INTERSPECIFIC PATTERNS IN CARNIVORE HABITAT USE AND THE IMPACT OF

HUMAN DISTURBANCE IN THE MANITOU EXPERIMENTAL FOREST

A Senior Thesis Presented To

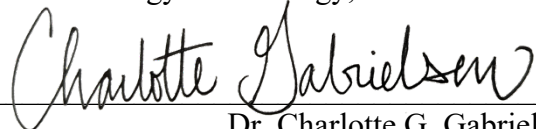The Faculty of the Department of Organismal Biology and Ecology

Colorado College

By

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Abstract

Diverse carnivore communities are important for maintaining top-down controls and protecting ecosystem function. It is important to understand what factors influence carnivore movement and behavior in order to effectively conserve predator communities. Both human activities and interspecific competition or predation by other carnivore species can impact habitat use and activity patterns of carnivores, and sometimes result in spatial or temporal avoidance of dominant carnivores. Previous research at the carnivore guild level in Colorado has been limited, and no previous carnivore studies exist for the Manitou Experimental Forest (MEF) in central Colorado. I used camera trapping to understand carnivore community composition and investigate the following research questions: (1) does human disturbance from developments or roads impact carnivore habitat use, and (2) do subordinate carnivore species spatially or temporally avoid dominant carnivores? To address these questions, I deployed 30 motion-triggered infrared cameras in the MEF for a period of approximately 86 days for a total trapping effort of 2,580 days. This trapping effort resulted in the detection of a total of 10 carnivore species, including 9 of the 11 species previously reported in the MEF and one new carnivore, the spotted skunk (*Spilogale gracilis*). Overall, human road disturbance did not negatively impact carnivore habitat use, although there was a trend of lower puma habitat use at high road disturbance sites. Fox species showed opposite patterns with human residential disturbance: gray fox (*Urocyon cinereoargenteus*) habitat use was negatively related to residential disturbance while red fox (*Vulpes vulpes*) habitat use was significantly positively related to residential disturbance. There was generally little evidence of interspecific avoidance among carnivore species except among canines, as gray foxes appeared to wait longer before using a site after a coyote and there may have been temporal segregation between the more nocturnal foxes and more diurnal coyote. I did find some preliminary evidence of mesocarnivores avoiding pumas (*Puma concolor*) at the seasonal scale, but more research is necessary to investigate this potential behavior. Positive associations among carnivores were more common, with spatial association between coyote (*Canis latrans*) and bobcat (*Lynx rufus*) and between striped skunk (*Mephitis mephitis*) and several larger mesocarnivores. I also found evidence that red fox may have followed pumas, likely in order to scavenge from puma prey carcasses. My research suggests that carnivore temporal and spatial coexistence is high within the MEF, which may be facilitated through dietary partitioning or more fine scale spatial or temporal segregation that I was unable to detect. The relatively low levels of human disturbance in the forest do not appear to disrupt habitat use patterns for most species, consistent with the hypothesis that low-density exurban development can represent suitable habitat for many carnivores. Future research should examine carnivore community interactions across a larger landscape and a broader gradient of human disturbance in order to better understand habitat use patterns in the carnivore guild of the Pikes Peak region of Colorado.

Introduction

Carnivores function as keystone species that exert important top-down controls on their ecosystems, influencing the size and structure of prey populations. The widespread loss of apex predators globally has demonstrated that apex predators, many of which are carnivores, exert large-scale influences on ecosystems through trophic cascades (Estes et al., 2011). Carnivores directly or indirectly have been found to control herbivore population dynamics, limit spread of disease, shape patterns in nutrient distribution throughout a landscape, and influence overall community structure and help maintain biodiversity (Frank, 2008; Peziol et al., 2023; Ripple et al., 2014; Ripple & Beschta, 2004).

Given the largescale effects of carnivores on their ecosystems, it is critical to understand how carnivores utilize habitat resources, since patterns in carnivore habitat use will determine how top-down controls are exerted across the landscape. While discussion of the importance of carnivores often focuses on the impact of a single apex predator, carnivore species usually do not exist in isolation, but rather within sympatric communities of multiple carnivore species that have many direct and indirect interactions. Within a carnivore guild, the pressures of competition for shared prey resources and intra-guild killing drive spatial and temporal differences in carnivore habitat use in order to minimize negative interactions. For instance, habitat use appears to be primarily driven by prey abundance for the apex predator tiger (*Panthera tigris*) , while spatial and temporal patterns of the mesopredators leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) are driven by prey abundance as well as avoiding tigers (Steinmetz et al., 2013). Since interspecific relationships can play such a large role in shaping carnivore movement behavior, in order to fully understand the processes that shape habitat use, research should focus on guild-level interactions and investigate the complete assemblage of sympatric carnivore species within particular areas (Boron et al., 2020; Cruz et al., 2018).

Anthropogenic disturbance can pose a serious threat to carnivore populations, and habitat degradation and fragmentation, land use changes, and increased human activity change patterns of carnivore habitat use. Human activity, in both urban and wild environments, can influence carnivore movement and predation behavior. For example, human activity caused pumas to reduce feeding time at prey carcasses and increased the rate of deer killed (Smith et al., 2017). Behavioral adaptions to human-disturbed environments translate into different patterns of resource use by carnivores, which could potentially have cascading effects on lower trophic levels. However, human disturbance does not impact all carnivore species equally, and this differential response to human activity or development can result in changes in the carnivore guild structure. In general, larger carnivores are expected to be more negatively impacted by human disturbance due to their greater land area demands and inability to tolerate habitat fragmentation (Crooks, 2002). In theory, if apex carnivores are more sensitive to human activity, smaller mesocarnivores may actually benefit from disturbances if they result in fewer larger carnivores in a landscape, resulting in mesopredator release (Crooks, 2002). Human disturbances also may impact carnivores differentially based on their degree of specialization; human

disturbance in Southeast Asia resulted in more specialist carnivores adapting with increased nocturnality compared to generalist species (Lee et al., 2024). With high levels of human activity, generalists and larger carnivores may encroach on smaller and more specialized carnivore species' niches, increasing competition among the carnivore guild (Smith et al., 2018). These varied responses by different carnivores to human activity mean that anthropogenic disturbance can often disrupt the existing carnivore guild structure (Prugh et al., 2009).

As many carnivore species have wide distributions with considerable variation in climate, ecosystem type and habitat structure, the factors influencing habitat use are likely to be highly regionally variable for a single species (Rubio-Rocha et al., 2023). The carnivore species assemblage can also vary tremendously over the range of widespread carnivores species; the puma (*Puma concolor*) has the widest distribution of any native terrestrial mammal in the Americas (LaBarge et al., 2022), overlapping with grizzly bear (*Ursus arctos horribilis*) and Canada lynx (*Lynx canadensis*) at its northern range limit, tropical carnivore species like jaguar (*Panthera onca*) and tayra (*Eira barbara*) in Central and South America, and culpeo (*Lycalopex culpaeus*) and Geoffrey's cat (*Leopardus geoffroyi*) in Patagonia. Given flexible guild structure over species' ranges, many carnivores appear to have highly plastic responses to interspecific competition (Monterroso et al., 2014). It is therefore critical that an understanding of what relationships drive patterns in resource use for a particular species be based on local research of focal carnivore guild members.

The Rocky Mountains contain some of the most intact carnivore guilds in North America, as apex carnivores have not been completely extirpated as in much of the eastern United States. However, much of the research on carnivore habitat use in the Rockies has focused on the Northern Rockies and particularly the Greater Yellowstone Ecosystem (Ripple & Beschta, 2004). Additionally, while there is more species-specific research on wolves (*Canis lupus*) and puma in the Rockies (Elbroch & Wittmer, 2012; Kertson et al., 2011; Nelson et al., 2012; Peziol et al., 2023), attempts to conduct research at the guild level are limited. Habitat modeling studies have recommended that conservation strategies in the Rockies should consider the habitat requirements of multiple carnivore species at once, and not only those of the apex carnivore that is assumed to be an umbrella species (Carroll et al., 2001). There is relatively limited research on habitat use patterns across the carnivore guild in Colorado (Goad et al., 2014; Kitchen et al., 2000; Lewis, Bailey, et al., 2015; Lewis et al., 2021; Lewis, Logan, et al., 2015), and to my knowledge there are no guild-level studies of habitat use in the Pikes Peak region.

I conducted a camera trap study of carnivores in the Manitou Experimental Forest (MEF), near Woodland Park, Colorado, in order to investigate carnivore guild structure and factors influencing habitat use patterns in this under-researched region. The MEF is part of the Pike-San Isabel National Forest, but contains a residential development within its boundaries, so it provides the opportunity to study how human disturbance in protected lands impacts carnivore habitat use. The only existing published report on the MEF mammal community was based on small mammal trapping and incidental observations of larger species from the 1950s through

1970s (Morris et al., 1977), with no systematic survey for large mammals. The development of camera trap technology in past several decades has been invaluable for carnivore surveys, as remote motion-triggered cameras can generate large datasets of wildlife observations and detect elusive species that are difficult or almost impossible to observe in person (Horn et al., 2020; Rodgers et al., 2015; Wood et al., 2021). I used camera trapping to conduct the first carnivore survey of the MEF and investigated the following questions on how carnivore habitat use is affected by human disturbance and interactions with other carnivore species: 1) How does human residential disturbance impact the likelihood of carnivore detection? 2) How does human road disturbance impact the likelihood of carnivore detection? 3) Do subordinate carnivores spatially avoid dominant carnivores? 4) Do subordinate carnivores temporally avoid dominant carnivores?

