come together, and I feel very lucky to learn from such excellent scholars and inspirational people. I additionally wish to thank all of the members of the WildCo lab past and present for their camaraderie and support, it's rare to be excited to go to work every day, and the group of people around me made this much easier. I would like to specifically thank Taylor Justason, Michael Procko, Jamie Clarke, Genevieve Hurd, Deb Sinarta, Isla Francis, Alexia Constantinou, and Madeleine Wrazej for their assistance in servicing cameras and tagging photos, as well as Charles White, Jessica Low, Annie Kim, Serena Sturton, Lucas Friesen, and Joey Krahm for their photo processing assistance. I thank Dr. Cat Sun, Dr. Joanna Burgar, Jamie Clarke, and Alexia Constantinou for useful reviews which greatly improved this thesis. Thanks to my WildCo twin Alexia for the many rants and raves in the coolest corner of the lab, and for putting some water on the fire cat.

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Tahkinee ayish paraaa'ntii kayaash eekwa lii zanimal

Chapter 1: Introduction

1.1 Wildlife under threat

Biodiversity is crucial to ecological functioning, with natural systems providing benefits and ecosystem services worldwide (Cimon-Morin et al., 2013; Johnson et al., 2017). Despite this knowledge, biodiversity is under threat in what has been termed the Anthropocene, where humans are having large-scale effects on the planet, resulting in dramatic declines and losses of wildlife witnessed globally (Dirzo et al., 2014; Johnson et al., 2017). Anthropogenic factors contributing to these impacts are numerous, ranging from overharvest of game species, to destruction of habitat by urban expansion, to emissions-fueled climate change (Dirzo et al., 2014; Newbold et al., 2015; Young et al., 2016). Compounding of these factors amongst many other human impacts can lead to range shifts, local extirpation, and even extinction of wildlife species (Butchart et al., 2010; Dirzo et al., 2014; Young et al., 2016).

While it is clear that vast issues such as climate change, environmental pollution, and permanent landscape change result in impacts on wildlife populations, smaller-scale impacts may also play a role in biodiversity decline (Larson & Reed, 2020; Nickel et al., 2020; Stewart et al., 2016). Anthropogenic impacts at the individual animal level may be more direct, such as harvest of wildlife for food or sport, fatal collisions with vehicles, or destruction due to conflict with humans or livestock (Barua et al., 2013; Wilkinson et al., 2020). Impacts at this individual animal level may also be less clear however, as activities commonly considered to be non-consumptive and low impact, such as non-motorized recreation or wildlife viewing may also have negative effects (Baker & Leberg, 2018; Gutzwiller et al., 2017; Larson et al., 2019).

With these impacts in mind, it is important to note the relationships and co-occurrence between humans and wildlife which have existed since time immemorial, where Indigenous Peoples have coexisted with and effectively supported healthy populations of wildlife across the globe (Berkes et al., 1998; Hessami et al., 2021; Suchet, 2002). The colonial tendency to separate humans from wildlife and the environments in which they live, both physically and morally, has resulted in an interruption to these relationships, to the detriment of people as well as wildlife (Suchet, 2002). With this knowledge of past and ongoing mutualistic relationships, as well as an

understanding of the colonial processes which have intentionally disrupted this balance, it is clear that there is potential for humans and wildlife to coexist.

1.2 Protected areas to the rescue?

One tool commonly proposed to mitigate the effects of the Anthropocene on wildlife is protected areas (PAs) (Graham et al., 2019; Haight & Hammill, 2020). Most PAs globally prevent land use change within their limits, providing vital habitat for wildlife in the face of expanding human footprint (Geldmann et al., 2013; Heino et al., 2015). PAs may provide refugia from climate change effects, though connectivity within PA networks is crucial for these refugia to be effective (Graham et al., 2019; Haight & Hammill, 2020; Stralberg et al., 2020). In addition to these broad-scale protections, PAs also provide opportunity for increased regulation of human behaviours when compared to unprotected lands, allowing for more effective conservation actions relating to human activity.

Particularly for species at risk, where small populations and increased sensitivity to anthropogenic factors can compound resulting in severe impacts, PAs may be even more crucial to long-term persistence (Deguise & Kerr, 2006; Geldmann et al., 2013; Watson et al., 2014). Understanding the status of these populations as a baseline is crucial to implementing conservation measures, especially in PAs where management actions may be easier to implement than under other land management regimes. While PAs may serve as refugia for at-risk species in decline, they may also serve as important source populations as species recover, allowing either natural or human-assisted dispersal into the broader landscape (Furlan et al., 2020; Heinrichs et al., 2018).

1.2.1 Dual mandate problem

Parks and PAs are often created with the goal of protecting wildlife and the habitats in which they live (Pringle, 2017; Watson et al., 2014), which has been broadly successful (Chen et al., 2022). However, many of these same areas are established and managed with an additional guiding principle to provide outdoor recreational opportunities to humans, leading to a dual mandate problem (Balmford et al., 2009; Reed & Merenlender, 2008). Engagement with nature

positively influences human well-being and is considered a cultural ecosystem service frequently provided by protected areas (Willis, 2015). PAs benefit humans through economic benefits from tourism, which also support conservation within these areas (Naidoo et al., 2019; Wittemyer et al., 2008). While these benefits are undeniable, with increasing growth of recreational activities in PAs worldwide, there may also be growing impacts on the wildlife these areas are mandated to protect (Balmford et al., 2015; Larson et al., 2016; Margules & Pressey, 2000; Pressey et al., 2015; Pringle, 2017).

With this dual mandate, PA management frequently involves a difficult balance between conservation actions and access for recreationists (Whittington et al., 2019). As such, linking science to decision making is a key factor in effective protected area management (Geldmann et al., 2013; Lemieux et al., 2018; Merkle et al., 2019; Pullin & Knight, 2009). Where decisions are made in the absence of strong evidence of impact, they may be subject to challenge from the public, whereas unrestricted use without monitoring may jeopardize conservation values. Scientists must consider the applicability of their research to informing management decisions in a conservation context, particularly under a framework of adaptive management (Tanner-McAllister et al., 2017). The iterative process of developing and testing hypotheses alongside management is crucial to adaptive management, ensuring recreation and conservation are compatible in PAs.

British Columbia, Canada is often considered one of the last areas of refuge for large mammals in North America, retaining the highest number of large mammal species in Canada, and the most species at risk (Shackleford et al., 2018; Westwood et al., 2019). The British Columbia protected areas system is the largest non-federal park system in North America and documented over 26 million visits (in person-days) over April 1, 2018 to March 31, 2019, with park usage steadily increasing in this province (B.C. Parks, 2020a). This immense and increasing use presents a large potential for negative impacts on wildlife within these areas, with current understanding of the interactions between human recreation and wildlife use of habitat being limited. Research gaps surrounding these interactions reduce science-informed management, which has the potential to degrade the protection afforded by PAs in British Columbia and elsewhere.

1.3 Tools to answer these questions

Past studies investigating relationships between recreation and wildlife have frequently lacked direct quantification of human use at ecologically relevant scales, limiting ability to effectively link animal responses to recreational impacts (Balmford et al., 2015; Buckley, 2009). Camera traps (CTs) provide an excellent source of such direct information, which can be collected with minimal effect on humans or wildlife. With the growing use of this technology for studying wildlife worldwide (Burton et al., 2015; Wearn & Glover-Kapfer, 2019), extension of camera deployments to directly quantify signals of human use of the same habitat as wildlife provides opportunity for further inference (Naidoo & Burton, 2020). Concerns over human privacy are increased where quantification of humans is a goal of CT surveys, though current methods allow for automated obscuring of individuals in CT images to help alleviate these concerns (Fennell et al., 2022; Sandbrook et al., 2021). Additionally, growing standardization of camera methodologies and reporting provides further options for the integration of data between spatially disjunct projects, building a stronger body of knowledge by “scaling up” localized survey efforts (Chen et al., 2022; Forrester et al., 2016; Meek et al., 2014; Steenweg et al., 2017).

CT data is commonly used to make inference about species habitat use in space or time (Steenweg et al., 2017; Naidoo & Burton, 2022). Beyond this, CTs also allow estimation of population parameters like density and abundance (Burgar et al., 2018b; Green et al., 2020). With increasing development of statistical techniques for estimating these parameters for naturally marked or unmarked species, CTs provide an exciting opportunity for minimally invasive monitoring of wildlife populations, which is a particular focus within many PAs (Chandler & Royle, 2013; Palencia et al., 2021; Zemanova, 2020). Using such tools allows PA and other land managers to better understand population status, evaluate population trajectories, and inform management actions, which are particularly crucial for conserving species at risk.

1.4 Thesis objectives

Capitalizing on the opportunities for ecological insight derived from this technology, I used an array of CTs deployed across one PA to first analyze relationships between human recreation and wildlife habitat use in space and time, and second to estimate the population density of an at-risk alpine ungulate species (mountain goat; *Oreamnos americanus*). By parsing

interactions between wildlife, habitat use, and human recreation at different spatial and temporal scales, I aimed to provide information to PA managers while also contributing to the greater field of knowledge around recreation ecology. I also integrated this CT survey with a spatially and temporally concurrent study which left visual markers on individual mountain goats to generate estimates of population density for this population of conservation concern, which is facing increasing recreational and other anthropogenic pressures (Balyx, 2022). This information serves to inform population management of mountain goats within the focal PA, while additionally proving the utility of CTs for density estimation. Density estimation using CTs has never before been used for this species, to my knowledge.

In my second chapter, I predicted that wildlife may differentially react to recreation across guilds based on ecological theory, where prey species might exploit human presence via a “predator shield”, while large carnivores would be repelled by humans under a “landscape of fear” framework, with mesocarnivores exhibiting a mixed response (Muhly et al., 2011; Oriol-Cotterill et al., 2015; Sarmiento & Berger, 2017). Further, I hypothesized that reactions to recreation may vary in space, time, or both for different species (Gaynor et al., 2018; Naidoo & Burton, 2020; Shamoon et al., 2018).

In my third chapter, I explored two statistical approaches integrating different CT data from marked and unmarked animals to generate mountain goat density estimates. This species is of key conservation concern within the study area, adding significant practical value to these estimates. Further, by directly comparing the precision of two analytical methods on the same dataset, I was able to test the efficacy of each approach, which may be beneficial for practitioners applying these methods in the future.

1.5 Study area description

Here, I focussed my study of these questions on Cathedral Provincial Park (hereafter Cathedral). Cathedral is in southern British Columbia, near the town of Keremeos, on unceded Syilx (Okanagan) Nation territory, particularly on the lands of the Smelqmix (Similkameen) Peoples. I gratefully and respectfully note that the Syilx Peoples have stewarded, existed upon, and inhabited these lands since time immemorial, including coexisting with the wildlife which

share these lands. While this thesis focusses on the currently recognized PA, it is important to note that this “protection” was established under a colonial framework that may have extinguished or inhibited the rights, traditions, and practices of the Syilx Peoples. Steps are currently taking place to enact Indigenous-led protection of the area encompassing and including Cathedral through the establishment of an Indigenous Protected and Conserved Area (IPCA; Lower Similkameen Indian Band, 2022).

Cathedral is a PA encompassing varied habitats across four predominant biogeoclimactic zones, containing numerous species, and providing extensive opportunities for non-motorized recreation (B.C. Parks, 2020). Cathedral covers an area of 330 km² and is bordered by the Snowy Protected Area to the east, areas of commercial forest harvest to the north and west, and the Pasayten Wilderness across the adjacent Canada-US border to the south. Cathedral is designated as a Class A Park, meaning park lands are “dedicated to the preservation of their natural environments for the inspiration, use and enjoyment of the public” (Park Act, 1996). The park receives over 4000 person-days of visitation by campers annually, although tracking of total visitor use is incomplete as non-camping visitors are not tracked (B.C. Parks, 2019). A small parcel of private land pre-dating the establishment of the park is centrally located at Quiniscoe lake in the core area and is operated as a backcountry lodge. Associated with this lodge is a private 4x4 access road paralleling Lakeview creek from the Ashnola river to Quiniscoe lake, which provides paid shuttle services for both lodge guests and campers.

Cathedral is located between the wet Coast Mountains and the far drier Okanagan Valley. There is a large elevational gradient within Cathedral, spanning from a low of 750 m along the park edge at the Ashnola River to over 2600 m at the top of Lakeview and Grimface mountains. Biogeoclimactic zones present within the park in order of predominance are Engelmann Spruce-Subalpine Fir (ESSF), Montane Spruce (MS), Interior Douglas Fir (IDF), and Interior Mountain-heather Alpine (IMA)(British Columbia Ministry of Forests, Lands, and Natural Resource Operations, 2020). Major tree species include ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) at lower elevations, mixed Engelmann spruce (*Picea engelmannii*) lodgepole pine (*Pinus contorta*) forest and higher elevation, and subalpine fir (*Abies lasiocarpa*), subalpine larch (*Larix lyallii*), and whitebark pine (*Pinus albicaulis*) at treeline. The park also

protects a high diversity of understory plants, various lichen species, and numerous wildflowers (M Fennell, personal observation, 2019).

Chapter 2: Using non-invasive methodology to assess the impacts of recreation on mammals in a protected area

2.1 Introduction

Under the founding doctrines of the “North American Model”, wildlife management and its related sciences have focused on consumptive interactions (hunting and fishing) with vertebrates (Hessami et al., 2021). The historical focus on hunting has meant that the science of ‘recreation ecology’ is relatively underserved, particularly in protected areas where hunting is often, yet not always prohibited (Buckley, 2013; Liddle, 1991; Marion et al., 2016; Monz et al., 2013; Kays et al., 2017). Understanding the impacts of non-consumptive recreation on various species is an important consideration for effective ecosystem management within and outside of PAs (Baas et al., 2020). outdoor recreation can affect wildlife and the ecosystems in which they live at local and range-wide scales, with impacts ranging from small-scale spatiotemporal shifts in habitat use to broad avoidance of entire areas due to high human use (Kays et al., 2017; Larson et al., 2019; Naidoo & Burton, 2020; Sarmiento & Berger, 2017).

Potential costs of these shifts for wildlife may include reductions in time available for foraging (Frey et al., 2017), reduced availability of quality habitat for forage or rearing young (Brown et al., 1999), increased risk of predation (Hamel & Côté, 2007), and chronic stress resulting in population-level effects (Clinchy et al., 2013). Nevertheless, little quantitative information about the relationships between recreation and individual species or entire animal communities is available to inform effective management, particularly where management actions may receive substantial public opposition (Pretty & Smith, 2004). A key factor in this lack of information is inadequate monitoring, in terms of biodiversity as well as visitor use across many protected areas (Balmford et al., 2015; Buckley, 2009). Examples of such actions that might receive opposition include trail closures, imposing quotas on human use, or temporal restrictions of protected area use (Whittington et al., 2019).

