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Spatial and Temporal Dynamics of Wildlife Use of a Human-Dominated Landscape

By

Cheryl Ellen Hojnowski

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Justin S. Brashares, Chair
Professor Steven R. Beissinger
Professor Maggi Kelly
Professor Eileen A. Lacey

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Abstract

Spatial and Temporal Dynamics of Wildlife Use of a Human-Dominated Landscape

by

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Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Justin S. Brashares, Chair

In many of the world's natural areas, humans now play, work, or live alongside large-bodied species of wildlife including ungulates, meso-carnivores, and even apex predators. The behavioral adjustments of these species to human activities have implications for individual fitness, population persistence, and community structure, as well as for human safety. Theory suggests that wildlife in human-dominated landscapes should modify their habitat use to avoid interactions with people, but that such avoidance may occur only in response to fine-scale spatial and temporal variation in human activity. Yet studies of the impacts of human disturbance on wildlife rarely quantify the fine-scale dynamics of human use. In this dissertation, I seek to link wildlife avoidance behavior more directly to the type, timing, intensity, and spatial distribution of human activity, thereby informing efforts to preserve relatively undisturbed spaces for large mammals in natural ecosystems regularly used by people.

I first consider spatiotemporal use of the landscape by grizzly bears (*Ursos arctos*) in areas of high recreation in Kananaskis Country, Alberta, Canada. For each day of the active bear season, I quantified numbers of people and vehicles using all trails, roads, and facilities located within the home ranges of GPS-collared bears. I estimated human disturbance at bear GPS positions as a function of both distance to human-use features and the average daily use on those features. Analyses revealed that when bears were in habitats adjacent to recreation infrastructure, they modified their behavior in response to daily, weekly, and seasonal fluctuations in human activity, avoiding the times and places of highest recreation. Bears responded to recreation patterns that were spatially and temporally consistent, highlighting the need to preserve predictable patterns of human use in the study area. This research demonstrates the value of quantifying fine-scale dynamics of human activity and focusing on areas of high overlap between wildlife and people to elucidate avoidance behavior of wild animals in human-dominated landscapes.

Further, I evaluate the effect of incorporating fine-scale estimates of recreation intensity on the predictive accuracy of resource selection function models developed to quantify habitat use of GPS-collared grizzly bears. Models that included static proxies for human disturbance were compared against those that estimated daily numbers of recreationists and vehicles within bear home ranges. When bears were in close proximity to trails, roads, and facilities, top models were those that rigorously quantified human use, indicating that bear habitat selection was

significantly influenced by the fine-scale dynamics of recreation activity. My results suggest that when spatial overlap between human activity and wildlife is high, static representations of human disturbance may be less effective for describing wildlife behavior.

Last, I expand my focus to multiple species. Spatiotemporal patterns of occurrence of large mammals, recreationists, and domestic dogs were assessed using camera traps deployed within critical wildlife habitat bordering the town of Canmore, Alberta. Recreation was categorized by type of user, and daily numbers of recreationists and domestic dogs were quantified over a twenty-month period. Coyotes (*Canis latrans*) demonstrated the clearest temporal shifts in response to recreation intensity, and hikers and off-leash dogs spatially displaced several species. Results also suggested that study species responded most to past rather than current levels of human activity. My findings underscore the importance of spatial scale in recreation impact studies and indicate that recreation can have measurable effects on fine-scale habitat use and diel activity of large mammals.

The research presented in this dissertation adds to the growing body of literature on wildlife behavioral responses to human disturbance in general and outdoor recreation in particular. Human activity is increasing in most natural ecosystems, and my work suggests timely new approaches for quantifying human use and measuring its impacts on wildlife behavior in landscapes where presence of people is widespread.

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1. Introduction

Maintaining space for wildlife is one of the key challenges facing conservation biologists on an increasingly human-dominated planet. Human encroachment on wildlife habitat has already led to drastic declines in populations of large mammals across the globe (Ceballos and Ehrlich 2002), while mounting evidence indicates that individuals of many species that persist in human-dominated landscapes are fundamentally changing their behavior in response to the presence of people (Frid and Dill 2002; Ordiz et al. 2011; Oriol-Cotterill et al. 2015a). In particular, wildlife behavioral responses to human disturbance are expected to resemble responses of prey species to risk of predation, even when human activity is non-lethal (Frid and Dill 2002, Beale and Monaghan 2004). That is, wild animals should perceive human disturbance as a form of risk that they seek to minimize or avoid.

For prey species, total avoidance of predation risk is typically impossible due to resource acquisition needs (Lima and Dill 1990; Lima 1998). Studies of predation risk effects have instead revealed mechanisms of fine-scale avoidance of predators by prey. By quantifying subtle variations in the behavior, density, and distribution of predators, researchers have revealed prey avoidance of predators within the space of minutes (Caro 1994) or hours (Creel et al. 2005), over distances as small as several meters (Broekhius et al. 2013). Detailed quantification of patterns of predation risk has also revealed that prey persistence depends on the existence of fine-scale spatial and temporal refugia, where risk of prey encountering predators is low (Durant 1998; Kaufmann et al. 2007).

Approaches to quantifying fine-scale patterns of predation risk should be relevant to investigations of wildlife behavior and persistence in natural areas used regularly by people. Wildlife in human-dominated landscapes also face trade-offs between acquiring resources and reducing risk of encounter with people, often making complete avoidance of human activity impossible (Basille et al. 2009; Oriol-Cotterill et al. 2015b). Therefore in human-dominated landscapes, coexistence between wildlife and people likely depends on preservation of spaces and time periods of low human activity, so that animals can avoid people at fine scales (Oriol-Cotterill et al. 2015a). Moreover, like predation risk, human disturbance is a dynamic process, and responses of wildlife can be expected to be influenced by the number of people on the landscape at any given time, their location, and the duration of their activity.

Investigations of the impacts of human disturbance on wildlife behavior have only recently begun to quantify fine-scale fluctuations in the intensity, timing, and spatial extent of human activity. Nonetheless, initial studies suggest that directly linking wildlife avoidance responses to the dynamics of human use could both inform conservation planning and facilitate a more mechanistic understanding of wildlife behavior in human-dominated environments. For example, Rogala et al. (2011) used hourly counts of people and vehicles on trails and roads, respectively, to estimate thresholds of human activity likely to spatially displace elk (*Cervus candadensis*) and wolves (*Canis lupus*) over variable distances. In Nepal, distinguishing types of human activity and spatial fluctuations in numbers of people on trails and roads demonstrated that tigers (*Panthera tigris*) offset their diel activity to coexist with people, indicating maintenance of tiger populations was possible even in high human-use areas, as long as the potential for temporal avoidance of people was preserved (Carter et al. 2012). By quantifying human disturbance at

multiple spatial and temporal scales, Oriol-Cotterill et al. (2015) showed that GPS-collared lions (*Panthera leo*) optimized their behavior to utilize resources in high human-use areas; the authors then suggested clustering human activity to provide lions more space to utilize resources and avoid people.

In this dissertation, I seek to advance the growing body of literature linking wildlife behavior to fine-scale spatial and temporal variation in human use of the landscape. I focus on the responses of large mammalian carnivores and ungulates to variations in the type, timing, intensity, and spatial distribution of recreation activity in provincial protected areas in the Rocky Mountains, Alberta, Canada. I aim to 1) better understand how animals adjust their spatiotemporal use of the landscape in response to fine-scale variation in intensity of human activity; 2) test whether quantifying human use improves our understanding of wildlife behavior, and 3) identify the characteristics of human activity that have the potential to displace wildlife.

Study system

I conducted my field studies in Kananaskis Country, Alberta, Canada, a 4,500 km^2 multiple-use area bordered by Banff National Park to the north and extending from the front ranges of the Canadian Rocky Mountains east toward Calgary. This region retains a number of large- and medium-sized carnivores and ungulates, including wolves, cougars (*Puma concolor*), grizzly bears (*Ursus arctos*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), lynx (*Lynx lynx*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*), moose (*Alces alces*), elk, bighorn sheep (*Ovis Canadensis*), mountain goats (*Oreamnos americanus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*). The mountainous provincial parks of western Kananaskis are also locally considered "Calgary's playground," with an estimated four million annual visitors. Though recreation is restricted to non-motorized use, networks of trails and facilities are extensive, roads are well-developed, and the combination of steep topography and low productivity largely confines both humans and wildlife to valley bottoms. Parts of western Kananaskis are among the most developed landscapes in the world where grizzly bears still persist (Gibeau et al. 1998).

Thus overlap between humans and wildlife is high in Kananaskis Country, making it an ideal location to study the impacts of human activity on spatiotemporal use of the landscape by large mammals. For the first two chapters of my dissertation, I use data collected on grizzly bears in Peter Lougheed Provincial Park and the adjacent Spray Valley Provincial Park (c. 600 km^2; 50.72°N, 115.12°W). During the grizzly bear active season, human use in these parks consisted primarily of hiking, bicycling, and drive-in and backcountry camping, plus associated vehicle traffic. Many bear food resources were found in valley bottom habitat, where human activities were also concentrated.

The study area for my third chapter was the northern boundary of Bow Valley Wildlife Provincial Park and adjacent municipal lands surrounding the town of Canmore (c. 100 km^2; 51.07°N, 115.36°W). While habitat and topography in this area was generally similar to Peter Lougheed and the Spray Valley Parks, human activity was substantially higher and consisted of recreation on dense trail networks, residential development, and vehicle traffic on high-volume roads and highways. This study area was also located in a broad valley that was considered a

movement pinch-point for large mammals traveling between Banff National Park and Kananaskis Country. Although the human activity was widespread in the valley, few alternative routes with similarly high-quality habitat existed for wildlife.

Overview of Dissertation

In chapter two, I investigate the behavior of grizzly bears in areas of high recreation intensity. I used Global Positioning System (GPS) radio-collars to obtain fine-scale locations on bears whenever they were within 500 m of a human-use feature, and I quantified spatial and temporal variation in daily numbers of people using trails, roads, and facilities. I calculated a human disturbance index for each bear GPS location, based on 1) the distance between the GPS location and nearby human-use features, and 2) the average daily human use on those features. Although study animals overlapped broadly with human activity, analysis of disturbance indices suggested that bears made fine-scale behavioral adjustments to avoid the times and places of highest recreation intensity. Avoidance varied with type of human use. Bears responded to daily fluctuations in human activity on roads, weekly and seasonal fluctuations in activity on trails, and seasonal fluctuations in activity in facilities. Bears also increased their selection for forest cover in high human-use areas. My results suggest that continued coexistence between bears and people in the study area depends on preserving predictable recreation patterns and limiting intensity of human use. My findings also underscore that in cases of broad-scale overlap between people and carnivores, new insights into carnivore avoidance behavior may be obtained by studies that focus within the more limited spatial extent of high human-use areas, and that quantify variation in human activity at multiple spatial and temporal scales.

In chapter three, I assess whether including estimates of average daily recreation levels improved models developed to predict grizzly bear habitat selection. Specifically, I compared three sets of habitat suitability models. The first set incorporated measures of distance to nearest trail, road, and facility, a conventional proxy for intensity of human use. The second model set also used distance to nearest feature, but categorized trails, roads, and facilities as having a high or low level of human use. The third model set included estimates of not only distance to nearest trail, road, and facility, but also the average daily number of people or vehicles using each of these features. I applied these models to describe the occurrence of GPS-collared grizzly bears at a relatively broad spatial scale, where human activity was diffuse, and at a finer scale, where bear-human overlap was high. I used Akaike's Information Criterion and k-folds cross-validation to evaluate model performance. I found that at a broad spatial scale, grizzly bear habitat selection was best predicted by the second model set, while at a fine spatial scale, bear habitat use was best predicted by the third set. I conclude that by rigorously quantifying human use dynamics, ecologists may better evaluate disturbance impacts on wildlife behavior and occurrence, particularly when wildlife-human overlap is extensive. My findings are applicable to other analytical approaches and other types of human disturbance.

In chapter four, I evaluate whether non-consumptive, non-motorized recreation influences diel activity patterns and space use of large mammals in the Bow Valley, Alberta, Canada, along the edges of Banff National Park, Bow Valley Wildland Provincial Park, and the town of Canmore. I used an existing camera trap data set to quantify spatiotemporal patterns of wildlife, human, and domestic dog detections at 66 survey sites over a 20 month period. To test for temporal

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displacement of large mammals by recreationists, I compared activity patterns of study species on wildlife versus human trails. I also developed models predicting the probability of wildlife detection during daily periods of high human activity. To test for spatial displacement of wildlife, I modeled the probability that study species would be detected at camera sites on any given day as a function of numbers of recreationists and domestic dogs, human infrastructure covariates, and habitat covariates. I also modeled the relative intensity of wildlife use of camera sites in relation to these covariates. Probability of daytime detection of most study species declined with increasing intensity of recreation, proximity to human infrastructure, or density of human infrastructure. Off-leash dogs were negatively associated with habitat use of black bears, elk, mule deer and white-tailed deer, and hikers were negatively associated with habitat use of cougars and white-tailed deer. My results provide evidence for stand-alone effects of recreation on spatiotemporal activity of large mammals. However, I suggest managers should also consider the potential combined impacts of outdoor recreation, expanding residential development, and increasing vehicle traffic at protected area boundaries.

In the final chapter of this dissertation, I draw general conclusions and make recommendations for future research to better understand and protect wildlife living in natural landscapes shared with humans.

2. Grizzly Bears Differentiate Fine-Scale Patterns of Human Activity in High-Use Recreation Areas

Summary

Some large carnivores spend significant time in high human-use areas, raising questions about whether and how such individuals modify their behavior to avoid people. In this study, I investigated the behavior of grizzly bears (*Ursus arctos*) when they were in areas of high recreation intensity in two provincial parks in Kananaskis Country, Alberta, Canada. I used Global Positioning System (GPS) radio-collars to obtain fine-scale locations on bears whenever they were within 500 m of a human-use feature, and I calculated a human disturbance index for each GPS location, based on 1) the distance between the location and nearby trails, roads, and facilities, and 2) the daily number of people or vehicles using these three types of anthropogenic features. Although study animals overlapped broadly with human activity, analysis of disturbance indices suggested that bears made fine-scale behavioral adjustments to avoid the times and places of highest recreation intensity. Avoidance varied with type of human use. Bears responded to daily fluctuations in human activity on roads, weekly and seasonal fluctuations in activity on trails, and seasonal fluctuations in activity in facilities. Bears also increased their selection for forest cover in high human-use areas. My results suggest that continued coexistence between bears and people in the study area depends on preserving predictable recreation patterns and limiting intensity of human use. In cases of broad-scale overlap between people and large carnivores, new insights into carnivore avoidance behavior may be obtained by studies that focus within the more limited spatial extent of high human-use areas, and that quantify variation in human activity at multiple spatial and temporal scales.

Keywords: grizzly bears, *Ursus arctos,* recreation, avoidance behavior, coexistence, fine scale

Introduction

Wildlife responses to human disturbance have been likened to the behavior of prey under risk of predation, even when human activity is non-lethal (Beale and Monaghan 2004, Frid and Dill 2002). Most commonly, wild animals simply seek to avoid people, whether through fleeing (Kerbiriou et al. 2009, Moen et al. 2012); hiding (Dickson et al. 2005, Kolowski and Holekamp 2009, Ordiz et al. 2011); or changes in habitat selection (Berger 2007, Dyer et al. 2001, Gill et al. 1996), timing of activity (Carter et al. 2012, Ordiz et al. 2012, Rasmussen and Macdonald 2012), or both (Hebblewhite and Merrill 2008, Theuerkauf et al. 2003). A number of recent studies emphasize that such avoidance behaviors are exhibited not only by typical wildlife prey species, but also by large carnivores in response to human activity (Oriol-Cotterill et al. 2015a).

As human populations increase, however, total avoidance of human disturbance appears impossible for some large carnivores, which are instead living within human-dominated landscapes (Carter et al. 2012; Llaneza et al. 2012; Oriol-Cotterill et al. 2015a). Studies of prey responses to predators suggest that in such cases of broad-scale overlap between people and wildlife, quantifying fine-scale patterns of human disturbance could better elucidate large carnivore avoidance strategies. For example, by closely examining the abundance, temporal activity, and shifting spatial distribution of predators, researchers have documented prey

responses to predation risk within the space of minutes (Caro 1994) or hours (Creel et al. 2005), over distances as small as several meters (Broekhius et al. 2013). Like predation risk, human disturbance is a dynamic process, and impacted species can be expected to respond to the number of people on the landscape at any given time, their location, and the duration of their activity. Yet most investigations of wildlife responses to people use static proxies to represent human disturbance, such as distance to or density of linear features (e.g., Basille et al. 2009). This practice may not only limit detection of fine-scale avoidance strategies of large carnivores in response to subtle changes in human use. It also has practical conservation implications, because management decisions about maintaining large carnivores in human-dominated environments are typically driven by concerns about human safety and therefore depend on reliable assessments of the degree to which carnivores avoid people.

In Kananaskis Country, Alberta, Canada, grizzly bears (*Ursus arctos*) overlap broadly with human activity due to distribution of bear food resources and widespread recreation. Though past research has identified a 500 m zone of influence around human use features such as trails, roads, and facilities (Ciarniello et al. 2009, IGBC 1998, Gibeau et al. 2001), some sub-adult and adult female bears regularly use these areas, which we hereafter refer to as the "front country". These front-country bears are not food-conditioned, and their behavior is likely driven instead by avoidance of predation by conspecifics, particularly adult males that depredate cubs and sub-adults and typically stay farther away from human activity (the despotic distribution, Elfstrom et al. 2014); presence of critical natural food resources near recreation infrastructure, and lack of alternative habitat (Gibeau et al. 2001, Gill et al. 2001). Avoidance of human disturbance by front-country bears is poorly understood, particularly as some individuals are seen by visitors on dozens of occasions each year and consistently display tolerant behavior toward people. Human activity in this region is also almost always non-lethal, so bears may not associate people with risk.

Recent studies have quantified fine-scale movements of brown bears following human approaches on foot (Ordiz et al. 2013, Moen et al. 2012) but have not considered spatiotemporal use of human-dominated landscapes by bears more comprehensively. Published research on grizzly bear behavior within areas of high human activity is scant (but see Donelon 2004). Because overlap between bears and people is so extensive in parts of the Kananaskis front country, this is an ideal system to investigate whether bears actively alter their fine-scale habitat selection and temporal activity patterns in response to human disturbance. Recreation levels are not uniform in the front country, which could allow bears to select for locations or times of low recreation intensity. Forest also comprises greater than 60% of available habitat and provides good cover for wildlife, so bears could conceal themselves from people at relatively small distances (Moen et al. 2012). A more nuanced understanding of the avoidance behavior of grizzly bears could inform efforts to conserve habitat and reduce encounters between bears and people, issues that are critical for both bear persistence and human safety in Kananaskis Country and beyond (Ordiz et al. 2013, Oriol-Cotterill et al. 2015).

In this study, we used GPS collars to collect fine-scale locations on grizzly bears that regularly used front-country habitats. We quantified daily human activity on all trails, roads, and facilities located within the home ranges of GPS-collared bears, and we asked whether, within the smaller spatial extent of the front country, bears were nonetheless attempting to avoid people. If bears

adjusted their behavior in response to fine-scale variations in human disturbance, while also exploiting the front country for important food resources and protection from conspecifics, then this could suggest a substantial degree of adaptive behavior. We expected that bears would avoid the areas of highest human disturbance, both spatially and temporally. We also expected that bears would select for forest cover more in the front country, compared to selection for forested areas at the scale of their full home range. This study provides important new information on the avoidance behavior of a large carnivore in areas of high overlap with people.

Materials and Methods

STUDY AREA

Kananaskis Country is a 4,200 km^2, multiple-use protected area located east of Calgary, Alberta, and stretching west to the Continental Divide. This study was conducted in Peter Lougheed and Spray Valley Provincial Parks (50.72°N, 115.12°W; area = approx. 600 km^2) in western Kananaskis Country (Fig. 1). Topography in these parks was defined by the Rocky Mountains, with elevation ranging from ~1600 m at valley bottom to greater than 3000 m along the Alberta-British Columbia border. Climate was continental and dry (~470mm annual precipitation), with relatively wetter winters than summers, and with more precipitation at higher elevations. Valley bottoms were dominated by coniferous forests, primarily lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*), mixed with Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at higher elevations. Conifer stands were interspersed with patches of wetland forest, shrubs and grassy meadows. Major waterways included the Kananaskis River and Upper and Lower Kananaskis Lakes.

Recreation in these parks was limited to non-motorized activities, chiefly hiking, biking, and camping, which were permitted only on designated trails and facilities. Road access into Peter Lougheed and the Spray Valley was via Highway 40, a two-lane paved highway, or the Smith-Dorrien Trail, a wide gravel road. My study area included ~70 km of roads, nearly all of which were paved (~40 km of Highway 40, the southernmost 17 km of which were closed annually from Dec 1 – June 15; ~five km of the unpaved Smith-Dorrien Trail; the 13-km paved Kananaskis Lakes Trail, and ~10 km of paved, secondary roads into campgrounds and other facilities; Fig. 1). The study area also included ~220 km of hiking and biking trails; eight auto-accessible campgrounds (~600 total campsites); three walk-in campgrounds (74 campsites); 17 day-use areas; two boat launches; a major visitor center; a lodge with 22 cabins and 13 additional campsites; and a 40-lot, seasonal cottage community along the Lower Kananaskis Lake shore. This infrastructure was located almost entirely in the valley bottoms. Visitation to all of Kananaskis Country was estimated at greater than 4 million people/year, and although rigorous figures for Peter Lougheed and the Spray Valley were not available, annual visitation was likely greater than 400,000 people, with the highest visitation occurring during the late spring through early fall, particularly July and August.

Grizzly bears were listed as a threatened species in Alberta, and the Kananaskis Country population was estimated at around 50 bears, with Peter Lougheed and the Spray Valley considered important areas for cub growth and survival. Bears in this region relied almost exclusively on plant foods, with meat constituting only about 10% of female and 20% of male diets (Felicetti et al. 2005). Bears may have been limited by the environment's productivity, and

reproductive outputs were low (Cattet et al. 2005). Bear food items included yellow hedysarum roots (*Hedysarum sulphurescens*), flower bulbs, grasses, sedges, dandelions, clover, and horsetail (*Equisetum arvense*) in the spring, and cow parsnip (*Heracleum maximum*), berries (particularly the buffaloberry *Shepherdia canadensis*), and hedysarum in the summer and fall; sources of animal protein included ant hills, ground squirrels, and occasional ungulates. Almost all bear plant foods were found in open areas, and many foods (e.g., buffaloberry, grasses, dandelions, clover) occurred in areas where human activity had opened the forest canopy, i.e., along trails, roadsides, and in facilities.

