Carnivore responses to urbanization and human presence along an urban-wildland gradient in western Washington

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Abstract

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Urbanization and human activity are primary drivers of wildlife habitat loss and degradation, but few studies to date have explored their impacts simultaneously. I investigated how anthropogenic infrastructure and the presence of humans affected habitat use of six carnivore species along an urban-wildland gradient of human development in western Washington, USA. Specifically, I deployed camera traps at 175 locations to quantify habitat use by American black bears (*Ursus americanus*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), Virginia opossums (*Didelphis virginiana*), and raccoons (*Procyon lotor*). I then used single-species, single-season occupancy models to characterize their respective patterns of habitat use. No covariate was significant for all six species, and I only detected significant relationships with any of the covariates for four of the species. Two species had significant relationships with distance to road but different responses; cougar occupancy increased while coyote occupancy probability decreased as the distance to road increased. Black bear occupancy was positively associated with increasing canopy cover and the probability of occupancy for opossums decreased with increasing elevation. Cougars were not detected at any sites ≤ 250 m from any buildings, suggesting that cougars may avoid using habitat in close proximity to these structures. I detected no significant response to the presence of humans by any of the species. My results reveal that carnivore spatial responses to human infrastructure and presence are species-specific and can be limited, highlighting the need for efforts to identify key drivers of species differences as well as tailored conservation and management approaches.

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INTRODUCTION

Urbanization is one of the primary drivers of wildlife habitat loss and fragmentation (Wilcove et al. 1998), and endangers more species than any other human activity in the United States (Czech et al. 2000). Between 1982 and 2012, urbanized area in the USA increased by 58.7%, raising the total developed land area in the conterminous USA from 3.7% to 5.9% (USDA 2015). The rate of development is also increasing, with current predictions suggesting that developed land area will reach 9.2% by 2025 (Alig et al. 2004). With the majority of the US human population now living in urban areas, most of this growth is expected to occur in and around existing cities, resulting in both higher urban densities and increased urban sprawl (Alig et al. 2004; Gehrt et al. 2010). Most of this new development comes from the conversion of forest, agriculture, grassland/shrublands, and wetlands (Auch et al. 2012), areas that normally provide habitat for wildlife. Indeed, between 1973 and 2000, the amount of US land covered by forests and agriculture both declined by 4.2%, while wetland cover declined by 4.5% (Sleeter et al. 2013). Of these land cover types, forest cover had the largest net decline in terms of area (97,000 km^2), followed by agriculture (90,000 km^2) and wetlands (14,000km^2). Alig et al. (2004) predict that the amount of US land covered by forests will decline another 3% by 2050.

Habitat loss and degradation cause myriad effects on wildlife. For example, increasing levels of urbanization reduce species richness of birds (Chace and Walsh 2006), invertebrates and non-avian vertebrates (McKinney 2008). Urbanization also homogenizes wildlife communities

(McKinney 2006), especially at high levels of development. Even the long-held notion that urbanization promotes increased animal abundance due to anthropogenic food subsidies and decreased predation pressure has been challenged by a meta-analysis by Saari et al. (2016) that found the abundance of many terrestrial animals is reduced in urban areas. While urban areas may still contain patches of remnant natural vegetation, these patches are often degraded and surrounded by a less permeable urban matrix (Gehrt et al. 2010).

Wildlife also face disturbances caused by the presence of humans engaging in recreational activities in patches of natural vegetation both within and surrounding urban areas (Nickel et al. 2020). Recreation is the second leading cause, after water development projects, of plant and animal species endangerment on US federal lands (Losos et al. 1995) and has been shown to reduce the effectiveness of protected areas (Reed and Merenlender 2008). At the same time, participation in outdoor recreational activities in natural areas is increasing globally (Balmford et al. 2015), putting pressure on land managers to provide more access and recreational opportunities. As access to trails and proximity to development are key predictors of human presence in natural areas (Nickel et al. 2020), wildlife seeking refuge in patches of remnant natural vegetation in and adjacent to urbanized areas likely still face acute anthropogenic pressure due to human presence. These factors all lead to increased and chronic stress for wildlife species (McPhearson et al. 2013).