Acknowledging the importance of understanding these human-wildlife relationships and impacts across a broad range of species, I seek to investigate the question: *does non-consumptive*

human recreation displace medium and large-bodied mammals? Specifically, I investigated whether human recreation impacts the spatiotemporal habitat use of medium and large-bodied mammals in Cathedral Provincial Park (hereafter Cathedral). I limited this study to medium and large-bodied mammals, as the decreased detectability of smaller species on CTs set to capture multiple species decreases the utility of this method for making unbiased inference about smaller animals (Kolowski & Forrester, 2017). Cathedral presents a useful case study relevant to other PAs, as it faces common issues of increasing human recreation, limited quantification of human use, and poor understanding of the compounding effects of these factors on management efforts.

I considered two general hypotheses that could explain wildlife responses to recreation. Firstly, wildlife may perceive risk from humans, similar to the risk perceived by prey from an apex predator (Dröge et al., 2017; Suraci et al., 2019). One possible response to this perceived risk is that wildlife may avoid areas used by humans, as predicted by hypotheses such as that of a landscape of fear, where wildlife are displaced with increased human use of potential habitat (Bleicher & Rosenzweig, 2018; Oriol-Cotterill et al., 2015; Støen et al., 2015). This pattern may be shaped by previous direct persecution, as well as ongoing threat from close human encounters leading to negative outcomes ranging from chronic stress to reduced fecundity (Carter & Linnell, 2016; Støen et al., 2015). Another possible response to risk is a temporal shift in habitat use, where individual animals become more nocturnal or crepuscular to avoid overlap with daytime human activity (Gaynor et al., 2018; Oriol-Cotterill et al., 2015; Shamoon et al., 2018). Animals sharing space with people may be partitioning time generally, resulting in low overlap with times of greater human activity across all sites, or more selectively where risk is higher in space, such as avoiding on-trail sites during the day. Where generalist species may be able to simply move to other habitats due to low costs of spatial avoidance, spatial overlap of recreation with essential habitat for specialist species may require other methods for avoiding conflict. As such, specialist species may be more likely to shift daily activities rather than moving to unsuitable habitats (Sarmiento & Berger, 2017).

Alternatively, wildlife may perceive benefits from proximity to humans, such as provision of resources or safety from predators. For prey species, moderate levels of human activity may repel large carnivores, providing a form of refuge under the predator shield hypothesis (Muhly et al., 2011; Sarmiento & Berger, 2017). Resource provision facilitated by human presence may

take multiple forms ranging from direct nutrient supplementation by humans (i.e. feeding, access to garbage, salt) to indirect effects such as increasing small prey availability for mesocarnivores under the predator shield hypothesis, where small prey move in when predators are repelled by humans (Muhly et al., 2011). Some species, such as mountain goats, may become dependent on humans for nutritional supplementation in the form of salt from urine or grey water disposal (Slabach et al., 2015), leading to positive spatial correlation and potential conflict. This dependence may result in an attractive sink, where costs associated with the attraction, such as direct human conflict, result in a net-negative impact (Robinson et al., 2008). Species may also show no response to human recreation, suggesting little direct impact from the recreation experienced.

In the context of Cathedral, I predicted that larger carnivore species (black bear; *Ursus americanus*, cougar; *Puma concolor*, grey wolf; *Canis lupus*) will avoid areas of human recreation due to risk of persecution under a landscape of fear, either from hunting where permitted, or destruction by managers (i.e. conflict mitigation; Klees van Bommel et al., 2020), with temporal avoidance exhibited where these species co-occur spatially with humans to reduce conflict (Table 2.1). Alternatively, potential for co-occurrence of large carnivores with humans may be influenced by easier travel on linear features such as trails (Dickie et al., 2017; Tattersall et al., 2020; Whittington et al., 2011). I predicted that mesocarnivore species (Canada lynx; *Lynx canadensis*, coyote; *Canis latrans*) would exhibit limited spatial avoidance of humans, and stronger temporal avoidance to minimize risk from larger predators. I also predicted mesocarnivores would maximize benefit from increased small prey (such as snowshoe hare; *Lepus americanus*) in proximity to humans under the predator shield hypothesis. Further, I predicted that mesocarnivores would still minimize risk of persecution by humans under a landscape of fear, resulting in increased cathemeral or nocturnal activity patterns in response to human impact (Frey et al., 2020; Table 2.1). I additionally predicted that ungulate species such as moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and mountain goats (*Oreamnos americanus*) would exhibit a positive spatiotemporal response to humans to benefit from the “predator shield” effect, but that specialist ungulates such as mountain goats might display a temporal shift away from mid-day due to the high overlap between key habitat and human recreation in alpine and sub-alpine environments at that time (Table 2.1).

Table 2.1. Predicted response to human recreation, for commonly encountered medium and large-bodied mammal species in Cathedral Provincial Park. Predicted responses spatially and temporally are listed for each species, with + representing a positive response to human recreation, - a negative, and +/- a neutral response. Also included is the hypothesis supporting the prediction and key associated references.

Species	Predicted Response		Hypothesis	Sources
	Space	Time		
Black bear <i>Ursus americanus</i>	-	-	Landscape of fear	Baker & Leberg, 2018; Erb et al., 2012
Cougar <i>Puma concolor</i>	-	-	Landscape of fear	Baker & Leberg, 2018; Nickel et al., 2020; Reilly et al., 2017
Grey Wolf <i>Canis lupus</i>	-	-	Landscape of fear	Kojola et al., 2016; Lesmerises et al., 2012; Musiani et al., 2010
Canada lynx <i>Lynx canadensis</i>	+/-	-	Predator shield (indirect exploitation of prey)	Kolbe & Squires, 2007; Squires et al., 2019
Coyote <i>Canis latrans</i>	+/-	-	Predator shield (indirect exploitation of prey)	George & Crooks, 2006; Kays et al., 2017; Nickel et al., 2020
Moose <i>Alces alces</i>	+	+/-	Predator shield	Naidoo & Burton, 2020
Mountain goat <i>Oreamnos americanus</i>	+	-	Predator shield & Human resource exploitation	Festa-Bianchet & Côté, 2008; Richard & Côté, 2016; Sarmiento & Berger, 2017
Mule deer <i>Odocoileus hemionus</i>	+	+/-	Predator shield	George & Crooks, 2006; Parsons et al., 2016; Reilly et al., 2017

2.2 Methods

2.2.1 Camera trap survey

Camera traps (CTs) are a non-invasive sampling tool that capture images triggered by a combination of heat and movement as detected by an infrared sensor (Meek et al., 2014). CTs provide an excellent opportunity for widespread sampling due to their relatively low maintenance and long temporal sampling ability limited only by battery and SD card capacity. Beginning in July 2019 until September 2021, I deployed 45 Reconyx HP2X (Reconyx, Holmen USA) CTs throughout much of the 330 km² area of Cathedral Provincial Park. Camera sites were selected using a stratified random design, accounting for effective spatial coverage as well as feasibility of access by field teams. The random point tool in ESRI ArcMap 10.7 (ESRI, Redlands USA) was used to generate points within two strata: a) on-trail points on linear features identified as recreational trails (n=19) or the lodge access road (n=2), and b) off-trail points within a bounding polygon delineated by a distance of greater than 350 m from the above linear features, but within 2 km as limited by reasonable access on foot (n=24, Fig. 2.1). My scope of inference therefore does not extend throughout the entire park, as I did not sample the least accessible areas, which may be used differently by wildlife. I attempted to sample similar landscapes (as shown by the mean and range of each predictor, Table 2.2), on- and off-trail, accounting for features such as vegetation, habitat attributes, and microtopography, with the only differences being the trail itself and human presence. Random points were also constrained to be a minimum of 750 m away from all other points to increase spatial independence among samples. Field teams navigated to each random point using coordinates on handheld GPS units, and deployed the camera as close to the point as possible given logistical constraints encountered such as topography and dense brush. Cameras were set facing an opening or feature (e.g. game trail) expected to maximize detections of animals using that random location.

Cameras were placed on trees with a minimum diameter > 10 cm, or a large boulder in one case above the treeline, at a height of 0.3-1.0 m above the ground. Camera sets were dependent on site characteristics and distance from the focal feature to provide a consistent detection zone for target animals. Focal features included human trails, game trails, and gravel roads. Similar detectability at each camera was confirmed with the camera walk test feature by field personnel

moving through the detection zone at different distances and heights (e.g. standing, crawling). At on-trail sites, cameras were placed perpendicular to the trail wherever possible to standardize detection probability across locations. Cameras were affixed 3-6 m from focal features. Cameras were set to take one image per trigger, with no delay between successive images, and high trigger sensitivity. Once deployed, CTs were checked bi-monthly between June and October for those in the higher use core area or other accessible areas, and annually for those in remote areas with limited human access. CT operability was high, resulting in over 26,000 camera-days of data collected, and a mean of 578 trap nights per camera (median: 616, range: 91-819). The few cases of camera failure were the result of wildlife damage, hardware malfunction, human tampering, or heavy snowfall. Ethics approval for this study was granted under UBC Animal Care Certificate #A18-0234 and UBC Behavioural Research Ethics Certificate #H21-01424. Approval for research within Cathedral Provincial Park was granted by BC Parks.

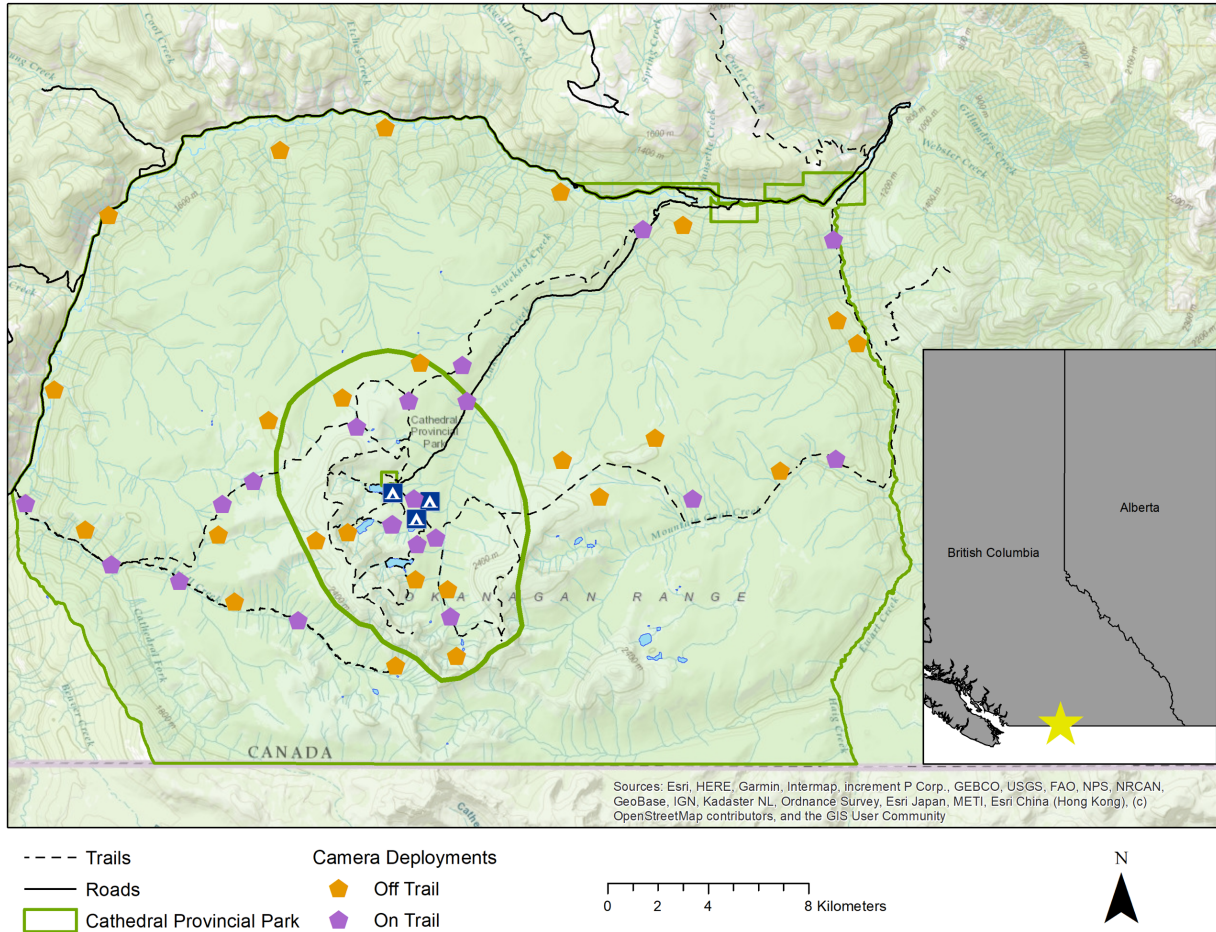


Figure 2.1. Map of camera trap deployments in Cathedral Provincial Park. The outer green polygon is the park boundary, while the inner is the park core area boundary where recreation is highest. Solid black lines are roads, and dashed lines are trails. Orange pentagons represent off-trail camera traps, and purple pentagons represent on-trail camera traps.

2.2.2 Data processing

Following collection of data from the field, images were blurred using an artificial intelligence (AI) algorithm to protect privacy by preventing identification of individual humans in CT images, while still allowing counting of human recreationists (Fennell et al., 2022). Images were then renamed and uploaded to a classification database in the WildCo lab at UBC (<https://wildlife.forestry.ubc.ca>). I additionally processed data through MegaDetector, a machine learning object detection model to identify humans, animals, vehicles, and blank images (Beery

et al., 2019; Microsoft, 2020). This step increases classification efficiency, particularly by allowing automated detection and filtering of blank and human images (Fennell et al., 2022).

The project team (undergraduate assistants, volunteers, and myself) classified animals in each image according to species, sex (where possible, e.g. mountain goats, deer, moose), and age class (adults, juveniles, and sub-adults where possible). We also tabulated a group count of the total number of distinguishable individuals within a sequence of related detections, with a sequence (hereafter called an independent event) defined as all images of the same species occurring within five minutes of the last image of that given species. Images of commonly confused species (lynx and bobcat) were each reviewed by myself a second time to ensure misclassification rates were minimized. Where there was uncertainty around the species within an image, an identification of “Unknown species” was assigned to the image.

Due to the immense number of human images captured, I used MegaDetector to automatically detect any images containing humans. Using a confidence threshold of 90% and manual visual confirmation, I classified all photos containing at least one human by the activity type. Human activity types include hiking, horseback riding, mountain biking, and motorized vehicles (the latter only at two sites on the private lodge access road).

2.2.3 Statistical analysis

I evaluated variation in wildlife habitat use using a Bayesian generalized linear mixed-modelling framework. Once images were classified, the number of independent detections per week at each site was summed for each of the focal species (Table 2.1), serving as an index of habitat use through space and time (Tattersall et al., 2020). I defined a week as the period Wednesday to Tuesday to overlap each weekend (including holidays) centrally within each weekly sample, as the weekend is typically the time of increased visitation of the park (Nix et al., 2018). Weekly counts permit evaluation of temporal trends within and across sites, and represents a balance between finer-scale temporal units, such as daily counts, that may be dominated by no detections (Naidoo & Burton, 2020), and coarse temporal units, such as months, that may not sufficiently capture the large seasonal changes in human recreation within Cathedral when access is concentrated in the snow-free periods between June and October. As

human use is limited outside of these months, I interpret results in relation to potential seasonal effects, which I attempted to account for via a continuous measure of vegetative productivity (NDVI).