Methods

Study Area

Camera trapping took place in the Manitou Experimental Forest (MEF), which is part of the Pike-San Isabel National Forest and located 48 km northwest of Colorado Springs near Woodland Park, Colorado. The total area of the MEF is 67.58 km^2, but I restricted my study area to the portion of the experimental forest east of Colorado state highway 67 (Figure 1). Elevation in the MEF ranges from 2280 m to 2840 m above sea level. The forest primarily consists of ponderosa pine (*Pinus ponderosa)* on south-facing, xeric slopes as well as in flat open grasslands along the western edge of my study area (directly east of the highway). In north-facing slopes and mesic regions, the forest is dominated by Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine, while quaking aspen (*Populus tremuloides*) and blue spruce (*Picea pungens*) are prevalent in drainage bottoms. In the northeast corner of the MEF, there is an area that contains almost exclusively lodgepole pine (*Pinus contorta*). The MEF is cut through by highway 67 and is bordered by the gravel Rampart Range Road to the east, but other roads within the experimental forest boundary and in surrounding National Forest are primarily single-track dirt roads. The MEF experiences low levels of recreational activity, and is used by hikers, campers, hunters, and off-road vehicle (ORV) drivers. There are also private inholdings inside the experimental forest boundary that predate establishment of the U.S. Forest Service (in 1905), so there is some amount of year-round residential disturbance present. The Ridgewood Subdivision, located in the central portion of the MEF, is approximately 2.84 km^2 large and contains approximately 160 residential structures. There are some additional smaller private land inholdings in the southern part of the study area, although these do not have well-maintained dirt roads and contain a lower density of residential structures than the Ridgewood development.
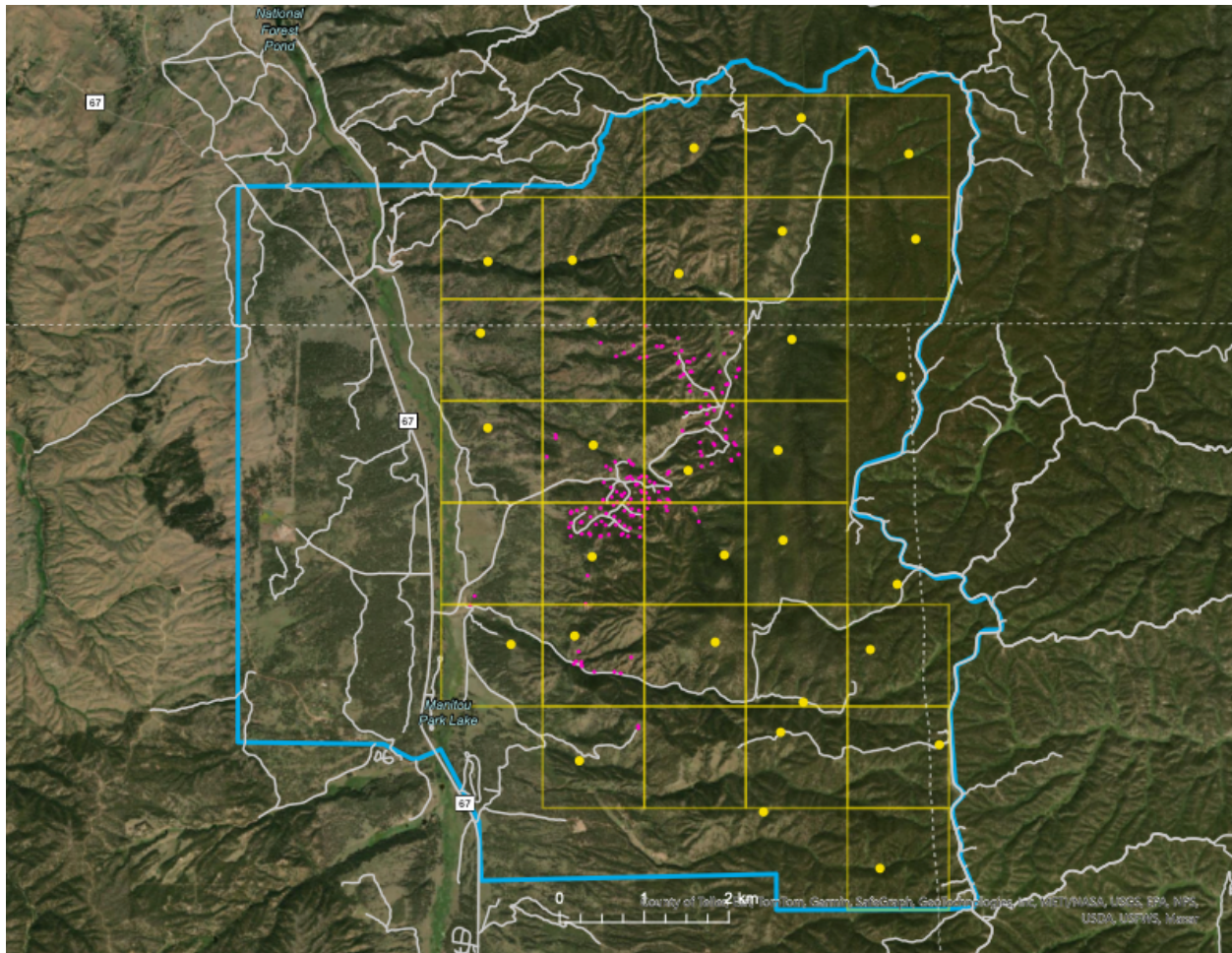
Figure 1. Map of camera trap project survey grid and individual camera stations (yellow dots) in the Manitou Experimental Forest (outlined in blue) showing roads (gray lines) and residences (pink dots). Grid cells measure 1.2 km to a side. Cameras were placed a minimum of 500 m apart and on movement corridors or paths/trails by carnivore scat.

Field Methodology

Carnivore observation data was collected by 30 motion-triggered camera traps set up throughout the MEF and operating for an average of 85 days (Figure 1, Figure 2). I used 30 cameras for the approximately 3 month survey duration because that trapping effort was experimentally determined to provide sufficient data for occupancy/habitat use modeling for most medium-sized carnivores in camera trap grids elsewhere in the Colorado Front Range. Although greater trapping effort would be preferable with a higher budget, I decided that increasing camera number and density over the area of MEF would produce too many redundant detections for carnivore target species, so more cameras would probably only be more helpful in a larger study area than the MEF. The study area was divided into grid cells of 1.2 km width, for a total grid area of 43.2 km^2 (Figure 1). I selected grid spacing based on reported spacing of around 1-2 km

for camera trap studies of medium sized feline/canine carnivores (Lombardi et al., 2020; Swinkels et al., 2023), and the advice of Dr. Jesse Lewis (Arizona State University, personal communication). I placed one camera in each grid cell so that each camera was at least 500 m apart from cameras in neighboring grid cells. Cameras were placed along trails, game paths or natural movement corridors in order to maximize the likelihood of detecting wide-ranging and low-density carnivore species. Whenever possible, I placed cameras near carnivore scat. I scouted out each grid cell area to familiarized myself with the topography and habitat and attempted to choose the best spot for carnivore detection. At each camera site I recorded information on site characteristics including tree species present, canopy cover and path type for potential future analysis of how habitat structure is related to carnivore detections. I set up cameras from August 12th through August 26th, visited all cameras once in October to switch SD cards and check on battery levels, and took down cameras from November 15th through November 20th (Figure 2). Several cameras were inoperable for periods during the survey because bears pushed down the camera, and because one SD card and one camera were stolen.
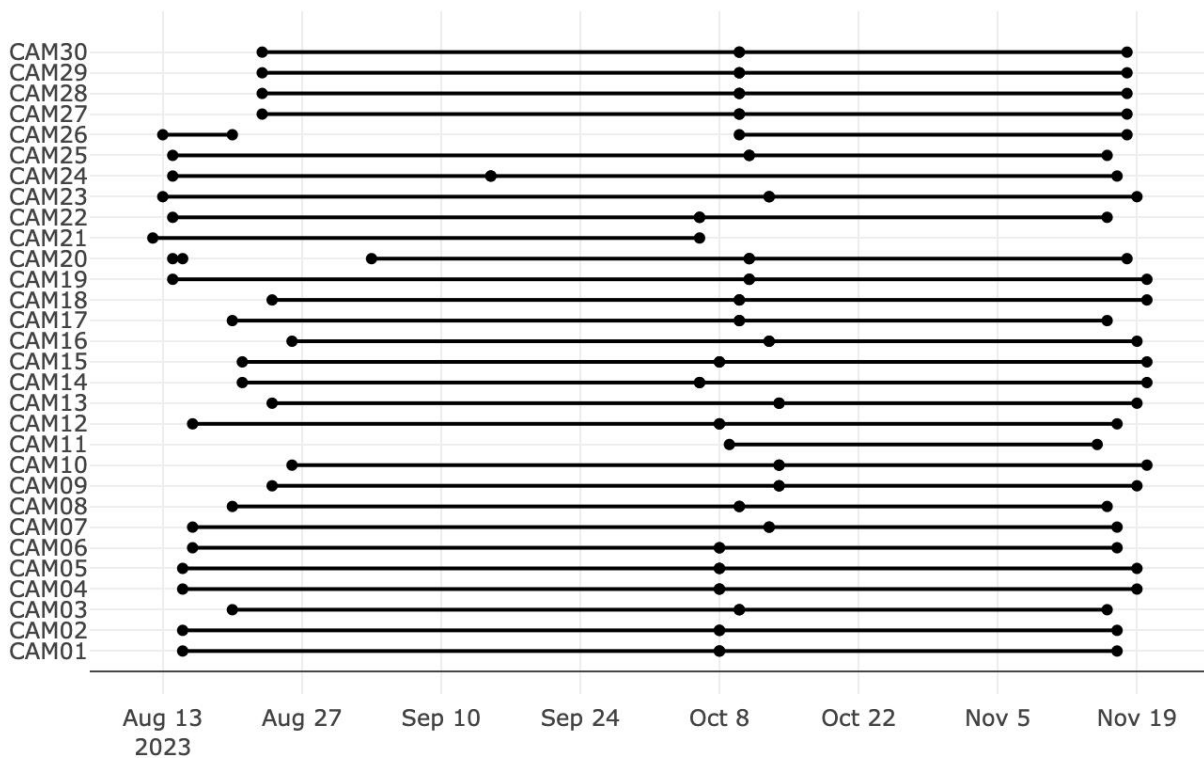
Figure 2. Plot showing periods when cameras in the MEF were operating over the survey duration. Dots represent dates cameras were deployed, visited and SD cards swapped, or taken down at the end of the survey. Total trapping effort was 2,580 days, with each camera operating for average of 85 days. Gaps in deployment represent cameras that were pushed down by bears or were stolen or had SD cards stolen.

Data Analysis

I manually processed photos (N = 45,456) and determined whether they contained images of animals. For those that did, I recorded camera ID, date and time of detection, animal species, and number of individuals. I counted detections of a species at a camera site that were more than an hour apart as independent detections.

In order to analyze the impact of human disturbance, I generated shapefiles for the human residences within the MEF and roads in the area using ArcGIS Pro Version 3.1.1. Using satellite imagery as a reference basemap, I manually digitized all exurban residences as points, using a Universal Transverse Mercator (UTM) coordinate system. The road layer was created by combining shapefiles for CO state roads (Colorado Department of Transportation) and trails (U.S. Forest Service), to which I digitized additional lines where trails were missing from the publicly-available datasets. In order to account for varying disturbance impacts of different road use levels, I created a disturbance level attribute and assigned each road into one of 5 classes (Figure 3B). High-use roads (including CO 67 highway) having concrete or asphalt surfaces and used for high-speed traffic (speeds $\geq$ 80 kph) were assigned class 5, residential roads and improved gravel surfaces (including Rampart Range Road) were assigned class 4, high use ORV roads were assigned class 3, and other F.S. roads were assigned classes 2 or 1 depending on use. Class 1 was assigned to F.S. roads within the main portion of the MEF but excluding roads or road segments around the research station lodge and office and by campgrounds that had higher activity. Class 0 was assigned to F.S. roads closed to public vehicle access.