DATA COLLECTION

Grizzly bear data

Bears were captured in culvert traps and through free-range darting in May – June 2014 and May – June 2015. Capture and immobilization methods followed Alberta Wildlife Animal Care Committee Class protocol and were approved by the Alberta Ministry of Environment and Sustainable Resource Development, Alberta Ministry of Environment and Parks, and University of California, Berkeley Animal Use and Care Committee. Capture operations were overseen by Alberta Environment and Parks staff, who targeted adult and sub-adult female bears that spent significant time in the front country and were known from previous, VHF telemetry-based monitoring. Female bears were targeted because their home ranges were contained entirely within the study area, while male bears in this region had home ranges up to 2,700 km^2 (Stevens and Gibeau 2005). Male bears also frequently slip their collars. Bears were fitted with GPS Iridium radio-collars (Vectronic Aerospace GmbH, Berlin, Germany and Followit, Lundesberg, Sweden) that were programmed to take a location once every 60 minutes (1 collar) or once every 30 minutes (all other collars) during the time of year when bears were active (May 1 – October 31). Only 3D GPS fixes with a dilution of precision (DOP) of < 10 (Frair et al. 2010) were used in analyses. To avoid bias associated with any changes in bear behavior related to the effects of handling, I excluded all locations within one week of an animal's capture and immobilization. Fixes associated with trapping locations and with two roadkill drop-off sites were also removed. With DOP ≥ 10 locations excluded, collar fix rates ranged from 92.5 – 96.6%.

Human use data

From June – Oct 2014 and May – Oct 2015, I estimated daily human activity on three classes of anthropogenic features located within the home ranges of GPS-collared grizzly bears (Fig. 1): 1) trails, including hiking and multiple-use hiking and biking trails (*n* = 26); 2) roads, including primary and secondary roads (*n* = 6); and 3) facilities, including campgrounds (*n* = 7), day-use areas (*n* = 5), and miscellaneous features such as a visitor's center, a lodge, and administrative buildings (*n* = 5). I used eight motion-triggered cameras (Bushnell, Overland Park, USA), 16 heat-triggered trail counters and eight magnetic vehicle counters (TrafX, Canmore, Canada) to quantify human use directly on 20 trails and four separate segments of two primary paved roads (Fig. 1). Trail counters were installed on hiking-only trails, and cameras were installed on multiple-use trails, because trail counters could not consistently detect bicycles. Trail counters and cameras produced timestamped data for each hiker, biker or group passing the counter or camera; these data were then summarized into hourly and daily totals. On trails less than 4 km in length (one-way; *n* = 17), only one counter or camera was deployed; on longer trails (*n* =3), trail counters were deployed every 3-5 km, since human use declined with distance from trailhead.

Vehicle counters were located in pairs, on opposite sides of the road, at two sites on Highway 40 and two sites on the Kananaskis Lakes Trail. Counter locations were selected to capture spatial variation in traffic flow, because traffic declined with increasing distance from the study area's northern boundary, as people exited roads to pull into trailheads, day-use areas and campgrounds. Each counter recorded the number of vehicles per hour in the nearest lane of traffic; these data were summarized into daily totals. Based on data collected by trail and vehicle counters, I extrapolated human-use counts on two additional secondary roads and six additional trails. To estimate daily use at facilities, I consulted with campground managers and conducted visual surveys of parking lots.

Vehicle counter accuracy was assessed against visual observations of vehicles. All counters over-counted slightly, but counter data were within 10% of visual observations. This discrepancy was of little consequence for analyses, since all vehicle counters over-counted and comparison of traffic levels between different roads and time periods was relative. Trail counters were known to be reliable based on previous studies in the region (J. Herrero, *personal communication*).

ANALYSES

My analyses consisted of three steps, which are described in detail below. First, I delineated grizzly bear home ranges. Next, to evaluate whether bears increased their use of forest cover when near human activity, I evaluated habitat selection of bears within their full home ranges, compared to bears' habitat selection within the front-country. Last, using only those GPS collar fixes obtained within 500 m of a trail, road, or facility, I examined whether the probability of bear occurrence at locations within the front-country was influenced by the timing and intensity of human activity. I carried out all statistical calculations in the statistical software R 3.3.1 (R Development Core Team 2016), and I extracted values of environmental and human disturbance variables using ArcGIS 10.2.2 (Environmental Systems Research Institute 2014) and Geospatial Modeling Environment 0.7.3 (GME; Beyer 2014). GIS layers for landcover and human-use features were provided by Alberta Environment and Parks.

Home range delineation

I randomly sampled 1,000 locations per bear to delineate each animal's full home range and 500 front-country locations per bear to delineate each animal's front-country home range. Front-country locations were those within 500 m of a trail, road, or facility. Home ranges were based on the 90% isopleth (Borger et al. 2006) from kernels created using the fixed Gaussian Kernel Density Estimate. Although GPS locations in these samples were probably auto-correlated, I did not sub-sample further, because auto-correlated data can contain important biological information (De Solla et al. 1999).

Habitat selection

To test whether bears selected for specific habitat types within their full home ranges and within their front-country home ranges, I conducted a compositional analysis (Aebischer et al. 1993) using the package 'adehabitatHS' in R (Calenge 2006). For each individual, I randomly selected 1,000 GPS locations in the full home range and 500 GPS locations in the front-country home range. The percentage of bear GPS locations that were located within each habitat type (habitat use) was compared to the percentage of the entire full or front-country home range covered by

each habitat type (habitat availability). Habitat type was described from an existing landcover map for the study area derived from Landsat imagery (Foothills Model Forest Grizzly Bear Research Program 2009). Major habitat types included forested (including closed and moderate coniferous and mixed tree stands); herbaceous / grassy; shrubs, and barren areas with <5% vegetation. Water (lakes and the Kananaskis River) was excluded. Overall landcover classification accuracy was estimated at 75% (Kappa = 0.46). To improve accuracy, I visually checked the landcover map against orthophotos in ArcMap (ArcGIS 10.2.2) to identify misclassified areas larger than five pixels in size. I corrected these misclassifications using ARIS Grid and Raster Editor (ARIS B.V. 2016).

To test whether bear selection for habitat types in their full home-ranges differed from habitat selection in the front country, I calculated the Ivlev's electivity index (Krebs 1999) for each habitat type in both the full and front-country home ranges. I used the formula $E = (p-q)/(p+q)$, where p is the habitat used and q is the habitat available, represented as proportions or percentages (Broekhius et al. 2013). When $E > 0$, preference occurred for a particular habitat type; when $E < 0$, avoidance occurred. I compared Ivlev's electivity indices for bears' full home ranges and front-country home ranges using a permutation test with $n = 1,000$ repetitions in the R package 'perm' (Fay and Shaw 2010). A permutation test was chosen to account for small sample sizes.

Bear occurrence in relation to human activity

Spatiotemporal patterns of human activity

Recreation levels in Peter Lougheed and the Spray Valley varied substantially by month and by day of the week. Therefore I divided all human-use data and bear GPS locations into 2 major seasons, non-peak season (1 May – 30 June and 1 Sept – 31 Oct) and peak season (1 July – 31 Aug), and also into weekends (including holidays) and weekdays. This created four main time periods: non-peak season-weekend; non-peak season-weekday; peak season-weekend, and peak season-weekday. Peak season and non-peak season dates were defined based on the local academic school year (which influenced vacation times for families using the study area) and exploratory analysis of the human-use data collected for trails, roads, and facilities.

I calculated average daily human-use events, N, for each trail, road, and facility, for each of the four time periods. A human-use event was defined as 1) for trails: all hikers or bikers passing a trail counter or camera within one minute of each other; 2) for roads: a vehicle passing a vehicle counter, and 3) for facilities: an occupied campsite or parking space. For trails, N was not an absolute count of people, because trail counters and cameras often could not differentiate between 1 and 2 hikers or bikers passing simultaneously, and because wildlife are likely more affected by the number of groups of people on a trail each day, rather than the absolute number of people (Herrero 2007; J. Herrero, *personal communication*). Human use was assumed to occur only on maintained linear features; i.e., I assumed people did not go off trails or roads. Some trails, roads, and facilities were closed during certain dates; human-use events on these dates were not included in calculations of N.

I used a Mann-Whitney U test with paired samples to test for significant differences in N between weekends and weekdays and between the peak and non-peak season. I used linear mixed effects (LME) models to test for differences in N between all four time periods, with the

name of the trail, road, or facility included as a random effect. I also used LME models to test for spatial variation in N; specifically, I tested whether N values differed significantly between individual trails, roads, and facilities, with time period included as a random effect.

Overall and diurnal patterns of bear space use

Next, I quantified the level of recreation-related disturbance that bears would experience at different times and locations in the front country. I randomly selected 200 front-country GPS locations per bear per time period, or a maximum of 50% of a bear's total front-country locations in the given time period, whichever was smaller (Table 1). I generated an equal number of random "absence" points within each bear's front-country home range. Based on diurnal fluctuations in N, I classified bear locations into three categories representing time of day: night (locations from 10:00 pm to 6:00 am, inclusive); morning/evening (6:30 am – 9:30 am and 6:30 pm – 9:30 pm), and daytime (10:00 am – 6 pm). Each absence point was assigned a time sequence (season, day of the week, and time of day) that matched that of an actual bear GPS location. I calculated a trail-specific, road-specific, and facility-specific disturbance index for each actual GPS location and each random absence point, using the formula $1 - (1 - 1/D)^N$ (Beale and Monaghan 2004), where N was equal to the average number of human-use events per day for any given anthropogenic feature in a particular time period (peak season-weekend, peak season-weekday, non-peak season-weekend, or non-peak season-weekday), and D was equal to the distance to that feature. Each actual GPS location and random absence point was assigned a separate disturbance index value for trails, roads, and facilities, because bears may perceive these features differently.

This formula assumes that the level of disturbance perceived by an animal is proportional to both the intensity of human use and the distance from that use (Beale and Monaghan 2004). At low values of N, disturbance indices declined exponentially with distance; at higher values of N, the decline approximated a negative logistic curve. The formula is artificially inflated at large values of N, so average daily vehicle counts were rescaled from 0 to 150 by dividing absolute counts by 20. For bear locations or random points that overlapped directly with a human-use feature, D was set equal to 1, resulting in a disturbance index of 1. For points that occurred during trail, road, or facility closure dates, N was equal to 0. Bears were often within 500 m of more than one trail, road, or facility, so disturbance indices were also cumulative; i.e., final disturbance index values reflected the sum of the disturbance indices for each trail, road, or facility within 500 m of a given point.

To assess whether the probability of bear presence at locations in the front country was influenced by the intensity and timing of human activity, I compared the disturbance indices at actual bear locations to those at random points using Generalized Linear Mixed Models (GLMMs) with a binomial error structure and logit link function (R package 'lme4', Bates et al. 2016). For the binomial response variable, "1" represented actual bear GPS locations and "0" represented randomly generated points. I built several candidate models with disturbance index (continuous) and habitat type (categorical) as spatial explanatory variables and with time of day (categorical) as a temporal variable interacting with disturbance index (Table 2). One-way ANOVAs suggested significant associations between trails and forested areas, between roads and both grassy and forested areas, and between campgrounds and shrubs. Therefore, an interaction between habitat and disturbance index was not included in candidate models. Elevation was also

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not included, as it did not vary significantly across front-country, valley-bottom locations. Food availability was excluded because bears in our study area use many different food resources, the availability of which has not been quantified at a fine enough resolution to be informative. At a coarse scale, bears select for greenness as a proxy for food (Mace et al. 1999), and all human-use features included in my analyses were located in medium-quality habitat based on greenness indices (Stevens 2005). To reflect differences in sample sizes (number of GPS locations) per bear, I included a random intercept in candidate models (Gillies et al. 2006). Backward elimination procedures were performed to exclude from final candidate models those covariates that did not contribute significantly ($p \geq 0.05$) to the variation in occurrence of bear locations. Models were ranked using the Akaike Information Criterion corrected for small sample sizes (AICc).

Weekly and seasonal patterns of bear space use

GLMMs were formulated to detect whether changes in bear space use occurred in association with daily fluctuations in recreation activity, because candidate models included an interaction between time of day and disturbance index. However, GLMMs could not pinpoint whether bears modified their habitat use in response to within-week or seasonal variations in human activity. Therefore I also used LME models to compare disturbance index values at actual (i.e., presence-only), daytime bear GPS locations, for the peak versus non-peak seasons and for weekends versus weekdays, for each type of human-use feature. The response variable was disturbance index (continuous), and the explanatory variable was season or day of the week. Bear ID was a random effect. I compared significant differences in average daily human-use events, N, to significant differences in disturbance index values. For example, if N on trails was significantly higher in the peak season than the non-peak season, then trail-related disturbance indices at bear locations would also be expected to be significantly higher in the peak season, if bears were not modifying their behavior to avoid people. Daytime bear locations were used because this is when bears were expected to respond most to human use, since human activity was highest during the day.

For further insight, I constructed analogous LME models with the distance to the nearest high-use trail, road, or facility as the response variable. High-use trails and facilities were those with $\geq$ 10 human-use events per day, and high-use roads were those with $\geq$ 100 vehicles per day. I compared distance from presence-only, daytime bear GPS locations to the nearest high use trail, road or facility, for the peak versus non-peak seasons and for weekends versus weekdays. If bears modified their behavior to avoid human disturbance, then distances between high-use features and bear locations should have been significantly greater during those time periods when N on those features was significantly higher.

Results

GPS location data were collected on five adult and sub-adult female grizzly bears from June – Oct 2014 and May – Oct 2015. I obtained 40,013 total GPS locations, or an average of 8,002 ± 3,921 locations per bear (range: 2,456 – 12,898 locations per bear). Of these, 16,430 locations were in the front-country, i.e., within 500 m of a trail, road, or facility. An average of 3,286 ± 1,778 locations per bear occurred in the front country (range: 816 – 5,337 locations per bear).

Front-country locations represented 40.9% ± 16.9% (range: 25.0% – 60.1%) of each bear's total locations.

The mean size of the full home ranges of study bears was 102.9 ± 38.1 km^2 (range: 57.3 – 148.1 km^2). Mean front-country home range size was 21.7 ± 5.1 km^2 (range: 16.1 – 28.6 km^2).

HABITAT SELECTION

Bears showed significant habitat preferences within both their full home ranges and their front-country home ranges, with grass and shrub significantly preferred over forest and barren areas (for full home ranges: $\lambda = 0.035$, $p = 0.008$; for front-country home ranges: $\lambda = 0.074$, $p = 0.021$) (Fig. 2). Bears selected for forest significantly more in the front country than at the full home range scale ($z = 1.974$, $p = 0.024$) (Fig. 2), and they selected for grass significantly less in the front country than at the full home range scale ($z = -1.67$, $p = 0.048$) (Fig. 2).

BEAR OCCURRENCE IN RELATION TO HUMAN ACTIVITY

Spatiotemporal patterns of human activity

For all three types of human-use features, the average number of daily human-use events, *N,* was significantly higher on weekends than weekdays and in the peak season than the non-peak season (Table 3). There was also significant temporal variation in *N* between each of the four time periods (peak season-weekend, peak season-weekday, non-peak season-weekend, non-peak season weekday); patterns of significance varied by type of human-use feature (Table 3). In all four time periods, *N* values differed significantly between individual trails ($F = 17.66$, $p < 0.001$), roads ($F = 17.66$, $p < 0.001$), and facilities ($F = 11.12$, $p < 0.001$) (Table A1), indicating high spatial variation in human use as well.

Overall and diurnal patterns of bear space use

There was strong support for only one GLMM predicting bear space use in relation to timing and intensity of recreation in the front country (Table 2). This model identified only habitat and an interaction between road-related disturbance and time of day as significant predictors of bear space use (Table 2). Study animals avoided road-related disturbance during the daytime ($z = -2.013$, $p = 0.044$), suggesting bears were more likely to be found at locations farther away from high-use roads during the day. During the mornings, evenings, and at night, bear avoidance of road-related disturbance was significantly less than during the daytime (for mornings and evenings, $z = 3.713$, $p < 0.001$; for nights, $z = 5.489$, $p < 0.001$) (Fig. 3), suggesting that bears moved closer to high-use roads during these hours. Consistent with habitat selection results, GLMMs indicated bears avoided forested habitat ($z = -2.009$, $p = 0.044$).

Trail-related disturbance and facility-related disturbance indices at bear locations did not contribute significantly to the explained deviance for any candidate models ($p > 0.05$), indicating that bear space in relation to human activity on trails and facilities was not significantly different than expected if space use was random. Interactions between time of day and trail- and facilities-related disturbance indices also were not significant, suggesting bears did not adjust their space use in response to diurnal fluctuations in human activity on these features.

Weekly and seasonal patterns of bear space use

LME models indicated that there was no significant difference in trail-related disturbance indices at daytime bear locations on weekends compared to weekdays ($F = 0.359$, $p = 0.550$) (Table 3; Fig. 4), even though trail N was significantly higher on weekends than weekdays ($t = -6.478$, $p < 0.001$). Bears were significantly farther away from the nearest high-use trail on weekends compared to weekdays ($F = 3.94$, $p = 0.049$) and during the peak season compared to the non-peak season ($F = 14.22$, $p < 0.001$) (Table 3; Fig. 4).

LME models also showed no significant difference in facility-related disturbance indices at daytime bear locations in the peak season versus the non-peak season ($F = 1.965$, $p = 0.161$), even though N was significantly higher in summer than in the spring and fall months ($t = 2.656$, $p = 0.012$). Bears were significantly further from the nearest high-use facility in the peak season than the non-peak season ($F = 15.830$, $p < 0.001$) (Table 3; Fig. 4).

Discussion

BEAR RESPONSES TO RECREATION IN THE FRONT COUNTRY

My results indicate that study bears attempted to avoid encountering people in the front country. Specifically, bears increased their use of forest cover when in high human-use areas, and they modified their behavior in response to fine-scale spatiotemporal variation in human activity on trails, roads, and in facilities. Although bears did not avoid high human disturbance for all features in all time periods, in no cases did bears prefer times and places of higher human disturbance, no matter the type of human use. Instead, bears appeared to use high human-use areas when risk of encountering people was low, and to avoid these areas when risk of detection by people was highest, as has been documented for other large carnivores (Oriol-Cotterill et al. 2015b).

Consistent with past studies (Gibeau et al. 2002, Northrup et al. 2012), bears avoided all roads or at least high-use roads during the day, but they demonstrated significantly less avoidance of roads during the mornings, evenings, and at night. Bears did not appear to modify their daytime habitat use in response to significantly lower traffic levels on weekdays and during the non-peak season. This may be because daytime road traffic was relatively high on all roads, even during non-peak season weekdays, and vehicles were the most lethal threat to bears in the study area. Bears foraged along grassy roadsides, which provided little cover, and used roads as movement corridors. Daytime traffic levels were likely always too high to provide consistent security for these activities.

In contrast to roads, bears did not exhibit a diurnal response to human activity on trails and in facilities. Bears' lack of adjustment to daily fluctuations in numbers of people on trails was unexpected, but most trails were located in fairly dense forest. This may have allowed bears to step into cover or use nearby, well-concealed game trails during the daytime as people approached, thereby reducing the need for increased avoidance during daily periods of high human use. Many facilities are campgrounds, where human use levels do not fluctuate widely over the course of a day. Campgrounds were fullest at night, when people were inactive, and in the morning and the evening, when people were active, but also had large numbers of occupants during daytime hours. Thus, there was likely no predictable daily quiet time in campgrounds that would signal lower levels of human disturbance to bears.

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Instead, study animals appeared to modify their spatial distribution in response to both within-week and seasonal fluctuations in trail-related disturbance, and in response to seasonal fluctuations in facility-related disturbance. Bears selected locations farther away from high-use trails throughout the day on weekends and during the peak season, when the number of hikers and bikers was greatest. Bears also selected for daytime locations farther away from facilities in the peak season, when daily visitation at facilities was significantly higher than in the spring and fall. Bears' use of locations closer to facilities in the non-peak season may be attributable not only to changes in human-use levels, but also to bears' attraction to natural food resources available near some facilities in the spring and fall.

Bears preferred grass and shrub over forest habitat in both the front country and at the full home-range scale. This is not surprising, given that almost all bear plant foods grew in open areas. Nonetheless, bears selected for forest significantly more, and open grassy areas significantly less, in the front country compared to their full home ranges. This suggests study animals may have used forest cover to conceal themselves from people and thereby reduce risk of encounters in the front country. Brown bears in Sweden have also been observed to use denser cover when closer to human activity (Ordiz et al. 2011), and this has been reported for other large carnivores as well (e.g., spotted hyenas (*Crocuta crocuta*): Boydston et al. 2003, Kolowski and Holecamp 2009; lions (*Panthera leo*): Schuette et al. 2013; cougars (*Puma concolor*): Dickson et al. 2005).

STUDY LIMITATIONS

While this study produces clear patterns regarding the spatial and temporal dynamics of bear avoidance of humans, its findings warrant consideration of potential weaknesses. First, my sample size of five bears is smaller than hoped, though it is consistent with similarly detailed, GPS-based studies of large carnivores (e.g., Broekhius et al. 2013). My population of interest was limited to those bears that consistently used front-country habitats, and this population was relatively small. The individuals sampled represented greater than 50% of front-country bears, and thus they should have provided a reasonable representation of bear behavior in the region. Second, my choice of home range estimator affected the distribution of random absence points within bears' front-country home ranges. A more liberal method, such as minimum convex polygon, likely would have generated more absence points located farther from human-use features, which may have led to disturbance indices at actual bear locations being greater than expected if space use was random. No home range estimator is free from bias, however. Minimum convex polygons tend to overestimate animal space use (Douglas-Hamilton et al. 2005, Macdonald et al. 1980), and my use of this method would have included large areas outside of the front country within bears' front-country home ranges.