The count of detections per site-week represents a combination of the number of individuals of a species using that site, and their movement patterns relative to the site. I assumed that animals moving through the camera detection zone were detected with high probability, although some individuals using the surrounding area may not have passed through the detection zone. Nevertheless, I was interested in the variation in detections as a signal of variation in site use, rather than sampling error as is assumed in some modelling frameworks (e.g. occupancy). I have no reason to expect unmodeled bias in detections and assumed they were proportional to site use. Further, occupancy may be more sensitive to variations in movement (including seasonally) than detection-based indices (Neilson et al., 2018).

To test the hypothesis that human recreation is a major determinant of wildlife habitat use, I derived camera trap indices of human use to provide a direct signal of recreational pressure. I calculated the number of independent human detection events, defined by a five-minute independence threshold, per active week at each camera site, as my primary predictor.

I also accounted for several environmental and sampling variables that could influence animal occurrence and detection at camera sites (Table 2.2). I included distance from camera sites to trails or roads (as an alternative but less direct measure of human disturbance, as well as a proxy for ease of animal travel), as well as elevation, and terrain ruggedness (vector ruggedness measure, Sappington et al., 2007) which may influence perceived or real predation risk, or ease of movement. I included percent open habitat within 500 m of the site, which may represent the level of concealment available to wildlife. I also included the Normalized Difference Vegetation Index (NDVI) as a proxy for vegetative productivity, which may influence forage, and by association prey availability for carnivores. NDVI also represents seasonal changes throughout the study area, which may influence habitat use unrelated to human influence. I calculated the distance to linear features with an exponential decay, such that $d = 1 - \exp(-1 \times \text{distance}/500)$, as I predicted that any influence of these linear features would quickly decrease with distance. NDVI was obtained from the MOD13Q1 product using the *MODISTools*

R package (Tuck et al., 2014), at a 16-day interval, within a 500 m buffer around each camera, resulting in consecutive weeks having the same value.

To parse the effects of recreation, environment, or a combination of these predictors I created three candidate models for each species and conducted model selection to discern the best supported set of predictors (Table 2.2). The three models for each species included:

- 1) Human detections and distance to linear features (the human model)
- 2) The environmental covariates described above without human detections or linear features (the environment model)
- 3) All predictors (the combined model)

I modelled the number of independent detections of each species per site-week as a negative binomial response and included the camera site as a random effect to account for potential nonindependence among repeated observations at the same site. All independent variables were standardized by subtracting the mean and dividing by one standard deviation to allow direct comparison of the direction and magnitude of effects on species use of habitat (Gelman, 2008). All predictor variables were assessed for collinearity (none were highly correlated, $|r| < 0.5$, Fig. S1; Dormann et al., 2013), and tested for multicollinearity using the Variance Inflation Factor (VIF; all had $VIF < 2$).

I conducted Leave One Out (LOO) cross validation and calculated the Leave One Out Information Criterion (LOOIC) for each candidate model (Vehtari et al., 2017). I selected the model with the lowest LOOIC as the most supported, with a threshold of eight $\Delta LOOIC$ signifying a large difference between models' predictive power (Sivula et al., 2022). All species other than wolves had the combined model as the most supported. Where the combined model was not the most supported, yet was within eight $\Delta LOOIC$ (wolves), I report the results of the combined model to allow comparison of the effects across species. For full model selection results including Bayesian R^2 values (Gelman et al., 2019) see Appendix A.3.

I ran models in R 4.1.0 (R Core Team, 2021), using the package *brms* (Bürkner, 2017). Models ran with default non-informative priors(uniform distribution, $-\infty$ to ∞) for 5000 iterations

on each of 4 chains with a thin rate of 1, following a burn-in of 2500 iterations. Model convergence was assessed through inspection of trace plots, and the Gelman-Rubin statistic ($R_{hat} < 1.1$; Gelman & Hill, 2007). All models were run with the full set of predictors (Table 2.2). I interpreted parameter estimates with Bayesian 95% credible intervals drawn from the posterior that does not include zero as signifying strong evidence of an effect of that variable in influencing species' use of sites, and Bayesian 80% credible intervals not overlapping zero as signifying weak evidence of an effect. I assessed effective sampling by calculating the number of effective samples against the number of total samples ($n_{eff}/N > 0.1$).

Table 2.2. Predictor variables used in Bayesian regression models of wildlife detections at 45 sites in Cathedral Provincial Park. I also provide the mean and range for each predictor at on and off-trail sites.

Variable	Description	Category	On-trail mean	Off-trail mean
Humans	# of human detection events per week at each camera site	Human use	12.13 (0-244)	0.049 (0-2)
Distance to linear ^a	Distance from camera to nearest trail or road (m) – with exponential decay	Human use	0	460 (117-1435)
Elevation ^b	Elevation at site (m)	Environmental	1821 (819-2261)	1675 (1080-2400)
VRM ^c	Site ruggedness within 90 m of the camera	Environmental	0.0018 (0.00004-0.013)	0.0028 (0.00007-0.019)
Open ₅₀₀ ^d	% of non-forested habitat within 500 m radius	Environmental	30 (4-99)	36 (1-99)
NDVI ^e	Normalized Difference Vegetation Index	Environmental	0.45 (0.0038 – 0.94)	0.46 (0.0036-0.98)

^a Trail features from BC Parks and OpenStreetMap

^b Field Measurement

^c Formula from Sappington et al. (2007)

^d <https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-inventory/data-management-and-access>

^e From MODIS MOD13Q1. <https://modis.gsfc.nasa.gov>

In addition to estimating the effects of recreation on wildlife at the weekly scale, I evaluated finer scale temporal interactions by analyzing changes in diel activity for each species. This method allows inference about fine scale temporal displacement of different species by analyzing the proportion of detections across a 24-hour period as calculated as radian-time (Frey et al., 2020; Ridout & Linkie, 2009; Rowcliffe et al., 2014). I calculated the coefficient of

overlap (Δ ; Ridout & Linkie, 2009; Schmid & Schmidt, 2006) between all independent detections of each species and humans, as well as the activity of each species at on- and off-trail sites. The coefficient of overlap quantifies the overlap of two activity patterns, and ranges from zero to one with values closer to one signifying higher overlap. Using the *overlap* R package (Meredith & Ridout, 2009), I generated 95% confidence intervals for each overlap estimate using 10,000 bootstraps, and present visual representations of each activity curve on a 24-hour axis. I used Δ_4 in cases with ≥ 50 observations in each group, and Δ_1 in cases with < 50 observations per group (Table 2.3) (Meredith & Ridout, 2009; Ridout & Linkie, 2009). To further quantify the difference between activity for on and off-trail sites, as well as between each species and humans, I generated a kernel density estimate from each activity distribution, using 10,000 bootstrap samples from the data for each, using the *activity* R package (Rowcliffe, 2014). I then conducted a Wald test to compare the difference between these kernel density estimates, testing the null hypothesis of no difference between groups, and with p values less than 0.05 representing statistically significant differences between activity patterns.

2.3 Results

Our most frequently detected wildlife species of interest was mule deer ($n=2186$), followed by coyote ($n=593$) and lynx ($n=419$) (Table 2.3). I recorded 21,646 human detections, as well as 154 domestic dog detections (generally alongside humans), despite dogs being banned in the park. For full records of species detected, see Appendix A.2.

Table 2.3. Number of independent detection events, as well as on- and off-trail detections and the ratio of on- to off-trail detections for each species of interest in Cathedral Provincial Park. Off-trail detections include the study team.

Species	Total detections	On-trail detections	Off-trail detections	On-trail:Off-trail
Humans	21 646	21 543	103	209.16
Mule deer	2 186	1 333	853	1.56
Coyote	593	510	83	6.14
Lynx	419	401	18	22.28
Mountain goat	333	257	76	3.38
Black bear	171	94	77	1.22
Moose	128	58	70	0.83
Wolf	78	66	12	5.50
Cougar	38	34	4	8.50

2.3.1 Spatial Effect

I found strong evidence that human recreation affected habitat use by mountain goats and mule deer, with a positive relationship between the number of human detections per site-week and the number of detections of these species (Fig. 2.2, Fig. 2.3). Coyotes were the only species where recreation had a strong negative effect on habitat use (Fig. 2.2, Fig. 2.3). I saw weak evidence that black bears had more detections where human use was higher (Fig. 2.2). There was weak evidence of more lynx detections where human use was higher, while recreation was not seen to influence moose, cougar, and wolf habitat use (Fig. 2.2). Distance to linear features was significantly negatively correlated for detections of all carnivore species, suggesting that predators are more frequently detected closer to recreational features such as roads or trails, which may increase the necessity of temporal partitioning to avoid conflict with humans (Fig. 2.3).

In terms of species associations with environmental features, wolves and bears were detected more often at lower elevations, while goats and lynx were detected more often at higher elevations (Fig. 2.3). The effect of terrain ruggedness was significant and positive only for explaining mountain goat habitat use, and the percent open habitat around a camera was significantly negatively correlated with cougar occurrence (Fig. 2.3). NDVI was significantly

positively correlated with all species other than moose (Fig. 2.3). Full model results for each species are available in Appendices A.4-A.11.

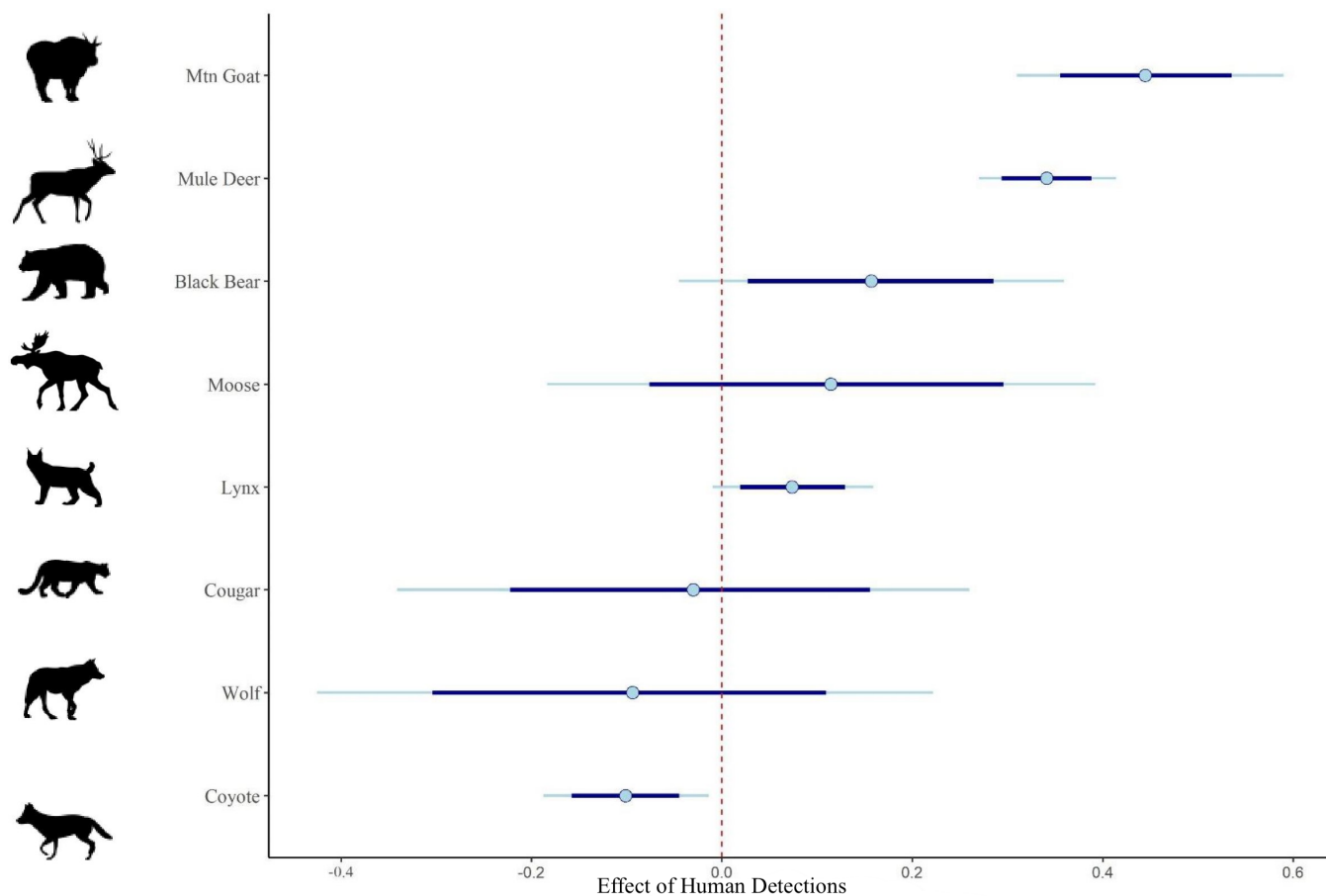


Figure 2.2. Effect of human detections on species habitat use. Shown are parameter estimates and credible intervals from Bayesian GLMMs at sampling sites at a weekly scale (see Table 2.2 for the full set of parameters included in models). Thick lines represent 80% credible intervals, and thin lines represent 95% credible intervals.