Mammalian carnivores are particularly vulnerable to the stresses created by both urbanization and human presence, owing to their relatively large home ranges, low population densities, and high levels of human persecution (Noss et al. 1996; Woodroffe and Ginsberg 1998). Consequently, urbanization has led to concomitant reductions in the geographic distributions of many mammalian carnivores (Woodroffe 2000; Randa and Yunger 2006; Bateman and Fleming

2012), with populations in these highly fragmented landscapes at greater risk of extirpation than those inhabiting more intact landscapes (Crooks et al. 2011). In areas where these species persist, urbanization may also alter carnivore density (Prange et al. 2003; Lewis et al. 2015b), spatial or temporal activity (Goad et al. 2014; Wang et al. 2015; Nickel et al. 2020), and interspecific interactions (Moll et al. 2018; Parsons et al. 2019). Similarly, human presence elicits a wide range of responses from carnivores, including changes in spatial or temporal activity (Wang et al. 2015; Nickel et al. 2020; Bandak et al. 2020), declines in density and community composition (Reed and Merenlender 2008), and altered intraguild competition (Moll et al. 2018). As urbanization continues to spread, carnivores will increasingly be forced to use urban or suburban areas, placing wildlife populations under even greater stress and increasing the risk and numbers of human-wildlife conflicts. Thus, urban planners and land managers, particularly those tasked with a dual mandate to manage for both conservation and recreation, will benefit from a more comprehensive understanding of how the process of urban development shapes patterns of carnivore occupancy, abundance, behavior, and interspecific interactions.

One challenge to conserving and managing carnivores in urbanizing areas is that wildlife species may respond variably to anthropogenic disturbance (Bateman and Fleming 2012). Whereas most research has focused on the negative effects of urbanization on carnivores, several species appear capable of adapting to or even exploiting areas with fairly extensive urbanization. For example, raccoons (*Procyon lotor*) are found in most metropolitan areas within their geographic range (Gehrt 2003), and reach higher densities in urban areas than in wildlands (Prange et al. 2003). Similarly, coyotes (*Canis latrans*) have expanded their range dramatically (Kays et al. 2010) and are thriving in many urbanized environments (e.g., Chicago, IL; Gehrt et al. 2009). Bobcats (*Lynx rufus*) have also been found in heavily developed areas (Gehrt et al. 2010). Even some larger-bodied carnivores appear to be capable of tolerating some types of urbanization. For example, black bears (*Ursus americanus*) will move in and out of the urban matrix (Bateman and Fleming 2012), most likely to capitalize on the availability of anthropogenic foods (Lewis et al. 2015a). Similarly, cougars (*Puma concolor*) exist on the urban fringes of many western cities and population centers including Boulder, CO (Alldredge et al. 2019), Seattle, WA (Kertson et al. 2013), and multiple cities in southern California including San Diego and Los Angeles (Ordeñana et al. 2010). Because carnivores can provide a number of ecosystem services including regulation of prey populations and zoonotic diseases, increased agricultural output, waste removal, reduced abundance of species that cause human injury, as well as social and aesthetic value (Ripple et al. 2014; O'Bryan et al. 2018), understanding the factors that contribute to their persistence in urbanized landscapes is of critical conservation concern.

Despite the growing body of knowledge about the effects of anthropogenic disturbances on carnivores, there is still limited research simultaneously examining the impacts of both urban infrastructure and human presence (but see Moll et al. 2018; Nickel et al. 2020). In addition, most studies of urban impacts have focused on single species (Larson et al. 2016), limiting inference as to how urbanization shapes wildlife communities. To address these knowledge gaps, I used camera traps to explore patterns of detection and occupancy for American black bears, bobcats, cougars, coyotes, and raccoons along an urban-wildland gradient of human development in western Washington, USA. I also included the Virginia opossum (*Didelphis virginiana*), a marsupial, as it occupies a similar ecological niche and presents similar management ramifications as many mesocarnivores in North America (Ginger et al. 2003; Root 2013). Western Washington is experiencing extensive development—between 1973 and 2000, the region experienced the highest overall land change in the US and was second-highest in the nation in changes due to development (Sleeter et al. 2013). The region similarly experienced extensive population growth: from 2010–2017, population levels in King and Snohomish counties increased by more than twice the national average (Office of Financial Management 2017). My primary objective was to quantify and contrast the extents to which occupancy patterns for these six carnivore species were shaped by urbanization and human presence.

METHODS

Study Area

I conducted fieldwork in an area of approximately 3000 km^2 located in King and Snohomish counties of western Washington, USA. Within this region, I was able to survey on more than 50 distinct properties (Fig. 1a) belonging to a variety of state, county, and municipal agencies, as well as privately owned residential properties. Property sizes ranged from approximately 0.1 to 94 km^2. Except for residences, all properties were open to the public and were managed for a variety of uses including hiking, camping, mountain biking, and wildlife viewing. Properties owned by the Washington Department of Natural Resources (WADNR) were also managed for hunting, fishing, and commercial resource extraction (i.e., timber and mining).