This study could be improved by inclusion of additional years of data, particularly data from a year in which there was a good *Shepherdia* berry crop. *Shepherdia* berries represent a critical bear food resource when present, and could motivate bears to tolerate higher levels of human activity in exchange for high nutritional reward (Lima and Dill 1990). At the same time, conservation officers close many trails and facilities during abundant berry seasons, thereby using a management intervention to reduce human disturbance for bears. In 2014 and 2015, there was a total berry crop failure in Kananaskis Country, and comparison to a good berry year could provide additional insights into bears' front-country behavior.

FINE-SCALE AVOIDANCE AS ADAPTIVE BEHAVIOR

By overlapping with human use at a broad scale, but actively avoiding people once they were within high recreation areas, Kananaskis' front-country bears demonstrated a behavioral flexibility that is arguably adaptive (Elfstrom et al. 2014). Because human activity was widespread but also non-lethal in the study area, complete avoidance of people was probably not only impossible for bears, but also would have come at too great a nutritional cost, as animals would have lost access to prime foraging areas located near human-use features (Lima and Bednekoff 1999, Sih and McCarthy 2002). Most front-country bears were sub-adults and young mothers with cubs, who may not have access to high-quality, backcountry habitat due to their dominance status, and for whom adult male bears are a greater threat than humans (Kaczensky et al. 2006, Nevin and Gilbert 2005, Steyaert et al. 2016). Thus these individuals were likely in high human-use areas because broad-scale avoidance of human use, at the level of the home range, would decrease the odds of their and their offspring's survival (Steyaert et al. 2016). Fine-scale avoidance, in contrast, may have been the most efficient strategy for front-country bears to reduce probability of encounter with people, minimize encounters with adult male bears, and maximize nutrition.

MANAGEMENT IMPLICATIONS

My results provide support for management interventions that facilitate bears' avoidance of people by 1) limiting overall recreation levels, and 2) maintaining spatial and temporal predictability in recreation patterns. Study bears appeared to recognize and take advantage of predictably quieter times and places in the front country, using habitats closer to roads or closer to high-use roads in the morning, evenings, and at night; habitats closer to high-use trails on weekdays and in the non-peak season; and habitats closer to high-use facilities in the non-peak season. Managing recreation intensity, timing, and spatial extent is essential not only to limit encounters between bears and people, which can have direct fitness costs for bears (Herrero et al. 2005), but also to prevent displacement of bears from important food resources. Ordiz et al. (2013) found that brown bears in Sweden reduced their foraging time when experimentally approached by hikers, even during hyperphagia. Recreation is increasing in Kananaskis Country, and if bears continue to avoid high disturbance intensity, as they did in this study, then they may lose access to important nutritional resources as more places in the front country become areas of high human use.

Management interventions like aversive conditioning, which aims to heighten animals' association of human activity with risk, may be a complementary strategy for maintaining or increasing bear avoidance of people in the study area. However, conditioned bears still require access to alternative, minimally-disturbed habitats where they can meet their dietary needs. Therefore attempts to manage bear behavior in the front country must be accompanied by efforts to ensure sustainable levels and patterns of recreation.

CONCLUSION

This work augments a handful of recent studies that have rigorously quantified human disturbance and, by so doing, have empirically confirmed fine-scale behavioral adjustments made by large carnivores living in human-dominated landscapes (Carter et al. 2012, Oriol-

Cotterill et al. 2015b, Rogala et al. 2011). I sought to quantify not only the distribution of human use, but also spatial and temporal fluctuations in its intensity, thereby going beyond coarse-scale estimates of human activity that blur variation in space and time. I also focused on areas of high overlap between grizzly bears and people, where the dynamics of human activity were most likely to have direct impacts on bear behavior. In complex, shared landscapes like the Kananaskis front country, investigations of human activity impacts on wildlife may profit from more detailed assessment of the behavior of both study animals and people, and from recognition that both human disturbance and wildlife response are dynamic processes, which vary over multiple spatial and temporal scales.

Tables and Figures

Table 1. Numbers of front-country bear GPS locations (presence points) per time period included in GLMMs. These numbers include bear locations during all times of day (night, morning/evening, and daytime). LME models used the same sample of points, but only daytime locations.

Bear ID	Peak weekend	Peak weekday	Non-peak weekend	Non-peak weekday	**Total**
39	75	200	200	200	**675**
104	194	200	200	200	**794**
139	165	200	200	200	**765**
151	87	200	42	75	**404**
152	90	200	200	200	**690**
Total	**611**	**1,000**	**842**	**875**	**3,328**

Table 2. Summary of model selection statistics for GLMMs analyzing the probability of bear occurrence in the front country in relation to habitat type, disturbance index, and an interaction between disturbance and time of day, denoted by ":". All models included a random intercept for bear. Final candidate models were only those for which all explanatory variables contributed significantly to the variation in probability of bear occurrence (the dependent variable). DistRD denotes disturbance related to roads. Models were ranked according to Akaike weights (w_i) based on AICc. Included are number of parameters, the log likelihood and AICc differences (Δ_i).

Rank	Model	K	log likelihood	AICc	Δ_i	w_i
1	Habitat + DistRD:time	7	-4552.2	9120.5	0	1.00
2	Habitat + DistRD	6	-4567.7	9147.4	26.9	0.00
3	Habitat	5	-4572.1	9154.3	33.8	0.00
4	DistRD:time	4	-4585.4	9180.7	60.2	0.00
5	DistRD	3	-4600.8	9207.6	87.1	0.00

Table 3. Comparison of differences in average daily human-use events (*N)*, disturbance indices at daytime bear GPS locations, and distance between daytime bear GPS locations and the nearest high-use anthropogenic feature, in different time periods. A '+' (or '–') indicates the given *N*, disturbance index, or distance value was greater (or less) in the first time period listed, compared to the second, but the difference was not significant. A '+++' (or '– – –') indicates the given value was significantly greater (or significantly less) in the first time period listed, compared to the second.

TRAILS	*N*	Disturbance Index	Distance
Weekend – Weekday	+++	+	+++
Peak – Non-peak	+++	+++	+++
Peak weekend – Peak weekday	+++	+	+
Peak weekend – Non-peak weekend	+++	+++	+
Peak weekend – Non-peak weekday	+++	+++	+++
Peak weekday – Non-peak weekend	–	+++	+
Peak weekday – Non-peak weekday	+++	+++	+++
Non-peak weekend – Non-peak weekday	+++	+	+++

ROADS	*N*	Disturbance Index	Distance
Weekend – Weekday	+++	+++	+
Peak – Non-peak	+++	+++	+
Peak weekend – Peak weekday	+++	+++	+++
Peak weekend – Non-peak weekend	+++	+++	–
Peak weekend – Non-peak weekday	+++	+++	+
Peak weekday – Non-peak weekend	–	–	–
Peak weekday – Non-peak weekday	+	+++	–
Non-peak weekend – Non-peak weekday	+	+++	+

FACILITIES	*N*	Disturbance Index	Distance
Weekend – Weekday	+++	+++	–
Peak – Non-peak	+++	–	+++
Peak weekend – Peak weekday	+	–	+
Peak weekend – Non-peak weekend	+	– – –	+++
Peak weekend – Non-peak weekday	+++	+	+++
Peak weekday – Non-peak weekend	–	– – –	+
Peak weekday – Non-peak weekday	+++	+	+++
Non-peak weekend – Non-peak weekday	+++	+++	+

Fig. 1. Map of study area with locations of trail counters, vehicle counters, and monitored facilities indicated by green, yellow, and orange dots, respectively. The extent of the front country considered in the study is shown in light beige, with front-country GPS locations of study bear 139 (in pink) overlain for illustration. The location of the study area within the province of Alberta is indicated by the red rectangle in the inset map.
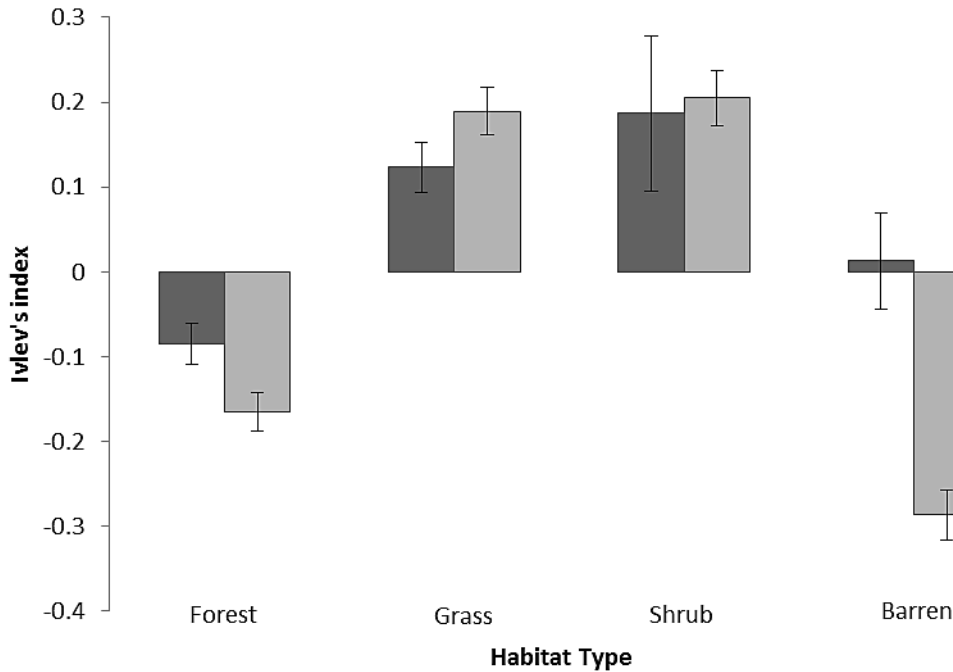
Fig. 2. Habitat selection for bears using Ivlev's index for preference/avoidance. Values > 0 indicate that a habitat type was used more than available (preference) and values < 0 indicate habitat type was used less than available (avoidance). The analysis was carried out for GPS locations vs. front-country home ranges (dark grey) and for GPS locations vs. full home ranges (light grey).
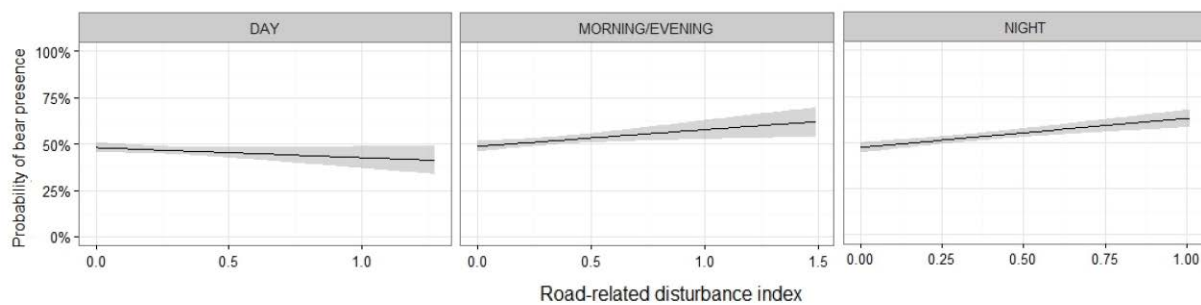
Fig. 3. The relationship between the road-related disturbance index and the probability of bear presence during the daytime (10:00 am – 6:00 pm), morning or evening (6:30 am – 9:30 am; 6:30 pm – 9:30 pm), and at night (10:00 pm – 6:00 am). Fitted lines displayed are averages ± 95% confidence intervals. The interaction between road-related disturbance and time of day was significant, suggesting that bear avoidance of human activity on roads was dependent on time of day. This interaction was not significant for trails or facilities.

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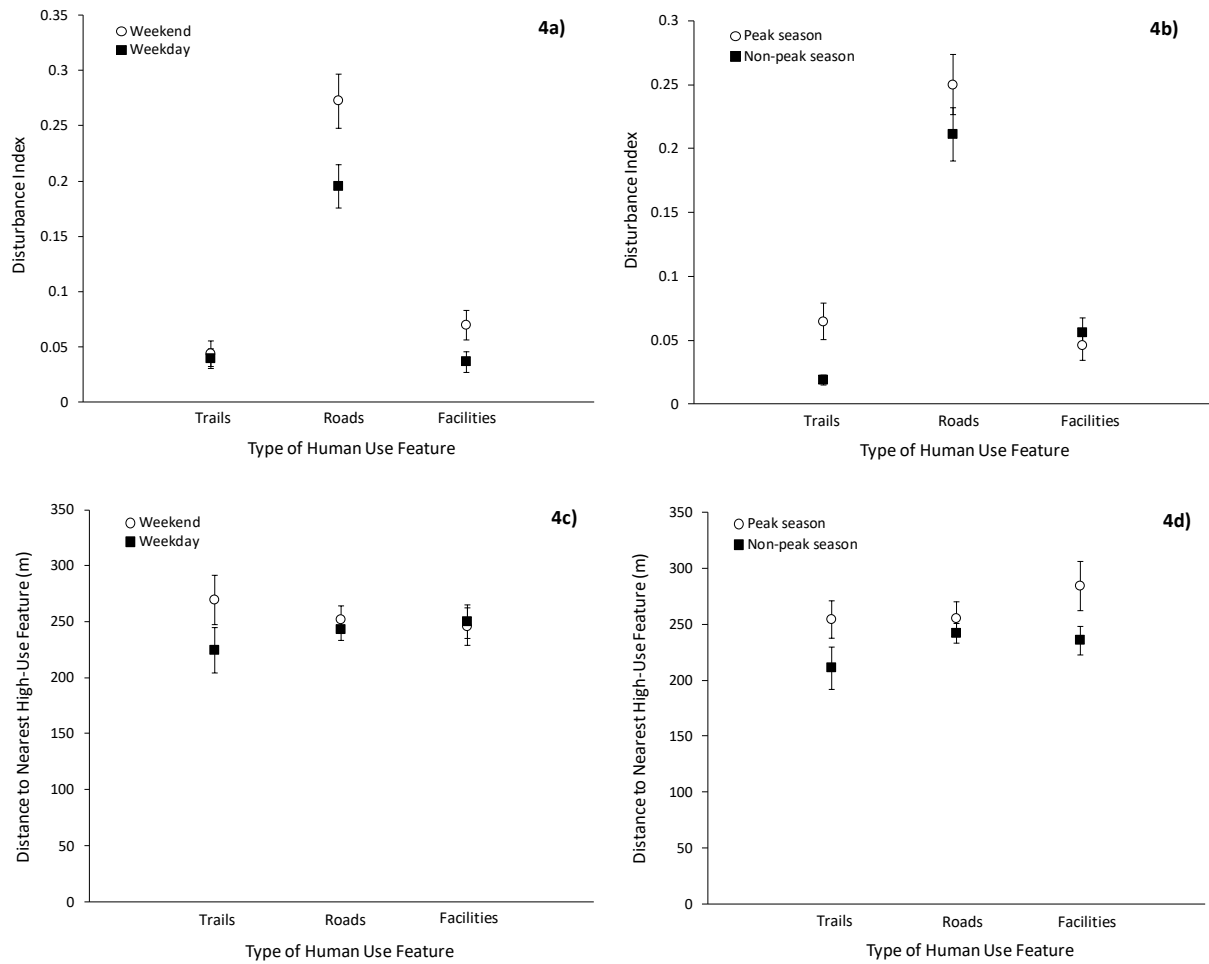
Fig. 4. Average disturbance index values (4a & 4b) and distance to nearest high human-use feature (4c & 4d) at daytime front-country bear locations, depending on type of human-use feature, day of the week, and season. For all types of human-use features, the average daily human use, *N,* was significantly higher on weekends than weekdays and in the peak season than the non-peak season. High human-use features were those for which $N \geq 10$ (for trails and facilities) or $N \geq 100$ (for roads). Error bars represent 95% confidence intervals.

Supplementary Material

Table S1. Summary of average daily human-use events, *N,* for trails and roads in the study area, by time period. For trails, estimated average daily absolute counts are in parenthesis and italics to the right of *N* values. For three trails longer than 4 km in length (one-way), counters are indicated by numbers "1" and "2" (e.g., "Three Isle 1", "Three Isle 2").

	Peak weekend	Peak weekday	Non-peak weekend	Non-peak weekday
TRAILS				
Wedge Pond	22 *(58)*	13 *(28)*	13 *(30)*	4 *(8)*
Elbow Lake 1	103 *(222)*	45 *(93)*	70 *(142)*	22 *(45)*
Highwood Meadows	51 *(136)*	26 *(66)*	46 *(128)*	20 *(43)*
Ptarmigan Cirque	90 *(280)*	39 *(105)*	76 *(269)*	22 *(52)*
Mt Everest Expedition	36 *(97)*	22 *(55)*	17 *(43)*	7 *(16)*
Lower Lake	17 *(40)*	7 *(16)*	8 *(18)*	3 *(5)*
Eau Claire Interpretive	10 *(22)*	4 *(10)*	4 *(2)*	2 *(4)*
Marl Lake Interpretive	25 *(63)*	19 *(44)*	15 *(39)*	4 *(7)*
Rockwall Interpretative	5 *(10)*	5 *(10)*	3 *(5)*	2 *(2)*
Boulton Interpretive	13 *(31)*	10 *(22)*	7 *(16)*	2 *(4)*
Three Isle 1	70 *(137)*	33 *(62)*	38 *(71)*	12 *(28)*
Elbow Lake 2	42 *(107)*	13 *(38)*	27 *(64)*	9 *(23)*
Upper Lake East	68 *(129)*	27 *(45)*	45 *(81)*	11 *(25)*
Galatea 2	84 *(263)*	20 *(48)*	69 *(198)*	14 *(34)*
Three Isle 2	39 *(88)*	19 *(45)*	18 *(36)*	6 *(13)*
Galatea 1	110 *(277)*	29 *(62)*	94 *(232)*	20 *(41)*
Terrace South	13 *(30)*	5 *(11)*	8 *(18)*	3 *(8)*
Lodgepole	29 *(73)*	22 *(52)*	8 *(20)*	4 *(7)*
Pocaterra south	3 *(8)*	2 *(4)*	2 *(3)*	1 *(1)*
Bill Milne	41 *(111)*	34 *(91)*	22 *(56)*	11 *(25)*
Lakeside	23 *(58)*	18 *(42)*	10 *(26)*	3 *(7)*
Pocaterra north	8 *(26)*	4 *(12)*	6 *(21)*	2 *(8)*
Wheeler	31 *(81)*	22 *(53)*	11 *(30)*	3 *(6)*
Spruce Rd	20 *(47)*	16 *(39)*	10 *(25)*	4 *(10)*
Elk Pass	12 *(39)*	6 *(18)*	9 *(31)*	3 *(8)*
Whiskey Jack	3 *(8)*	2 *(4)*	2 *(3)*	1 *(2)*
Fire Lookout	5 *(12)*	3 *(6)*	3 *(7)*	2 *(6)*
Bill Benson	20 *(48)*	16 *(40)*	10 *(24)*	4 *(8)*
WWL Lodge Connector	20 *(47)*	16 *(35)*	10 *(24)*	4 *(8)*
ROADS				
Hwy 40 Elpoca	1,251	640	915	386
Hwy 40 Eau Claire	3,133	1,816	1,736	995
KLT Boulton	1,454	807	789	302
KLT PVIC	1,731	969	1,072	477
Smith-Dorrien south	838	508	488	154
Lakeshore Dr	34	20	22	11

3. Quantifying human activity improves wildlife occurrence models: A case study with grizzly bears

Summary

Conservation biologists are increasingly concerned about the diverse impacts of human disturbance on wildlife behavior. Yet most investigations of wildlife response to human activity do not estimate directly either the intensity of human use or its spatial and temporal variation. Instead, analyses typically rely on proxies to represent human impacts. In this study, I assessed whether including estimates of average daily recreation levels improved models developed to predict grizzly bear (*Ursus arctos*) habitat selection in two protected areas in Kananaskis Country, Alberta, Canada. Specifically, I compared three sets of habitat suitability models. The first set incorporated measures of distance to nearest trail, road, and facility, a conventional proxy for intensity of human use. The second model set also used distance to nearest feature, but categorized trails, roads, and facilities as having a high or low level of human activity. The third model set included estimates of not only distance to nearest trail, road, and facility, but also the average daily number of people or vehicles using each of these features. I applied these models to describe the occurrence of GPS-collared grizzly bears at a relatively broad spatial scale, where human activity was diffuse, and at a finer scale, where bear-human overlap was high. I used Akaike's Information Criterion and *k*-folds cross-validation to evaluate model performance. I found that at a broad spatial scale, grizzly bear habitat selection was best predicted by the second model set, while at a fine spatial scale, habitat selection was best predicted by the third set. By rigorously quantifying human use dynamics, ecologists may better evaluate disturbance impacts on wildlife behavior and occurrence, particularly when wildlife-human overlap is extensive. Paradigms from community ecology may suggest improved methods for measuring human activity. My findings are applicable to other analytical approaches and other types of human disturbance.

Keywords: grizzly bears, *Ursus arctos,* human disturbance, habitat suitability models, resource selection function

Introduction

Human activity occurs in nearly all of the world's natural areas, with wide-ranging implications for wildlife behavior, population dynamics, and community structure (Frid and Dill 2002, Hebblewhite and Merrill 2008, Oriol-Cotterill et al. 2015a). Ecologists investigating the impacts of human disturbance on large mammals are frequently interested in habitat selection of study animals, which is commonly assessed using habitat suitability models (e.g., Beckmann et al. 2012, Berland et al. 2008, Llaneza et al. 2012, Oriol-Cotterill et al. 2015b). These models estimate the likelihood that an animal will occur in a particular location on the landscape, given a number of predictor variables associated with that location (Hirzel and Le Lay 2008), including estimates of human disturbance. However, the human disturbance variables used in most habitat suitability models do not represent direct estimates of human activity or its spatiotemporal variation. Instead, wildlife ecologists commonly use proxies meant to reflect the intensity of human use, such as distance to nearest settlement, road or trail; or density of these anthropogenic features within a pre-defined radius. This practice allows the relatively straightforward

quantification of human disturbance from existing maps or remote sensing products, but it may have two key shortcomings. First, reliance on static proxies limits the ability of researchers to assess how temporal changes in the number of people on the landscape impact wildlife habitat selection. Second, proxies typically fail to account for spatial variation in activity across different human use features. A number of studies have shown that wildlife responds not to the presence or number of anthropogenic features per se, but rather to the number of people using those features (Coleman et al. 2013, Hebblewhite and Merrill 2008, Whittington et al. 2005). This suggests that a more mechanistic understanding of wildlife behavior may be achieved by rigorously quantifying the spatiotemporal dynamics of human activity.