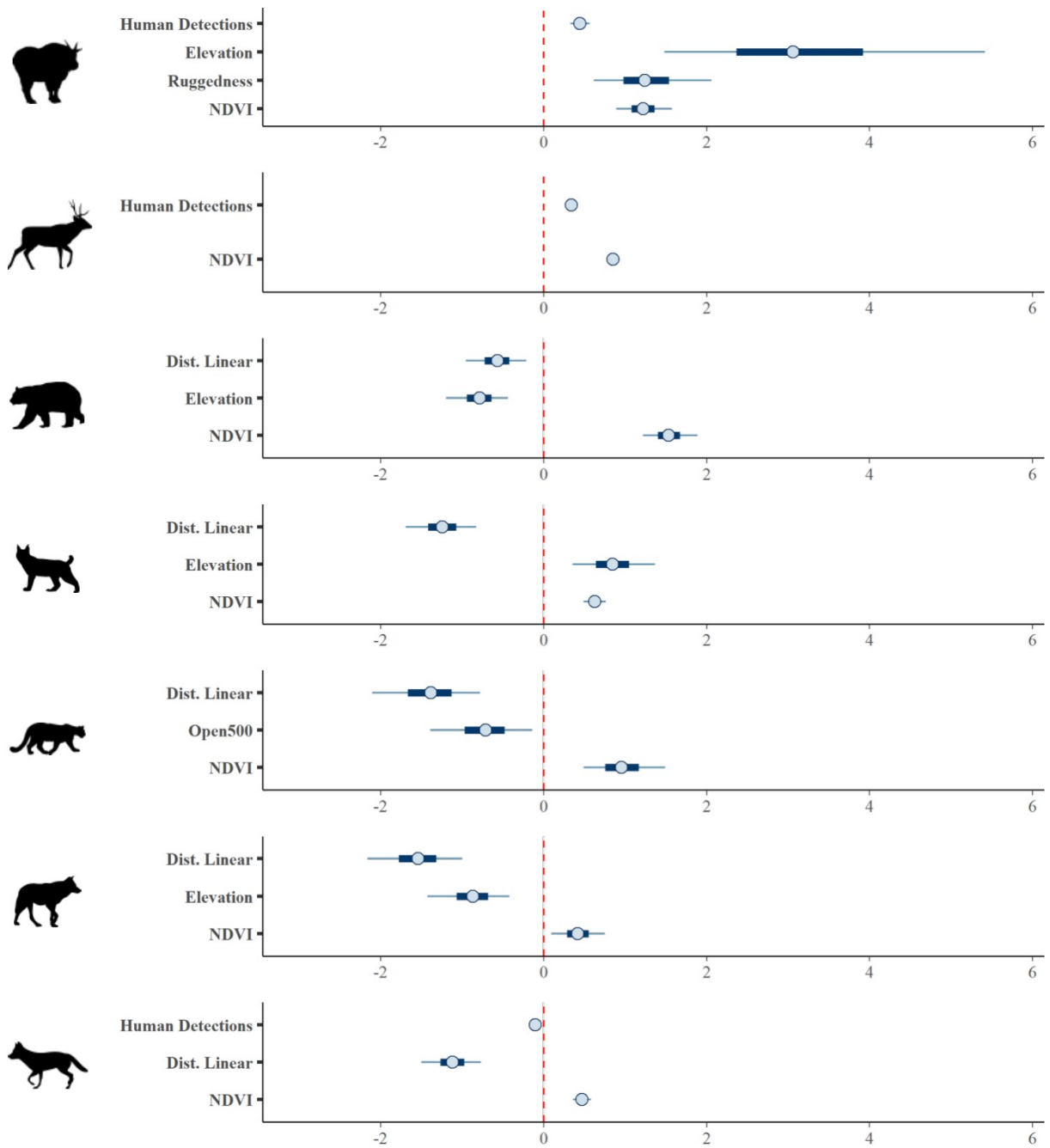


Figure 2.3. Parameter estimates for predictors strong predictors of wildlife habitat use. Shown are parameter estimates from Bayesian GLMMs. Strong predictors are defined as 95% credible interval not overlapping zero. Species are (top to bottom): mountain goats, mule deer, black bears, Canada lynx, cougars, wolves, and coyotes. Thick lines represent 80% credible intervals, and thin lines represent 95% credible intervals. Credible intervals are not visible for some estimates at this scale. All predictors were standardized to have a mean of 0 and standard deviation of 1. Moose are not shown due to no significant predictors.

2.3.2 Temporal Partitioning

All species showed relatively low temporal overlap with humans in their diel activity patterns, supporting my prediction of temporal partitioning across large carnivores and mesocarnivores, though ungulate activity was contrary to my prediction of higher temporal overlap with people (Fig. 2.4, Table 2.4). Cougar activity patterns were not significantly different from humans, though this was potentially due to few cougar detections (Fig. 2.4, Table 2.4). Most predator species were more nocturnal than humans, except for black bears which, like people, exhibited a diurnal activity pattern. Ungulates were generally more crepuscular than predators or humans. Mountain goats and wolves were the only two species with significant differences in their diel activity patterns between on and off-trail sites (Fig. 2.5, Table 2.4). Mountain goat activity occurred earlier in the day at on-trail sites in comparison to off-trail sites (Wald test, $W=6.85$, $d.f.=1$, $p=0.0089$), and wolves used on-trail sites significantly more at night than during the day (Wald test, $W=4.36$, $d.f.=1$, $p=0.037$).

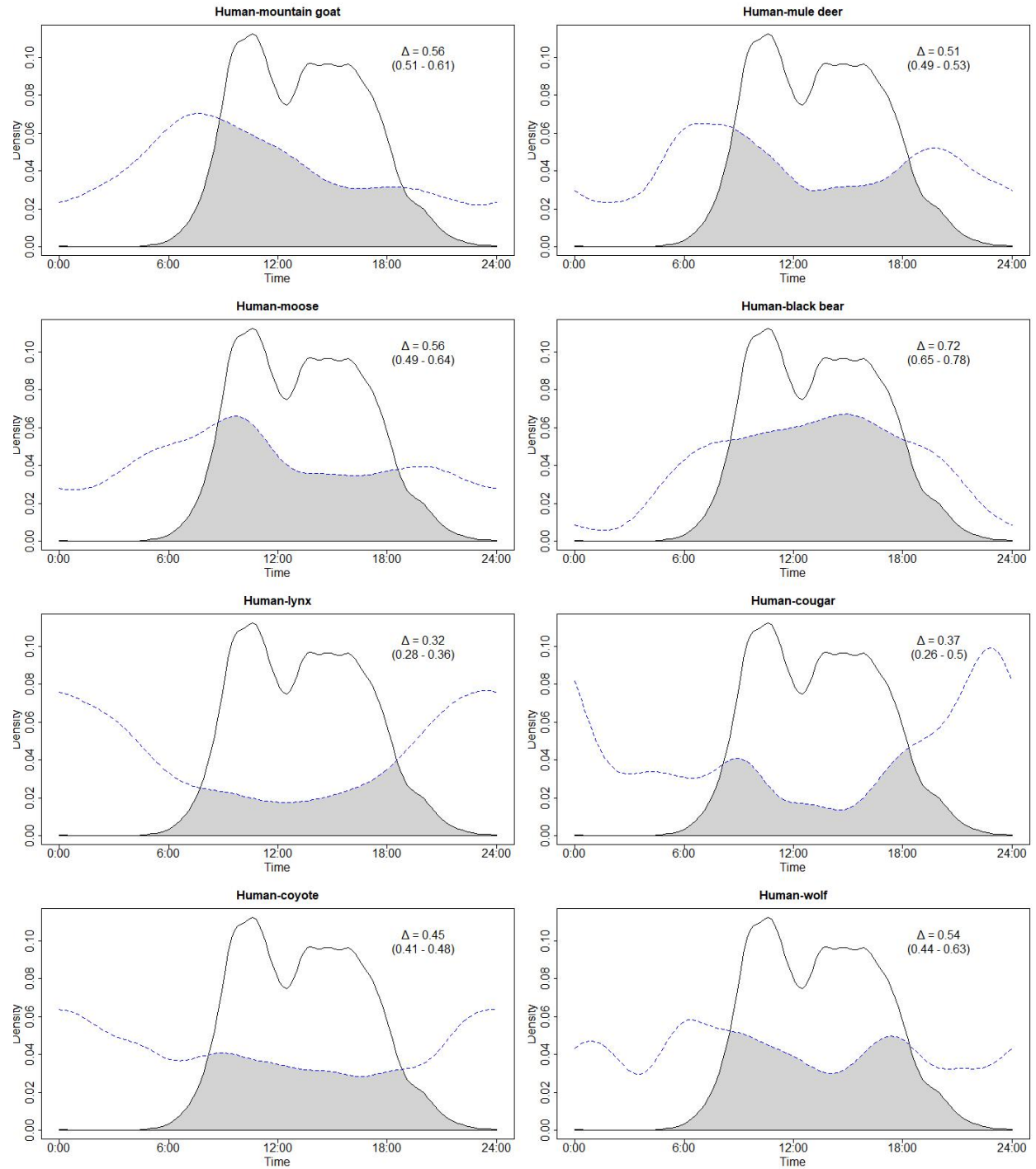


Figure 2.4. Human (solid line) and animal (dashed line) comparisons of activity for eight focal species, with overlap coefficient (Δ) estimates (generated with 10 000 bootstraps).

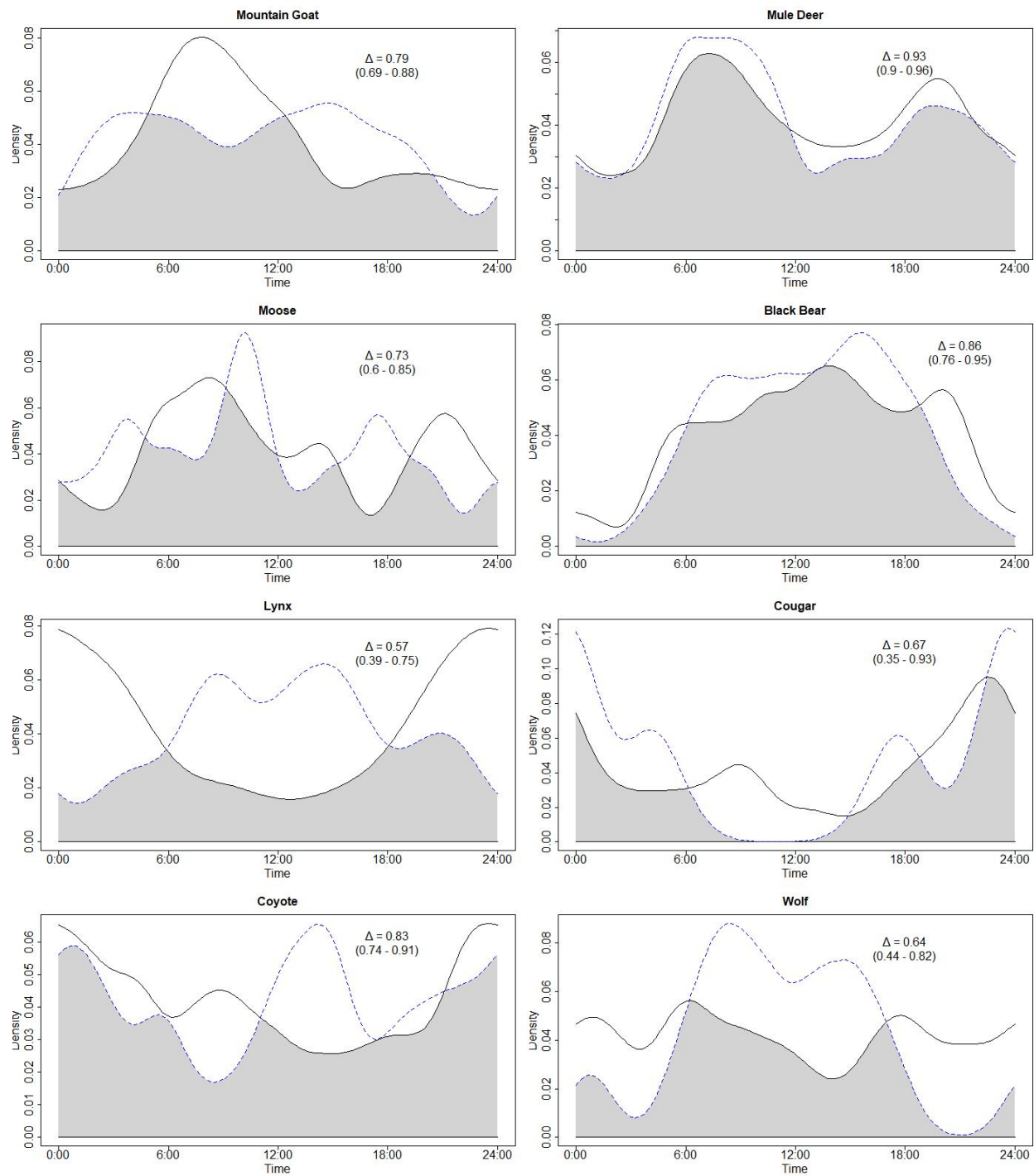


Figure 2.5. Comparisons of diel activity for each species between camera trap sites on (solid line) vs. off (dashed line) of recreation trails, with overlap coefficient (Δ) estimates (generated with 10 000 bootstraps). Note the varied Y-axis scale between each plot, which represents the kernel density estimate.

Table 2.4. Overlap coefficient (with 95% confidence interval as generated by 10,000 bootstrap samples), Wald statistic, and Wald test *p*-value for activity patterns of single species on- versus off-trail and human versus each species. Statistically significant differences between activity patterns are denoted in bold.

Species	On vs. Off-trail			Overlap with Humans		
	Δ (95% CI)	W	<i>p</i>	Δ (95% CI)	W	<i>p</i>
Mountain goat	0.79 (0.69-0.88)	6.85	0.0089	0.56 (0.51-0.61)	22.09	<0.0001
Mule deer	0.93 (0.90-0.96)	1.15	0.2842	0.51 (0.49-0.53)	109.05	<0.0001
Moose	0.73 (0.60-0.85)	0.93	0.3360	0.56 (0.49-0.64)	8.71	0.0032
Black bear	0.86 (0.76-0.95)	1.01	0.3155	0.72 (0.65-0.78)	19.99	<0.0001
Lynx	0.57 (0.39-0.75)	0.81	0.3685	0.32 (0.28-0.36)	23.19	<0.0001
Cougar	0.67 (0.35-0.93)	0.41	0.5202	0.37 (0.26-0.50)	0.24	0.6218
Coyote	0.83 (0.74-0.91)	<0.01	0.9808	0.45 (0.41-0.48)	31.03	<0.0001
Wolf	0.64 (0.44-0.82)	4.36	0.0368	0.54 (0.44-0.63)	14.55	0.0001

2.4 Discussion

Human recreation can lead to changes in species use of habitat; however, these shifts in space and time are highly variable across species. This study found that only coyotes displayed habitat use patterns consistent with strong spatial displacement from recreation. For smaller ungulate species, my prediction of positive spatiotemporal correlation with human recreation was supported, providing partial evidence for the predator shield hypothesis, though my expectation of predators avoiding areas of higher human use was not strongly supported (Muhly et al., 2011). My prediction of either displacement or neutral temporal responses for mountain goats and mule deer respectively was also supported, as behavioural plasticity may allow these species to spatially co-occur with human recreation as suggested by the positive correlation between co-occurrence with humans at the weekly scale (George & Crooks, 2006).

Mountain goats significantly shifted diel activity overall when compared to recreation, while being one of two species to significantly shift activity patterns between on and off-trail sites, suggesting either a high level of plasticity, a high level of disturbance, or a balance between the two. A potential mechanism for this shift may be the balancing of negative effects from direct human interaction during the day with positive nutritional benefits of human-derived salt sources (such as urine, grey water, or sweaty clothing) at night (Kroesen et al., 2020; Sarmiento & Berger, 2017). Mule deer exhibited minimal changes in activity pattern between on and off-trail sites, and exhibited crepuscular activity patterns, which follows the findings of Reilly et al. (2017). Moose detections were not significantly correlated with human recreation spatially, though this species was infrequently detected in Cathedral, potentially resulting in a weak signal. Moose exhibited a significant difference in overall activity patterns when compared to humans, with moose activity peaking earlier in the morning.