I used the Kernel Density tool in ArcGisPro to create a raster layer of human disturbance levels for both the residences and roads (Figure 4, Figure 3A). For residences, I chose a radius of 1500 meters around each residence point to represent the area around the residence that the impact of disturbance would extend to (sensu Lewis et al. 2015A). For kernel density applications with the road layer, the disturbance class attribute was used for the population field so that high-use roads were weighted more heavily in the output. Since there were no published values for radius of disturbance effects from roads in this ecosystem, I tested several radius values as well as the tool's default setting of no specified radius, then used the regression feature to determine which raster output best explained variation in detections; all produced similarly low R^2 values, so I used the default settings. Next, I used the Extract Values to Points tool to assign each camera location the kernel density raster value for that pixel. To assess how much carnivore detections varied in accordance with the disturbance levels, I used these values as continuous variables in single species habitat use models. I also classified each camera site into low or high residential disturbance and low or high road disturbance and used these as categorical variables in single species habitat use models.
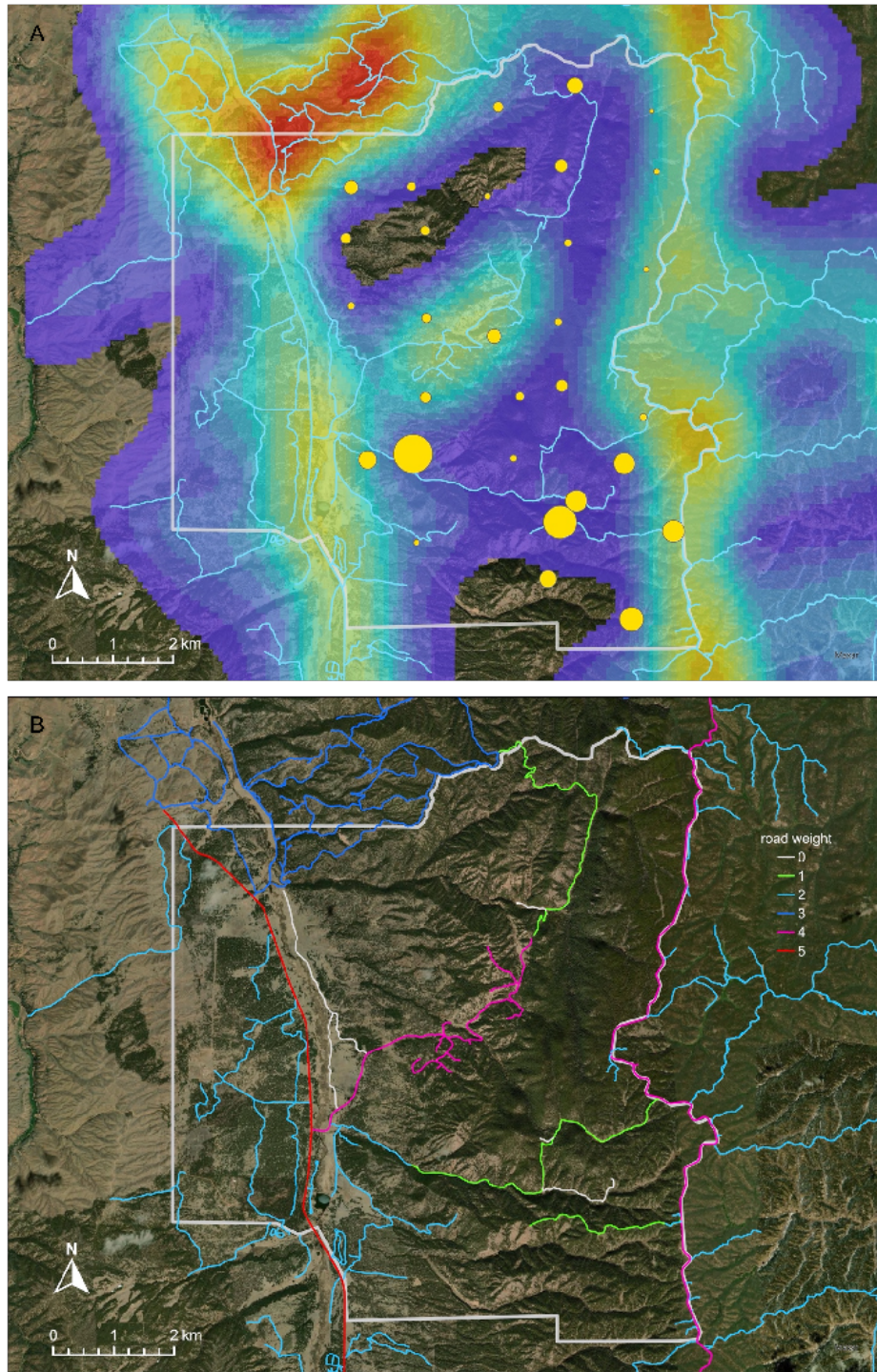
Figure 3. A) Heat map showing kernel density output raster for road disturbance in the MEF with circles at camera locations scaled proportional to total carnivore capture rate. No relationships were found between kernel density output values and detection rates of any carnivore species. B) Road weight classes used to weight roads with kernel density tool in ArcGIS. Class 5 was used for the highway, class 4 for residential roads and improved gravel surface roads (Rampart Range Rd), class 3 for high-use ORV roads, class 2 for F.S. roads by the research station/lodge and campground and outside experimental forest boundary, class 1 for internal MEF F.S. roads, and 0 for roads closed to public access.
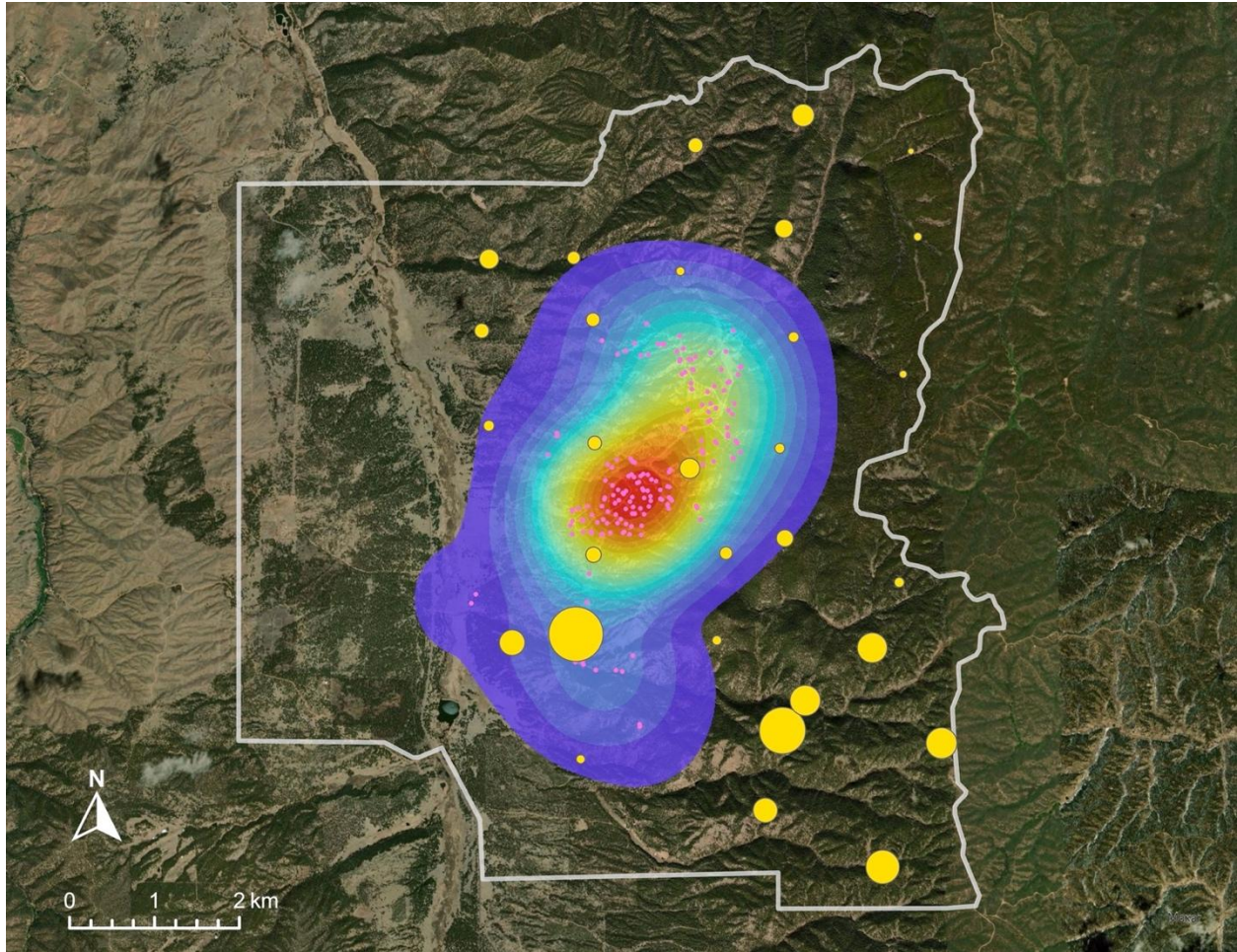
Figure 4. Heat map showing kernel density output raster for residential disturbance in the MEF with circles at camera locations scaled proportional to total carnivore capture rate; pink dots show individual human residences. No relationship was found between kernel density output values and detection rates of any carnivore species.

I quantified periods of temporal avoidance by calculating the mean interval from a detection of species A to the first detection of species B at the same camera site, and the mean interval from a detection of species B to the next detection of species A at the same camera site. I performed one-tailed t-tests assuming unequal variance in Microsoft Excel Version 16.83 to compare the mean AB and mean BA intervals and determine if species A waited longer than expected to return to a site after it was used by species B. I used a significance level of ⟨=0.05. Using the University of British Columbia Wildlife Coexistence Lab's "An Introduction to Camera Trap Data Management and Analysis In R" as a guide (Beirne, 2022), I modified code to perform occupancy estimation, single species habitat use models, species detection correlation analysis, diel activity analysis and activity coefficient of overlap tests in RStudio Version2023.12.1+402. I calculated raw occupancy, or the proportion of sites occupied by a species to provide an additional metric of carnivore presence in the MEF. To investigate the impact of human disturbances on carnivore habitat use, I fit single-species linear models of habitat use

(independent capture rate) with human disturbance covariates. I used both continuous variables (kernel density raster values) as well as categorical variables for road and residential disturbance to model habitat use in each focal species. To investigate spatial patterns of carnivore coexistence, I used the *corrplot* package to create a plot showing pairwise correlations between different carnivore species detections. In order to identify general patterns in the timing of wildlife activity, I plotted diel activity. I used the *activity* package to fit a model of activity adjusted for sunrise/sunset times for each focal carnivore species. To measure how much activity overlapped between pairs of carnivore species, I used the *overlap* package to calculate the coefficient of overlap (Δ), which varies from 1 (complete overlap) to 0 (no overlap).

Results

In 2,580 total trap-days from August 12 to November 20, my cameras were triggered a total of 5,682 times. Animals (including humans and domestic animals) accounted for 61% of these triggers (N = 3,455). Wild mammals made up 49% of triggers (N = 2759). I detected a total of 20 mammal species excluding humans and domestic animals, including 10 carnivore species: coyote, red fox, gray fox, puma, bobcat, black bear, western spotted skunk, striped skunk, raccoon, and long-tailed weasel (Table 1, Appendix 1). Canines were the most frequently detected carnivore species (Table 1), with coyote most common (N=116), followed by red fox (N=104) and gray fox (N=86). Striped skunk (N=44) and bobcat (N=39) were also detected somewhat frequently, while detections of black bear (N=30), puma (N=25) and spotted skunk (N=17) were less frequent (Table 1). The least detected carnivores were raccoon, with 10 detections, and the long-tailed weasel, which was only detected once (Table 1). I excluded raccoon and weasel from further analysis due to the low number of observations. Less frequently detected carnivores had higher occupancy estimates relative to those of the species with highest capture rate (Figure 5). Additionally, both fox species had higher estimated occupancy than coyote, despite having a lower number of raw captures (Table 1).