Recreation is one type of human disturbance that is well-suited to more rigorous estimation in the context of habitat suitability models. In protected areas, recreation and associated vehicle traffic are often confined to defined trails, roads, and facilities, which makes robust monitoring of human use feasible. In areas where recreation is well-developed, human presence on the landscape is regular (often daily), persistent over time, and spatially widespread (Beeco and Brown 2013), potentially impacting wildlife across multiple spatial and temporal scales. Technology for counting people on trails and vehicles on roads is also readily available, and visitor monitoring studies have recently applied a number of new tools to estimate intensity of recreation activity (D'Antonio et al. 2010, Meijles et al. 2014, Wolf et al. 2012). However, these tools have been used primarily to understand visitor behavior, while efforts to assess visitor impacts on the surrounding biotic and abiotic environment remain limited (Monz et al. 2010, Larson et al. 2016). This may be because visitor impact studies require not only financial resources to purchase needed equipment, but also substantial staff time to conduct field work and analyze data. Yet participation in outdoor recreation and ecotourism is increasing worldwide (Balmford et al. 2009, Cordell 2012), underscoring the need to evaluate whether investment in more robust human use monitoring can improve our understanding of wildlife behavior.

In this chapter, I seek to assess whether rigorous estimates of recreation intensity improve predictions of habitat selection patterns of grizzly bears (*Ursus arctos*) living in two provincial parks in Alberta, Canada. My previous work demonstrated significant spatial and temporal variation in recreation intensity across this landscape (Chapter 1). I constructed habitat suitability models for bears at broad and fine spatial scales, and all models included a measure of human disturbance as a predictor variable. The broad spatial scale corresponded to the full extent of grizzly bear home ranges, which included sizeable areas where presence of people was rare. Fine-scale models, in contrast, focused on valley bottom portions of bear home ranges, where human activity was pervasive. Within each spatial scale, I compared the fit and predictive success of models that incorporated only static proxies for human disturbance, to those of models that rigorously quantified the spatial and temporal characteristics of human use. Since large parts of the full home ranges of study bears were separated from human activity by considerable distances, I hypothesized that proxies would be sufficient to develop a robust, broad-scale habitat suitability model. At a fine scale, however, I expected that bear behavior would be more directly influenced by recreation, due to close proximity of bears to people. Therefore I hypothesized that the best fine-scale model would directly quantify intensity of human use.

Materials and Methods

STUDY AREA

This study was conducted in Peter Lougheed and Spray Valley Provincial Parks (50°N, 115°W; area = approx. 600 km^2) on the eastern slopes of the Rocky Mountains in western Kananaskis Country, Alberta, Canada (see Fig. 1, Chapter 1). Elevation in the study area ranged from ~1600 m at valley bottom to greater than 3000 m along the Alberta-British Columbia border. Climate was continental and dry (~470mm annual precipitation), with relatively wetter winters than summers, and with more precipitation at higher elevations than valley bottoms. Valley bottoms were dominated by coniferous forests, primarily lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*), mixed with Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at higher elevations. Conifer stands were interspersed with patches of wetland forest, shrubs and grassy meadows. Major waterways included the Kananaskis River and Upper and Lower Kananaskis Lakes.

Recreation in these parks was limited to non-motorized activities, chiefly hiking, biking, and camping, which were permitted only on designated trails and facilities. Road access into Peter Lougheed and the Spray Valley was via Highway 40, a two-lane paved highway; the Kananaskis Lakes Trail, a two-lane paved road, and the Smith-Dorrien Trail, a wide gravel road (see Fig. 1, Chapter 1). The study area included ~220 km of hiking and biking trails; ~70 km of roads, nearly all of which were paved; 8 auto-accessible campgrounds (~600 total campsites); 3 walk-in campgrounds (74 campsites); 17 day-use areas; a major visitor center; a lodge with 22 cabins and 13 additional campsites; and a 40-lot, seasonal cottage community along the Lower Kananaskis Lake shore. For the purposes of this study, I classified this recreation-related infrastructure into three categories: 1) trails, including both hiking and biking trails; 2) roads, including primary and secondary, paved and unpaved roads; and 3) facilities, which comprised all campgrounds, day-use areas, and the visitor's center and other buildings. These human-use features were almost entirely concentrated in the valley bottoms. Visitation to Peter Lougheed and the Spray Valley was estimated to be greater than 400,000 people/year (D. Fizor, *personal communication*), with the highest visitation occurring from the late June through early September.

SPECIFICATION OF HABITAT SUITABILITY MODELS

I used resource selection function (RSF) models (Manly et al. 1993) to investigate the probability of grizzly bear presence in relation to spatial environmental and human disturbance variables. I specified all RSF models as generalized linear models (GLMs) with a binomial error structure and a logit link function (Boyce et al. 2002); the binomial response variable was either 0 or 1, with 1 representing actual bear presence and 0 representing randomly generated absence points. All statistical analyses were conducted using R 3.3.1 software (R Development Core Team 2016). I extracted values of environmental and human disturbance covariates using ArcGIS 10.2.2 (Environmental Systems Research Institute 2014) and Geospatial Modeling Environment 0.7.3 (GME; Beyer 2014).

Grizzly bear data

I used GPS collar locations collected from five adult and sub-adult female grizzly bears during 2014 – 2015. Data from female bears were used because their home ranges were fully contained within the study area and because all female bears retained their collars for at least one complete non-hibernation season (May – Oct). Collars were programmed to record a location once every

60 minutes (one collar) or once every 30 minutes (four collars). For a complete description of grizzly bear GPS data collection and analysis, see Chapter 1.

Habitat selection of grizzly bears varies seasonally (Gibeau 2000); therefore I used only bear locations collected during hyperphagia, when bear behavior is focused on eating to gain weight for hibernation (July 15 – Oct 31; Donelon 2004). Locations obtained during the spring breeding season were excluded. There was no berry crop in 2014 or 2015, limiting the need to divide hyperphagia into summer and fall components. Because I was interested in evaluating models that accounted for the effect of human disturbance on bear behavior, I used only GPS locations taken during the daytime (9:00 – 18:00), when recreation activity was highest (Chapter 1).

Recreation occurred in the home ranges of all study animals but was concentrated in specific areas such as valley bottoms. Therefore I considered bear habitat selection at two spatial scales, based on the degree of overlap with human activity. First, I classified all bear GPS locations occurring within 500 m of a road, trail, or facility (25-60% of locations per bear, Chapter 1) as "front-country" locations, in accordance with previous grizzly bear studies that identified a 500 m zone of influence around human-use features (Ciarniello et al. 2009, IGBC 1998, Gibeau et al. 2001). I expected that within this zone, recreation dynamics may be very important to bear habitat selection. I randomly sampled 300 front-country locations per bear to delineate the front-country home range of each animal. Next, I considered the extent of each bear's full home range, which can be quite large in Kananaskis Country (up to 1,000 km^2 for females, Stevens and Gibeau 2005), with some areas separated from human activity by several kilometers or by significant physical features such as mountain ranges. I expected that when bears were in these more remote areas, their behavior would be less influenced by human disturbance. I randomly sampled 600 locations per bear to delineate the full home range of each study animal. Home ranges were based on the 90% isopleth (Borger et al. 2006) from kernels created using the fixed Gaussian Kernel Density Estimate.

I constructed separate sets of RSF models to predict the distribution of bear locations within 1) the full home ranges of individuals (a relatively broad spatial scale) and 2) the subset of individual home ranges located in the front-country (a finer spatial scale, where human-bear overlap was high). In addition to the randomly sampled presence points, I generated 600 random absence points within each bear's full home range and 300 random absence points within each front-country home range. I estimated the value of six environmental and three human disturbance predictor variables at each actual bear location and at each random absence point, as described below. Values at random points represented availability of resources, while values at presence points represented bears' resource use.

Predictor variables

I considered the following environmental covariates as predictor variables in RSF models: landcover, elevation, slope, aspect, greenness, and edge density. Landcover type was described from an existing landcover map for the study area derived from Landsat (Eastern Slopes Grizzly Bear Project 2000), collapsed to five major landcover types: avalanche slopes (the reference category); forested (including both coniferous and mixed coniferous-deciduous forests); herbaceous; shrubs; and barren areas with less than 5% vegetative cover. Overall classification error was estimated at $24 \pm 3.2\%$. To reduce this error, I visually checked the landcover map

against orthophotos in ArcMap (ArcGIS 10.2.2) to identify misclassified areas larger than five pixels in size. I then corrected these misclassifications using ARIS Grid and Raster Editor (ARIS B.V. 2016). Elevation (m), slope (degrees), and aspect class (northeast, southeast, southwest, northwest, and flat) were derived from a 30x30 m Digital Elevation Model (DEM). To estimate greenness, I used a seamless greenness vegetation map generated by Wierzchowski (2000) on the basis of tasseled-cap transformations of spectral reflectance from Landsat images. Edge density was included as an indicator of landscape complexity and was derived in FRAGSTATS (McGarigal et al. 2012) on the corrected landcover map using a 250-m diameter moving window.

I also considered three human disturbance covariates: disturbance related to trails, disturbance related to roads, and disturbance related to facilities. Trails, roads, and facilities were treated separately because bears likely perceive them differently (J. Paczkowski, *personal communication*). Values of human disturbance covariates were estimated in three ways:

Distance to nearest human-use feature. Using existing anthropogenic GIS layers, I calculated the distance in meters from each bear presence and absence point to the nearest trail, road, and facility. Distance to nearest human-use feature is a common and simple proxy used in wildlife habitat suitability modeling.

Distance to nearest *high-use* human feature. Habitat selection of grizzly bears and other large carnivores has previously been evaluated by categorizing anthropogenic features into high- and low-use and considering only high-use features in analyses (e.g., Gibeau et al. 2002, Hebblewhite and Merrill 2008). I used a combination of motion-triggered cameras (Bushnell, Overland Park, USA), heat-triggered trail counters, magnetic vehicle counters (TrafX, Canmore, Canada), and consultations with Kananaskis Country staff to estimate daily human use on 29 trails, six roads, and 17 facilities located within the home ranges of GPS-collared bears. Data were collected from June – Oct 2014 and May – Oct 2015. Trail counters were installed on 15 hiking-only trails, and cameras were deployed on eight multiple-use trails and bike paths. Trail counters and cameras produced timestamped data for each hiker or biker, which were then summarized into daily totals. For trails longer than 4 km ($n =4$), trail counters or cameras were deployed every 3-5 km, because human use declined with distance from trailhead. Vehicle counters were located in pairs, on opposite sides of the road, at two sites on Highway 40 and two sites on the Kananaskis Lakes Trail. Vehicle counter locations were selected to capture spatial variation in traffic flow, since traffic decreased with distance from the Trans-Canada Highway, which is located approximately 35 km from the study area's northern boundary. Each counter recorded hourly counts of vehicles in the nearest lane of traffic; these data were summarized into daily totals. Counter accuracy was assessed against visual observations of vehicles. Based on data collected by trail and vehicle counters, I extrapolated human use counts on six additional trails and two additional secondary roads. To estimate use at facilities, I consulted with campground managers and conducted visual surveys of parking lots. See Chapter 1, Fig. 1 for a map of monitored trails, roads, and facilities.

For each bear presence or absence point, I calculated the distance in meters to the nearest high-use trail, road, or facility. High-use roads were those with greater than 100 vehicles per day, and high-use trails or facilities were those with greater than 10 human-use events per day. A human-

use event was defined as a group of hikers or bikers passing a trail counter or camera within one minute of each other, or an occupied parking space or campsite in facilities (Chapter 1). I considered this second approach to estimating human disturbance to be a mixed-proxy approach, since it included a coarse approximation of the intensity of human activity on anthropogenic features.

Human disturbance index. I estimated a trail-related, road-related, and facilities-related disturbance index at each bear GPS location and each randomly generated absence point (Fig. 1). This represented an attempt to quantify human disturbance directly, without use of proxies. The disturbance index was calculated using the formula $1 - (1 - 1/D)^N$ (Beale and Monaghan 2004), where N was equal to the average number of human-use events or vehicles per day on any given anthropogenic feature, and D was equal to the distance to that feature in meters. This formula assumes that human disturbance is proportional to both the intensity of human use and the distance from that use (Beale and Monaghan 2004). At low values of N, the disturbance index declines exponentially with distance; at higher values of N, the decline approximates a negative logistic curve.

For all types of human-use features, values of N differed significantly between weekends and weekdays, and between the summer (1 July – 31 Aug) and the fall (1 Sept – 31 Oct) (Chapter 1). Therefore unique values of N were assigned to each bear GPS location depending on the season and day of the week when it was obtained (summer-weekend, summer-weekday, fall-weekend, or fall-weekday). Each random absence point was assigned a date that matched that of an actual bear location and was given a corresponding N value.

Disturbance indices were artificially inflated at large values of N, so average daily vehicle counts were rescaled from 0 to 100 by dividing absolute counts by a constant. For bear GPS locations and random absence points that occurred during trail, road, or facility closure dates, N was equal to 0. For bear locations or absence points that overlapped directly with a human-use feature, D was set equal to 1.

In calculating disturbance indices, I capped D at a maximum of 500 m. When bears were greater than 500 m from a human-use feature, the influence of human activity was considered to be 0. The reasons for this were twofold. First, locations greater than 500 m from human-use features were outside of the above-defined zone of influence (Ciarniello et al. 2009, Gibeau et al. 2001) where bear behavior is most likely to be affected by human use. Second, disturbance indices typically levelled off at or very close to zero at distances beyond 500 m.

Bears were often within 500 m of more than one trail, road, or facility, so disturbance index values were also cumulative; i.e., final values of trail-related, road-related, and facilities-related disturbance covariates reflected the sum of the disturbance indices for each trail, road, or facility within 500 m of a given point.

I used a Spearman's rho (ρ) correlation analysis and analysis of variance inflation factors (VIF) to test for collinearity between predictor variables and between predictor variables and the dependent variable. VIF analysis was conducted using the 'fmsb' package in R (Nakazawa 2017). For all pairwise combinations of predictor variables, ρ was less than 0.60 and the VIF was

less than 4.0, providing no evidence of collinearity; thus all variables were retained in candidate models.

MODEL EVALUATION

Based on the three approaches to estimating human disturbance covariates described above, I constructed three sets of RSF models. The first set of models used distance to nearest trail, distance to nearest road, and distance to nearest facility as the three human disturbance covariates. I termed these RSF models "distance-proxy models." In the second set of RSF models, termed "mixed-proxy models," the three human disturbance covariates were distance to nearest *high-use* trail, distance to nearest *high-use* road, and distance to nearest *high-use* facility. The third set of RSF models, or "disturbance index models," used the trail-related disturbance index, road-related disturbance index, and facilities-related disturbance index as human disturbance covariates. All combinations of environmental predictor variables were included in each set of RSF models. Separate models were constructed for the full home range and front-country home range.

Model selection

Within each set of models, I used the Akaike Information Criterion for small sample sizes (AICc) to select the model that best fit the data. That is, I used AICc to select the top model among distance-proxy RSF models, the top model among mixed-proxy RSF models, and the top model among disturbance-index RSF models, for both the full home range scale and the front-country home range scale. This resulted in three top candidate models at each spatial scale (Table 1). I then compared the AICc scores of these three top models to determine which model type (distance-proxy, mixed-proxy, or disturbance-index) best fit the data overall. I conducted an analysis of deviance to ensure that final candidate models retained only those environmental and human disturbance covariates that contributed significantly to the variation in bear presence. Starting from a full model that included all predictor variables, I performed backward elimination procedures to exclude those covariates that did not contribute significantly ($p \geq 0.05$) to the explained deviance. I estimated coefficients for all covariates retained in the top models selected by AICc (Table 2).

Model prediction

While AIC assists in selecting the model that best fits the data, it provides little insight into the degree to which model predictions correspond to actual habitat use. That is, if all candidate models poorly predict actual bear habitat selection, AIC will simply select the best model among these poor candidates. Therefore, I used *k*-folds cross validation to assess the predictive accuracy of the top distance-proxy, mixed-proxy, and disturbance-index models identified by AICc at each spatial scale (Boyce et al. 2002). Because grizzly bear GPS locations fit a presence/available (use-versus-availability) design, rather than a presence/absence design, other methods commonly used to assess predictions of logistic regression models (e.g., classification tables, confusion matrices, receiving operating characteristics) were not appropriate (Boyce et al. 2002).

I followed Huberty's (1994) rule of thumb to partition the data in each of the top models into five groups, with an equal number of data points in each group. I trained each model iteratively on four of the five data sets, with the fifth data set serving as a test group. I first used each best-fit

model to predict the RSF scores for the training data. Predicted RSF scores represented the probability of grizzly bear presence on a scale from 0 to 1. In a good model, it would be expected that low predicted RSF scores would be associated with absence points, and high scores with presence points. I binned the predicted RSF scores into ten geometric interval bins scaled between the minimum and maximum scores for each model; these bins represented the range of RSF scores available on the landscape. Next, I used the training model to predict RSF scores for presence locations *only* in the testing data set. Thus, each presence-only cross-validation point was assigned a predicted RSF score. I calculated the proportion of cross-validation use points that fell into each of the ten RSF bins (Fig. 2, 3), and I computed the Spearman's rank correlation (ρ) between the proportion of cross-validation points within individual bins and the bin rank (Table 3). A strong positive correlation would indicate a model with good predictive performance, as more presence points would fall into higher RSF bins. I repeated this process for all training and test groups and each of the six top models. I compared the average Spearman's ρ for the top distance-proxy, mixed-proxy, and disturbance-index model at each spatial scale to determine which model best predicted bears' habitat selection within both their full home ranges and within the front country.

Results

Mean home range size for the five female grizzly bears monitored was 102.9 ± 38.1 km^2 (range: $57.3 - 148.1$ km^2). Mean front-country home range size for these animals was 21.7 ± 5.1 km^2 (range: $16.1 - 28.6$ km^2).

HABITAT SELECTION IN THE FULL HOME RANGE

All three top models (distance-proxy, mixed-proxy, and disturbance-index) included all predictor variables except elevation, which was excluded based on results of analysis of deviance (Table 1). All top models indicated that bears selected for higher greenness and higher edge density, and that they selected against steep slopes and forested habitat (Table 2a). The top distance-proxy and mixed-proxy models also suggested bears selected areas further from roads and closer to trails and facilities (Table 2a).

The top mixed-proxy model had the lowest AICc score. The top distance-proxy model also received some weight, but the mixed-proxy model was nearly four times as likely to be the best fit model (Table 1). Cross-validation indicated that the mixed-proxy model also had the best predictive accuracy at the full home range scale, although all three top models (distance-proxy, mixed-proxy, and disturbance-index) displayed significant positive Spearman-rank correlations across RSF bins (Table 3a, Fig. 2), suggesting all models predicted actual bear habitat selection relatively well. The mixed-proxy model was slightly more significant overall, however, and this model also showed the most consistency between *k*-folded sets (Table 3a, Fig. 2).

HABITAT SELECTION IN THE FRONT COUNTRY

Analysis of deviance excluded elevation, slope, and edge density from all three model types (distance-proxy, mixed-proxy, disturbance-index); all other predictor variables were retained (Table 1). All top models indicated that bears selected for areas of higher greenness and for grass and shrub habitat, and that bears avoided roads and/or road-related disturbance in the front

country (Table 2b). The top distance-proxy and mixed-proxy models also suggested bears selected for areas closer to facilities (Table 2b).

The disturbance-index model was the best model overall, in terms of both fit and predictive accuracy. This model had the lowest AICc score and was the only model to receive weight (Table 1). It also displayed the most significant positive average Spearman rank correlations across RSF bins (Table 3b, Fig. 3) and showed the strongest differentiation between low, middle and high RSF bins (Fig. 3).

The average Spearman rank correlation for the top distance-proxy model was not significant (Table 3b, Fig. 3), suggesting this model did not predict bear habitat selection well in the front country. For the mixed-proxy model, the average Spearman rank correlation was significant, but there was high variation between k-folded sets, and correlations were not significant for three individual sets (Table 3b). Both the mixed-proxy and distance-proxy models poorly discriminated the proportion of grizzly bear presence points in the middle RSF bins (Fig. 3).

Discussion

Differentiation of human use levels improved the success of RSF models in predicting grizzly bear occurrence. For full home ranges of study animals, the best model fit and predictive accuracy was demonstrated by the mixed-proxy model. Even though the spatial extent of bear-human overlap was limited at this broader scale, this result indicates that rough approximations of human use intensity (i.e., high versus low use) nonetheless improved predictions of grizzly bear habitat selection. Within the front country, the disturbance-index model was the best predictor of bear presence, suggesting that when overlap between people and bears was high, bear habitat selection was more heavily influenced by the dynamics of human activity. These results are consistent with analyses of fine-scale responses of wolves (*Canis lupus*) and elk (*Cervus canadensis*) to human activity on trails and roads in Banff National Park, which showed that wolf and elk space use were best predicted by models that included an interaction between distance to anthropogenic feature and numbers of people or vehicles using that feature (Rogala et al. 2011).

Although all three top models performed well at the full home range scale (Table 3; Fig. 2), this was not the case for the front country (Fig. 3), where proxy-based models were relatively poor predictors of bear habitat selection. This is likely because the two proxy-based models did not adequately account for the dynamics of human activity, which appeared to have a greater effect on bear behavior in the front country. Habitat and terrain are also more uniform in the front country, and therefore proxy models may not have distinguished as clearly between used and available locations based primarily on environmental covariates. Bears' full home ranges, in contrast, contained more diverse values for environmental variables, such as sizeable barren areas above tree-line that are not found in valley bottoms.