Large predator species exhibited largely neutral spatiotemporal relationships with human recreation, contrasting my prediction of negative response. Black bears were weakly positively correlated with the number of weekly human detections, suggesting that this species coexists with humans in space, contrary to my predictions under the predator shield hypothesis, though use of habitat near humans may be influenced by easier travel by predators on linear features (Dickie et al., 2017). Temporal results again varied by species for carnivores, with black bears

and cougars showing no significant difference in activity pattern at on and off-trail sites, while wolves significantly increased their use of on-trail sites at night suggesting temporal avoidance of humans. Cougar activity patterns were non-significantly different from human activity patterns, despite trending heavily towards increased nocturnal activity, while wolves were significantly more active at night, and black bears were significantly more active during cathemeral periods than people.

Mesopredator spatiotemporal responses to human recreation were mixed, with lynx habitat use being weakly positively correlated with human activity as predicted, while coyotes were strongly negatively correlated contrary to my prediction of exploitation of the predator shield to maximize prey. Lynx and coyotes each had significantly different diel activity patterns than humans, with both being more active at night than humans, as shown by prior studies (Reilly et al., 2017; Nickel et al., 2020). While both mesopredator species had non-significant differences in on- and off-trail activity patterns, lynx did trend towards more nocturnal use of trails, similar to wolves. In areas of co-occurrence with wolves, prior studies have shown increased cathemeral (irregular throughout day and night) activity by coyotes, potentially due to competition or intraguild predation by wolves (Frey et al., 2020; Shores et al., 2019). While I did not statistically test this potential interaction, it may explain the observed difference in on and off-trail diel patterns between these canid species. Additionally, I did not directly investigate patterns of occurrence for predominant mesocarnivore prey (squirrels and hares) due to their small body size resulting in inconsistent detectability on CTs. Investigation of these smaller wildlife and their influence on mesocarnivore habitat use is an exciting direction for further study in the future.

Trends in the increased use of trails at night by mountain goats and wolves suggests that these linear features may play an important role as travel corridors, while potentially facilitating resource acquisition. For mountain goats, trails may allow faster travel to natural mineral licks, while also providing a source of salt themselves due to trailside urination by humans, as well as leading to campgrounds that may serve as artificial mineral licks due to concentrated human use (Kroesen et al., 2020; Sarmiento & Berger, 2017). Predators, particularly wolves, use linear features to increase hunting efficiency in other environments (Dickie et al., 2017). While wolves may not be able to use these corridors during the daylight hours when they are dominated by

human recreationists, trails may be directly resulting in increased exploitation of prey species by these predators at night, resulting in indirect negative effects of recreation infrastructure on prey. This effect is further supported by the negative correlation between detections of all predator species and distance to linear features, suggesting that the five carnivore species are frequently closer to roads or trails. The possibility of predators preferentially selecting to travel on trails, yet less than they would in the absence of humans is an interesting avenue for future research not directly investigated here.

Expansion of the “human niche” in terms of habitat use in space and time results in species-specific responses by wildlife. Although I did not specifically investigate the consequences of observed behavioural responses for individual fitness or population demography, prior research has shown effects ranging from decreased time for foraging (Coppes et al., 2017) or hunting (Musiani et al., 2010), to reduced fecundity (Phillips & Alldredge, 2000), to wholesale abandonment of territory (Pauli et al., 2017). Despite the potential for positive impacts to ungulate survival under the predator shield hypothesis, human alteration of natural food webs via recreation is contrary to the mandate of many PAs to preserve and protect natural environments. The plasticity of animal responses to human disturbance does provide for a landscape of coexistence, though thresholds of sensitivity may vary by species (Kronfeld-Schor & Dayan, 2003; Oriol-Cotterill et al., 2015). Sensitive species might be more readily lost from landscapes facing human pressures, presenting a form of ecological filtering of the wildlife community. Examples of species particularly sensitive to disturbance which have historically been present in this study area, yet are rarely detected and potentially extirpated include wolverine (*Gulo gulo*; Stewart et al., 2016) and grizzly bear (*Ursus arctos*; Sarmento & Berger, 2017).

While understanding animal responses to recreation is interesting from a theoretical standpoint, this knowledge is critical to informing effective management of human recreation in and outside of protected areas. Protected areas in particular frequently face a dual mandate dilemma, where balancing ecological integrity with quality recreational opportunities requires a thorough understanding of the potential impacts of different management decisions. Where these impacts may be on recreationists through limiting access, it can result in significant upset and disagreement, especially when based upon limited information or data (Gundersen et al., 2015).

While human enjoyment is crucial to the mandate of many PAs, impacts on animals may be even more significant, leading to negative effects for individuals and populations (Baker & Leberg, 2018; Larson et al., 2016; Larson et al., 2019). To establish an effective compromise between these dual mandates, optimizing outcomes for humans as well as animals, direct quantification and understanding of these impacts is essential. Here I have shown that recreation may not be having strong impacts on wildlife at the levels measured (i.e. spatial displacement), though I have provided evidence of disruption to natural dynamics (i.e. diel patterns).

PAs assist in maintaining mammal diversity (Chen et al., 2022), reduce population declines (Geldmann et al., 2013), and are potential refugia from climate change (Haight & Hammill, 2020). Using the best available science to inform management decisions serves to ensure that PAs will continue to provide these benefits to wildlife in the future, while also ensuring opportunities for human enjoyment of these landscapes. Translating research into effective management requires collaboration between researchers and practitioners, providing research outputs linked to management questions in a readily available and interpretable (Lemieux et al., 2018; Merkle et al., 2019). Here I provide insight on the relationships between recreation and a range of wildlife species within one PA, providing results that may be used by park managers to inform management actions. These results are specific to the levels of recreation tested, which may serve as a baseline in the face of increased recreation within the same area, or as a comparison for a similar system facing higher levels of recreation currently. Further, these analyses are based upon habitat use by each species, but do not account for factors such as population abundance or demography, which are equally important to consider when informing effective management at the landscape scale, as is commonplace in PAs. Additional studies at finer scales of habitat use may additionally inform our understanding of potential anthropogenic impacts, as is currently taking place within Cathedral in relation to mountain goats, recreation, and helicopters (Balyx, 2022).

It is important to note that these findings should be considered with potential caveats. While I did show statistically significant relationships between recreation and habitat use spatially and temporally for a number of species, I do not quantify what the physiological or population effects of these responses may be. Prior research has suggested impacts from perceived risk (whether from predators or humans) may include reduced fecundity or decreased

body condition, leading to negative effects individually and for the population (Clinchy et al., 2013; Creel et al., 2009; Phillips & Alldredge, 2000). Additionally, while I report results showing a significant recreational effect, I do so via a correlational framework that does not prove causation of these patterns. Further, due to logistical constraints, I did not explore these relationships at distances beyond 1500 m from roads or trails, which may have provided insight as to responses in areas with even further reduced potential influence of recreation. Alongside this consideration, many species may make seasonal movements throughout the study area naturally, which I did not directly account for in my modelling framework, although exploration of seasonal effects may be an exciting future direction for research (Ager et al., 2003; Aikens et al., 2017; Merkle et al., 2016). I was unable to fully separate the effect of the presence of a trail from human use of that trail, though I was able to observe varied levels of human presence on different trails throughout the course of the study, including periods with very limited or no human use. In light of potential preference for trails by many species, I suggest that future research directly account for this factor, which may only be possible through experimental closure of certain areas for a duration of time.

Opportunities for further study on this topic are broad, particularly with increasing tools becoming available for monitoring animals as well as recreationists where they co-occur. Collation of CT data across multiple independent projects may allow the “scaling up” of inference, eliminating potential bias related to individual landscapes or species assemblages (Steenweg et al., 2017). Fine scale monitoring of animal movement is becoming increasingly accessible due to improvements in technology (Kays et al., 2022), while direct monitoring of human movement is also facilitated by the widespread use of GPS technology (Marion et al., 2020). The potential for inference on animal responses to recreationists at very-fine spatial and temporal scales with concurrent movement monitoring provides an exciting opportunity to explore this topic further. Additional sources of recreational data are also being trialed to investigate similar questions, including the use of publicly available social media to produce indices of human use and spatial maps of recreational intensity (Kupfer et al., 2021). Direct analysis of the biophysical impacts of recreation on wildlife via stress hormones may also allow direct quantification of responses not measured by methods such as the CTs used in this study (Clinchy et al., 2013; Creel et al., 2009).

2.5 Management Implications

I directly quantified recreational use in one relatively small and isolated PA representing a heavily impacted yet rare ecosystem in the province, and investigated the potential for impacts of recreation on eight mammal species. While I observed significant negative spatiotemporal displacement at the weekly scale only for coyotes, my results do suggest that human recreation may result in temporal displacement of predators and prey from on-trail areas, with multiple species becoming more active at night in response to recreation. Consideration of inference at further scales, both finer and coarser, may provide further insight as to these relationships. This information may inform improved management in Cathedral Provincial Park, but also serves to expand the volume of knowledge surrounding recreation ecology broadly. Based on these results, I suggest that recreation management strategies in Cathedral as well as other areas consider the importance of allowing adequate temporal availability of habitat free of people for wildlife, potentially via restrictions on the timing of daily recreational use. Such restrictions may provide a balance of the dual mandates mentioned above, where the daytime hours provide for extensive recreational opportunities, while the period from dusk until dawn allows wildlife use of habitat without human stressors (Whittington et al., 2019). Taking this a step further, the expansion of these “wildlife hours” pre-dusk and post-dawn, even by a few hours, may result in a significant increase in the temporal niche breadth available to the wildlife community. Additionally, I suggest carefully considering potential impacts of linear features, such as trails, in shaping the use of habitat by wildlife. While I did not directly explore interspecies relationships due to trail infrastructure, the increased detection of all five predator species on linear features suggests that increasing the density of these features may result in increased predation risk for ungulates (Dickie et al., 2017). Finally, I suggest that managers continue to monitor wildlife responses to recreation in order to inform targets and thresholds of impact upon which to build effective management plans for PAs around the province.

Chapter 3: Density estimation of a partially marked mountain goat (*Oreamnos americanus*) population of conservation concern

3.1 Introduction

Knowledge of population status is crucial for informing effective management of wildlife species, providing information that can be used as a baseline against which to assess changes in population status over time, allowing more effective prioritisation of conservation actions for species of concern. Species at risk often occur in small populations, prone to an ‘extinction vortex’, i.e., a compounding threat of extinction from both abiotic and biotic processes (Gilpin and Soulé 1986). Potential threats range from inbreeding depression due to limited genetic diversity, to disease outbreaks, to stochastic abiotic events such as avalanches or wildfires. These threats can be compounded by anthropogenic pressures, whether they be from development, climate change, or non-consumptive recreation (Dirzo et al., 2014; Newbold et al., 2015; Young et al., 2016). Beyond conservation of species at risk, knowledge of population status is needed to inform decisions such as setting sustainable harvest levels of game species or evaluating the functioning of metapopulation dynamics (e.g. source populations; Robinson et al., 2008) across a protected area network (Morris & Doak, 2002).

To understand population trajectory, knowledge of population abundance (N) is needed (Williams et al., 2002). Evaluating changes in abundance, or calculating the population growth rate (λ), are common ways to assess gains or losses to a population over time. While this information is useful for comparing changes within the same area, ecologists often wish to assess status between different populations (Kane et al., 2015; Morin et al., 2022). Evaluating population density ($D = N/area$) is an approach that allows the comparison of spatially disparate populations by standardizing to include sampling area (animals per area) providing a comparable metric across populations (Borchers & Efford, 2008; Efford, 2004). Challenges associated with acquiring data to calculate such metrics include survey cost, technical difficulty, and the selection of appropriate analytical methods (Green et al., 2020).

Mountain goats (*Oreamnos americanus*) are an alpine dwelling ungulate species, unique due to their ability to climb near-vertical rock faces, hardiness against harsh alpine climates, and proclivity for procuring minerals at natural or human-sourced licks from urine or grey water (Festa-Bianchet et al., 2008). Globally, mountain goat populations are considered secure, yet in British Columbia this species is on the provincial blue list signifying vulnerability to extirpation or extinction (B.C. Ministry of Environment, 2010). The conservation of mountain goats is particularly crucial in British Columbia, as the province contains the majority of goats in the world (B.C. Ministry of Environment, 2010). Within British Columbia, mountain goat populations in the Okanagan region are particularly vulnerable due to small population sizes (B.C. Conservation Data Centre, 1994). The most recent publicly available population estimates for the entirety of the Okanagan region are 200-300 individuals, with a declining trend (B.C. Ministry of Environment, 2010; Gyug, 2006). Threats to mountain goats include historical overharvest, warming climate resulting in reduced habitat, and negative impacts from motorized and non-motorized recreation (B.C. Ministry of Environment, 2010; Festa-Bianchet et al., 2008; Richard & Côté, 2016; Sarmiento & Berger, 2017).

Additionally, fragmentation of habitats leading to decreased connectivity between populations presents a high risk of inbreeding depression and associated negative effects for populations in the South Okanagan and adjacent regions (Parks et al., 2015). Mountain goats are a species of key conservation concern in Cathedral Provincial Park (hereafter Cathedral), particularly in the face of increasing human use leading to potential for human-goat conflict around anthropogenically sourced salt licks in campgrounds and on trails (K. Safford, BC Parks Conservation Specialist, *personal communication*, June 2019). The last recorded aerial survey (2006) of this population recorded no goats in the Cathedral population, with a past maximum of 38 individuals in 1953 (Gyug, 2006), while recent minimum number alive surveys estimated a population size of 24 to 28 individuals (K Safford, BC Parks Conservation Specialist, *personal communication*, July 2022).

Common methods for estimating mountain goat population sizes in British Columbia are based on aerial transect surveys of known populations via helicopter, with occasional additional information from ground-based surveys included (B.C. Ministry of Environment, 2010; Poole et al., 2011). While this method may produce reliable population estimates, it is infrequently

implemented due to high costs, with many populations facing decade or longer gaps between successive surveys (B.C. Ministry of Environment, 2010). An additional downside of aerial survey methods is the potential for negative effects of helicopters on the animals being surveyed, which has been shown for mountain goats (Balyx, 2022; Festa-Bianchet & Côté, 2008). Here I evaluate the extent to which camera traps (CTs) offer a lower-cost, minimally invasive alternative for surveying mountain goat populations.

With the increasing deployment of CTs across the world (Burton et al., 2015; Steenweg et al., 2017), spatial and temporal overlap with studies using other sampling tools presents opportunities to combine data from multiple sources for ecological inference. Many CT studies are focussed on multi-species investigation, though data are easily subset to provide information on single species that may be used for purposes such as estimating density. In Cathedral, an opportunity to capitalize on two co-occurring studies was presented when a number of mountain goats were captured and collared for a separate telemetry-based study of human-goat interactions and goat ecology (Balyx, 2022), while this multi-species CT study was also occurring (see Chapter 2). The marking process facilitated by the collar study provided visually distinct identifiers in the form of numbered cattle tags attached to each collar, which are generally distinguishable in CT images (Fig 3.1).