Several carnivores were uniquely distributed throughout the MEF (Figure 6). Bobcats were detected at 14 cameras, and capture rates were greatest in the southern half of the MEF. Pumas were detected at 14 cameras and showed greatest capture rates in the middle and northern parts of the MEF. Red foxes were detected at 19 cameras, but detections were unevenly distributed throughout the MEF, with camera #22 representing 45% of all detections. Gray fox captures were fairly evenly detected throughout the MEF and were detected at 21 cameras. Coyotes were detected at 15 cameras, and detections were highly concentrated within the southeastern corner of the MEF. Bears were detected at 17 cameras and detections were distributed throughout the MEF. Spotted skunks were detected at 7 cameras and striped skunks at 17 cameras, and detections of both skunks were distributed throughout the forest but with few detections in the central part of the MEF. All carnivore species were detected across habitat types, including ridgelines and drainage bottoms and in different tree communities. However, very few carnivores and no canines or felines were detected at camera sites in the lodgepole pine plantation type forest.

Table 1. Numbers of raw detections and independent detections (detections of a species above the 1-hour threshold) for all wild mammals detected in the Manitou Experimental Forest. 20 mammal species were detected in total, including 10 carnivore species. Of carnivore species, canines were detected very frequently, bobcat and striped skunk were detected somewhat frequently, and black bear, puma, and spotted skunk were detected infrequently. Detections of raccoon and long-tailed weasel were very rare, and these species are excluded from analysis.

| species	detections	independent detections	species	detections	independent detections
coyote	116	112	red squirrel	1010	822
red fox	104	100	mule deer	566	394
gray fox	86	86	mountain cottontail	379	334
striped skunk	44	43	elk	101	82
bobcat	39	39	Colorado chipmunk	89	77
bear	30	28	Abert's squirrel	42	42
puma	25	25	moose	41	41
spotted skunk	17	16	golden-mantled ground squirrel	31	27
raccoon	10	10	mouse/rat spp.	25	24
long-tailed weasel	1	1	white-tailed jackrabbit	3	3
total carnivores	**472**	**460**	**total mammals**	**2759**	**2306**
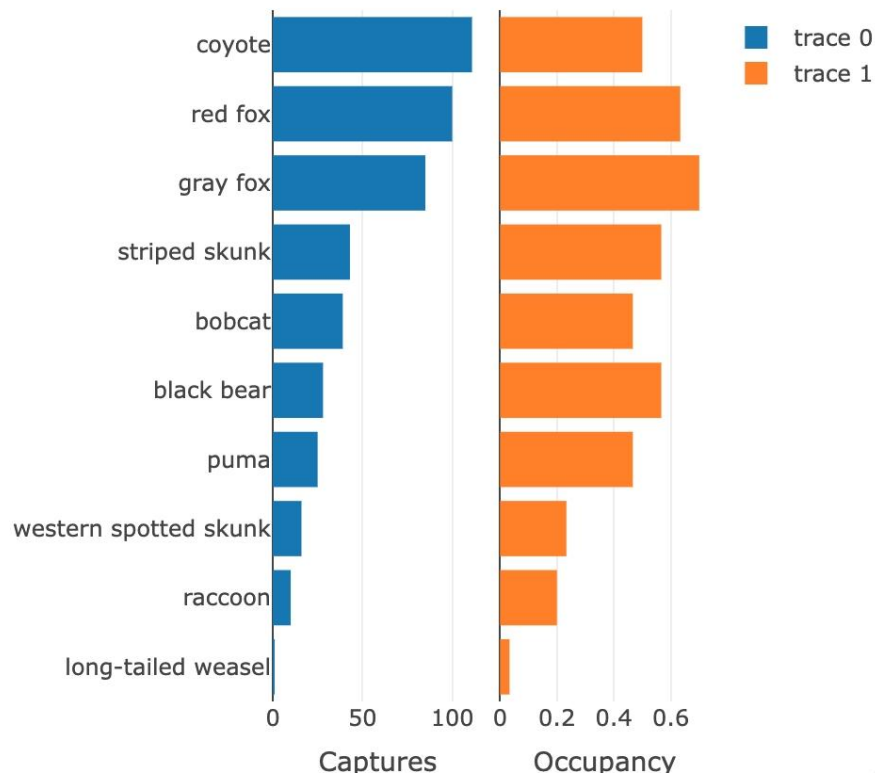
Figure 5. Number of captures (detections) compared to occupancy (proportion of sites occupied) for each carnivore species in the MEF. Canine species were detected most frequently, although occupancy levels were similar for all medium and large carnivores as well as striped skunks.
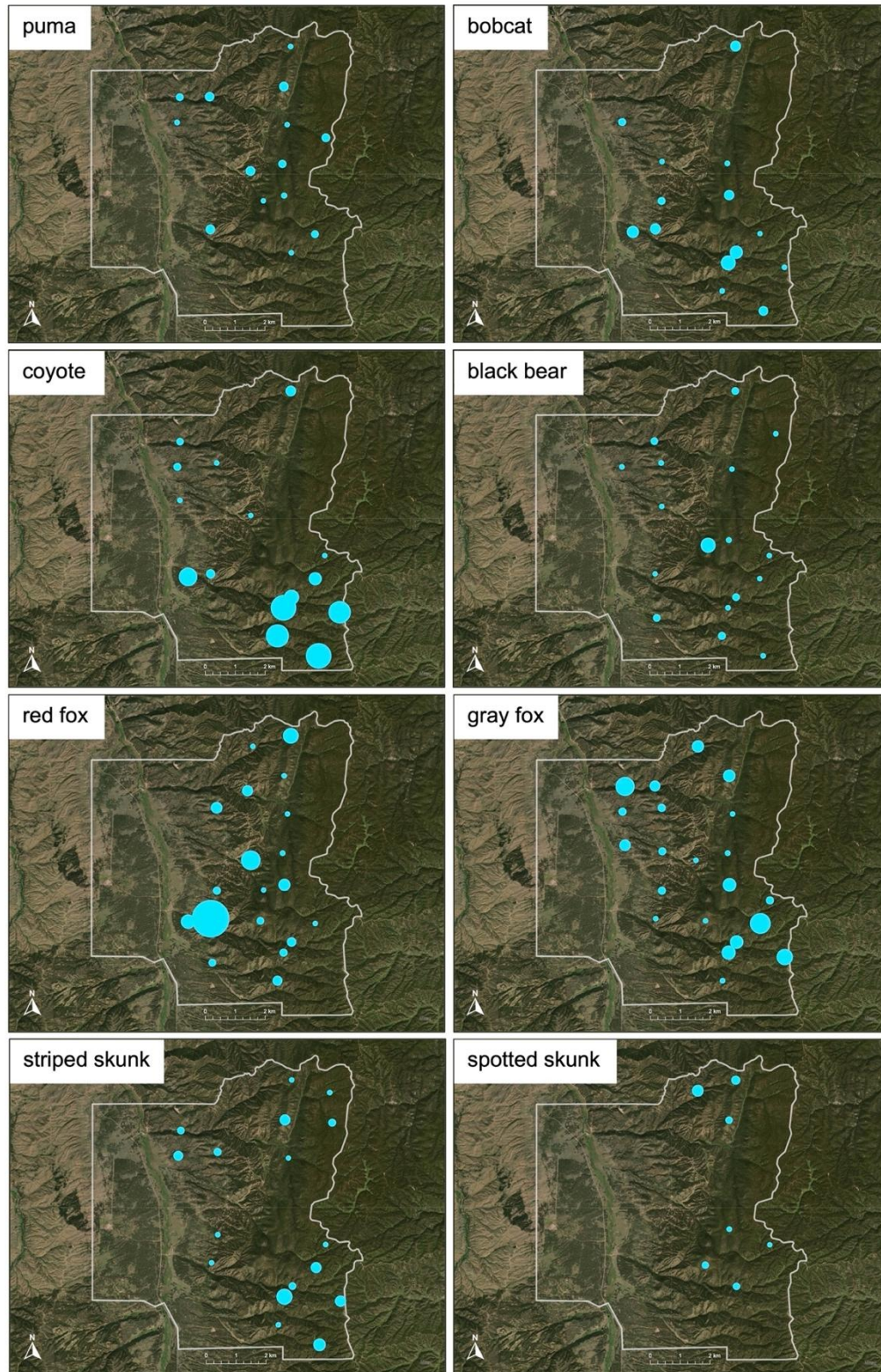
Figure 6. Spatial patterns in detection rates of carnivores across the MEF. Circles are scaled proportionally to the detection rate at each camera. Puma detection rates were highest in the central and northern parts of the MEF, while

bobcat detection rates were greatest in the southern part of the MEF. Coyote detections were strongly concentrated in the southern corner of the MEF. Black bear detections were distributed fairly evenly throughout the MEF. Both foxes were detected throughout MEF, but red fox detections were more unevenly distributed and concentrated at one camera. There were few striped and spotted skunk detections in the central part of the MEF.

Carnivore activity was generally crepuscular or nocturnal, but the degree of nocturnality varied among species (Figure 7). Skunk species were the most nocturnal, and both foxes also had very limited activity during the day. Coyote, bobcat, and black bear were more diurnal than other species, and were active throughout the entire day, with coyote activity peaking in mid-morning and bobcat activity peaking around dawn. Puma activity pattern was mostly crepuscular/nocturnal, but with a few daytime detections.
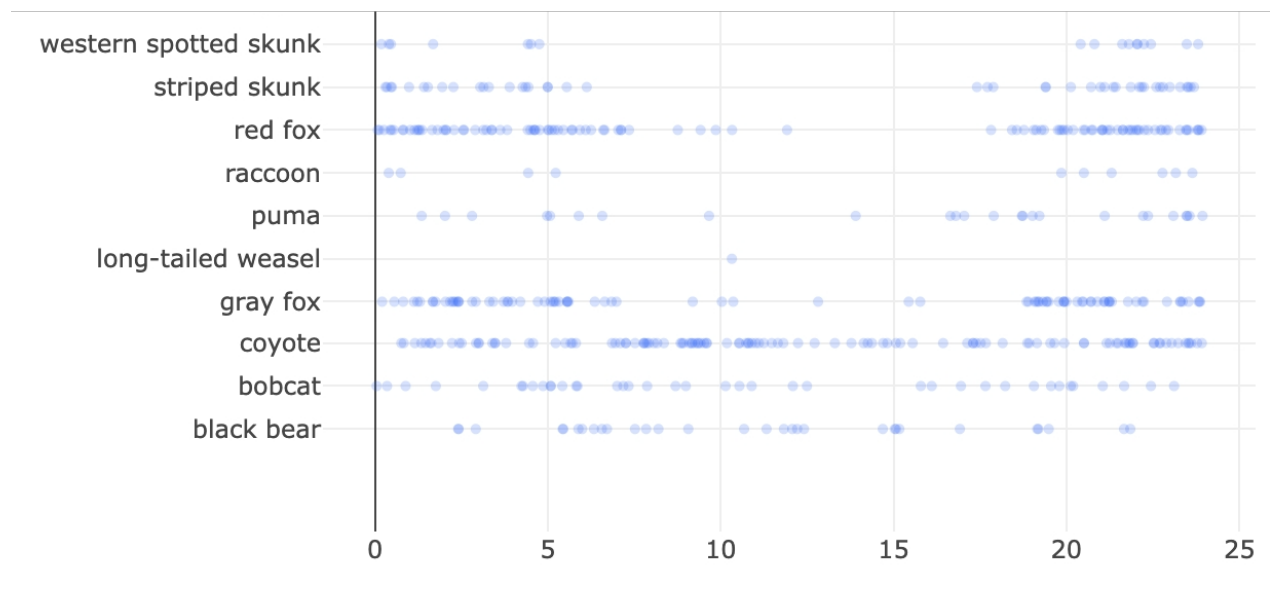
Figure 7. Diel activity patterns of carnivores. Detections are represented by blue dots; x-axis is the number of hours from midnight. Times shown in this plot are not adjusted for the change in sunrise/sunset over the fall. Bobcat, coyote, and black bear were active throughout the day, while red and gray fox were more strongly nocturnal. Puma were also active throughout the day but were less diurnal than bobcats.