INTERPRETING BEAR BEHAVIOR

For front-country habitat in which bears were more likely to encounter humans, the disturbance-index model allows a more nuanced interpretation of bear behavior. For example, this model indicated that bears neither avoided nor selected for facilities-related disturbance, while the two

proxy-based models suggested that bears selected for areas near facilities (Table 2b). In contrast to the proxy models, the disturbance-index model accounted for variability in human use levels among different facilities, on different days of the week, and across different seasons. Thus the disturbance-index model could discriminate between bear selection for a given location (such as areas near facilities), versus bear selection for disturbance levels at that location. The results of this model can be interpreted in two ways. First, bears may have responded to spatial differences in human use, avoiding the highest-use facilities in the study area and using areas closer to less-busy facilities. Second, bears may have responded to temporal variation in activity at facilities, selecting for areas closer to facilities on weekdays or during the fall, when human use lower. Habitats close to facilities provide key food resources for bears in the study area, and the disturbance-index model suggests that bears may balance these benefits against potential costs of proximity to human activity by using facility-adjacent areas when and where human use is lower. In fact, previous analyses (Chapter 1) showed that bears selected for human use associated with facilities in the fall, when human activity was lower and seasonal bear foods were available, but bears avoided facilities in the summer, when human activity was very high. Because the distance-proxy and mixed-proxy models did not rigorously quantify the dynamics of human use, they do not allow for an interpretation that bears may optimize their behavior when in areas of high human activity. Instead, they appeared to overemphasize bear selection for areas near facilities in the fall months.

IMPLICATIONS FOR MODELING IMPACTS OF HUMAN ACTIVITY

Grizzly bears and many other wildlife species respond to human activity in ways that resemble the responses of prey species to predators (Frid and Dill 2002, Ordiz et al. 2011, Oriol-Cotterill et al. 2015a). Studies of predator-prey interactions typically examine variation in both the density and the distribution of the predators, and in this paper, I attempted to quantify human activity with similar rigor. My human disturbance index was derived from a simple model of predation risk, which assumes that behavioral changes among prey are a function of both the number of and distance to predators (or recreationists, in this case) (Beale and Monaghan 2004). In this way, my disturbance-index models treat humans as just one more species on the landscape. This conceptualization may be particularly apt when the presence of people in wildlife habitat is regular, long-term, and spatially widespread. Such steady human activity can occur in a variety of contexts, e.g., in protected areas that allow extensive recreation; in and around settlements built within wildlife habitat (Llaneza et al. 2012); in former wildlife habitat that animals have recolonized, including urban areas (Magle et al. 2016, Northrup et al. 2012, Poessel et al. 2016); and in multiple-use landscapes where people engage in subsistence practices such as grazing livestock and gathering timber and non-timber forest products (Carter et al. 2012). The superior performance of disturbance-index models in the front country suggests that when human-wildlife overlap is high, application of tools from community ecology could improve insights into human impacts on wildlife behavior.

The results of this study also highlight an opportunity to test the value of rigorously quantifying human disturbance in other contexts. In addition to the RSF models used here, occupancy models (MacKenzie et al. 2005) can also easily incorporate measures of human use. Moreover, telemetry is not required to study wildlife habitat selection in relation to people; studies based on camera trap images, wildlife sign and visual observations are also appropriate. Counting people can be a starting point for investigations of wildlife response to different types of recreation activity, such

as hiking versus biking (Taylor and Knight 2003), or to different types of human use, e.g., tourism versus subsistence harvest of forest products (Carter et al. 2012). Moreover, rigorous investigations of human activity and its impacts on wildlife need not be limited to quantifying intensity of human use. For example, proliferation of GPS technology makes it increasingly feasible to track human movements on a very fine scale, and a recent study incorporated this technology to investigate real-time changes in grizzly bear movements in response to encounters with hikers (Ordiz et al. 2013).

Overall, I encourage a more dynamic approach to investigating the effects of human disturbance on wildlife species. If rigorous estimation of the intensity of human use is not possible, researchers can improve relevant proxies by better accounting for spatial and temporal variation in human activity. For example, levels of human use could be estimated for a subset of sample localities and then combined with expert opinion to define multiple categories of human use intensity (e.g., low, medium, high) across a study area. Ecologists can also distinguish between levels of disturbance during the day versus the night and, where relevant, between different days of the week and seasons of the year. Although collection of detailed human use data and its subsequent analysis may be challenging, this theme is ripe for development of new methods and analytical techniques. When counting people on the landscape is feasible, doing so is a logical first step toward understanding wildlife responses to humans on a finer scale.

Tables and Figures

Table 1. Summary of model selection statistics for resource selection function (RSF) models analyzing the probability of grizzly bear occurrence in relation to environmental and human disturbance predictor variables, at the scale of full home ranges and at the scale of front-country home ranges. TR denotes trails; RD denotes roads, and FAC denotes facilities. Models were ranked according to Akaike weights (w_i) based on AICc. All full home range models had 16 parameters, and all front-country models had 14 parameters.

FULL HOME RANGE RSF

Rank	Model type	Description	AICc	Δ_i	w_i
1	Mixed-proxy	Habitat + Greenness + Slope + Aspect + Edge Density + Distance.High.TR + Distance.High.RD + Distance.High.FAC	7766.4	0	0.79
2	Distance-proxy	Habitat + Greenness + Slope + Aspect + Edge Density + Distance.TR + Distance.RD + Distance.FAC	7768.9	2.5	0.21
3	Disturbance-index	Habitat + Greenness + Slope + Aspect + Edge Density + Disturbance.TR + Disturbance.RD + Disturbance.FAC	7809.4	43.0	0

FRONT-COUNTRY HOME RANGE RSF

Rank	Model type	Description	AICc	Δ_i	w_i
1	Disturbance-index	Habitat + Greenness + Aspect + Disturbance.TR + Disturbance.RD + Disturbance.FAC	4519.9	0	1.00
2	Mixed-proxy	Habitat + Greenness + Aspect + Distance.High.TR + Distance.High.RD + Distance.High.FAC	4535.6	15.7	0
3	Distance-proxy	Habitat + Greenness + Aspect + Distance.TR + Distance.RD + Distance.FAC	4542.2	22.3	0

Table 2a. Model coefficients, z-scores, and p-values for significant variables in the top distance-proxy, mixed-proxy, and disturbance-index resource selection function (RSF) models of grizzly bear habitat selection within the full home ranges of study animals.

DISTANCE-PROXY RSF

Variable	Estimate	Standard Error	z-score	p-value
Landcover: Forest	-0.815	0.106	-7.675	<0.001
Slope	-0.018	0.003	-5.791	<0.001
Edge density	3.47×10^{-3}	4.01×10^{-4}	8.665	<0.001
Greenness	0.015	2.65×10^{-3}	5.792	<0.001
Distance.TR	-5.38×10^{-5}	1.47×10^{-5}	-3.665	<0.001
Distance.RD	6.65×10^{-5}	2.21×10^{-5}	3.003	0.003
Distance.FAC	-3.77×10^{-5}	1.23×10^{-5}	-3.072	0.002

MIXED-PROXY RSF

Variable	Estimate	Standard Error	z-score	p-value
Landcover: Forest	-0.818	0.106	-7.699	<0.001
Slope	-0.018	0.003	-5.683	<0.001
Edge density	3.45×10^{-3}	4.00×10^{-4}	8.623	<0.001
Greenness	0.015	2.65×10^{-3}	5.837	<0.001
Distance.High.TR	-4.12×10^{-5}	1.13×10^{-5}	-3.653	<0.001
Distance.High.RD	5.95×10^{-5}	2.18×10^{-5}	2.724	0.006
Distance.High.FAC	-4.65×10^{-5}	1.18×10^{-5}	-3.932	<0.001

DISTURBANCE-INDEX RSF

Variable	Estimate	Standard Error	z-score	p-value
Landcover: Forest	-0.798	0.104	-7.664	<0.001
Slope	-0.022	0.003	-6.905	<0.001
Edge density	3.16×10^{-3}	3.98×10^{-4}	7.948	<0.001
Greenness	0.015	2.65×10^{-3}	5.692	<0.001

Table 2b. Model coefficients, z-scores, and p-values for significant variables in the top distance-proxy, mixed-proxy, and disturbance-index resource selection function (RSF) models of grizzly bear habitat use within the front-country.

DISTANCE-PROXY RSF

Variable	Estimate	Standard Error	z-score	p-value
Landcover: Grass	0.498	0.223	2.235	0.025
Landcover: Shrub	0.473	0.213	2.219	0.027
Greenness	0.017	4.59×10^{-3}	2.561	0.010
Distance.RD	2.41×10^{-4}	7.80×10^{-5}	3.085	0.002
Distance.FAC	-7.16×10^{-5}	2.26×10^{-5}	-3.174	0.002

MIXED-PROXY RSF

Variable	Estimate	Standard Error	z-score	p-value
Landcover: Grass	0.490	0.223	2.198	0.028
Landcover: Shrub	0.469	0.213	2.199	0.028
Greenness	0.015	4.57×10^{-3}	2.505	0.012
Distance.High.RD	2.39×10^{-4}	7.83×10^{-5}	3.047	0.002
Distance.High.FAC	-7.15×10^{-5}	2.19×10^{-5}	-3.264	0.001

DISTURBANCE-INDEX RSF

Variable	Estimate	Standard Error	z-score	p-value
Landcover: Grass	0.726	0.226	3.217	0.001
Landcover: Shrub	0.671	0.210	3.191	0.001
Greenness	9.41×10^{-3}	4.57×10^{-3}	2.060	0.039
Disturbance.RD	-0.597	0.140	-4.248	<0.001

Table 3a. Cross-validated Spearman rank correlations (ρ) between resource selection function (RSF) bin ranks and proportions of cross-validated use locations for individual and average model sets, for full home ranges of study bears. Results are presented by model type: distance-proxy, mixed-proxy, and disturbance-index.

Set	Distance-proxy RSF		Mixed-proxy RSF		Disturbance-index RSF	
	ρ	p-value	ρ	p-value	ρ	p-value
1	0.867	0.001	0.855	0.001	0.784	0.007
2	0.900	<0.001	0.964	<0.001	0.840	0.002
3	0.855	0.001	0.915	<0.001	0.827	0.003
4	0.967	<0.001	0.936	<0.001	0.806	0.004
5	0.855	0.001	0.976	<0.001	0.830	0.003
Average	0.988	<0.001	0.999	<0.001	0.964	<0.001

Table 3b. Cross-validated Spearman rank correlations (ρ) between resource selection function (RSF) bin ranks and proportions of cross-validated use locations for individual and average model sets, for front-country home ranges of study bears. Results are presented by model type: distance-proxy, mixed-proxy, and disturbance-index.

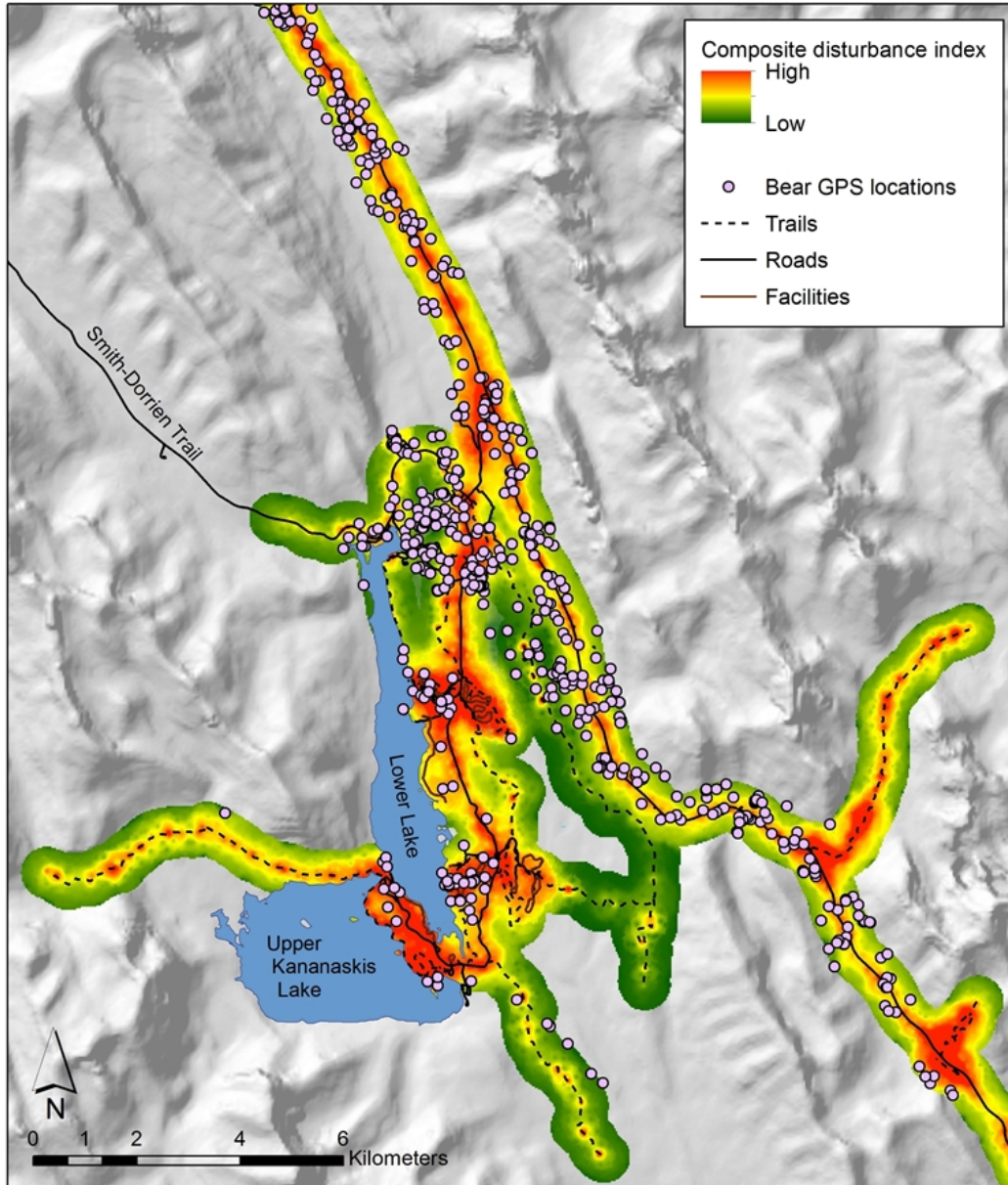| Set	Distance-proxy RSF		Mixed-proxy RSF		Disturbance-index RSF	
	ρ	p-value	ρ	p-value	ρ	p-value
1	0.689	0.028	0.259	0.469	0.851	0.002
2	0.772	0.009	0.634	0.049	0.875	<0.001
3	0.245	0.496	0.626	0.053	0.978	<0.001
4	0.665	0.036	0.729	0.017	0.821	0.004
5	0.098	0.789	0.394	0.260	0.867	0.001
Average	0.515	0.128	0.709	0.022	0.964	<0.001

Fig 1. Map of front-country disturbance indices for trails, roads, and facilities for weekends during the fall (1 Sept – 31 Oct), for the southern portion of the study area. GPS locations for grizzly bears (*Ursus arctos*) are also from fall weekends. For map display purposes, individual disturbance indices for trails, roads and facilities were re-scaled from 0-1 and overlaid to show a composite index. In disturbance-index RSF models, however, trail-related, road-related, and facilities-related disturbance indices were included as separate covariates, because response of bears to human activity may differ depending on type of human-use feature.

Fig. 2. Frequency of categories (bins) of resource selection function (RSF) scores for withheld use locations (i.e., testing data) of grizzly bears, for the top RSF models of bear habitat selection at the scale of full home ranges. (A) depicts the top distance-proxy model; (B) depicts the top mixed-proxy model, and (C) depicts the top disturbance-index model. Mean ($\pm$ S.D.) frequency values by RSF-score bin are illustrated. Spearman rank correlations for mean frequency values by bins indicated that all models were good predictors of cross-validated use locations, with the mixed-proxy model having the highest correlation ($\rho = 0.999$, $p < 0.001$).
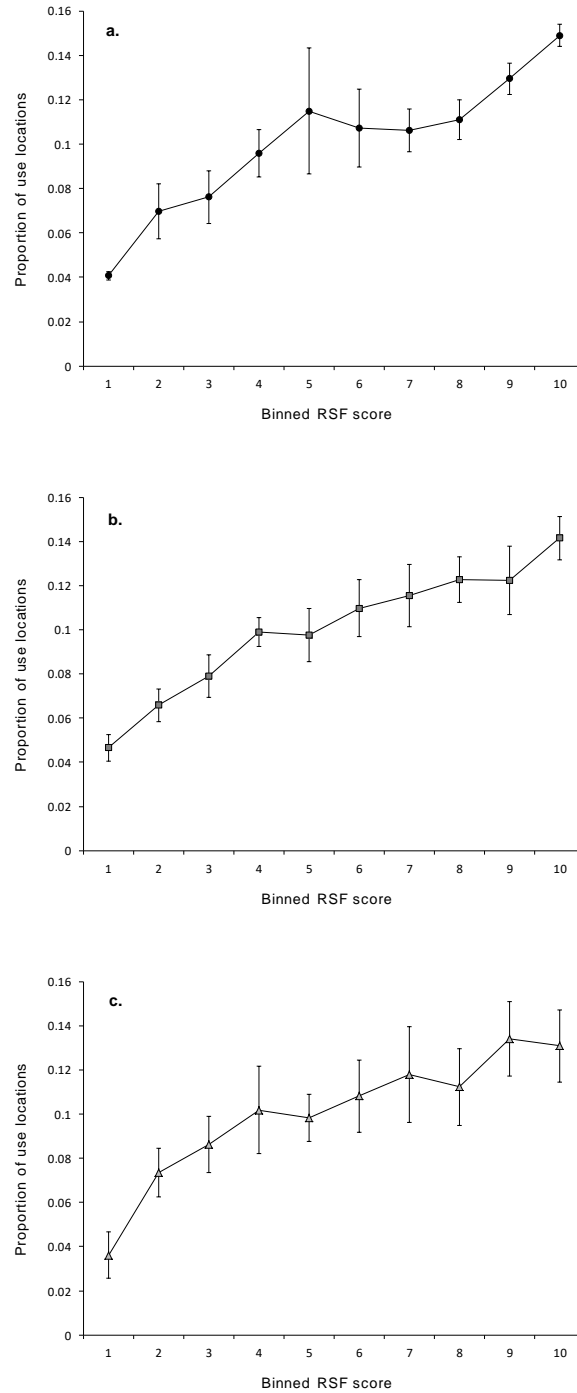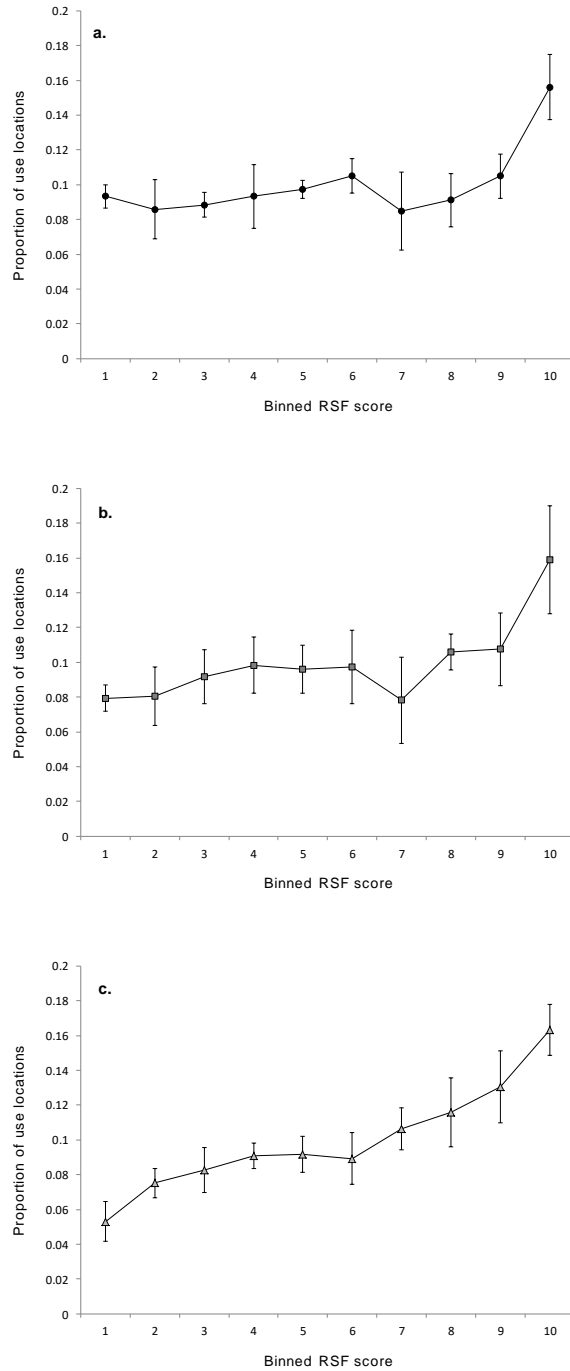
Fig. 3. Frequency of categories (bins) of resource selection function (RSF) scores for withheld use locations (i.e., testing data) of grizzly bears, for the top RSF models describing bear habitat selection within the front country. (A) depicts the top distance-proxy model; (B) depicts the top mixed-proxy model, and (C) depicts the top disturbance-index model. Mean ($\pm$ S.D.) frequency values by RSF-score bin are illustrated. Spearman rank correlations for mean frequency values by bins indicated that the disturbance-index model had the highest correlation ($\rho = 0.964$, $p < 0.001$) and best predicted cross-validated use locations. The mixed-proxy model was also significant ($\rho = 0.709$, $p = 0.022$), while the distance-proxy model was not ($\rho = 0.515$, $p = 0.128$).

4. Spatial and temporal displacement of large mammals by recreationists and domestic dogs in the Bow Valley, Alberta

Summary

Public demand for outdoor recreation is a key contributor to increased human activity at the boundaries of North American protected areas. However, the impacts of recreation on wildlife remain unclear. In this study, I assessed whether non-consumptive, non-motorized recreation influenced diel activity patterns and space use of large mammals in the Bow Valley, Alberta, Canada, along the edges of Banff National Park, a neighboring provincial park, and the town of Canmore. I used camera trap data to quantify spatiotemporal patterns of wildlife, human, and domestic dog detections at 66 locations monitored over a 20-month period. To test for temporal displacement of large mammals by recreationists, I compared activity patterns of study species on wildlife versus human trails. I also developed models predicting the probability that study species were photographed during daily periods of high human activity. Coyotes were less active during the day on trails used by humans, and probability of daytime detection of most study species declined with increasing intensity of recreation, proximity to human infrastructure, or density of human infrastructure. To test for spatial displacement of wildlife, I modeled the probability that study species would be detected at camera sites on any given day as a function of numbers of recreationists and domestic dogs, density of or proximity to human infrastructure, and habitat characteristics. I also modeled the relative intensity of wildlife use of camera sites in relation to these parameters. Off-leash dogs were negatively associated with habitat use of black bears, elk, mule deer and white-tailed deer, and hikers were negatively associated with habitat use of cougars and white-tailed deer. My results provide evidence for stand-alone effects of recreation on spatiotemporal activity of large mammals. However, managers should also consider the combined impacts of outdoor recreation, expanding residential development and increasing vehicle traffic on patterns of wildlife occurrence at protected area boundaries.