Capture-recapture based methods of population estimation have become increasingly prevalent, building from models incorporating imperfect sightability of individuals with natural or artificial (human applied) marks, to more complex models focused on populations without identifiable individuals (Becker et al., 2022, Royle et al., 2014; Tourani, 2022). Data used for capture-recapture estimates can be acquired from genetic, live-trap, or CT surveys (Efford, 2004; Royle et al., 2014). Building on capture-recapture models, spatially explicit capture-recapture (SCR) estimates incorporate spatial information about a distinct sampling area and the explicit location of recaptures within it, allowing more precise estimation of population density (Borchers & Efford, 2008; Efford, 2004; Royle et al., 2014).

Individual identifiability is often a crucial aspect of SCR modelling, where natural marks such as spots or unique pelage patterns may allow identification, or humans may apply artificial marks to animals (e.g. collars, tags, bands) (Royle et al., 2014). SCR models use information

about detections of marked individuals to populate an area of inference known as a state-space, defined by traps in space with a buffer around them encompassing all possible home ranges. Detection data are used to estimate activity centers for each identifiable individual, as well as for undetected individuals based on their detections at traps within the state-space and assumptions about detectability and movement (Efford, 2004).

Detections of unmarked or unidentifiable individuals are not incorporated in SCR modelling approaches, resulting in data being discarded despite its potential utility. Such data may be particularly important in studies with few marked individuals relative to unmarked. Spatial mark-resight (SMR) models are an extension of SCR models, and allow for the use of information about a marked subset of individuals to parameterize detection probabilities of unmarked individuals (Chandler & Royle, 2013; Jimenez et al., 2019; Sollmann et al., 2013; Whittington et al., 2018). Further, SMR models integrate detections of marked individuals that cannot be accurately identified, as can occur with CT images at night or with fast (blurry) movements (Augustine et al., 2018; Jimenez et al., 2019; Murphy et al., 2019). Both SCR and SMR approaches to density estimation have been increasingly fitted with CT data, providing crucial population information at lower costs or with less impact than alternative methods (Augustine et al., 2018; Bugar et al., 2018b; Rich et al., 2014; Sun et al., 2017).

By using CTs to resight marked individuals, as well as to record detections of unmarked individuals, I sought to provide an accurate estimate of mountain goat population density in Cathedral using both SCR and SMR approaches. I predicted that SCR median density estimates would be lower yet more precise due to being fitted with data only from individually identifiable animals, while SMR estimates would be higher with lower precision due to the inclusion of unmarked and unidentifiable goats. While this study will provide important and relevant local knowledge to park managers on a population of conservation concern for the first time in over a decade, it will also serve as an example of the first known application of CT-based density estimation for mountain goats, while additionally providing a direct comparison between two density estimation methods.

3.2 Methods

3.2.1 Camera trap survey

I used 17 camera traps within the known summer range of mountain goats, as determined by GPS telemetry data on 11 goats from July 2019 to August 2021. I constrained sampling to summer because telemetry data showed that goats use different areas of the park in different seasons, with habitat used in seasons other than summer being poorly sampled by these CTs (Balyx, 2022). CTs from the broader multispecies survey (Chapter 2) excluded from this analysis did not detect any goats across the three years, outside of one detection (a likely dispersal event by a young male goat), further validating the telemetry-based home range estimates. Additionally, given this knowledge around seasonal movement and the model assumption of population closure, I constrained the number of cameras to reduce the likelihood of violating this assumption. Balyx (2022) deployed GPS collars on 12 goats beginning in June 2019, allowing individual identifications in CT images based on number tags. All goats collared were adults, ranging in age from 4-8 years. There were four males collared, and eight females.

The 17 cameras consisted of 10 from the broader multispecies survey (Chapter 2) as well as 7 set to target goat summer range. As CTs were removed as the study progressed, the number used decreased from 17 in 2019, to 15 in 2020, to 10 in 2021 (Fig. 3.2, Table 3.1). CTs were set both on and off recreational trails, and images were classified as described in Chapter 2, except using a coarser thirty-minute lag-threshold to establish independent events. Images of mountain goats were classified for sex (using features such as face shape, horn shape and size, size of supraoccipital glands), age, mark status (collared/uncollared), and if marked, individual identity where possible based on legible number tags (Fig 3.1). Mean spacing between CTs was 715 m in 2019, 858 m in 2020, and 853 m in 2021. This spacing resulted in multiple CTs falling within each animal's summer home range based on telemetry analysis, with mean summer home range sizes estimated as 29 km² for females and 14 km² for males (Balyx, 2022).



Figure 3.1 Example camera trap images of A) unmarked, B) marked and identifiable, C) marked and unidentifiable mountain goats.

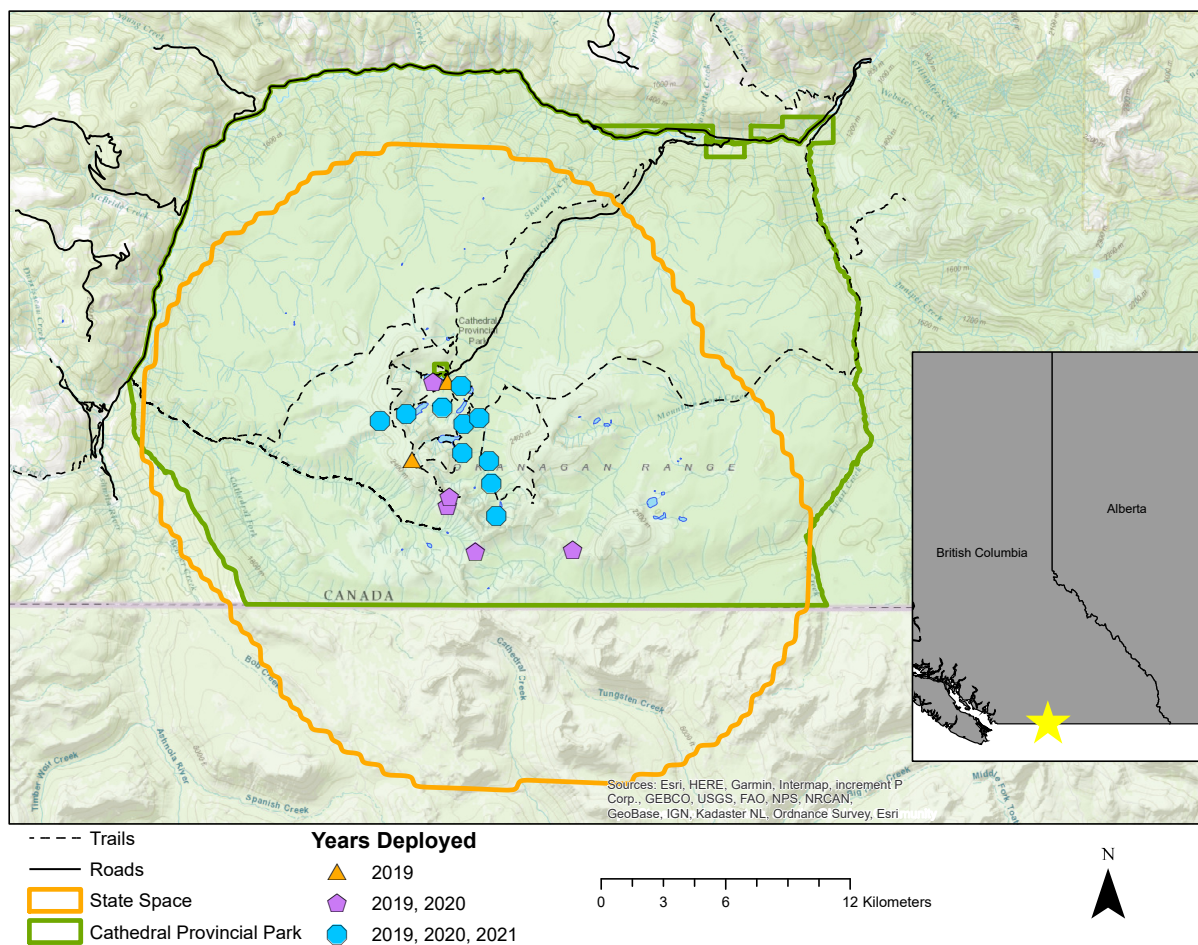


Figure 3.2 Map of camera trap deployments in Cathedral Provincial Park used for mountain goat density estimation, and the years each camera was active. The orange polygon is the state space (322 km²) and the green polygon is the park boundary. Solid black lines are roads, and dashed lines are recreation trails.

3.2.2 Statistical analysis

I fit SCR and SMR models to CT data to estimate mountain goat population density across three summers of sampling, from 2019 to 2021. Using data from processed CT images, I totalled marked and unmarked goat detections across weekly sampling occasions for the summer of each year, providing 14 occasions for 2019 and 2020 (July to September) and 9 occasions for 2021 (July to August).

I used the R (R Core Team, 2021) package *secr* version 4.5.4 (Efford, 2022a) to generate SCR and SMR estimates of density under a maximum likelihood framework. I fit multi-session models with each summer defined as a session, using a half-normal detection function, using default settings in the function ‘*secr.fit*’ for SCR and SMR models. The multi-session models used the same state-space of 322 km² for each year, which was defined with a 7500 m buffer around all cameras as suggested by the *secr* function ‘*suggest.buffer*’ (Fig 3.2.). I accounted for imperfect operability of CTs within sessions due to failure or removal at different points by including a trap operability matrix, improving the fit of detection models (Efford et al., 2013).

For SCR models, I used only the detections of identifiable marked individuals, summed as the count of independent detections per individual per weekly occasion. For SMR models, I included the same information, while also adding un-identifiable marked individuals (where number tags were visible but not legible), as well as detections of unmarked adult individuals, excluding juveniles to allow comparison to other populations and survey methods that do the same (Gyug, 2006). SMR estimates were adjusted for overdispersion to provide improved confidence interval coverage by fitting an initial model, estimating the overdispersion at these initial values 10 000 times, and re-fitting the model using an adjusted pseudo-likelihood (Efford, 2022a). I did not include additional environmental covariates or allow for variability in parameters other than density for each year in the multi-session (year) model.

I provide estimates of the following parameters: mountain goat density, abundance across the state-space, σ (the spatial scale parameter, representing decreasing likelihood of detection with increased distance from activity centers, which relates to home range size), g_0 (the likelihood of detection at distance = 0). I measured the precision of estimates using relative

standard error (RSE), sometimes denoted as the coefficient of variation (CV). It is general practice to consider RSE values <0.2 as useful for wildlife management (Green et al., 2020; Pollock et al., 1990; Williams et al., 2002). Goodness of fit was evaluated using the function ‘*secr.test*’, calculating devdf (the deviance divided by the residual degrees of freedom) for 100 simulations under the model, with p values greater than 0.05 suggesting support for the null hypothesis that these values were generated by the model. All p values were ~ 1 , suggesting good model fit.

I conducted post-hoc simulations to assess the robustness of my estimates of density by generating 100 simulated capture histories, with density, σ , and g_0 fixed at the estimates I generated for each year and model type, including the same number of occasions and traps as described above. I used the R package *secrdesign* version 2.6.0 (Efford, 2022b) to conduct and evaluate simulations under an SCR modelling framework for each set of known parameters. I calculated the mean RSE value across the 100 models fit to simulated populations, providing insight around the expected precision under my sampling design, and allowing comparison of the RSE values for these models.

3.3 Results

CTs were deployed from the beginning of July to the end of August (2021) and September (2019 and 2020) for 9 and 14 sampling occasions, respectively (Table 3.1). I recorded 552 adult mountain goat detections across the three summers, of which 400 were unmarked, 121 were individually identifiable, and 31 were marked but not individually identifiable (Table 3.1). There were 10 marked individuals in summer 2019 and 2020, and 9 individuals in summer 2021. I recorded at least one identifiable image of 9, 7, and 6 of these marked individuals in 2019, 2020, and 2021 respectively. The kid:nanny ratio was 0.50, 0.75, and 0.46, and the billy:nanny ratio was 0.50, 0.49, and 0.55 for 2019, 2020 and 2021 respectively (Appendix A.1).

Table 3.1. Mountain goat detection summary from 17,15, and 10 camera traps sampled for 98, 98, and 63 camera-days in summer 2019, 2020 and 2021 respectively in Cathedral Provincial Park. The total number of detections are provided for identifiable marked individuals (Marked-ID), unidentifiable marked individuals (Marked-noID) and unmarked individuals. The number of marked and recaptured individuals are also provided.

CT detections					Sampling			
Year	Marked-ID	Marked-noID	Unmarked	Total	Marked	Recaptured	Cameras	Occasions
2019	54	8	157	219	10	9	17	14
2020	49	15	135	199	10	7	15	14
2021	18	8	108	134	9	6	10	9

Density estimates ranged from 6.32 goats per 100 km² (95% CI; 2.98-13.40) for SCR in 2019 to 11.54 (95% CI: 6.97-19.13) for SMR in 2021. The estimates were similar between years and model approach, with SMR models being more precise, with a mean RSE value of 0.2 for SMR and 0.4 for SCR estimates (Fig. 3.3, Table 3.2). Using SCR, I estimated mountain goat abundance across the 322 km² state space at 20 adults for 2019 and 21 for both 2020 and 2021. Using SMR, I estimated abundance at 24 goats for 2019, 30 for 2020 and 37 for 2022 (Table 3.2). RSE values from the simulations were higher than those generated for each model, with values based on the SMR derived density, σ and g_0 parameters ranging from 0.21 to 0.30 and the SCR derived estimates ranging from 0.61 to 2.44 (Appendix A.2). This suggests that these estimates, particularly for SCR, may not be highly robust using the CT data available.