Total detections of all wildlife species declined over the survey period, with peak detection rate of over 100 animal detections per 100 camera trap days occurring in September and sharply declining over October and November to around 60 animal detections per 100 camera trap nights (Figure 8). Detection rates of carnivore species also exhibited this general pattern, with the exception of puma, of which detection rate increased over the fall and peaked in November (Figure 9). Black bear detections peaked earlier in August and rapidly declined to 0 by mid-

September when they entered hibernation. Because I only detected black bear activity during a short period immediately prior to hibernation, I excluded them from further analysis as the timing of my survey is not well suited to drawing conclusions about temporal and spatial patterns in their habitat use.
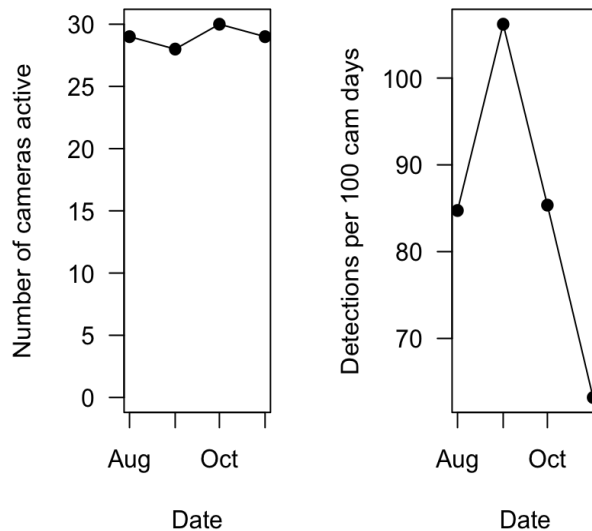
Figure 8. Seasonal variation in A) number of cameras in operation and B) total wildlife detection rate for carnivores in the MEF. Detections of wildlife generally declined over the survey period, with peak wildlife detection rate in September and sharply decreasing from September through November.

Human Disturbance Impacts

Neither residential disturbance or road disturbance kernel density variables predicted capture rate of any carnivore species in single-species habitat use models. However, using the categorical disturbance variables, some trends were apparent. Puma road habitat use was lower at high road disturbance sites than at low road disturbance sites (Figure 10), although this pattern was not significant (p = 0.17). Puma habitat use did not differ between low and high residential disturbance levels (p = 0.46; Figure 11). Bobcat habitat use did not differ between low and high road disturbance sites (p = 0.33), or between low and high residential disturbance sites (p = 0.93). Coyote habitat use was higher at high road disturbance (p = 0.47) and lower at high residential disturbance (p = 0.28), but not significantly so. Gray fox habitat use did not differ between high and low road disturbance levels (p = 0.81), and neither did habitat use of red fox (p = 0.49). However, there was a strong trend with gray fox habitat use and residential disturbance, with higher habitat use at low residential disturbance sites than at high residential disturbance sites (p = 0.08). Red fox habitat use was significantly lower at low residential disturbance than at high residential disturbance (p = 0.04).
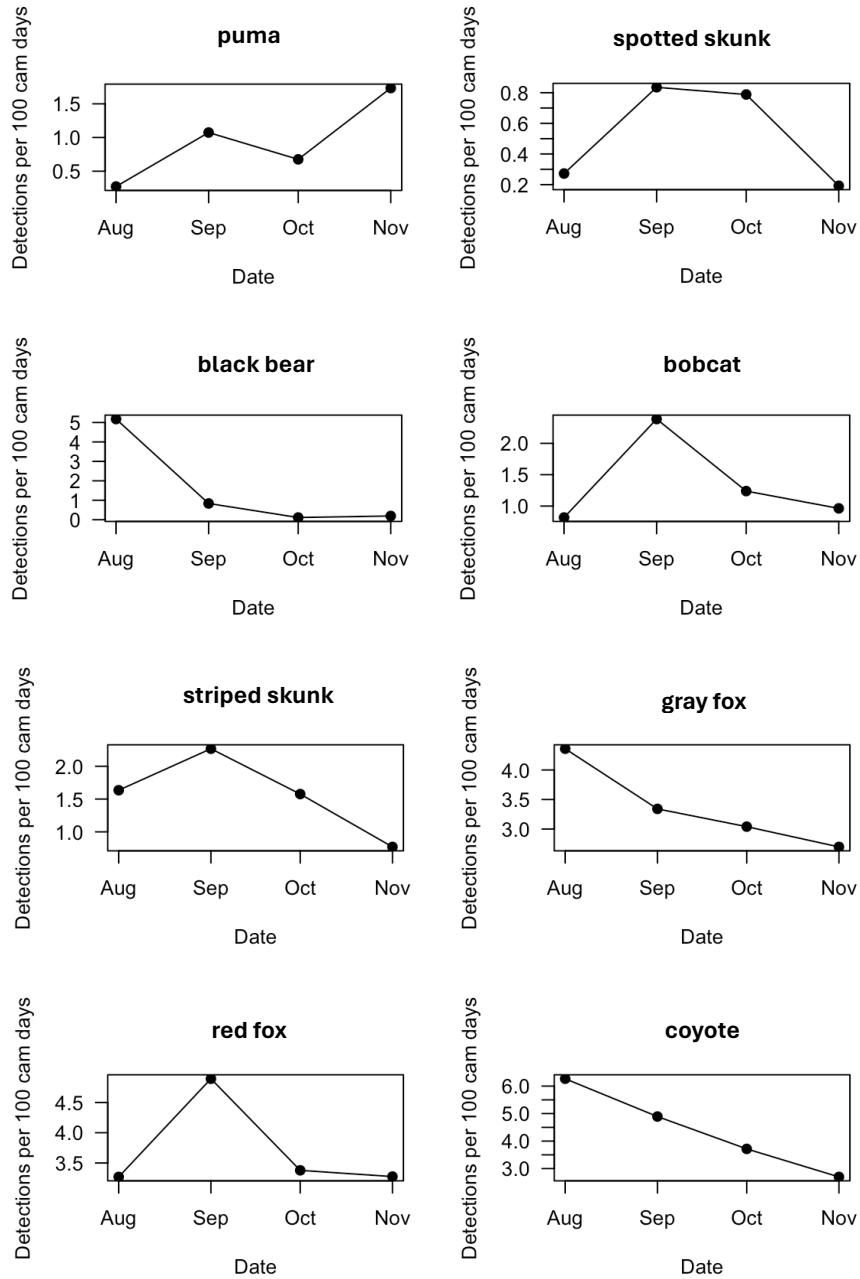
Figure 9. Seasonal variation in detection rates of carnivores in the MEF. Detection rates of all carnivores declined in November with the exception of puma, which peaked in November.
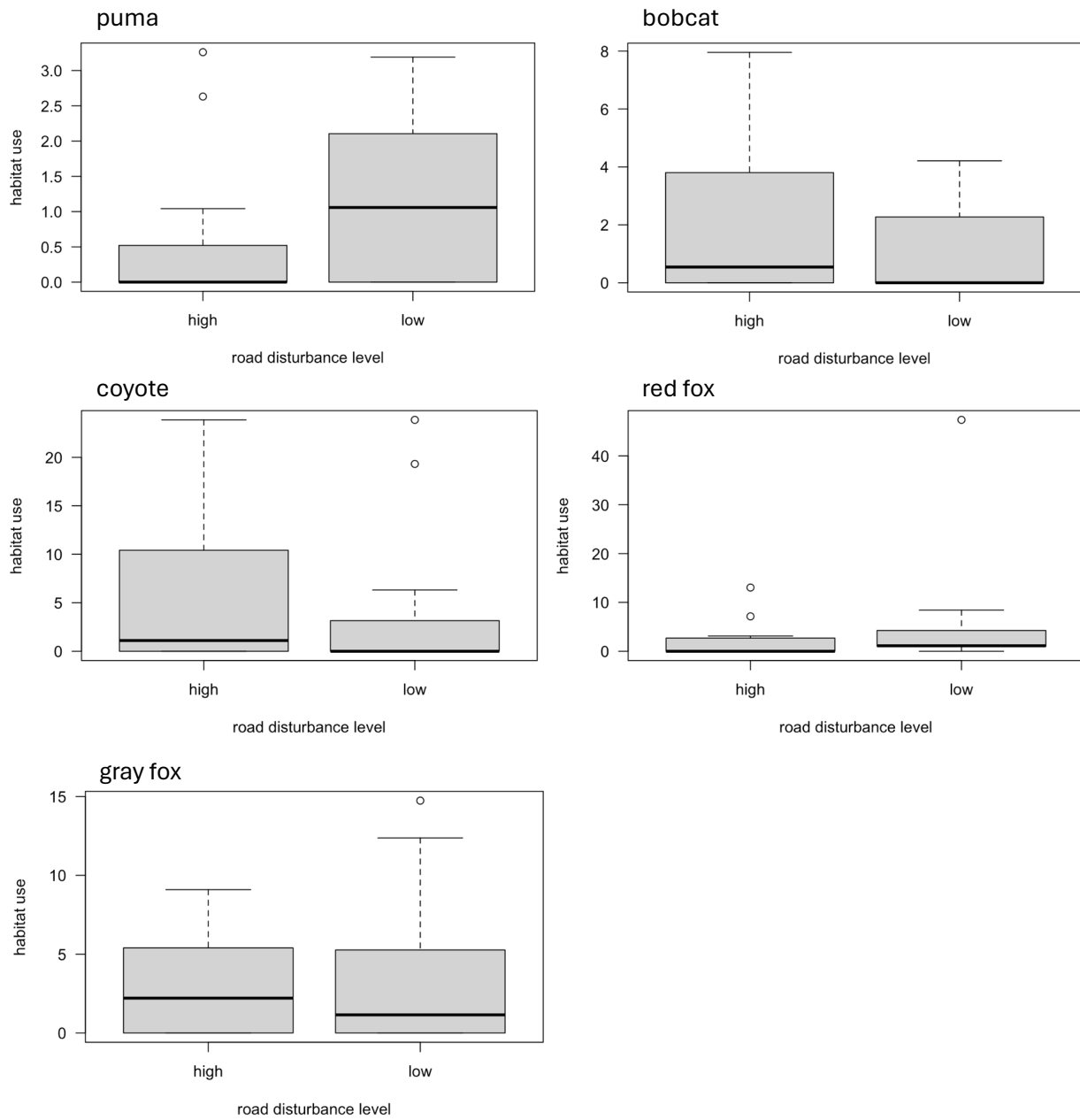
Figure 10. Habitat use of felines and canines in the MEF at high and low levels of road disturbance. Habitat use did not differ between road disturbance levels for bobcats, gray fox, or red fox. Puma habitat use was lower at high road disturbance (P=0.17), and coyote habitat use was higher at high road disturbance (P=0.47).
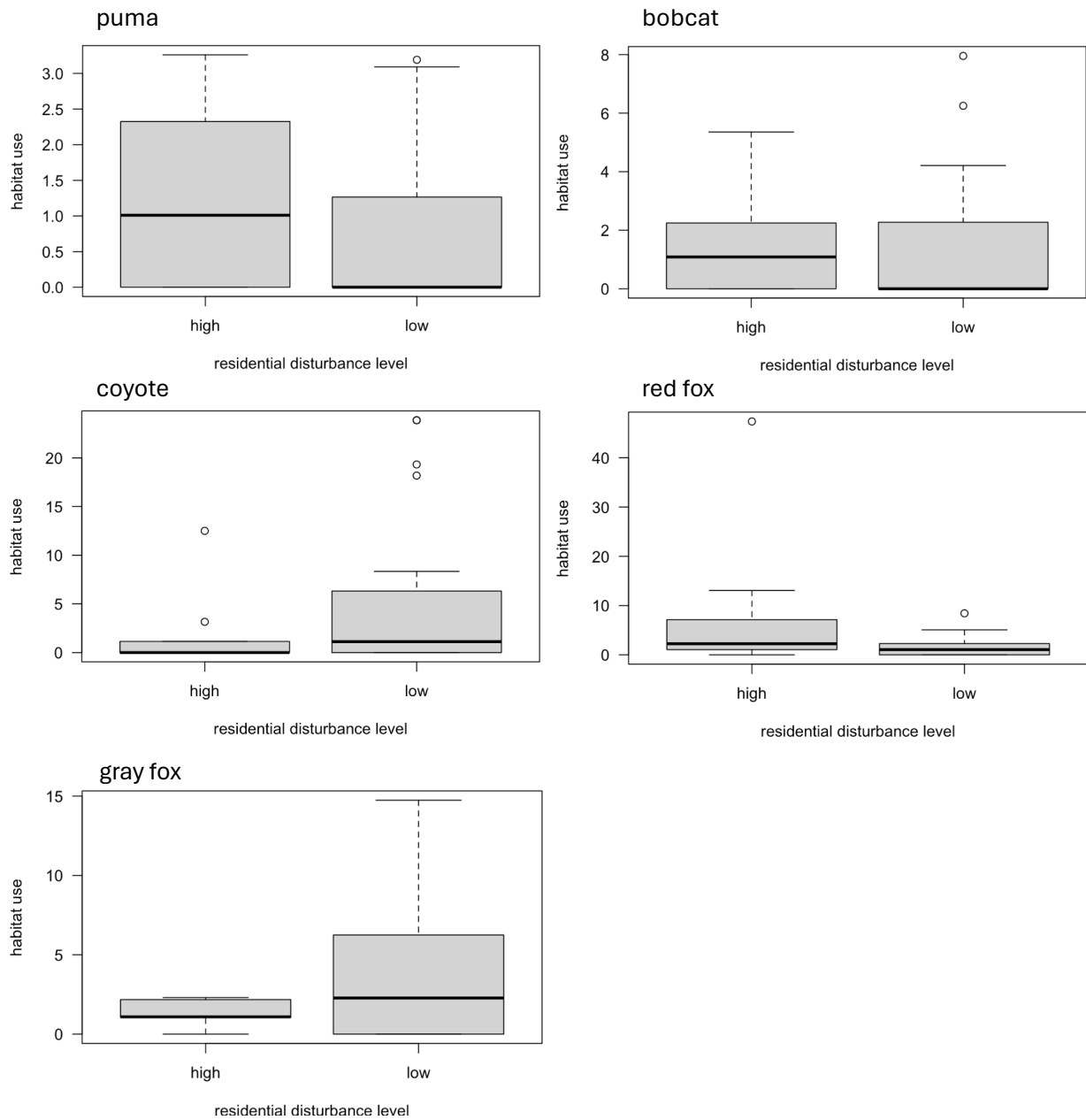
Figure 11. Habitat use of felines and canines in the MEF at high and low levels of residential disturbance. Habitat use between high and low residential disturbance levels did not differ for pumas or bobcats. Habitat use of coyote (P=0.28) and gray fox (P=0.08) was higher at low levels of residential disturbance, while habitat use of red fox was significantly lower (P=0.04) at low levels of residential disturbance.