Land cover types for this region were varied and included a mixture of urbanized landscapes (e.g., commercial, residential, and mixed-use), park lands, agricultural croplands, and coniferous forests typically dominated by stands of Western hemlock (*Tsuga heterophylla*) and Douglas fir (*Pseudotsuga mensiezii*). Topography in the study area was generally hilly, with elevations ranging from sea level to approximately 1500 m. Annual precipitation ranged from 85–200 cm, mostly as rainfall, with the western portion of the study area generally drier and precipitation increasing toward the east. Development intensity was highest at the western edge of the study area and decreased toward the east approaching the foothills of the Cascade Mountain Range.

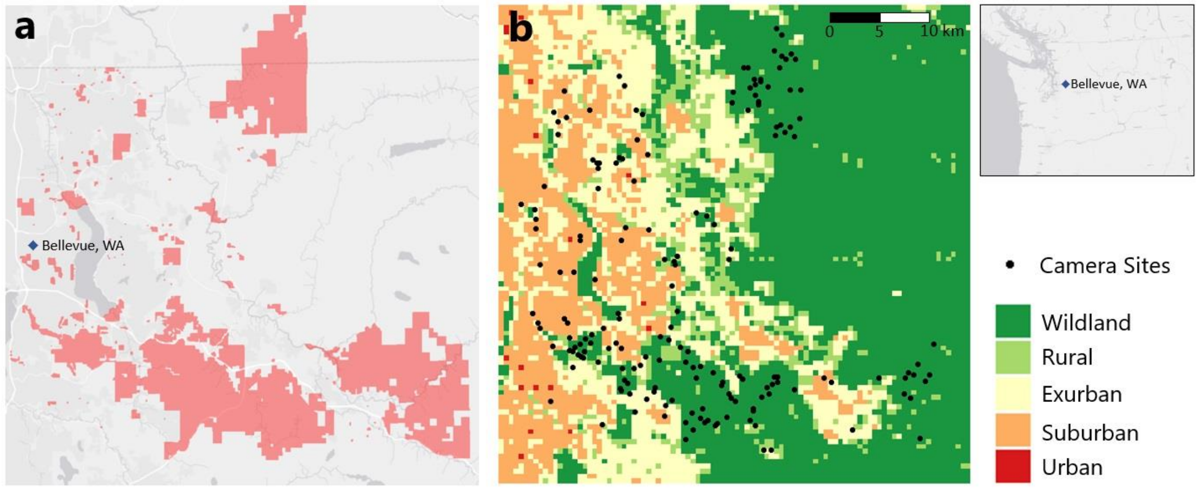

Figure 1. Properties available for camera site deployment in western Washington, USA, shown as light-red polygons (a) and camera site locations along the urban-wildland gradient between July 2016 to August 2017 (b). Urban-wildland gradient levels are defined by the average number of buildings per hectare (Urban > 10, Suburban = 1.4706-10, Exurban = 1.1265-1.4705, Rural = 0.005-1.1264, Wildland < 0.005).

Camera Trap Survey

I used ArcMap 10.4 (ESRI 2016) to create a building density layer using tax parcel records by first identifying all parcels with a structure present and then placing a centroid within those parcels (Kertson 2010). I then overlaid a grid of 500 by 500 m cells on the study area and classified each cell by development zone (e.g., urban, suburban, exurban, rural, or wildland; Theobald 2005) based on the number of points that fell within each cell. I then used the R (R Core Team 2018) package “Sampling” (Tillé and Matei 2016) to randomly select cells within the available properties for camera trap deployment, with the selection stratified among each development zone in proportion to the total available area of each zone within the study area.

From July 2016 to August 2017, I placed Reconyx (Hyperfire and Ultrafire; Reconyx, Inc., Holmen, WI) or Bushnell (Trophy Cam HD Aggressor; Bushnell Corporation, Overland Park, KS) camera traps at 175 different locations in public parks ($n = 151$) and private residences ($n = 24$) throughout the study area to monitor carnivore activity along an urban-wildland gradient of human development (Fig. 1b). At each site, I placed a camera along a trail or unpaved service road to maximize carnivore detection (Cusack et al. 2015). For sites located at residences that lacked a trail feature, I placed a camera along other linear features (e.g., hedge rows, fences, outbuilding walls, or streams) that could guide an animal’s movement on the property (Andersen et al. 2017). I limited camera deployments to a maximum elevation of 700 m above sea level because elevations exceeding that threshold could be inaccessible during the winter owing to high snow levels. Cameras were deployed for a minimum of 28 days (mean = 46.4, sd = 26.2), then moved to a different location. I attempted to place all cameras ≥ 500 m from any other camera. Trigger sensitivity for all cameras was set to high and cameras recorded three photos per trigger, re-triggering immediately if the animal was still in view. If consecutive photo triggers were less than 60 seconds apart, I grouped the resulting images into sequences and counted the animals in the sequence, not in the individual photos. Undergraduate volunteers made initial species identifications for each sequence using eMammal software (eMammal.si.edu), and I then used the eMammal Expert Review Tool to confirm or correct all volunteer species identifications. I used the R package “camtrapR” (Niedballa et al. 2016) to create detection/non-detection encounter histories from the sequence data for each species for use in occupancy modeling.