Keywords: recreation, protected areas, large mammals, camera trap, habitat use, diel activity patterns

Introduction

Increased human population density has been documented at the edges of protected areas (PAs) around the world (Brambilla and Ronchi 2016, Radeloff et al. 2010, Wittemyer et al. 2008), with concomitant declines in biodiversity and connectivity of wildlife habitat (Wade and Theobald 2010, Wood et al. 2015). In Western Europe and North America, residential development near PAs has been driven primarily by access to scenic open space and outdoor recreation opportunities (Gimmi et al. 2011, Kramer and Doran 2010). While outdoor recreation experiences may increase public support for conservation (Zaradic et al. 2009), a recent review found frequent negative impacts of non-consumptive, non-motorized recreation on wildlife behavior, physiology, and fitness (Larson et al. 2016), suggesting recreation may be limit the occurrence of wildlife in PA buffer zones. Moreover, if recreation is associated with growing residential areas and management resources are limited, recreation at PA edges may be more intensive, more dispersed, and less well-regulated than recreation within PAs, potentially increasing the likelihood of negative effects on wildlife.

Nonetheless, the evidence for displacement of wild animals by recreationists remains mixed, with relatively few studies conducted explicitly to examine this issue (Larson et al. 2016). In the case of large-bodied mammals, species and individuals often differ in their tolerance of human activity (Frid and Dill 2002). Working in southern Alberta, Canada, Muhly et al. (2011) found that large mammalian carnivores were displaced from trails used by greater than three recreationists per day, while ungulates were tolerant of recreation levels nearly ten times higher. Two studies of mammalian meso-carnivores in California PAs suggested that coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) avoided non-motorized human activity on trails both spatially and temporally (George and Crooks 2006, Reed and Merenlender 2008), but mule deer (*Odocoileus hemionus*) adjusted their behavior only temporally (George and Crooks 2006). More recently, two large-scale, multi-species occupancy studies found few associations between non-motorized recreation and space use or diel activity of large mammals, suggesting instead that habitat variables were most important in predicting wildlife occurrence (Kays et al. 2017, Reilly et al. 2017). Wildlife spatial and temporal responses to people may also be dependent on local context, with relevant factors including the presence of domestic dogs (Weston and Stankowich 2014), intensity of other forms of anthropogenic activity in the area (Erb et al. 2012), and availability of alternative wildlife habitat (Gill et al. 2001).

On the southeastern border of Banff National Park in the Canadian Rocky Mountains, participation in non-consumptive, non-motorized recreation is growing rapidly in association with expanding residential development in and around the town of Canmore (Fig. 1). This area provides an ideal opportunity to investigate the effects of recreation on wildlife use of critical habitat along PA edges. Located just 3 km from the national park boundary, Canmore is situated within the Bow River Valley, a wide floodplain that is a key movement corridor for large carnivores and ungulates traveling between Banff National Park and Kananaskis Country, a group of large provincial protected areas to the southeast (Fig. 1). In the early 1990s, the Alberta government designated formal wildlife corridors in the lands surrounding Canmore, providing legal recognition of the Bow Valley's significance as an animal movement pinch-point. Since this time, however, the human population of Canmore has tripled, from 5,000 to nearly 18,000 permanent and semi-permanent residents. Alongside this urban growth, a network of official and unofficial recreation trails has proliferated adjacent to and within animal movement corridors. Understanding wildlife responses to human activity on these trails on wildlife is an urgent conservation and management need.

In this study, I analyzed camera-trap data to assess whether non-motorized recreation was displacing large mammals from the habitat patches and wildlife corridors remaining around the town of Canmore. I focused on eight species of conservation and management interest: wolves (*Canis lupus*), cougars (*Puma concolor*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), coyotes, elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), and mule deer. I used camera trap images to estimate numbers of recreationists on trails and to quantify spatiotemporal patterns of wildlife detections. For each study species, I assessed whether timing and intensity of recreation was associated with 1) changes in diel activity patterns (i.e., temporal displacement of wildlife) and 2) changes in habitat use (i.e., spatial displacement). I also quantified the influence of nearby human infrastructure and habitat characteristics on timing and location of wildlife occurrence. Based on previous studies, I expected wildlife

responses to human activity to vary by species (Crooks 2002), with large carnivores most likely to be negatively associated with recreationists, and ungulates most likely to be unaffected or positively affected by recreation activity (Kays et al. 2017, Muhly et al. 2011, Reilly et al. 2017). These analyses provide the first quantitative assessment of the impacts of recreation on large-bodied mammals in the Canmore and Bow Valley area and generate new insights into interactions between recreation and persistence of wildlife along PA boundaries.

Materials and Methods

STUDY AREA

This study was conducted in the Bow Valley, Alberta, along the boundary of Bow Valley Wildland Provincial Park and on adjacent, undeveloped municipal lands surrounding the town of Canmore (50°N, 115°W; Fig. 1). Bow Valley Wildland Provincial Park borders Banff National Park and is part of a larger group of provincial PAs collectively referred to as Kananaskis Country. Climate in the study area is continental and dry (~470mm annual precipitation), with relatively wetter winters than summers, and with more precipitation at higher elevations than valley bottoms. Vegetation types included mixed coniferous/deciduous forest stands, coniferous forest, open grasslands, and riparian areas along the Bow River and other watercourses in the valley bottom. Common tree species included lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and trembling aspen (*Populus tremuloides*), while buffaloberry (*Shepherdia canadensis*) and a variety of willows, shrubs and grasses were common in the understory. Elevation in Bow Valley Wildland Park ranges from 1300 m to greater than 3000 m, though all areas surveyed in this study were below 1650 m.

Human activity was widespread both within and immediately adjacent to the study area (Fig. 1). A variety of non-motorized recreation activities, particularly hiking and mountain biking, occurred on an extensive network of official and unofficial trails within the wildland park and on municipal land. Domestic dogs were allowed with hikers on all trails, although municipal and provincial regulations required that dogs be leashed. Recreationists included both residents of the town of Canmore and out-of-town visitors, with Canmore receiving greater than 4 million visits per year (Government of Alberta, *unpublished data*). The study area was adjacent to a number of secondary roads in the town of Canmore and was bisected by the Trans-Canada Highway (Highway 1), where traffic levels can exceed 25,000 vehicles per day (Rogala et al. 2011), and the Bow Valley Trail (Highway 1A), which is used by up to 3,300 vehicles per day (Rogala et al. 2011).

DATA COLLECTION

Alberta Parks Ecology Department staff and volunteers deployed camera traps at 66 survey sites beginning in May 2015. Cameras were deployed for a two-year period and were serviced approximately monthly; the analyses presented here include those data collected from deployment through December 31, 2016. Survey locations were selected by overlaying the study area with a 1x1 km grid and placing one camera trap on a human or wildlife trail within each grid cell (Fig. 1). Camera placement within the grid cell was not random but rather occurred at a location thought to maximize the probability of capturing wildlife. Many human trails were longer than 1 km, but cameras were located on a different human trail within each grid cell

whenever possible. Cameras were primarily Reconyx Hyperfire and Silent Image; Reconyx Rapidfire and Ultrafire were also used (Reconyx Inc., Holmen, WI, USA). All cameras used no-glow infrared technology to minimize disturbance to wildlife and make cameras less noticeable to people. When triggered, cameras took a burst of 5 photos, 1 second apart, with no delay between consecutive bursts. Cameras were placed on trees approximately 40 cm above the ground on human trails, and approximately 80 cm above the ground on wildlife trails. All camera models except Silent Image were placed inside security boxes, and cameras were locked to trees using steel cables. The minimum distance between cameras was 430 m.

Photos and data were stored in TimeLapse2 Image Analyser (Greenberg 2016) and Microsoft Access, respectively. Photos of humans were permanently deleted after data entry, in accordance with Government of Alberta protocols. All human and wildlife images were coded as events, with one event consisting of all individuals captured within one minute of each other. Thus, a group of four hikers was entered as one event comprised of four individuals; two mule deer traveling together were recorded as one event comprised of two individuals. Only event data were used for subsequent analyses, and in the following text, "detections" refer to events, not individuals. Wildlife photos taken within 30 minutes of a prior detection of the same species were not considered independent captures and were not used in analyses (Ohashi et al. 2013, Wang et al. 2015).

COVARIATES

I characterized each camera site by the number of hikers, bikers, runners, on-leash dogs, and off-leash dogs recorded on the given trail (recreation covariates); distance to urban edge, distance to the nearest parking lot, road density, and trail density (human infrastructure covariates); elevation, slope, greenness, ungulate relative abundance, enhanced vegetation index (EVI) value, and percent forest cover (habitat covariates); and trail type, season, and number of days each camera functioned per month (nuisance covariates) (Table 1). All human infrastructure and habitat covariates were projected in Universal Transverse Mercator, North American Datum of 1983, Zone 11N, which was also the projection used in subsequent analyses. Hiker, biker, runner, and on-leash and off-leash dog events were summed for three time periods: the given day (e.g., May 24, 2015), the two weeks immediately prior to the given day (e.g., May 11 – 24, 2015), and the month (e.g., May 2015). Distance from camera locations to urban edge and nearest parking lot were extracted in ArcMap 10.4 (Environmental Systems Research Institute 2014) using existing anthropogenic layers maintained by Alberta Environment and Parks. I used the kernel density tool in ArcGIS to calculate road and trail density within 500 m, 1 km, and 2 km radii of each camera site, and in subsequent analyses I chose the radius that minimized model Akaike's Information Criterion (AIC) for each species. Due to large differences in vehicle traffic, the Trans-Canada Highway was assigned a weight of 10 for road density calculations, while all other roads were assigned a weight of 1. Elevation (m) and slope (degrees) were derived from a 30x30 m Digital Elevation Model (DEM). Greenness was used only in bear models and was estimated from a seamless greenness vegetation map generated by Wierzchowski (2000) on the basis of tasseled-cap transformations of spectral reflectance from Landsat images. Relative ungulate abundance was the total number of mule deer and white-tailed deer events per month, divided by the number of days the camera operated during that month; this covariate was used in cougar models only. EVI values were included in coyote and ungulate models and were obtained from MODIS data available for the southern Canadian Rocky

Mountains; I used the maximum EVI value recorded at each camera location during the study period. I calculated percent forest cover by reclassifying an existing landcover map for the study area as forested or not forested and using the kernel density tool in ArcMap to calculate the percent forest at 300 m, 500 m and 1 km radii from the camera (Wang et al. 2015). In analyses, I chose the radius for percent forest cover that minimized model AIC for each species. Trail type was human trail or wildlife trail. Season was spring (Apr – June); summer (July – Aug); fall (Sept – Oct); or winter (Nov – March).

I standardized all continuous covariates by subtracting by the mean and dividing by the standard deviation (z-transformation). To test for associations between variables, I conducted an analysis of variance inflation factors (VIF) and correlation analyses between covariate pairs in R version 3.3.1 (R Development Core Team 2016); VIF analysis was implemented in the 'fsmb' package (Nakazawa 2017). I discarded variables for which $r > 0.60$ or VIF > 3.0. On-leash dogs were correlated with hiker and runner events at all three temporal scales (daily, biweekly, and monthly; $r > 0.70$), and therefore on-leash dog events were excluded from subsequent analyses.

TEMPORAL ANALYSES

I used two approaches to test the influence of human activity on diel activity patterns of study species. First, I quantified overlap between the overall daily activity pattern of recreationists in the study area and the activity patterns of wildlife species on human trails and wildlife trails. Second, I created diel activity models to describe the probability that study species were photographed during daily periods of high human activity.

Overlap between recreationist and wildlife activity patterns

I used the non-parametric kernel density estimation technique described in Ridout and Linkie (2009) to 1) estimate the overall diel activity pattern of recreationists in the study area; 2) estimate the diel activity patterns of each study species on human trails and on wildlife trails; 3) calculate overlap between the overall recreationist activity pattern and the diel activity patterns of each study species on human trails, and 4) calculate overlap between the overall recreationist activity pattern and the diel activity patterns of each study species on wildlife trails. Ridout and Linkie's technique treats the times of all camera images (i.e., capture times) as random variables from a continuous circular distribution. Capture times are converted to radians, and kernel density estimation is used to generate a probability density function that represents the activity pattern of a given species. A coefficient of overlap (Δ) can then be calculated to quantify the degree of overlap between two activity patterns. The coefficient of overlap (Δ) is the integrated difference between the two kernel density functions and ranges from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap (Ridout and Linkie 2009).

I first combined all hiker, biker, and runner events at all cameras, for the entire study period. I used the capture times for these events to calculate an overall activity pattern for recreationists in the study area (Reilly et al. 2017). Next, I categorized wildlife detections by trail type, and I created separate probability density functions describing the activity pattern of each study species on human trails and on wildlife trails. All wildlife detections for the entire study period were used. I then calculated the coefficient of overlap, $\hat{\Delta}$, between the activity pattern of each study species on human trails and the overall activity pattern of recreationists in the study area. I

used $\hat{\Delta}_4$, which is recommended for sample sizes > 50 (Ridout and Linkie 2009). I did the same for wildlife trails, calculating the overlap between the activity pattern of each study species on wildlife trails and the overall recreationist activity pattern. I obtained 95% confidence intervals for each $\hat{\Delta}_4$ estimate by generating 1,000 bootstrap samples. For each study species, I compared the 95% confidence interval for $\hat{\Delta}_4$ for human trails to the corresponding 95% confidence interval for $\hat{\Delta}_4$ for wildlife trails. I considered the difference in activity patterns to be significant if confidence intervals did not overlap. All statistical procedures were carried out in the R 3.3.1 using the package 'overlap' (Meredith and Ridout 2017).

Diel activity models

Because recreationist activity patterns differed substantially between months of the year and between weekends and weekdays, I also used the kernel density estimation approach described above to estimate separate weekend and weekday probability density functions for recreationist activity for each month in the study period. I first combined hiker, biker, and runner events at all cameras. I then categorized these events by year, month, and day of the week (weekend or weekday), resulting in 40 separate probability density functions describing recreationist activity (i.e., one activity pattern for May 2015 weekdays, one for May 2015 weekends, etc.). For each probability density function, I considered the time interval that corresponded to 40% of recreationist detections on either side of the mean (analogous to an 80% confidence interval) to be the high human activity period for the day. I classified wildlife detections that occurred during this high human activity period with a "1", and those that occurred outside of this period with a "0", for the appropriate month and day of the week. I used Generalized Linear Mixed Models (GLMMs) to predict the probability of species' detection during high human activity periods as a function of recreation covariates, human infrastructure covariates, trail type, and season (Table 1). GLMMs had a binomial error structure (0/1) and used the logit link function; separate models were constructed for each study species. Camera was included as a random effect, and hours of daylight was included as an offset. Starting with a null model with no predictor variables, I used forward stepwise procedures to include only those covariates and interactions that contributed to the explained deviance ($p < 0.05$). To test whether species responded to current versus past levels of recreationist activity, I compared models that included hiker, biker, runner, and off-leash dog events on the day that the wildlife detection occurred to models that summed these events over the two weeks prior to the given detection. I then chose the time period (one day or two weeks) that minimized model AIC. Final candidate models included only significant covariates, and AIC was used to select the top model. Analyses were carried out in the 'overlap' (Meredith and Ridout 2017) and 'lme4' (Bates et al. 2017) packages in R 3.3.1.

SPATIAL ANALYSES

To quantify habitat use of study species, I constructed daily occurrence models to evaluate the probability that species would be detected at camera sites on a given day, and I created visit frequency (VF) models (Kays et al. 2017) to assess relative intensity of wildlife use of surveyed locations.

Daily occurrence models

Daily occurrence models predicted the probability of detecting each study species on a given day as a function of recreation covariates, human infrastructure covariates, habitat covariates, trail

type and season (Table 1). Models were GLMMs with a binomial response and logit link function, and camera was included as a random effect. For each study species and for each day that cameras operated, I recorded a "1" if the species was detected that day, and a "0" if the species was not detected. As for diel activity models, I compared the AIC of models that included the total hiker, biker, runner, and off-leash dog events for the given day, against the AIC of models that included the total recreationist and off-leash dog events over the previous two-week period. Separate models were created for each species, and I used forward stepwise procedures to retain only significant variables in final candidate models. AIC was used to select the top model. Analyses were carried out in the 'lme4' (Bates et al. 2017) package in R 3.3.1.

Visit frequency models

While daily occurrence models predicted the probability of detecting a species on a particular day, VF models quantified the intensity with which study species used a given camera location over the course of a month. I considered that concordance between these two types of models would bolster study results. For each study species, I totaled the number of detections per month at each camera; this was the monthly visit frequency (VF) for each species. I also summed all hiker, biker, runner, and off-leash dog events at each camera for each month. I used GLMMs with a Poisson response and log link to model the monthly VF of each species as a function of recreation, human infrastructure, habitat, and nuisance covariates (Table 1). The number of days that each camera functioned during the given month was included as an offset, and camera was a random effect. As described above, I used forward stepwise procedures to retain only those covariates that significantly contributed to the explained deviance, and I used AIC to select the top model. I checked for over-dispersion by assessing the residual deviance against the residual degrees of freedom. For mule deer and white-tailed deer, the residual deviance was more than twice the residual degrees of freedom and therefore the monthly number of detections of each of these species was treated as a negative binomial response rather than a Poisson response. Analyses were carried out in the 'lme4' (Bates et al. 2017) package in R 3.3.1.

Results

Thirty-three wildlife trails and 33 human trails were surveyed for a total of 36,145 camera days, capturing 116,266 independent images of people and 6,948 images of the eight study species (Table 2). On average, cameras were functional for $93.7 \pm 8.4\%$ of days deployed. Hikers, bikers, and runners comprised greater than 96% of human detections (Table 2); other types of non-motorized recreation included climbing, horseback riding, skiing, and snowshoeing. Hiker, biker, runner, and off-leash dog activity varied substantially in space and time (Table 3). For wildlife species, I considered 100 detections to be the minimum necessary to ensure model convergence and statistical rigor. Images of wolves and grizzly bears did not meet this threshold (Table 2), and therefore these species were excluded from analyses of temporal activity and space use.

TEMPORAL ACTIVITY

With the exception of coyotes, there were no significant differences in overlap between the overall activity pattern of recreationists in the study area and the activity patterns of study species on wildlife trails versus human trails (Table 4). Coyote overlap with the overall recreationist activity pattern was significantly higher on wildlife trails compared to human trails

(Fig. 2, Table 4). Cougars overlapped the least with human activity, while white-tailed deer and black bears overlapped the most (Table 4).

Diel activity models indicated that probability of detecting coyotes during daily periods of high human activity was negatively associated with the number of hiker events and that the detecting probability of black bears was negatively associated with off-leash dog events (Table 5). For both these species, models that summed hiker and off-leash dog events over a two-week period had lower AIC (i.e., were more parsimonious for the given data) than models that totaled hiker and dog events on the given day. Recreation covariates were not significant predictors of diel activity of other study species.

Human infrastructure covariates were negatively associated with detections of cougars, elk, and white-tailed deer during daily periods of high human activity, with different infrastructure covariates identified as significant for each of these species (Table 5). Associations between human infrastructure covariates and black bear activity patterns were mixed, with probability of daytime bear activity negatively associated with road density but positively associated with proximity to urban edge (Table 5). Infrastructure covariates were not significant predictors of diel activity of coyotes or mule deer.

Consistent with the results of the overlap analysis, diel activity models suggested that coyotes were significantly more likely to use wildlife trails than human trails during daily periods of high human activity. Season was a significant determinant of timing of diel activity of black bears, elk, mule deer, and white-tailed deer (Table 5).

SPACE USE

Recreation covariates were significant predictors of habitat use of all study species (Table 6). In particular, hikers and off-leash dogs had negative impacts on several species. For black bears, elk, mule deer, and white-tailed deer, daily occurrence models indicated that probability of detection on a given day declined as off-leash dog events increased. Monthly visit frequencies (VF) of black bears, elk, and white-tailed deer were also negatively associated with off-leash dogs (Fig. 3, Table 6). Hiker events were negatively associated with daily probability of occurrence of both cougars and white-tailed deer and with the monthly VF of white-tailed deer (Fig. 3, Table 6). Coyote spatial responses to dogs and human recreationists were mixed, and bikers, hikers, and runners did not impact space use of black bears, elk, and mule deer (Table 6). For all species, daily occurrence models that included the sum of hiker, biker, runner, and off-leash dogs events over the previous two weeks had lower AIC than models that incorporated events on a given day.

The impact of human infrastructure covariates on daily probability of occurrence and monthly VF varied by species. Space use of coyotes and mule deer was positively associated with human infrastructure. Daily probability of coyote detection increased with increasing road density and decreasing distance to parking lots; coyote monthly VF also increased at higher road density (Table 6). Daily probability of mule deer detection increased with increasing trail densities (Table 6). Elk responses to human infrastructure were mixed, with daily probability of elk detection and elk monthly VF increasing with higher road densities but decreasing with higher trail densities. Trail density was negatively associated with monthly VF of cougars (Table 6; Fig.

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3). Human infrastructure covariates were not significantly related to space use of black bears and white-tailed deer.

Habitat covariates were significant predictors of daily occurrence and/or VF of black bears, mule deer, and white-tailed deer (Table 6). Black bears, cougars, and coyotes all preferred human trails over wildlife trails, and season was a significant predictor of daily detections and/or VF for all species except coyotes (Table 6).

The results of the daily occurrence and VF models were generally similar, although daily occurrence models tended to identify a greater number of significant associations than VF models (Table 6). Of 31 significant variable associations, daily occurrence and VF models had 17 variables in common. Daily occurrence models identified 12 significant associations that were not identified by VF models, and VF models produced 2 significant associations not identified by daily occurrence models. Model predictions did not contradict each other for any covariates.