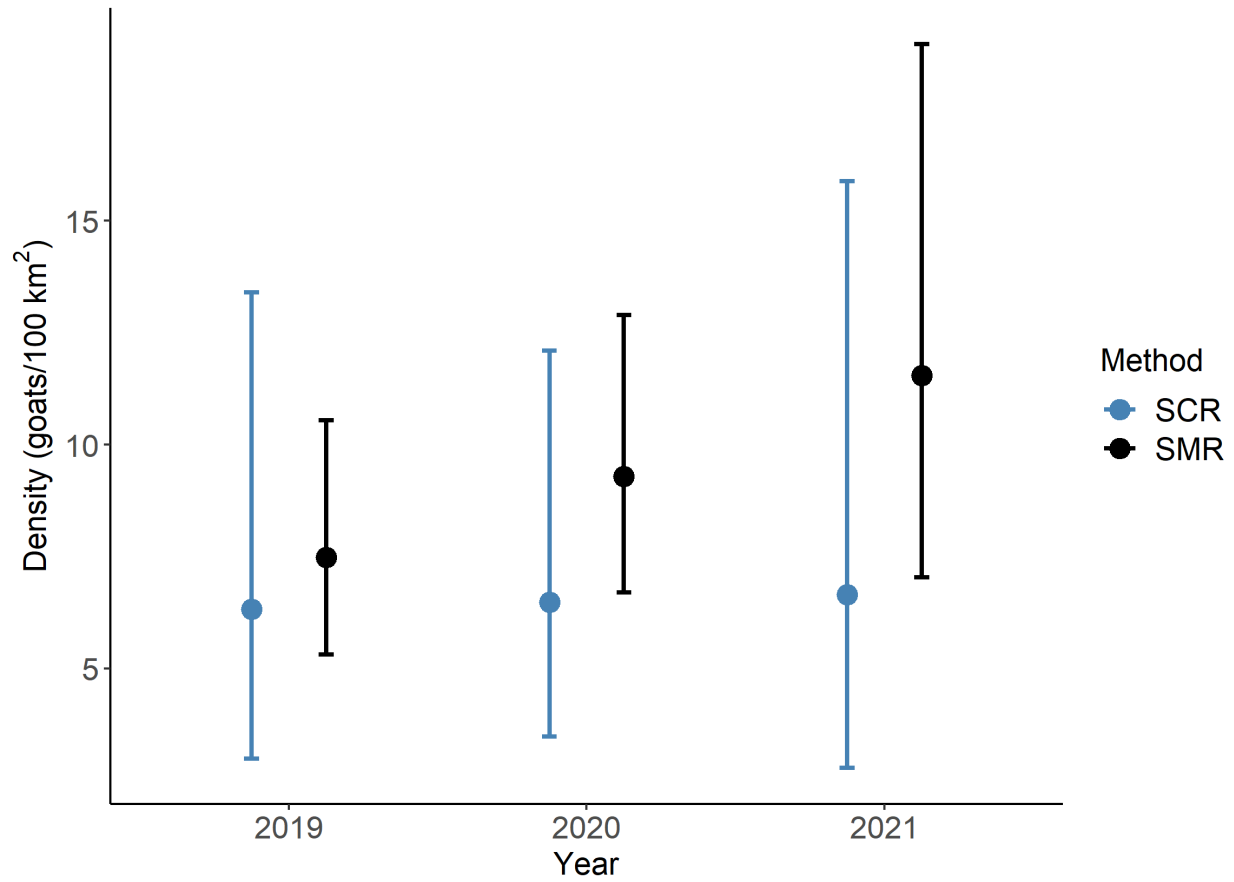


Figure 3.3 Mean (point) and 95% CI (bars) estimates of adult mountain goat population density from spatial capture-recapture (SCR) and spatial mark-resight (SMR) models in Cathedral Provincial Park from 2019 to 2021.

Table 3.2. Results for SCR and SMR models of mountain goats in Cathedral Provincial Park, from 2019 to 2021. Estimates of density (\hat{D} , goats/100km²), abundance (\hat{N}), σ (in meters), and g_0 with 95% CIs in parentheses. RSE is relative standard error, a measure of the precision of the density estimate.

Year	Method	\hat{D} (goats 100km ⁻²)	\hat{N}	σ (m)	g_0	RSE(\hat{D})
2019	SCR	6.32 (2.98-13.40)	20 (10-42)	2018 (1512-2694)	0.13 (0.09-0.17)	0.40
2019	SMR	7.48 (5.27-10.61)	24 (17-34)	3612 (2968-4397)	0.16 (0.11-0.24)	0.18
2020	SCR	6.48 (3.47-12.09)	21 (11-38)	2018 (1512-2694)	0.13 (0.09-0.17)	0.33
2020	SMR	9.29 (6.67-12.95)	30 (22-42)	3612 (2968-4397)	0.16 (0.11-0.24)	0.17
2021	SCR	6.65 (2.78-15.88)	21 (9-49)	2018 (1512-2694)	0.13 (0.09-0.17)	0.47
2021	SMR	11.54 (6.97-19.13)	37 (23-61)	3612 (2968-4397)	0.16 (0.11-0.24)	0.25

3.4 Discussion

Here I provide the first population estimates (mean estimates: 6.32 -11.54 goats/100 km²) for mountain goats in Cathedral in over a decade. These density estimates are lower than other mountain goat populations in southern British Columbia, which average from 45-80 goats/100 km² (coastal and interior populations respectively), underscoring the conservation concern of this population (B.C. Ministry of Environment, 2010; Gyug, 2006; Jessen et al., 2022; Parks et al., 2015). Based on population viability analysis, mountain goat populations with fewer than 25 individuals have a 50% chance of extirpation within 40 years, while populations with fewer than 50 individuals have an 18% chance of extirpation over the same period (Hamel et al., 2006). Considering these projections, there is an 18-50% chance that the Cathedral population will be extirpated within 40 years.

Mountain goats face threats from climate change, hunter harvest, and anthropogenic activity, leading to a status of special concern in British Columbia (B.C. Conservation Data Centre, 2015; B.C. Ministry of Environment, 2010; Festa-Bianchet et al., 2008; Jessen et al., 2022). Recent studies showing declines in other mountain goat populations around the province suggest that our understanding of the status of this elusive ungulate is limited, which calls for increased monitoring at finer scales and with new methodologies (Jessen et al., 2022). While aerial surveys have been the common tool for monitoring this species in the past, other less invasive options such as incorporation of Local Ecological Knowledge (LEK), community science, and genetic or CT based capture recapture methodologies are increasingly being used (Jessen et al., 2022; Poole et al., 2011).

I applied two approaches to estimating population density using images from CTs, providing an example of estimating mountain goat population density with only some marked individuals. The first approach, SCR, uses only images of marked mountain goats, while the second, SMR, additionally incorporated images of unmarked and marked yet unidentifiable individuals. For each of the three years of sampling, mean point estimates were higher with SMR, but confidence intervals overlapped. I also saw higher precision for the SMR method in each year. Only two of the three years of SMR models (2019 and 2020) generated RSE values below 0.2, while none of

the three years of SCR models had RSE values below this threshold that is considered a common cut-off for use in wildlife management (Palencia et al., 2021, Williams et al., 2002). I did not see any significant trend in density estimates over the three years of sampling. The 2021 estimate was less precise than the prior two years, likely due to the shorter sampling period and gradual removal of CTs as shown by the higher RSE values from the simulations, despite higher point estimates of density.

Tools have been developed to assist in simulations of sampling design, facilitating testing of potential designs for density estimation studies (Efford & Boulanger, 2019). My post-hoc use of these tools to assess density estimate robustness via simulation of populations of known density reinforced the importance of deploying more CTs for a longer time in generating precise estimates, particularly for low density populations. I strongly suggest that pre-sampling evaluation via power analysis and simulation is an important aspect in developing robust estimates useful for wildlife management and conservation (Burgar et al., 2018b, Rees et al., 2011, Sun et al., 2014).

With a limited number of CTs and marked individuals, I was able to generate relatively precise estimates of density and abundance for a partially marked population of mountain goats, though feasibility is highly dependent on the number of recaptures recorded, as witnessed by four of the six estimates being above commonly used thresholds of precision. In comparison to more common survey methods for alpine ungulates, such as helicopter surveys, this approach is safer, more aligned with goals to decarbonize research, and may be more cost effective. While the marking portion of SCR and SMR studies may require some of the same trade-offs (if using helicopter capture techniques or access), and is invasive on individual animals, the CT component of the method provides for low impact assessment of populations. To overcome this aspect, methods to estimate density without marked individuals continue to be developed and tested, which would be an exciting extension of this study (Amburgey et al., 2021; Burgar et al., 2018b, Palencia et al., 2021). An additional benefit of the use of CTs is the ability to survey multiple species, as well as multiple periods rather than providing a single day snap shot of the population as in aerial methods (Burgar et al., 2018a).

Monitoring the status of species at risk is an essential conservation action both in and outside of protected areas, particularly in the face of declining biodiversity worldwide, and increasing human impact (Butchart et al., 2010; Watson et al., 2016). Despite this crucial need, methods to acquire such information are often difficult to implement, inefficient, or costly, although new methods such as smaller GPS trackers, improved CTs, and remote sensing-based approaches leveraging observation or analytical technology are increasingly making it possible to census populations (Burgar et al., 2018b; Poole et al., 2011). Particularly for sensitive species, invasive sampling methods such as aerial surveys or GPS collaring may cause harm to varying extents, providing increased incentive for non-invasive methods of acquiring animal data (Latham et al., 2019; Zemanova, 2020). While this CT study capitalized on a concurrent capture and marking based study of mountain goats, researchers continue to investigate the possibility of application of SCR-based methods to non-marked or naturally identifiable species (e.g. Spatial Count models; Burgar et al., 2018b; Chandler & Royle, 2013). Extension of the SMR methods used here to incorporate knowledge around partial identities (sex, age, pelage pattern; e.g. SPIM models) is a promising avenue for generating increasingly precise estimates of population parameters (Augustine et al., 2018; Jimenez et al., 2019, Sun et al. *in review*). Further, new methods continue to emerge, including those attempting to estimate density from CT data without requiring information about individual identity (Amburgey et al., 2021; Becker et al., 2022, Palencia et al., 2021). Here, I show the utility of combining a relatively small number of CTs from a multi-species study with a limited number of marked individuals from a spatially and temporally concurrent study to provide reasonable estimates of density for an understudied population of conservation concern, providing a starting point for further study of similar methods in other populations and species.

Chapter 4: Synthesis and conclusions

With wildlife under threat from numerous human pressures in the Anthropocene, better understanding the impacts of our actions and activities is crucial to long-term persistence and ecosystem health (Dirzo et al., 2014; Johnson et al., 2017; Young et al., 2016). Particularly where we as a society have commonly considered our own recreational activities as non-consumptive and low impact, we must better understand the ways in which our own enjoyment of the natural world may impact it negatively (Boyle & Samson, 1985; Kays et al., 2017; Larson et al., 2019). By growing this understanding, we are better able to mitigate any impacts, ensuring a balance between the dual mandates of provision of human enjoyment and protection of ecological integrity that are the basis of many protected areas. With this thesis I assessed the potential for recreation-caused displacement in spatial or temporal habitat use across eight mammal species in a temperate PA via CT sampling. Additionally, I used data from these same CTs deployed for multispecies sampling to estimate density for a mountain goat population of conservation concern within the PA.

In my second chapter, I examined wildlife responses to recreation at a weekly scale, as well as through analysis of changes in daily activity patterns. To answer the question of whether recreation displaces wildlife, I examined temporal and spatial shifts against predictions rooted in ecological theory. I found mixed spatial responses, with only coyotes showing strong negative relationships with recreation, while mule deer and mountain goats may have benefited from recreation via a form of predator shield. Temporal responses were more pronounced, with all species other than cougars exhibiting significantly different activity patterns than humans. Together these results suggest that human recreation may be displacing wildlife temporally more than spatially within Cathedral. Despite relatively low impact in comparison to other anthropogenic activities, human powered recreation may in fact “consume” portions of the temporal niche used by wildlife, which I suggest may rebuke framing of these activities as non-consumptive.

Building on the multispecies CT study in chapter two, I focused on a species of conservation concern within Cathedral. Considered at risk throughout British Columbia, mountain goats are a major draw of recreationists to the park where they are easily viewed at

close ranges (B.C. Conservation Data Centre, 2015). Despite this threatened status and high potential for direct conflict with recreationists, the population status of the Cathedral herd is poorly understood, with population size not being formally assessed for a number of decades (B.C. Ministry of Environment, 2010; Gyug, 2006). Capitalizing on a concurrent collaring study, I used resightings of marked and unmarked goats to build SCR and SMR models of goat density for the population within the park. Density was lower than most other populations in the province (Jessen et al., 2022), and the estimated population size suggests an 18-50% chance of extirpation in the next 40 years according to projections from other regions (Hamel et al., 2006). Estimates of population size based on local knowledge and minimum number alive surveys (24 - 28 goats) were within the 95% confidence intervals of these estimates, suggesting that they are relatively accurate (K. Safford, BC Parks Conservation Specialist, *personal communication*, July 2022). This baseline estimate of population density can be used by managers to inform appropriate actions, including potential future measurement using similar methods to generate an estimate of population trend.

4.1 Research strengths and limitations

This study is based on a multispecies framework, where I generated insights about single species responses to recreation for eight focal species across the wildlife community. By using the same methodology on- and off-trail I was able to directly quantify human recreation at fine spatial and temporal scales, allowing inference across a gradient of use, which is a frequent shortcoming of prior studies (Balmford et al., 2015; Larson et al., 2019; Naidoo & Burton, 2020). Quantification of recreation at these scales is infrequent in many PAs, which may severely limit the ability of decision makers to assess the impact of management decisions (Balmford et al., 2015; Lemieux et al., 2018; Pressey et al., 2015). Particularly under adaptive management frameworks, this information is crucial to improving conservation outcomes (Tanner-McAllister et al., 2017).

With this research I capitalized on a concurrent collaring study to estimate population density for mountain goats. By having an array of CTs deployed throughout the landscape of Cathedral, I was able to maximize the benefit from potential risks to individual animals due to their capture and handling. Further, this opportunity allowed for information on population

status, which can be used by managers in conjunction with findings from the recreation study to enact informed conservation planning for this at-risk species.

One limitation of this study is the lack of a true “control” for human use, as I was not able to reach the most remote areas of the park. While I did sample across a gradient of human recreation, as well as a range of distances from trails, additional insight may have been gained from sampling areas even further from recreational influence. Alongside this limitation is the lack of a control for the effect of trails without humans. While I was able to survey across a range from low to high use trails across the study area, no trails were entirely free of humans during the study period. Additionally, Cathedral is a moderately used park, though with increasing visitation year over year (B.C. Parks, 2019). The patterns observed here may not be the same with higher or lower use. Future analyses may be an excellent avenue to explore this aspect, in addition to studies in other PAs. Further, the implementation of true adaptive management in PAs, where experiments or manipulations (such as trail closures, quota systems, or temporal restrictions) are made, measured, and learned from would provide insights with much further depth than I am able to provide here.

A limitation to the density estimation is the summer-only sampling. Mountain goats shift their range seasonally, with this migratory behaviour effectively removing goats from the sampling area from fall to spring (Festa-Bianchet & Côté, 2008; Kroesen et al., 2020). This limited the effective sampling period, potentially reducing the precision of density estimates. Small sample size particularly exacerbated this issue in 2021, when cameras were gradually removed throughout the study period.

4.2 Applications and future research

Findings from this research can be incorporated into structured decision making, a key aspect of adaptive management of Cathedral, while also being highly applicable to decision making in other PAs. By showing that human expansion into the temporal niche space may “crowd” animals more in time than in space, limiting use of trails to certain hours may be supported. Further, the use of trails and roads by all carnivores in this study may be relevant to future planning and development decisions. These effects together should be considered when

developing park management plans. In Cathedral, mountain goats exist in a relatively small, low density population within habitat that is facing increasing recreational pressure with growing park visitation. I suggest that a species-specific management plan should be enacted to continue monitoring the status of this population, as well as to further understand factors relating to recreation (urine, campground management, photography) that might influence potential conflict.