Interspecific Relationships

There were only weak negative correlations in carnivore detections between species pairs, but several moderate and strong positive correlations between species (Figure 12). Striped skunk was strong positively correlated with coyote, and somewhat strongly correlated with bobcat and gray fox as well. Bobcat and coyote were also strongly positively correlated. Red fox was moderately correlated to puma, and more weakly correlated to bobcat. Gray fox was weakly correlated to puma.
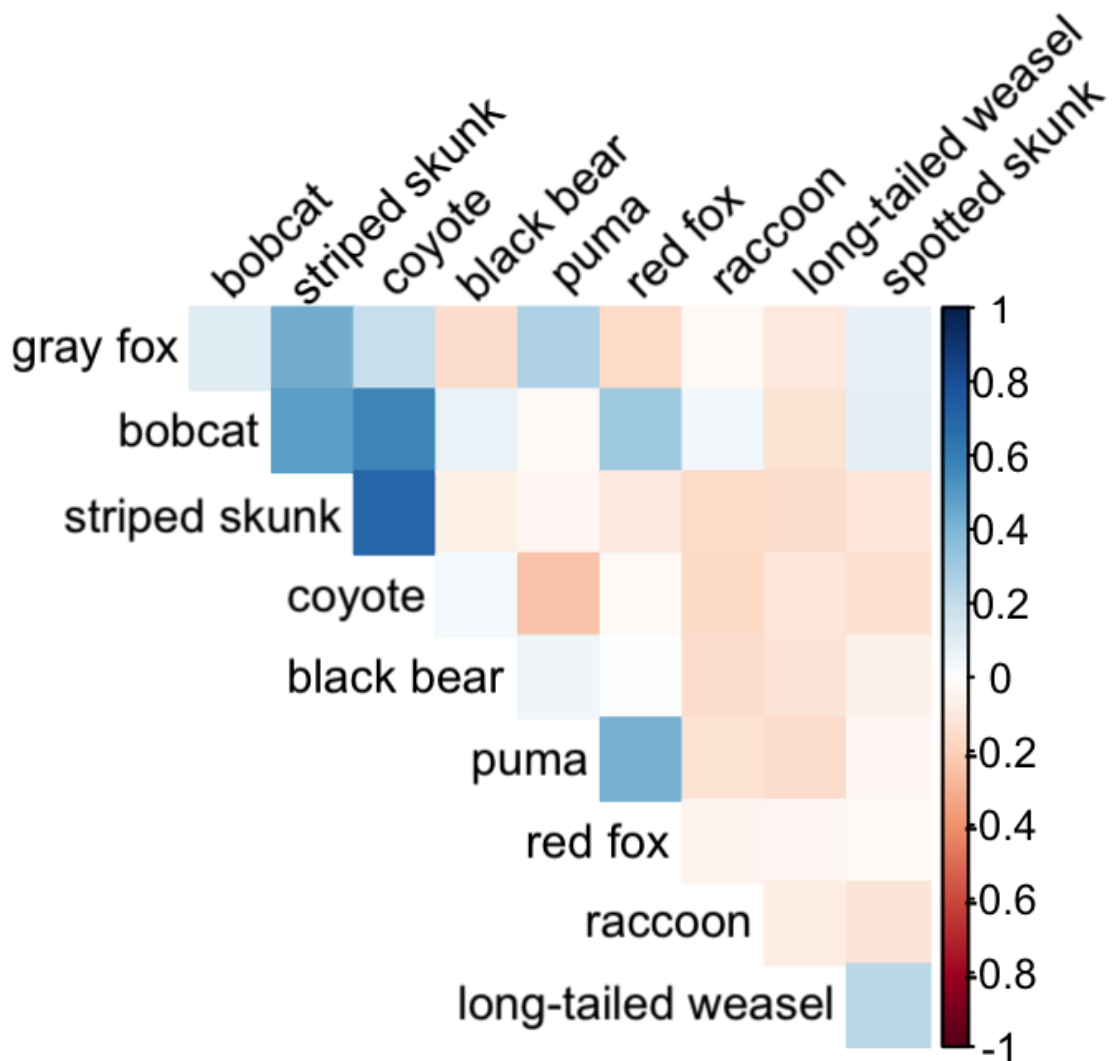
Figure 12. Spatial correlation in carnivore detections for different species pairs. Red indicates negative correlations and blue indicates positive correlations. Bobcat and coyote are strongly positively correlated. Striped skunk is strongly positively correlated with coyote, and somewhat strongly correlated with gray fox and bobcat. Red fox was moderately positively correlated to puma, and gray fox was weakly positively correlated to puma.

All canine and feline species pairs relatively high amounts of overlap in their activity patterns as all species were at least somewhat nocturnal (Figure 13). The species with the greatest degree of overlap were red and gray fox ($\Delta = 0.87$), bobcat and coyote ($\Delta = 0.81$) and puma and red fox ($\Delta = 0.77$). Peaks in bobcat activity in the morning and evening were slightly offset from coyote activity peaks during those periods of the day. Slightly lower degree of activity overlap was found between puma and bobcat ($\Delta = 0.72$), puma and coyote ($\Delta = 0.70$), puma and gray fox ($\Delta = 0.72$), bobcat and gray fox ($\Delta = 0.69$), and bobcat and red fox ($\Delta = 0.70$). The degree of overlap was notably lower between coyotes and gray foxes ($\Delta = 0.59$) and between coyotes and red foxes ($\Delta = 0.60$), and these species pairs showed the clearest separation in activity level during the daytime.

For most species pairs, there was no difference in the mean interval between detections at a site of species A after species B compared to the interval between species B after species A. The mean interval between a coyote detection and a subsequent bobcat detection was 5.94 days, while coyotes were detected an average of 8.94 days after a bobcat, but this trend was not significant (p = 0.15). The mean interval for red fox detections following coyote detection was 6.25 days, which was longer than the mean interval of 4.29 days for coyote detections following red fox detections, but not significantly so (p = 0.20). There was a strong trend in that gray fox detections following coyote detections occurred later than coyote detections following gray fox detections (p = 0.098). The mean interval between puma and subsequent red fox detections was significantly shorter than the mean interval between red fox and subsequent puma detections (p = 0.026).