Discussion

Recreation covariates were significant predictors of habitat use of all study species analyzed (Table 6). In particular, hikers and off-leash dogs appeared to have the potential to spatially displace wildlife from habitat patches and corridors located along the edges of several PAs and the town of Canmore, Alberta. In addition, either recreation or human infrastructure covariates were significant predictors of diel activity for all species except mule deer (Table 5). These results differ from those of two recent, regional-scale studies that emphasized the importance of environmental variables over recreation in predicting wildlife occupancy and habitat use (Kays et al. 2017, Reilly et al. 2017). In contrast to these studies, my analyses focused on a relatively small spatial area (~90 km^2; Fig. 1), within which habitat variables did not vary greatly. Human activity dynamics were clearly a more important determinant of wildlife behavior at this fine scale.

This study also provides novel insights into the temporal scale over which wildlife adjust their behavior to human activity. By comparing diel activity and daily occurrence models that included daily versus biweekly numbers of recreationists, I found strong evidence that animals responded to recreation over extended periods (e.g., two weeks), rather than simply real-time (daily) human use.

SPATIOTEMPORAL RESPONSES TO HUMAN ACTIVITY

Of the species considered, coyotes exhibited the strongest temporal response to human activity. Spatial responses of coyotes were also strong, with models of space use identifying more significant associations with human activity covariates for coyotes than for any other study species. Both daily occurrence and VF models identified only positive associations between coyotes and human infrastructure, a finding that is consistent with other studies documenting increases in coyote occurrence with greater proximity to and intensity of urbanization (Ordeñana et al. 2010). VF models also identified positive relationships between coyotes and recreation covariates, although daily occurrence models suggested a mix of positive and negative associations between coyote space use and recreation activity. This result contradicts those of George and Crooks (2006) and Reed and Merenlender (2008), both of which reported spatial

displacement of coyotes by recreationists. However, other studies have demonstrated increases in coyote occurrence on hiking trails, even when human use is high (Kays et al. 2017), or no relationship between coyote space use and recreation (Reilly et al. 2017). Previous research has found that coyotes are able to persist in areas of high human activity by shifting their temporal activity, rather than their spatial habitat use (Kays et al. 2017, Reilly et al. 2017, Tigas et al. 2002), and in this study, coyotes were the only species to significantly decrease their daytime activity on human trails compared to wildlife trails that had no recreation.

The impacts of recreation on temporal activity of other study species were less clear. Although the activity patterns of cougars, elk, mule deer, and white-tailed deer on human trails overlapped less with the overall pattern of recreationist activity, compared to activity patterns of these species on wildlife trails (Table 4; Fig. 2), these differences were not statistically significant. Cougars in this study were primarily nocturnal, and ungulates were crepuscular (Fig. 2). This may have limited their baseline level of overlap with the peak hours of human activity, perhaps making strong activity shifts unnecessary. Temporal overlap between black bears and recreationists was relatively high, but black bears likely foraged on berries throughout the day and night during the summer (Nelson et al. 1983), and berries were abundant on human-use trails in the study area. Nonetheless, for all study species except mule deer, diel activity models identified at least one negative relationship between recreation or human infrastructure covariates and probability of wildlife detection during daily periods of high human activity.

Daily occurrence and VF models provided clear evidence of the negative impacts of off-leash dogs on space use of black bears and all three ungulate study species. Indeed, off-leash dogs had the most consistently negative influence on wildlife space use of any recreation covariate (Table 6). Relatively few studies of the effects of human disturbance on wildlife explicitly consider domestic dogs (Weston and Stankowich 2014), although dogs on hiking trails have been implicated in declines of bighorn sheep (*Ovis canadensis*) in the southwestern United States (Krausman et al. 1995). In addition to spatially displacing wildlife, dogs may affect animals' physiology and energy expenditures by raising stress levels or increasing flight distances (Martinetto and Cugnasse 2001, Pelletier 2006). Off-leash dogs move unpredictably and can chase animals, which may lead to 'sensitization' of wildlife and increased intensity of responses like avoidance, flight, or stress (Glover et al. 2011, Weston and Stankowich 2014). Surprisingly, off-leash dogs did not appear to negatively impact space use of cougars or coyotes in the study area. These two species may be less likely to perceive dogs as a potential predator, although cougar occurrence has been negatively associated with domestic dogs in northern California (Reilly et al. 2017).

In contrast to off-leash dogs, human recreationists on trails and human infrastructure did not elicit negative spatial responses in most study species. Human presence is pervasive in the Bow Valley near Canmore, and all study species were likely habituated to people to some degree, perhaps allowing them to use suitable habitats close to town that their wilderness counterparts would avoid (Papouchis et al. 2001). Nonetheless, habitat use of cougars and white-tailed deer was negatively impacted by either hikers or increasing trail density in both daily occurrence and VF models, suggesting these two species are susceptible to spatial displacement by people on trails. This result was somewhat unexpected for white-tailed deer, but it was not surprising for cougars, which are known to be sensitive to human activity (Dickson and Beier 2002, Dickson et

al. 2005). Even though cougars, black bears, and coyotes all preferred human trails to wildlife trails, cougars avoided human trails when hiker numbers or overall density of human trails was high. These three carnivore species likely selected human trails not because of any attraction to people, but because human trails were wider and less obstructed than wildlife trails, thereby facilitating movement for hunting and traveling (Harmsen et al. 2010).

STUDY LIMITATIONS

My spatial analyses did not account for imperfect detection of study species at camera trap locations, which could have biased estimates of wildlife space use in relation to human activity (Gu and Swihart 2004). While occupancy models (MacKenzie et al. 2002, MacKenzie et al. 2005) could have addressed this issue, I chose not to use an occupancy approach, due to the limited capacity of occupancy models to include temporal variability in covariates predicting wildlife space use. Because the cameras used in this study functioned for an extended time period, the resulting dataset captured significant daily, weekly, and seasonal differences in recreation levels at camera locations. I expected that this temporal variation in human activity would influence both the probability that study species used camera locations and the probability that species were detected at cameras. However, occupancy models can only incorporate temporal variation into covariates predicting the probability of detecting study species, while covariates for habitat use or occupancy must remain constant at each site over the course of a sampling season. I concluded that for this study, using constant values for recreation-related occupancy covariates risked obscuring the effects of finer-scale temporal dynamics of human activity on wildlife habitat use. Revealingly, my daily occurrence models, which accounted for day-to-day variation in recreation levels, identified seven more significant relationships between wildlife occurrence and recreation covariates than did VF models, which summed hikers, bikers, runners, and off-leash dogs for a given month, thereby masking finer-scale temporal variability in human activity.

I attempted to minimize the uncertainty caused by imperfect detection by developing two different spatial models, the results of which were largely concordant. Kays et al. (2017) also found that VF models produced similar results to occupancy models that accounted for detectability. Moreover, detection rates in this study were likely high and consistent across camera survey sites. All study species were large-bodied; all cameras were Reconyx brand, programmed identically, and placed set at standardized heights and distances from trails; vegetative cover was similar across camera locations; bait was not used; and the "sites" that I was interested in included only the area within the immediate vicinity of each camera, i.e., sites were equivalent to the range of the camera, and not further. Variables that are often included as detection covariates in occupancy models, such as trail type, season, and effort, were included as predictors in my spatial analyses.

My analyses also did not address potential spatial dependence between cameras. However, the minimum distance between cameras was consistent with other, similar studies of recreation and human development impacts on large mammals (e.g., Reilly et al. 2017, Wang et al. 2015). While typical home ranges for cougars, black bears, coyotes, and elk were as large as or larger than the study area, I was interested in relative habitat use by study species within this area, and whether variation in recreation levels drove differential space use. In addition, placement of

cameras on independent trails should have minimized the probability that humans would have visited multiple camera locations on a given day.

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

My results suggest that hikers and, in particular, off-leash dogs are displacing some species of large mammals from habitat along the edges of Banff National Park, Kananaskis Country provincial parks, and the town of Canmore, Alberta. Land managers could reduce the impacts of recreation in the study area by decommissioning trails, particularly unofficial trails that have emerged within wildlife corridors, or by limiting the number of recreationists on trails (e.g., through a day-use fee system). Further, while some species of wildlife may have been habituated to the presence of humans, this effect did not extend to off-leash dogs, which displaced most study species. Since the majority of all dogs on trails in the study area were off-leash (58.2%; Table 2), even though leashing is required, off-leash dogs appear to pose a major management challenge. Compliance with leash laws could be increased by increasing enforcement effort, raising fines, developing outreach programs to foster leashing as a community social norm, and better informing the public about the detrimental effects of dogs on wildlife (Williams et al. 2009). My analyses could not test the impacts of on-leash dogs on study species due to high correlations between numbers of on-leash dogs and recreationists. Managers seeking to better understand the relationship of dogs and wildlife should consider closing some trails entirely to domestic dogs, and then comparing wildlife use of dog-free areas to wildlife use of trails that allow domesticated canids.

Wildlife species are rarely impacted by one type of human disturbance in isolation from others (Didham et al. 2007, Sala et al. 2000). Increased human activity in the study area occurred primarily in the form of outdoor recreation, residential development, and vehicle traffic. Notably, increases in these forms of human activity appear to be common at the edges of North American PAs (Gimmi et al. 2011, Kramer et al. 2010), and they are likely to be interconnected. A comprehensive study of threatened and endangered species in the United States identified outdoor recreation as a leading independent cause of species decline, but recreation was also highly associated with urbanization and residential development, with 39% of species endangered by recreation also endangered by urbanization (Czech et al. 2000). Urbanization, in turn, was also highly associated with the presence of roads (Czech et al. 2000). While my results provide evidence that recreation alone impacts wildlife, land managers should consider the cumulative and interacting impacts of recreation, urbanization, and vehicle traffic on wildlife in the study area. Notably, the two most sensitive species in this study, wolves and grizzly bears, were not detected with sufficient frequency to be included in analyses. These two species are likely already being limited by the individual or combined effects of recreation, residential development, and high-use roads. Moreover, the impacts of human activity on rare species inhabiting PA edges may not be immediate but rather become evident only after several decades (Wood et al. 2015), suggesting that policy makers should consider the potential for time lags and cumulative effects when weighing proposals for future developmentand associated recreation infrastructure.

My analyses focused on a relatively small area of habitat at the edges of Banff National Park, Bow Valley Wildland Provincial Park (Kananaskis Country), and the town of Canmore. While recreation covariates were generally important to spatiotemporal use of the study area by large

mammals, these effects also clearly varied across species. It seems likely that these effects also vary across habitats or spatial scales, suggesting that a regional-level investigation of large mammal occupancy patterns across the eastern slopes of the Canadian Rocky Mountains would be valuable for contextualizing the results presented here. Such a study could examine the responses of wildlife to a variety of anthropogenic and environmental factors, with the goal of identifying those variables that are most important in shaping wildlife occurrence and temporal activity at broad versus fine spatial scales.

Tables and Figures

Table 1. Covariates used in diel activity (DA), daily occurrence (DO), and visit frequency (VF) models.

Category	Covariate	Description	Model
Recreation	Hikers	Total number of hiker events recorded by each camera on a given day (DA, DO), over the previous two-week period (DA, DO), and per month (VF)	DA, DO, VF
Recreation	Bikers	Total number of biker events recorded by each camera on a given day (DA, DO), over the previous two-week period (DA, DO), and per month (VF)	DA, DO, VF
Recreation	Runners	Total number of runner events recorded by each camera on a given day (DA, DO), over the previous two-week period (DA, DO), and per month (VF)	DA, DO, VF
Recreation	Off-leash dogs	Total number of off-leash dog events recorded by each camera on a given day (DA, DO), over the previous two-week period (DA, DO), and per month (VF)	DA, DO, VF
Human Infrastructure	Dist.Urban	Distance (m) from each camera to urban edge	DA, DO, VF
Human Infrastructure	Dist.Parking	Distance (m) from each camera to the nearest parking lot	DA, DO, VF
Human Infrastructure	Road.Density	Density of roads within a 500 m, 1 km, and 2 km radius of each camera	DA, DO, VF
Human Infrastructure	Trail.Density	Density of trails within a 500 m, 1 km, and 2 km radius of each camera	DA, DO, VF
Habitat	Elevation	Elevation (m) at camera location	DO, VF
Habitat	Slope	Slope (degrees) at camera location	DO, VF
Habitat	Greenness	Greenness vegetation map (Wierzchowski 2000) based on tasseled-cap transformations of spectral reflectance from Landsat images (bears only)	DO, VF
Habitat	Ung.RAI	Number of deer detections per month, divided by the number of days the camera operated (cougars only)	DO, VF
Habitat	max.EVI	Maximum value of the Enhanced Vegetation Index during the study period (coyotes, ungulates)	DO, VF
Habitat	Percent.forest	% forest within 100 m, 300 m, or 500 m radius of the camera	DO, VF
Nuisance	Season	Spring (Apr-June), summer (July-Aug), fall (Sept-Oct), winter (Nov-Mar)	DA, DO, VF
Nuisance	Trail.type	Human trail or wildlife trail	DA, DO, VF
Nuisance	Effort	Number of days the camera was operational each month	VF

Table 2. Summary statistics for recreationists, domestic dogs, and wildlife study species captured by cameras. Events are all individuals captured within one minute of each other, and mean event size is the number of individuals per event.

Species	Cameras captured (out of 66) (%)	Number of detections (events)	Mean event size ± SD
Hikers	49 (74.2%)	66,107	1.59 ± 0.52
Bikers	38 (57.6%)	28,566	1.99 ± 0.61
Runners	39 (56.0%)	17,053	1.48 ± 0.42
All human trail use	55 (83.3%)	116,266	1.94 ± 0.62
On-leash dogs	41 (62.1%)	12,473	1.12 ± 0.09
Off-leash dogs	52 (78.8%)	17,365	1.16 ± 0.17
Black bears	57 (86.3%)	397	1.09 ± 0.19
Cougars	47 (71.2%)	170	1.11 ± 0.25
Coyotes	53 (80.3%)	989	1.12 ± 0.17
Elk	50 (75.8%)	972	1.73 ± 0.65
Grizzly bear	20 (30.0%)	28	1.58 ± 0.47
Mule deer	66 (100%)	1,653	1.51 ± 0.31
White-tailed deer	65 (98.5%)	2,695	1.36 ± 0.18
Wolf	24 (36.4%)	44	1.32 ± 0.62

Table 3. Summary statistics for recreation covariates included in temporal and spatial analyses.

Recreation covariate	One-day average ± SD (range)	Two-week average ± SD (range)	Monthly average ± SD (range)
All trails			
Hikers	1.84 ± 5.13 (0 – 197)	25.99 ± 60.20 (0 – 983)	51.34 ± 109.05 (0 – 1279)
Bikers	0.76 ± 2.89 (0 – 59)	10.80 ± 34.06 (0 – 480)	22.18 ± 69.73 (0 – 777)
Runners	0.46 ± 1.52 (0 – 24)	6.49 ± 17.74 (0 – 164)	13.22 ± 35.64 (0 – 276)
Off-leash dogs	0.42 ± 1.16 (0 – 17)	5.83 ± 12.47 (0 – 131)	11.16 ± 23.62 (0 – 200)
Human trails			
Hikers	3.09 ± 6.62 (0 – 197)	43.81 ± 76.44 (0 – 983)	100.76 ± 137.90 (0 – 1279)
Bikers	1.45 ± 3.91 (0 – 59)	20.58 ± 45.40 (0 – 480)	26.34 ± 47.00 (0 – 777)
Runners	0.85 ± 2.01 (0 – 24)	12.01 ± 23.29 (0 – 164)	43.88 ± 93.86 (0 – 276)
Off-leash dogs	0.64 ± 1.28 (0 – 17)	8.96 ± 12.63 (0 – 131)	22.03 ± 29.73 (0 – 200)

Table 4. Overlap ($\hat{\Delta}_4$) between the overall activity pattern of recreationists in the study area and activity patterns of study species on wildlife trails and on human trails. The difference in overlap is statistically significant for coyotes (bolded row) at $p < 0.05$; 95% confidence intervals do not coincide. Wolves and grizzly bears are not included due to insufficient detections.

Species	Wildlife Trail $\hat{\Delta}_4$ (95% CI)	Human Trail $\hat{\Delta}_4$ (95% CI)	Difference (Human – Wildlife)
Black bear	0.577 (0.500 – 0.654)	0.637 (0.579 – 0.695)	0.060
Cougar	0.371 (0.248 – 0.493)	0.292 (0.223 – 0.362)	-0.079
Coyote	**0.590 (0.521 – 0.656)**	**0.481 (0.450 – 0.517)**	**-0.109**
Elk	0.505 (0.457 – 0.554)	0.466 (0.425 – 0.507)	-0.039
Mule deer	0.561 (0.526 – 0.596)	0.542 (0.504 – 0.580)	-0.019
White-tailed deer	0.637 (0.609 – 0.665)	0.608 (0.573 – 0.643)	-0.029

Table 5. Significant variables from top diel activity models describing the probability of species' detection during daily periods of high human activity as a function of recreation, human infrastructure and nuisance covariates (Table 1). Times of hiker, biker, and runner events were combined, converted to radians, and fitted with a kernel density function; "high human activity periods" correspond to the interval of the day that contained 40% of recreationist detections on either side of the mean (80% of total detections). Models were binomial Generalized Linear Mixed Models built separately for each species. Top models were those with the best Akaike's Information Criterion (AIC); all top models had >2 units difference with other candidate models (Burnham and Anderson 2002).

Species	Variable	Estimate	SE	z	p
Black bears	Off-leash dogs	-0.577	0.189	-3.059	0.002
	Dist.urban	-0.381	0.111	-3.440	<0.001
	Road.density	-0.315	0.139	-2.273	0.023
	Season:spring	0.896	0.434	2.062	0.039
Cougars	Dist.urban	0.438	0.221	1.981	0.047
Coyotes	Hikers	-0.300	0.127	-2.359	0.018
	Trail.type:wildlife	0.627	0.318	1.974	0.048
Elk	Dist.parking	0.276	0.129	2.136	0.033
	Road.density	-0.203	0.098	-2.072	0.038
	Season:winter	0.974	0.260	3.748	<0.001
Mule deer	Season:summer	-0.513	0.158	-3.253	0.001
	Season: winter	0.428	0.188	2.276	0.023
White-tailed deer	Trail.density	-0.198	0.064	-3.109	0.002
	Season:summer	-0.390	0.106	-3.687	<0.001

Table 6. Significant variables from the top daily occurrence and visit frequency (VF) models, by species. For daily occurrence models, binomial Generalized Linear Mixed Models (GLMMs) were used to model the probability that a species was photographed on a given day at a given camera, as a function of recreation, human infrastructure, habitat, and nuisance covariates (Table1). For VF models, Poisson GLMMs were used, and the response variable was the total number of detections of the species per month at each camera. For both sets of models, camera was a random effect. Top models were those with the best Akaike's Information Criterion (AIC); all top models had >2 units difference with other candidate models (Burnham and Anderson 2002).