Future research approaches might attempt to overcome some of the limitations listed above, such as examining areas further from recreation, expanding sampling to incorporate goat home-ranges throughout the year, and by sampling for longer. An additional interesting avenue for research is to measure the effects of spatial or temporal closures on habitat use. Experimental closures of specific areas within PAs have shown promise in other regions, and would serve as a direct test of the effectiveness of management actions (Whittington et al., 2019). Investigating responses to recreation in different areas, particularly with higher and lower levels of use would be an excellent opportunity to extend this work, potentially allowing for a meta-analytical framework to answer these same questions at broader scales. In terms of density estimation, evaluating other methods relative to CTs for factors such as cost and risk, accuracy, the validity of sightability corrections commonly used for aerial surveys would be an interesting and useful avenue for investigation.

Parks and protected areas form an integral part of widespread conservation strategies globally, but to avoid the creation of “paper parks” we need to ensure that these PAs are effective (Di Minin & Toivonen, 2015). Use of evidence to inform both proactive and adaptive management approaches is crucial in ensuring PA effectiveness, while also being relevant to fostering human-wildlife coexistence more generally across the landscape. I focus here on traditional PAs as examples of good management but would be remiss not to acknowledge the fact that effective management may not be universal across PAs. Further, many examples exist of Indigenous-led, community-based, or privatized land management that show how management can be effective, evidence-based, and beneficial to both people and wildlife. Together, conservation strategies incorporating all of these approaches are key to mitigating the threats of the Anthropocene far into the future.

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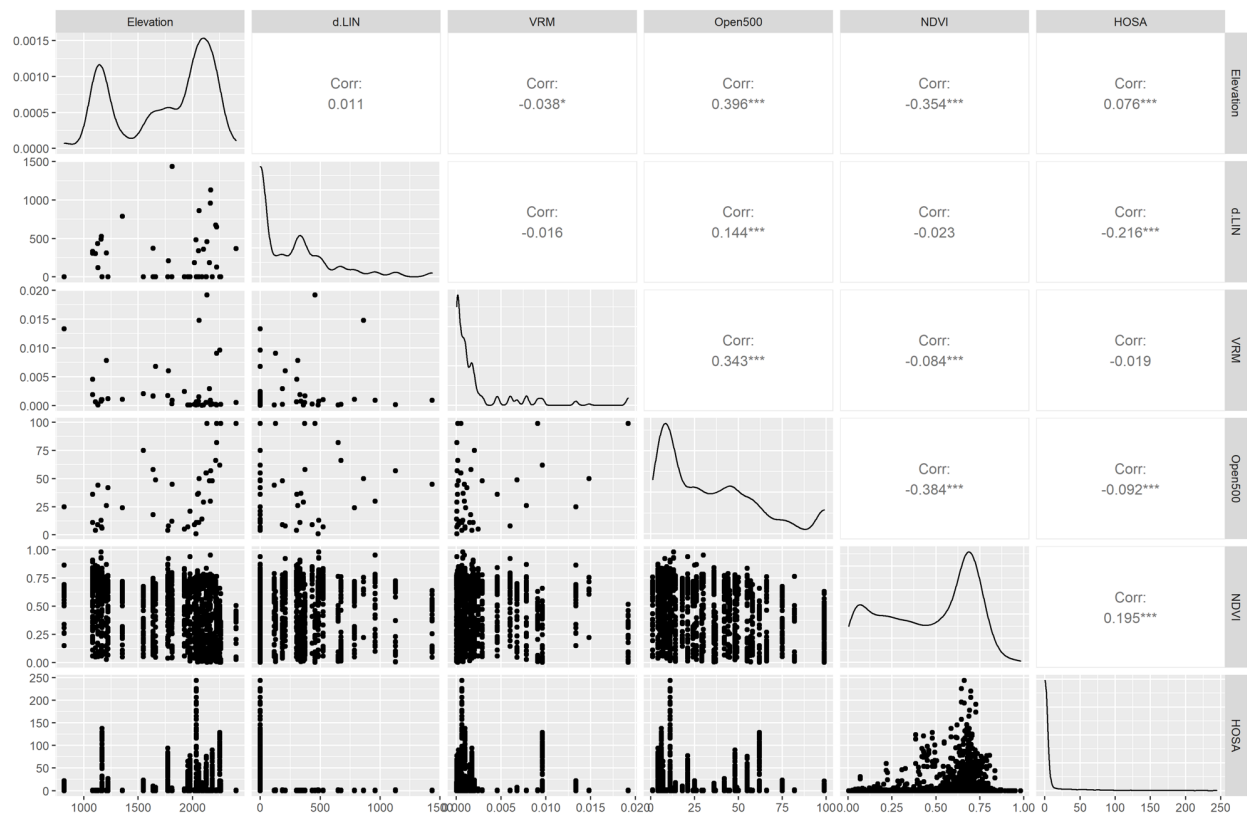
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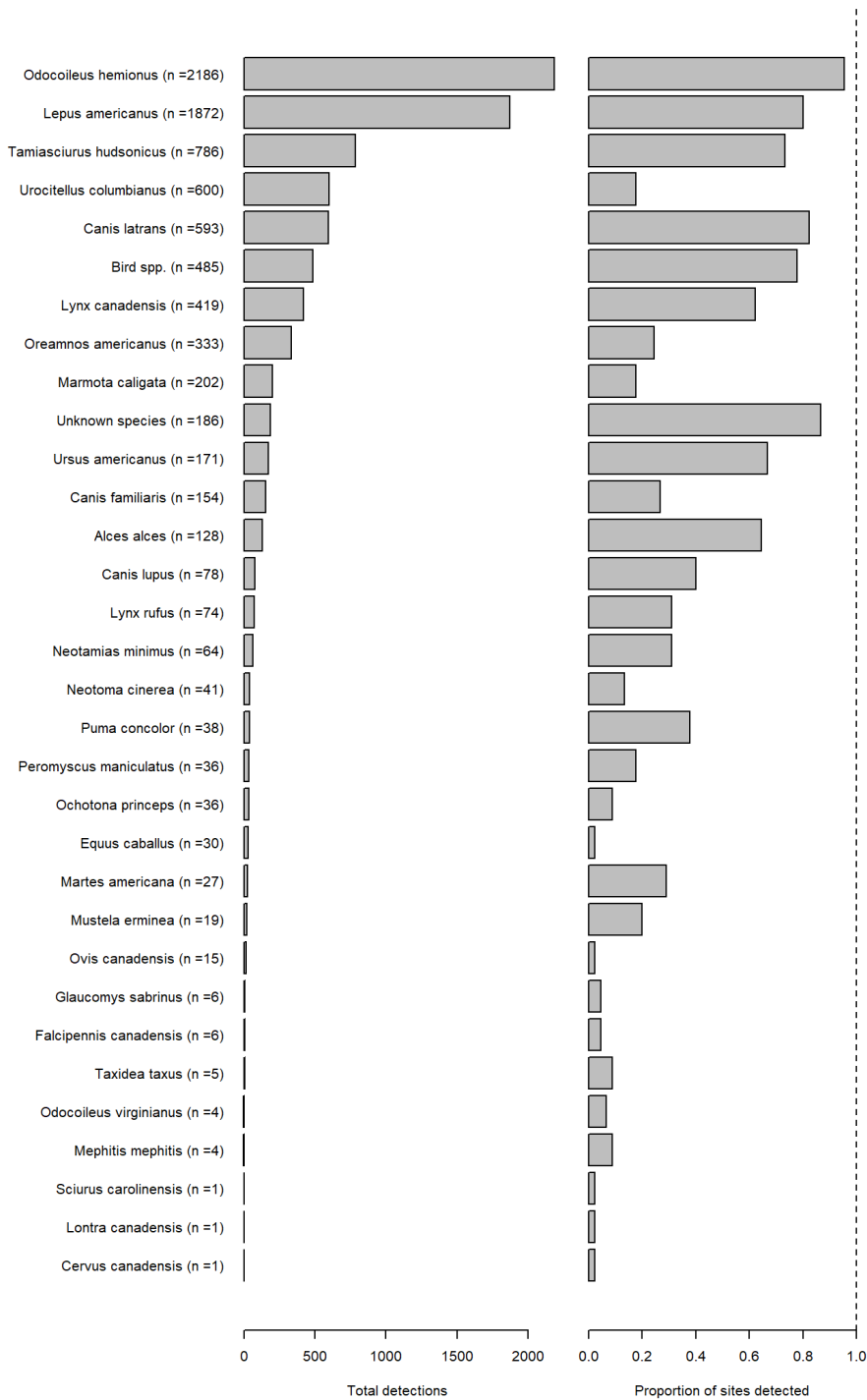
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Appendices

Appendix A Chapter two supporting information



A.1. Correlation coefficients between all predictors used in single species Bayesian models of mammal habitat use in Cathedral Provincial Park. See Table 2 for further description of predictors.



A.2. Number of independent detections for each wildlife species recorded in Cathedral Provincial Park (left) and the proportion of sites the species was detected at (right).

A.3. Model selection results for all species, using the Leave One Out Information Criterion.

LOOIC values within 8 are considered similarly predictive. Bayesian R^2 values represent the explanatory power of each candidate model.

Species	Model	LOOIC	Δ LOOIC	R^2
Moose	Combined	1030.6	0.0	0.030
	Environment	1031.9	1.3	0.029
	Human	1032.5	1.9	0.026
Coyote	Combined	2711.4	0.0	0.248
	Environment	2717.4	6.0	0.244
	Human	2764.6	53.2	0.213
Wolf	Environment	614.2	0.0	0.035
	Combined	614.7	0.5	0.035
	Human	620.3	6.1	0.024
Lynx	Combined	1906.2	0.0	0.236
	Environment	1906.2	0.0	0.228
	Human	1965.8	59.6	0.231
Mule deer	Combined	6264.1	0.0	0.397
	Environment	6363.4	99.3	0.239
	Human	6594.8	330.7	0.497
Mountain goat	Combined	796.1	0.0	0.626
	Environment	834.2	38.1	0.422
	Human	837.7	41.6	0.580
Cougar	Combined	374.1	0.0	0.029
	Environment	382.6	8.5	0.025
	Human	389.7	15.6	0.016
Black Bear	Combined	1144.0	0.0	0.089
	Environment	1148.3	4.3	0.086
	Human	1238.1	94.1	0.050

A.4. Moose Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-4.20	0.30	-4.81	-3.66
Human Detections	0.11	0.15	-0.18	0.39
Dist. Linear	-0.15	0.27	-0.72	0.36
Elevation	-0.19	0.30	-0.82	0.39
Ruggedness	-0.16	0.31	-0.83	0.41
Open500	-0.14	0.32	-0.78	0.49
NDVI	0.24	0.13	0.00	0.48

A.5. Coyote Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-3.05	0.23	-3.51	-2.63
Human Detections	-0.10	0.04	-0.19	-0.01
Dist. Linear	-1.13	0.22	-1.59	-0.70
Elevation	0.12	0.24	-0.36	0.60
Ruggedness	0.01	0.21	-0.39	0.42
Open500	0.32	0.24	-0.15	0.82
NDVI	0.47	0.07	0.34	0.60

A.6. Wolf Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-5.33	0.40	-6.23	-4.65
Human Detections	-0.09	0.16	-0.43	0.22
Dist. Linear	-1.56	0.36	-2.30	-0.89
Elevation	-0.89	0.31	-1.57	-0.34
Ruggedness	-0.20	0.31	-0.82	0.39
Open500	0.04	0.31	-0.59	0.64
NDVI	0.42	0.20	0.04	0.81

A.7. Lynx Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-4.17	0.30	-4.82	-3.64
Human Detections	0.07	0.04	-0.01	0.16
Dist. Linear	-1.25	0.26	-1.78	-0.76
Elevation	0.85	0.31	0.25	1.47
Ruggedness	-0.64	0.36	-1.40	0.05
Open500	-0.20	0.30	-0.82	0.38
NDVI	0.63	0.08	0.47	0.79

A.8. Mule deer Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-1.39	0.18	-1.75	-1.03
Human Detections	0.34	0.04	0.27	0.41
Dist. Linear	-0.10	0.17	-0.44	0.24
Elevation	0.11	0.20	-0.29	0.51
Ruggedness	-0.25	0.18	-0.61	0.11
Open500	-0.02	0.22	-0.46	0.39
NDVI	0.85	0.05	0.76	0.95

A.9. Mountain goat Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-8.94	1.29	-12.04	-6.95
Human Detections	0.44	0.07	0.31	0.59
Dist. Linear	-1.14	0.65	-2.56	0.01
Elevation	3.21	1.22	1.23	6.04
Ruggedness	1.28	0.45	0.49	2.26
Open500	0.75	0.64	-0.48	2.06
NDVI	1.22	0.21	0.84	1.65

A.10. Cougar Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-6.37	0.50	-7.47	-5.51
Human Detections	-0.03	0.15	-0.34	0.26
Dist. Linear	-1.41	0.41	-2.27	-0.65
Elevation	-0.11	0.30	-0.70	0.49
Ruggedness	-0.68	0.52	-1.81	0.23
Open500	-0.73	0.38	-1.54	-0.05
NDVI	0.97	0.30	0.41	1.60

A.11. Black bear Bayesian model parameter estimates, including standard error, lower and upper 95% credible intervals. All predictors were standardized to have a mean of 0 and standard deviation of 1.

Term	Estimate	Std.error	Lower	Upper
Intercept	-4.71	0.29	-5.33	-4.19
Human Detections	0.16	0.10	-0.05	0.36
Dist. Linear	-0.57	0.23	-1.04	-0.13
Elevation	-0.80	0.23	-1.29	-0.37
Ruggedness	0.05	0.23	-0.39	0.50
Open500	0.39	0.26	-0.15	0.89
NDVI	1.54	0.20	1.16	1.96

Appendix B Chapter three supporting information

B.1. Number of detections of nanny, billy, and kid mountain goats per year from 2019 to 2021, as well as the kid to nanny ratio.

Year	Nanny	Billy	Total Adult	Kid	Kid:Nanny Ratio	Billy:Nanny Ratio
2019	141	71	212	70	0.50	0.50
2020	136	67	203	102	0.75	0.49
2021	78	43	121	36	0.46	0.55

B.2. Mean RSE values from SCR models of 100 simulated populations with fixed values of density, σ , and g_0 , sampled with the number of occasions and trap design in our empirical study for each year.

Year	Density	σ (m)	g_0	Mean RSE	RSE _{SE}	Occasions	Traps
2019	6.32	3612	0.16	0.22	0.0018	14	17
2019	7.48	2018	0.13	0.61	0.031	14	17
2020	6.48	3612	0.16	0.21	0.00076	14	15
2020	9.29	2018	0.13	0.81	0.074	14	15
2021	6.65	3612	0.16	0.30	0.018	9	10
2021	11.54	2018	0.13	20.44	20.05	9	10