Discussion

Comparison with Previous Mammal Survey

My results demonstrate that the Manitou Experimental Forest is home to a robust carnivore guild. I detected 9 of the 11 carnivore species listed in the only previous report of MEF mammals, based on small-mammal trapping and observations from 1957 through 1974 (Morris et al., 1977). The exceptions were mink (*Neovison vison*) and badger (*Taxidea taxus*), which were both considered "rare" and associated with wetlands and more open habitats that I did not sample (Reid, 2006). In addition to these species, I detected spotted skunk, which was not listed in this report and apparently never trapped or observed in the MEF as of 1974. It is unclear whether this is because camera traps are more effective at detecting spotted skunk, or due to spotted skunks only moving into the MEF in the past 50 years. Morris et al. (1977) also assign relative abundance categories to each carnivore, stating that coyote are abundant, raccoon, black bear, bobcat, long-tailed weasel, and striped skunk are common, while gray fox, red fox, and mountain lion are casual visitors that "may venture on Experimental Forest occasionally". Camera trap detections indicate that both fox species are actually fairly common and may be some of the most abundant carnivores in the area. My camera trap data suggests mountain lions are more than casual visitors, as at least one individual incorporates the MEF into its home range,
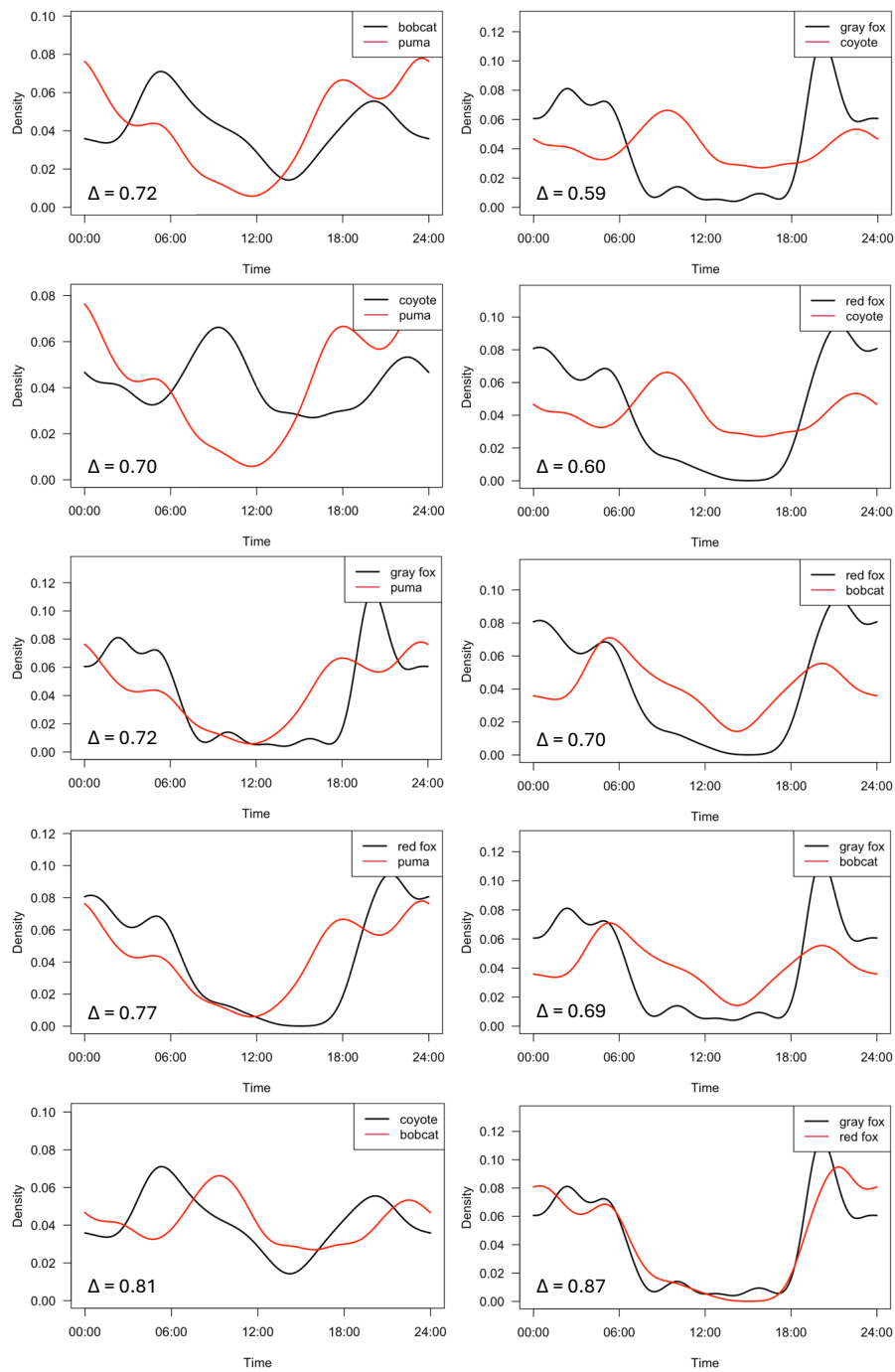
Figure 13. Activity pattern comparison and the coefficient of overlap (Δ) between pairs of canine and feline carnivore pairs. Δ ranges from 1.0 (complete overlap) to 0.0 (no overlap). Red and gray foxes, red fox and puma, and bobcat and coyote exhibited the highest degree of overlap with each other. Both fox species had a notably lower degree of overlap with coyotes.

which aligns with observations of a puma denning site in the central part of the MEF for multiple years over the past three decades (B. Linkhart, Colorado College, personal communication). Long-tailed weasel and raccoon were considered common, and I detected these species 10 times or fewer, however my cameras were deployed to target canines and felines and were likely not appropriately positioned to photograph raccoon and weasel. There have likely been changes to MEF carnivore populations in the 50 years since those abundance categories were assigned, and long-term monitoring projects have shown that carnivore populations can exhibit significant changes in density over a much shorter period of time (Durant et al., 2011). However, the disparity between estimates based on personal observations and systematic camera trapping clearly demonstrate the value of camera traps for surveying elusive carnivore species (Alldredge et al., 2019; Pettorelli et al., 2010), even if the efficacy of camera trapping is variable by species (Gompper et al., 2006). With a trapping effort of 2580 days, my camera grid was able to detect species that are extremely difficult to observe in person, and estimates of occupancy suggest that some species' habitat use within the survey grid may in fact be higher than what is reflected by raw number of photo captures. This is consistent with findings that larger camera trap surveys are necessary to improve detection probability for elusive or rare wildlife species than for common and easily detectable species (O'Connor et al., 2017; Shannon et al., 2014).

Human Disturbance

Overall, my results provide little evidence that feline or canine habitat use is impacted by roads within the MEF. There was one nonsignificant trend for categorial road disturbance variables: puma habitat use was lower at higher road disturbance sites. While puma occupancy was shown to be negatively correlated to road density in Chile and road use intensity in California and puma occupancy in Arizona increased at greater distances to roads (Baker & Leberg, 2018; Cifuentes-Ibarra et al., 2023; Markovchick-Nicholls et al., 2008), other research has demonstrated that pumas exhibit no preference or even select for habitat closer to roads (Kertson et al., 2011; Sollmann et al., 2012). However, my puma detections in the MEF may only represent one or two individuals, based on home range size estimates (Hansen, 1992), so it is unclear whether pumas in this region of Colorado actually show a negative response to road disturbance. Puma movement behavior and habitat use has been shown to be highly variable among individuals (Burdett et al., 2010; Kertson et al., 2011; Wilmers et al., 2013), so studies of larger puma populations would be needed to identify effects of disturbance beyond individual personalities.

The two fox species displayed contrasting patterns of habitat use in response to human residential development, with red foxes using higher disturbance habitat significantly more and gray foxes using lower disturbance habitat more. These results align with previous findings on red fox behavior and response to human activity. Another Colorado study found that red fox habitat use along a development gradient was strongly positively correlated with human housing (Goad et al., 2014), and red foxes in both rural and suburban regions elsewhere in North America have been shown to prefer low density residential areas over more wild habitat (Adkins & Stott, 1998; Gosselink et al., 2003). This ability to make use of habitat with greater human disturbances

likely reflects both the generalist strategy of red foxes and in some areas may also allow red foxes to find refuge from larger carnivores that are more avoidant of human development (Gosselink et al., 2003; Moll et al., 2018). There is less clarity on how human disturbance influences gray fox habitat use. While gray fox occupancy was positively related to an overall human disturbance index in Southern Arizona, occupancy has also been found to be negatively related to roads, housing density and urbanization (Baker & Leberg, 2018; Markovchick-Nicholls et al., 2008; Ordeñana et al., 2010). A North Carolina study determined that while gray foxes select for lower housing density in the absence of coyotes, when coyotes are present and forest cover is low, gray foxes actually select habitat with higher housing density (Parsons et al., 2022). If gray foxes are spatially avoiding human residential habitat in the MEF, this might be driven by inherent preferences in habitat structure or by interactions with other carnivores. For example, gray foxes appear to be more specialized than and sensitive to competition with red fox (Morin et al., 2022), so gray fox and red fox may exhibit habitat partitioning along a human disturbance gradient. Recent research on gray foxes suggests that their ability to tolerate and make use of habitat in suburban and exurban areas is highly regionally variable and dependent on interspecific competition with species like coyotes and red foxes (Wang et al., 2015; Smith et al., 2018).

I did not find any impact of residential disturbance on pumas, or of residential or road types of human disturbance on bobcats or coyotes. Other research has found that human disturbance can influence habitat use by these species, although the degree and direction of human impact appears to be highly regionally variable. In general, pumas have been found to be fairly sensitive to human residential development; pumas spatially avoided residential areas in Washington and California (Kertson et al., 2011; Wilmers et al., 2013), and puma occupancy and density were lower in exurban developments (Lewis, Logan, et al., 2015; Wang et al., 2015). Bobcats have also frequently been found to be sensitive to human disturbances. Bobcat density or habitat use has been shown to be negatively associated with human recreational activity and exurban development elsewhere in Colorado (Lewis et al., 2015B; Lewis et al., 2021), and urban areas negatively impacted California bobcat habitat use (Ordeñana et al., 2010; Riley, 2006). However, my results are consistent with one California study that showed that bobcat occupancy was not impacted by exurban development (Wang et al., 2015). In fact, research on carnivores in protected areas of varied disturbance levels in Arizona found that while bobcat occupancy was negatively related to human disturbance in the more popular Saguaro National Park, in a protected area with less visitation and human disturbance, Chiricahua National Monument, bobcat occupancy was actually positively related to human disturbance (Baker & Leberg, 2018). Research on coyote response to human disturbance is also variable, and while studies in Illinoi and Northern Colorado found that coyotes avoided residential areas (Goad et al., 2014; Gosselink et al., 2003), other researchers have found that coyotes do not alter habitat use in response to human activity (Lewis et al., 2021), are not impacted by exurban development (Wang et al., 2015), or may even be positively associated with roads or urban areas (Baker & Leberg, 2018; Ordeñana et al., 2010). The small, low-density development and relatively low

level of disturbance in the MEF may not represent a threat to coyotes or bobcats, which seem able to tolerate lower amounts of human disturbance.

Although most species did not exhibit spatial trends with respect to road or residential disturbance, it is still possible that carnivores in the MEF could be temporally responding to human activity. Carnivore species such as coyotes, pumas, bobcats and ocelots have been found to shift to more nocturnal activity patterns in order to avoid periods of greatest human activity or in response to human persecution (Cruz et al., 2018; Kitchen et al., 2000; Lewis et al., 2015A; Lewis et al., 2021; Wang et al., 2015). It is also important to consider that the overall disturbance level of the MEF is relatively low compared to more suburban areas or protected areas with higher recreational activity. Residential areas with low density housing and substantial forest area such as those in the MEF may not be considered disturbed habitat for these carnivore species and might not be utilized differently than the surrounding National Forest. Additionally, while some roads bordering the MEF experience fairly high recreational use, vehicle activity may not be frequent enough to impact the habitat use patterns of carnivores. Telemetry research on pumas suggests that avoidance is focused on consistent and not intermittent disturbance (Wilmers et al., 2013), and moderate recreational use of Forest Service roads may not represent a consistent disturbance to primarily nocturnal carnivores.