Species	Variable	Daily occurrence model				Visit frequency model			
		Estimate	SE	z	p	Estimate	SE	z	p
Black bears	Off-leash dogs	-0.258	0.130	-1.988	0.047	-0.390	0.1565	-2.493	0.013
	Greenness	0.359	0.130	2.758	0.006				
	Trail.type:wildlife	-0.757	0.280	-2.707	0.007	-0.839	0.292	-2.871	0.004
	Season:spring	1.749	0.183	9.562	<0.001				
	Season:summer	1.655	0.177	9.354	<0.001				
Cougars	Hikers	-0.490	0.181	-2.703	0.007				
	Trail.type:wildlife	-1.603	0.370	-4.331	<0.001	-1.166	0.300	-3.889	<0.001
	Season:winter	0.508	0.163	3.122	0.002	0.700	0.154	4.546	<0.001
	Trail.density					-0.353	0.165	-2.143	0.032
Coyotes	Bikers	0.136	0.047	2.907	0.004				
	Hikers	-0.138	0.048	-2.889	0.004				
	Runners	-0.192	0.055	-3.467	<0.001				
	Off-leash dogs	0.277	0.050	5.483	<0.001	0.237	0.072	3.310	<0.001
	Dist.parking	-0.493	0.199	-2.469	0.014				
	Road.density	0.485	0.194	2.502	0.012	0.732	0.162	4.523	<0.001
	Trail.type:wildlife	-1.860	0.374	-4.975	<0.001	-1.428	0.342	-4.178	<0.001
Elk	Runners	0.179	0.075	2.387	0.017				
	Off-leash dogs	-0.453	0.077	-5.920	<0.001	-0.247	0.056	-4.392	<0.001
	Road.density	1.203	0.214	5.616	<0.001	1.126	0.213	6.150	<0.001
	Trail.density	-1.072	0.223	-4.803	<0.001	-1.050	0.225	-4.662	<0.001
	Season:winter	-1.017	0.091	-11.175	<0.001	-1.085	0.087	-12.485	<0.001
Mule deer	Off-leash dogs	-0.337	0.074	-4.584	<0.001				
	Trail.density	0.342	0.143	2.398	0.016	0.269	0.121	2.231	0.026
	Slope	0.422	0.142	2.956	0.003				

Species	Variable	Daily occurrence model				Visit frequency model			
		Estimate	SE	z	p	Estimate	SE	z	p
	Season:winter	-1.106	0.070	-15.704	<0.001	-1.016	0.100	-10.115	<0.001
	Elevation					0.504	0.121	4.154	<0.001
White-tailed deer	Bikers	-0.135	0.067	-2.009	0.045				
	Hikers	-0.172	0.080	-2.143	0.032	-0.263	0.109	-2.420	0.016
	Runners	0.147	0.066	2.226	0.026				
	Off-leash dogs	-0.344	0.078	-4.391	<0.001	-0.260	0.101	-2.566	0.010
	Elevation	-0.757	0.129	-5.883	<0.001	-0.579	0.117	-4.960	<0.001
	Percent.forest	0.308	0.133	2.328	0.020				
	Season:winter	-0.699	0.050	-13.860	<0.001	-0.532	0.079	-6.713	<0.001
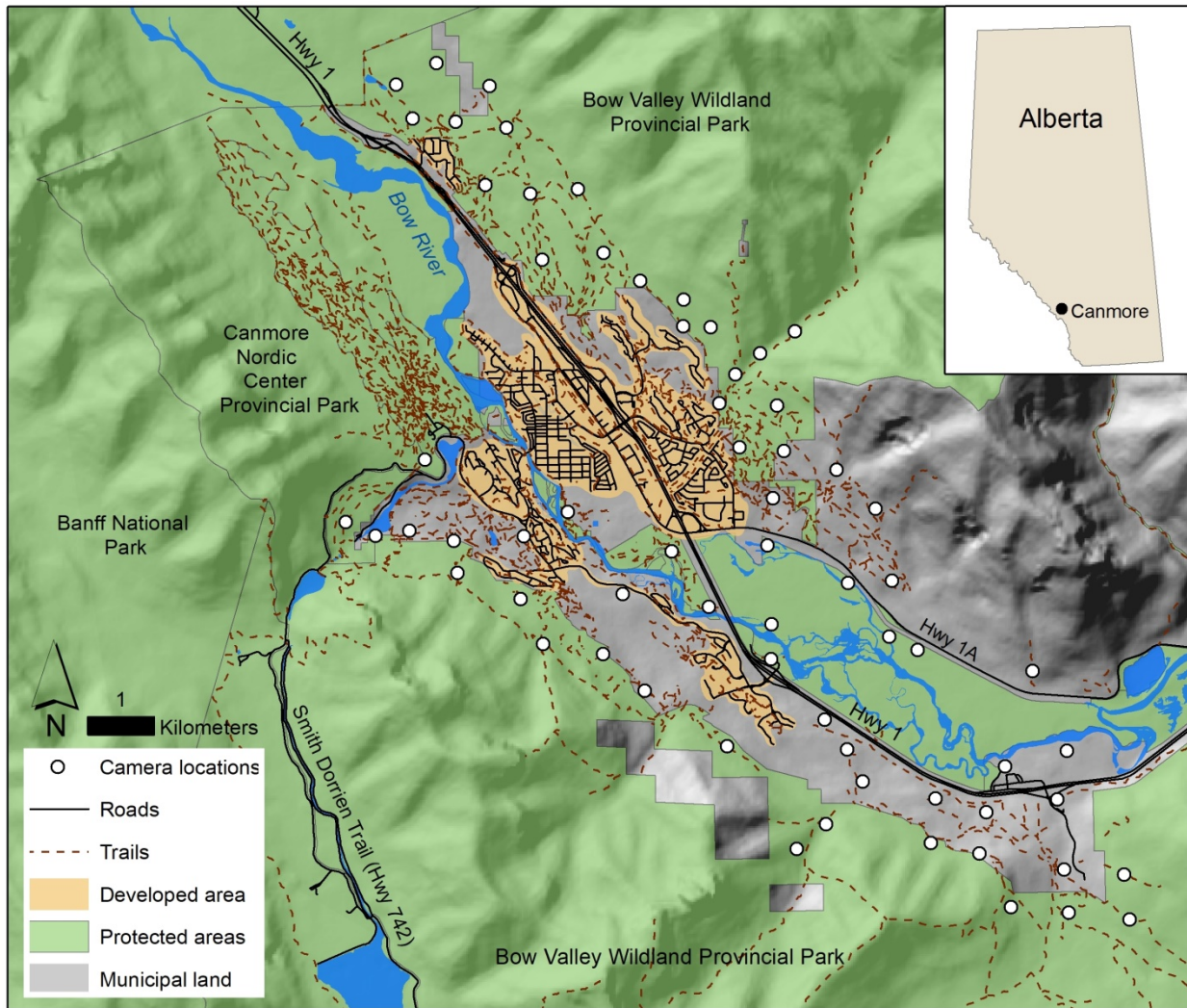
Fig. 1. Map of the study area showing the locations of cameras, roads, trails, protected areas, and the town of Canmore and its associated development footprint. Bow Valley Wildland and Canmore Nordic Center Provincial Parks are part of Kananaskis Country, a 4,200 km² protected area that extends to the south and east. Inset: location of Canmore in the province of Alberta, Canada.
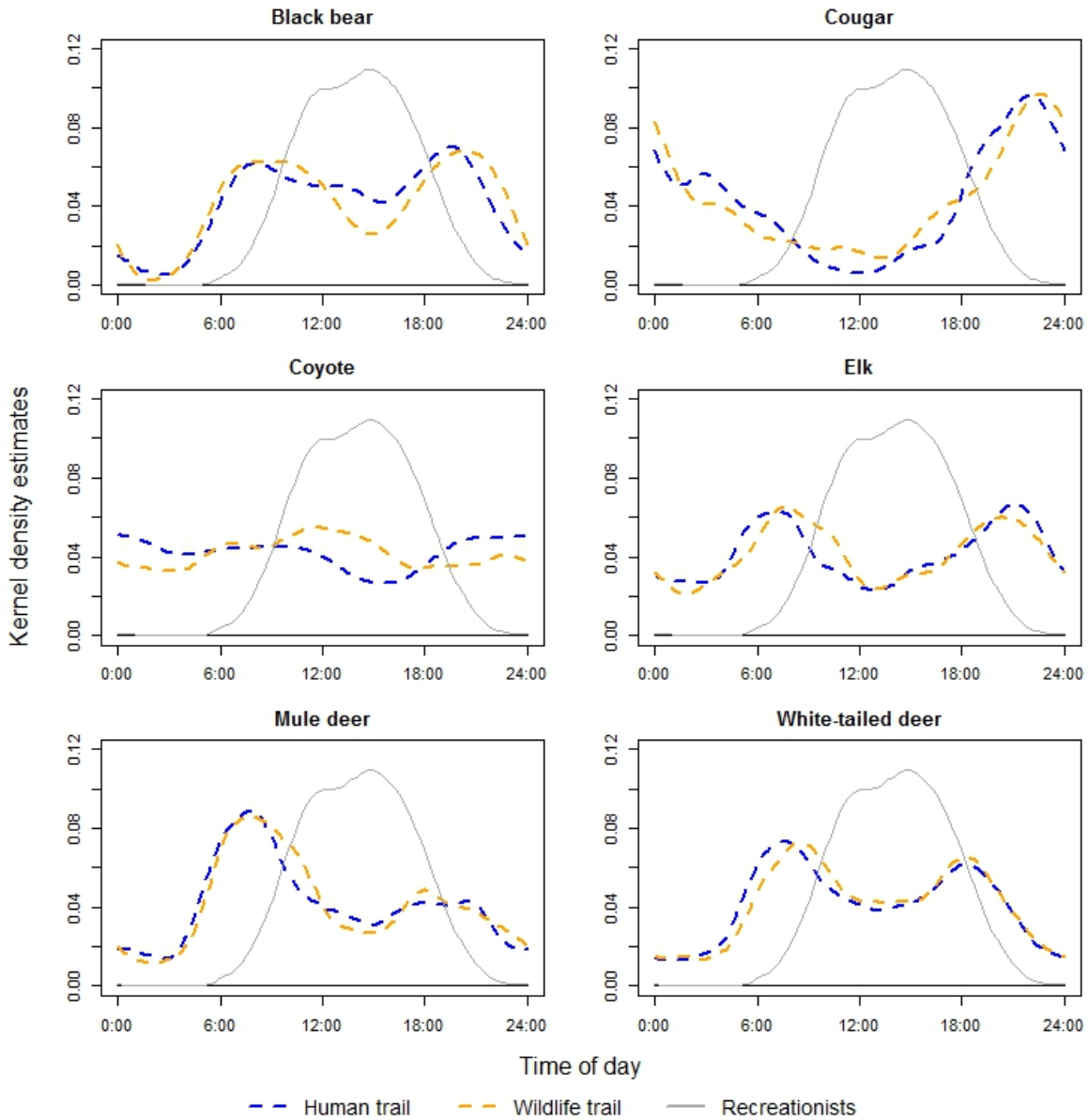
Fig. 2. Kernel density estimates of daily activity patterns of six study species on human trails (blue dotted line) and wildlife trails (orange dotted line); data for grizzly bears and wolves are not shown due to small sample sizes. The activity pattern of recreationists is shown in gray.. Overlap between the overall activity pattern of recreationists in the study area and coyote activity patterns on human trails was significantly lower than the overlap between recreationist and coyote activity on wildlife trails (95% confidence intervals did not coincide). Overlap of other species with recreationist activity was not significantly different on human versus wildlife trails.
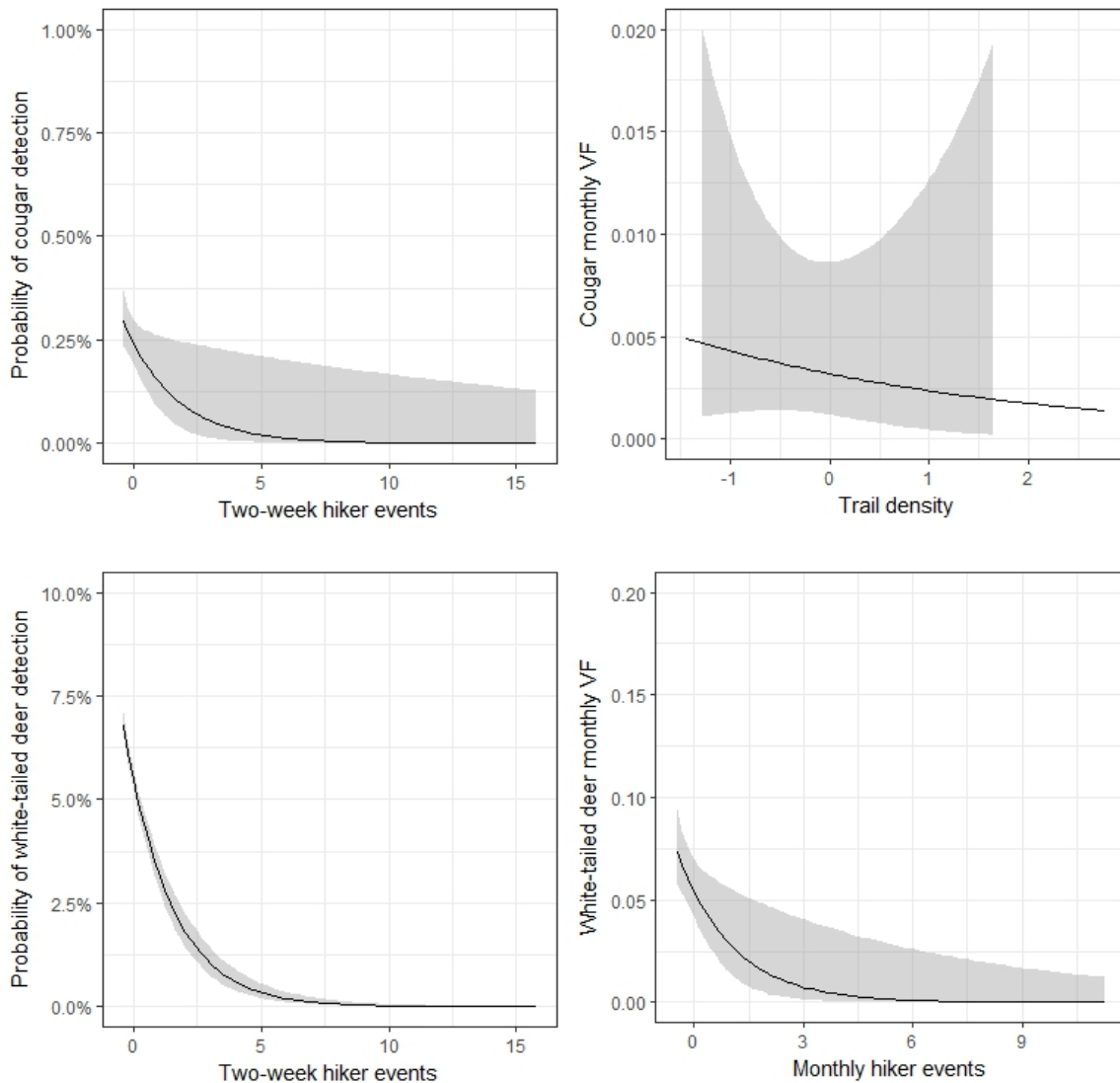
Fig. 3. Relationships between (left panels) total hiker events over the previous two weeks and probability of cougar and white-tailed deer detection on a given day (daily occurrence model results), (upper right panel) the density of human trails and monthly visit frequency (VF) of cougars, and (lower right panel) monthly hiker events and monthly VF of white-tailed deer (VF model results). Monthly VF was the number of detections of each species per month at each camera. The x-axis values are *z*-transformed; units are standard deviations above or below the mean, which is centered at zero. See Table 3 for mean and standard deviation of hiker events. Shading represents 95% confidence intervals. Confidence intervals for the cougar VF model are truncated due to limited detections.
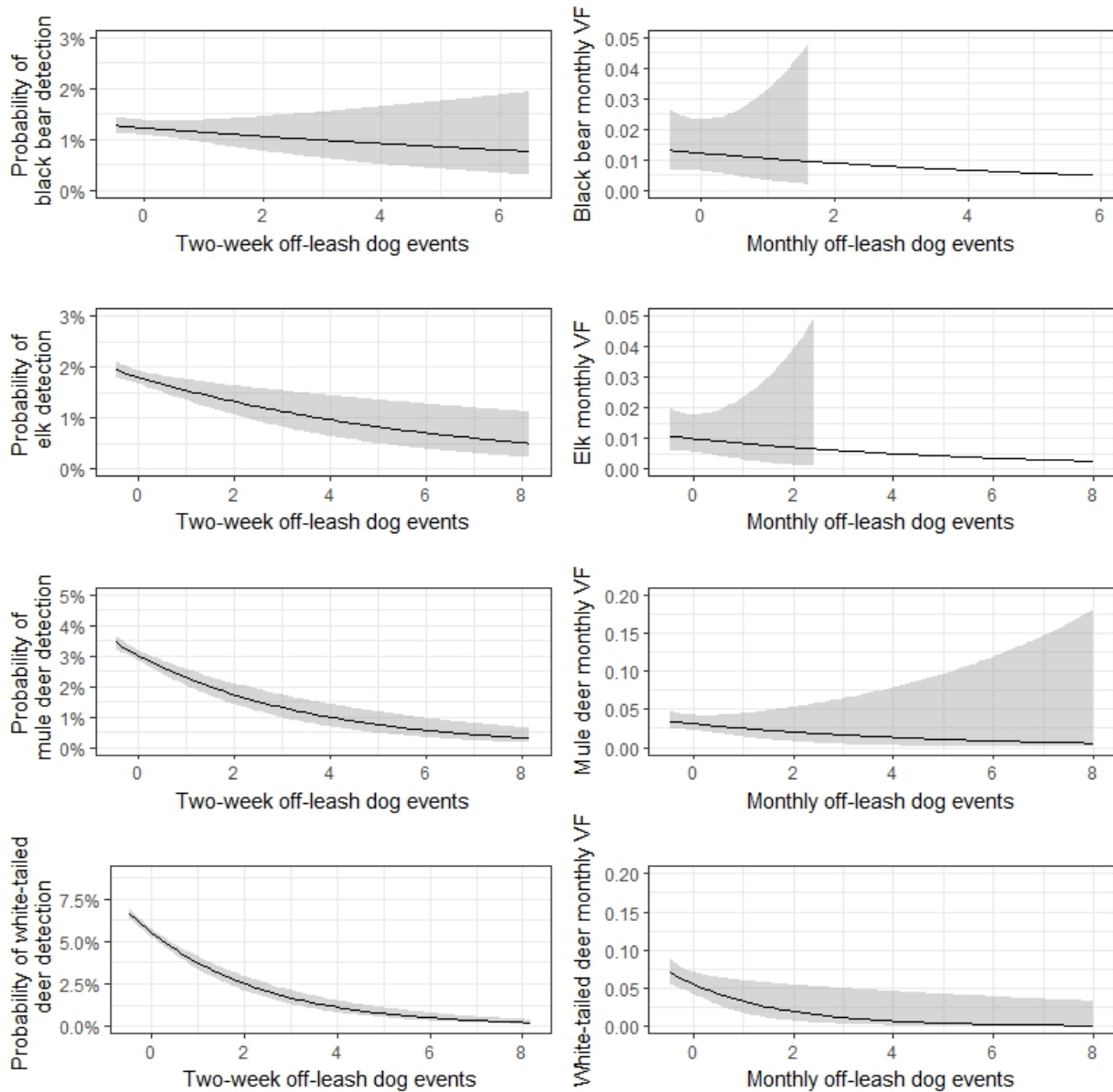
Fig. 4. Relationships between (left panels) total off-leash dog events over the previous two weeks and probability of black bear, elk, mule deer, and white-tailed deer detection on a given day (daily occurrence model results) and (right panels) monthly off-leash dog events and monthly visit frequency (VF) of black bear, elk, mule deer, and white-tailed deer (VF model results). Monthly VF was the number of detections of each species per month at each camera. The x-axis values are z-transformed; units are standard deviations above or below the mean, which is centered at zero. See Table 3 for mean and standard deviation of off-leash dog events. Shading represents 95% confidence intervals. Confidence intervals for bear and elk VF models are truncated due to limited detections of these species.

5. Conclusion

Key findings

As human populations continue to grow, it is likely that more natural areas across the globe will become landscapes that are shared between wildlife and people. Large mammals inhabiting these landscapes must navigate the complex dynamics of human disturbance, which will be determined by spatial and temporal variation in density and type of human activity. Taken together, my studies suggest approaches for achieving a more nuanced interpretation of wildlife avoidance behavior in relation to human use. This dissertation is novel in its focus on areas of high overlap between people and wildlife, and in its rigorous quantification of the timing, intensity, and spatial distribution of human activity.

My second and third chapters clearly demonstrate that spatiotemporal variation in levels of human disturbance can shape the habitat selection patterns of wildlife living in areas where human activity is widespread. In my first chapter, analyses showed that grizzly bears adjusted their behavior in response to daily, weekly, and seasonal fluctuations in recreation on roads, trails, and in facilities, using areas near busier anthropogenic features at times when human activity on those features was lower. Bears also increased their use of forest cover when close to recreation infrastructure, lending support to recent studies documenting that large carnivores utilize multiple strategies to avoid people in areas of high human activity (Oriol-Cotterill et al. 2015b). My second chapter confirmed that quantifying spatiotemporal variation in human activity improves prediction of grizzly bear habitat selection in high human use areas. My results suggested that, at minimum, conservation biologists should distinguish high- and low-intensity categories of human use, both in space and time, and that in areas of high overlap between wildlife and people, continuous estimates of human activity levels best describe wildlife behavior.

My fourth chapter identifies types and levels of non-motorized recreation that displaced large mammalian carnivores and ungulates from critical habitat linking two large protected area systems. I used camera trapping data to demonstrate that most study species shifted their temporal activity patterns to avoid human disturbance associated with trails, roads, or residential development, while also spatially avoiding off-leash dogs and/or hikers. This final chapter retains a fine-scale approach, but it expands my focus from one to multiple species.

Landscapes where people and wildlife coexist have been characterized by peaks and troughs of human disturbance. Throughout my dissertation, I investigate ways to quantify these fluctuations in human activity and measure wildlife response. My final chapter also moves toward identification of those peaks of human activity that are too high or occur too frequently for wild animals to continue to utilize an area.

Future research

This dissertation suggests several directions for future research. First, investigations of wildlife behavioral responses to the fine-scale dynamics of human activity are few, and future studies should continue to evaluate the utility of rigorously quantifying human disturbance to gain a

more mechanistic understanding of wildlife behavior in landscapes shared with people. My work focuses on non-motorized recreation, but regular human presence in wildlife habitat can take a number of forms, including residential development and other activity near settlements, livestock grazing, and gathering of timber and non-timber forest products. Unique approaches will likely be needed to estimate the timing, intensity, and spatial extent of these different activities, and the scales of estimation best suited for assessing impacts on wildlife may also vary. Future research could begin to elucidate best practices for quantifying human activity in diverse landscapes.

While my studies focus on habitat selection and diel activity of wildlife, the development of technology to track both human and wildlife movements creates an additional opportunity to measure wildlife behavioral adjustments to people in real time. For example, Ordiz et al. (2013) quantified brown bear movement patterns in response to experimental approaches by people, finding that bears increased their energy expenditures and reduced foraging time after encounters with humans, with potential demographic consequences. Moreover, many studies of wildlife behavioral responses to human disturbance refer to the possibility of population-level consequences, but these have rarely been confirmed with empirical data. In one example, researchers linked reduced population viability of an endangered bird to altered habitat selection patterns and foraging regimes during tourist seasons (Kerbiriou et al. 2009). Connecting reproduction and survivorship of wild animals to their behavioral responses to humans will be essential to assess whether wildlife populations in human-dominated landscapes are equally viable as their wilderness counterparts.

While this dissertation adds to the growing body of literature investigating the mechanisms by which wildlife adjust their behavior around people, the ability of large carnivores and ungulates to navigate and avoid human activity is only one determinant of whether these species will persist. Human attitudes and behaviors are at least as important, if not more so. For example, my research demonstrates that the willingness of private citizens to limit their recreation activity and to follow regulations, such as leashing of off-leash dogs, will be critical to wildlife conservation in my study area. The Theory of Planned Behavior (Azjen 1985) and other paradigms employed in human dimensions of wildlife research could help to reveal those factors shaping human behavior in coexistence landscapes, with the goal of promoting behaviors that facilitate persistence of wildlife (Marchini and MacDonald 2012).

Traditional approaches to conservation have advocated large-scale separation between wildlife and people. Though large reserves and wilderness areas are doubtless still needed, recent studies suggest they may be complemented by efforts to maintain wildlife populations in habitats regularly used by people (Llaneza et al. 2012; Carter et al. 2012; Oriol-Cotterill et al. 2015a). However, biologists and managers seeking to conserve wildlife in human-dominated landscapes are in need of models of success. Some factors affecting long-term, sustainable coexistence between people and wildlife cannot be controlled, such as wildlife life history traits, but many other factors can be managed. These include tolerance of local people for wild animals; social norms related to the environment and responsible behavior; presence of effective incentives for human behavioral change; planning of infrastructure in a way that maintains space for wildlife; and efforts to modify animal behavior when needed, such as aversive conditioning. Researchers working in shared landscapes across the globe should record and communicate lessons learned

and strategies that appear effective for maintaining viable populations of wildlife in the midst of human activity.

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