If human activity does cause carnivores to modify habitat use to avoid interaction or conflict with humans and domestic species, which may be the case for the gray fox, this could lead to carnivores using lower quality habitat that may negatively impact fitness. Carnivores that respond to disturbance by altering their activity to become more nocturnal may be forced to alter their diet if their preferred prey are not active at the same time. While some carnivore species are habitat or dietary generalists and may readily adapt to high levels of human activity (Smith et al., 2018), specialized species may be especially threatened by development and other human land use changes. Even if low levels of human disturbance do not result in spatial or temporal modifications in carnivores' habitat use, there could still be associated costs to carnivore fitness. Individual pumas in California who made use of low-density exurban residential habitat experienced significantly higher mortality than pumas who made use of wild habitat (Burdett et al., 2010). If individual carnivores equally or even preferentially utilize human-altered habitats but suffer fitness costs as result, than these low disturbance level areas may represent 'ecological traps' (Hale & Swearer, 2016), which carnivores have not adequately evolved to deal with due to the rapid expansion of human development.

Interspecific Avoidance

I did not find any clear evidence of avoidance of puma by smaller carnivores, with the correlation plot analysis showing only weak negative correlations between species pairs. There was a slight negative correlation between detections of coyote and puma, and coyote detections were largely concentrated at four sites in the south-eastern corner of the MEF, where there were no puma detections. Coyote activity also peaked during mid-morning when puma activity is

lowest. These observations may suggest some level of spatial or temporal avoidance of pumas by coyotes, but my data is not conclusive. If coyotes are avoiding pumas spatially, that would be consistent with results in California that showed coyote detection probability is lower where pumas are present (Wang et al., 2015). Mesocarnivores have been found to avoid pumas throughout their range, with ocelot, tayra and crab-eating fox avoiding puma temporality in the Brazilian Pantanal (Finnegan et al., 2021), and Geoffrey's cat and hog-nosed skunk avoiding puma spatially in Argentina (Zanón Martínez et al., 2022). Bobcats avoided sites following a puma detection in wild habitat but not in exurban development habitat in the Colorado Western Slope (Lewis et al., 2015A), but I found no evidence of that behavior in the MEF. This could indicate that exurban residential areas in the MEF similarly force greater overlap between the feline species, although average intervals between bobcat and puma detections were much longer, which could be due to low trapping effort or because feline density in this region is lower than the other Colorado study sites.

It was interesting to note that the detection rate of bobcats, canines and skunks fell when puma detection rate peaked during the month of November. It could be that mesocarnivores utilized habitat out of the study area more frequently during this time in response to the puma spending more time within the MEF boundaries. Since my cameras likely only detected one or two individual pumas, it is unclear whether the seasonal pattern in puma detection is driven by an individual's behavior or representative of more widespread seasonal changes in habitat use. Research in Idaho has shown that when puma prey species are restricted to lower elevation habitat in the winter, puma overlap more with bobcats and coyotes, resulting in increased competition for prey and more bobcats and coyotes being killed by pumas (Koehler and Hornocker, 1991). It is possible that subordinate mesocarnivores reduce habitat use in the MEF when puma use increases in order to escape this increased competition and predation pressure resulting from seasonal effects on puma prey.

I found some evidence of temporal avoidance among the canine species. The lowest levels of activity pattern overlap were between coyote and gray fox, and between coyote and red fox, as the foxes were strongly nocturnal and coyotes more diurnal. This temporal segregation may allow foxes to minimize competition and reduce conflict with the larger coyotes. Additionally, the longer interval between coyote and subsequent fox detections compared to fox and subsequent coyote detections suggests that both fox species may avoid returning to a site with coyote scent trails, although this pattern was more pronounced for gray fox. This behavior is consistent with findings suggesting gray foxes used scent trails to avoid coyotes temporally in North Carolina (Parsons et al., 2022). Another study found a complete lack of avoidance among canine species, with red fox, gray fox and coyote occupancy independent of each other, although they attribute this lack of segregation to high levels of human disturbance (Morin et al., 2022). Most research on interspecific relationships of these three canines has also taken place in the Midwest or Eastern U.S., in very different ecosystems and without larger apex predators like

pumas present, so there is a need for more research on canine avoidance to understand patterns in Colorado.

Positive Associations Among Carnivores

Bobcat and coyote detections were correlated somewhat strongly, which indicates that these two species are able to coexist spatially. Despite the theory that their similar body size should result in avoidance, studies in California and Texas also found that bobcats and coyotes did not avoid each other and even that bobcat detection probability increased with higher coyote activity (Lombardi et al., 2020; Wang et al., 2015). Coyotes and bobcats in the MEF had a high degree of overlap in daily activity patterns, although coyote activity peaks were slightly offset from peak bobcat activity in the morning and evening. This fine scale difference in activity may be enough to enable coexistence, or some other mechanisms might enable coexistence between these species, such as dietary partitioning or differential hunting strategies.

Striped skunk detections were strongly correlated to detections of coyotes, bobcats, and gray foxes, indicating that striped skunks are positively associated spatially to these larger mesocarnivores. There has been very limited research on coexistence and potential positive associations between skunks and canines or felines, and it is unclear what drives the spatial coexistence between skunks and these larger carnivores. Striped skunk and coyote co-occurrence increased with increasing human activity in Detroit city parks, and this pattern was attributed to the human-shield hypothesis (Gámez & Harris, 2021), which suggests that human activity should benefit subordinate carnivores and shield them from apex predators who are more negatively affected by human disturbance. However, the MEF represents a much less human-disturbed landscape than parks in Detroit, so human activity would not be expected to exert the same pressures on larger carnivores as in a more urban habitat. An experimental study in Illinois found that striped skunks did not spatially avoid coyote howling playback or coyote urine as predicted (Prange & Gehrt, 2007), so it is possible that striped skunks do not consider coyotes and maybe other mesocarnivores intense threats, or that they have other ways of avoiding negative interactions besides spatial avoidance. Skunk species were more strictly nocturnal than coyote and bobcats, so some amount of temporal segregation may enable this coexistence. The association with larger carnivores could also be driven by benefits to the skunk of associating with larger predators, such as increased ability to scavenge leftover prey carcasses. I did find multiple instances of striped skunk and spotted skunk being photographed within the same 8 second motion trigger sequence as coyotes and gray foxes, suggesting interactions between skunks and canines occur frequently, although I could not determine the nature of these interactions.

I found evidence of a positive association between red fox and puma. There was a significantly shorter interval between a puma and subsequent red fox at a site compared to a red fox and subsequent puma detection, and it is unlikely that the larger and dominant puma is avoiding returning to sites following red fox use. This would suggest that red foxes may be seeking out

and following puma scent trails, even though they are subordinate to pumas. One other study documented this behavior, and found that red foxes in Grand Teton National Park and the Bridger-Teton National Forest followed pumas to prey carcasses in order to scavenge carrion (O'Malley et al., 2018). Although risk of intra-guild killing is often thought to cause mesocarnivores to avoid apex carnivores temporally or spatially (Finnegan et al., 2021), pumas provision disproportionally large amounts of carrion to scavengers (Elbroch & Wittmer, 2012), so the benefits of scavenging puma caches may outweigh the risks of predation. O'Malley et al. (2018) also showed that red foxes were more tolerant of puma presence at carcasses and fed for longer periods of time during the winter when prey resources were more limited, so it is possible this behavior is also influenced by seasonality in the MEF.

There are many mechanisms that may enable the generally high level of coexistence among carnivore guild members in the MEF. Human disturbance can force greater overlap between species that typically avoid each other in wild systems as carnivores attempt to escape interaction with humans (Lewis, et al., 2015A; Parsons et al., 2022; Smith et al., 2018). Although I have limited evidence of human disturbance impacts, the lack of a strong gradient in human activity in the MEF may prevent me from identifying patterns with human activity that could be altering carnivore behavior and reducing spatial or temporal segregation within the guild. Coexistence has also been shown to vary seasonally; the carnivores of the Brazilian Pantanal exhibited significantly less temporal segregation during the wet season than during the dry season when resources were more limited (Finnegan et al., 2021). Future research should investigate how observed patterns of habitat use in the MEF change throughout the year over a longer survey period. The presence of certain keystone species and particularly apex predators can also alter guild structure and impact the degree of spatial and temporal overlap among carnivores. Raccoons detections were only negatively related to coyote activity in the absence of pumas (Wang et al., 2015), suggesting that when an apex predator is present, avoidance behaviors among mesocarnivores and small carnivores may be minimized. The loss of apex predators may also result in mesopredator release (Prugh et al., 2009), increasing populations of mesocarnivores and altering competition dynamics within the guild. While puma are still present in the MEF, the loss of wolves, Colorado's other native apex predator, has likely had large impacts on mesocarnivores habitat use over the last century. With the recent reintroduction of wolves to the state, baseline research focused on carnivore guild interactions is even more important to monitor how wolves may potentially change these dynamics in the near future. Finally, while I did not investigate potential drivers of habitat use patterns apart from interactions with other carnivores and human activity, bottom-up controls can also be critical in determining how carnivores move through and utilize habitat. Plant community structure can influence carnivore habitat selection by shaping patterns of prey distribution or by providing preferred conditions for hunting. Topography also may explain patterns in carnivore habitat use, since elevation, slope, and terrain ruggedness influence ease of movement through a landscape. In the future, I hope to investigate how factors like forest community type, slope position, water availability, and relative prey abundance are related to carnivore detections in the MEF.

Conclusions

Overall, with the exception of the gray fox, my study did not find strong evidence that human activity from road use or within the residential development negatively affects carnivore habitat use. This provides some support for the idea that low-density residential areas surrounded by protected land can support complete carnivore guilds without restricting habitat use. However, future research in the Pikes Peak region of Colorado should investigate whether carnivores alter activity patterns in response to activity on roads or in developments and should also examine a larger gradient of human disturbance than is present in the MEF.

My results point to an overall high degree of coexistence between large and medium carnivores within the MEF. Although there is some evidence of temporal segregation among canines, bobcats and coyotes, striped skunks and mesocarnivores, and red foxes and pumas all exhibited positive spatial or temporal associations. Spatial and temporal coexistence among the carnivore guild may be enabled by other forms of niche partitioning or could be explained by seasonal factors or even seasonal variation in the habitat use of an apex predator like the puma.

My research adds to the limited body of carnivore habitat use research in the Colorado Front Range, but the small size of the MEF study area and the relatively low trapping effort limit the utility of this dataset. There is still a need for larger scale camera trap surveys of carnivores in the Pikes Peak region, as well as more long-term camera grids that are operable over multiple seasons and years. Larger surveys would be particularly useful in understanding patterns with larger carnivores like puma for which an area the size of the MEF could represent only a fraction of their home range. A better understanding of how human disturbances and interspecific relationships influence carnivore behavior and habitat utilization in this region of Colorado would be useful for conservation decision making and for facilitating coexistence between carnivores and people.

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Appendix 1. Example images of the ten carnivore species detected:

Puma *(Puma concolor)*

Bobcat *(Lynx rufus)*

Coyote *(Canis latrans)*

Red fox *(Vulpes vulpes)*

Gray fox *(Urocyon cinereoargenteus)*

Black bear *(Ursus americanus)*

Spotted skunk *(Spilogale gracilis)*

Striped skunk *(Mephitis mephitis)*

Raccoon *(Procyon lotor)*

Long-tailed weasel *(Mustela frenata)*

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