Model Covariates

I modeled variation in black bear, bobcat, cougar, coyote, opossum, and raccoon occupancy probability (ψ) using covariates (Table 1) that represented urbanization (i.e., building density, trail density, distance to road), human presence (i.e., average number of human detections per day), and habitat features (i.e., percent canopy cover, distance to edge, elevation). Building density, trail density, and percent canopy cover were calculated within a 250 m radius buffer surrounding each camera site—a scale consistent with habitat selection by smaller carnivores (Kelly and Holub 2008). Building density was calculated using the same landcover layer used for site selection described above in the Camera Trap Survey section. To represent the density of linear anthropogenic landscape features (hereafter referred to as "trail density") present in areas of natural vegetation, I combined trail data from the Washington Recreation and Conservation Office (https://rco.wa.gov/recreation-and-conservation/maps-and-data/) with data on closed, unpaved service roads from the WADNR (https://fortress.wa.gov/dnr/adminsa/gisdata/metadata/road.html). Percent canopy cover was calculated by averaging canopy cover values from the 2016 United States Forest Service Tree Canopy Cover dataset (https://data.fs.usda.gov/geodata/rastergateway/treecanopycover/). Using data from the Washington State Department of Transportation (https://www.wsdot.wa.gov/mapsdata/geodatacatalog/), I measured the distance from each camera to the nearest major road. To calculate distance to edge, I first used the 2016 National Land Cover Database dataset (https://www.mrlc.gov/data/nlcd-2016-land-cover-conus) and reclassified landcover types as either open (including Open Space, Low Intensity Development, Medium Intensity Development, High Intensity Development, Barren Land, Shrub/Scrub, Grassland/Herbaceous, Pasture/Hay, Cultivated Crops, and Emergent Herbaceous Wetlands) or closed (including Deciduous Forest, Evergreen Forest, Mixed Forest, and Woody Wetlands) to create a landcover layer representing the boundary between open and closed habitats (Moll et al. 2018), and then measured the shortest distance to this boundary for each site. I measured elevation above sea level using United States Geological Survey 10-meter digital elevation models (https://gis.ess.washington.edu/data/raster/tenmeter/). To account for the intensity of human presence at each camera location, I divided the number of humans detected at each site by the number of days during which the camera operated.

I included five covariates (Table 1) in the model for detection probability (p). Because carnivore detectability can be affected by human activity (Nickel et al. 2020) and trail width (Harmsen et al. 2010; Cusack et al. 2015), I included covariates for both. I also included three-day period of the year (for coyotes) or week of the year (for all other species) as a detection covariate because carnivore activity varies by season (Ellington et al. 2020), particularly for species that hibernate (e.g., bears; Gaines 2003). Further, as different camera types have different trigger speeds and fields of view, I added a categorical covariate for camera type to account for potential differences among the three camera types used. I also included a binary covariate for whether a site was located in a public park (=0) or private residence (=1). None of the continuous covariates were strongly correlated (Pearson's correlation matrix, $|r| < 0.6$), so all were retained. All continuous covariates were standardized to have a mean of 0 and standard deviation of 1.

Table 1. Descriptions and ranges for covariates used to model occupancy probability (ψ) and detection probability (p) for black bears, bobcats, cougars, coyotes, opossums, and raccoons in western Washington, USA, in July 2016-August 2017.

Covariate	Description	Parameter
Building density	Number of buildings per hectare within a 250 m buffer; range 0–6.26	ψ
Trail density	Linear length (m) of trails and closed, unpaved service roads per hectare within a 250 m buffer; range 0–110.01	ψ

Covariate	Description	Parameter
Distance to road	Euclidean distance (m) to nearest public road; range 19.01–3670.89	ψ
Human activity	Average number of humans detected per day; range 0–352.93	ψ
Percent canopy	Average percent canopy cover within a 250 m buffer; range 12.44–84.05	ψ
Elevation	Meters above sea level; range 10.42–675.42	ψ
Distance to edge	Euclidean distance (m) to nearest habitat edge; range 0.22–1090.23	ψ
Time of year	Calendar 3-day period (coyote; range 1–122) or calendar week (all other species; range 1–52)	p
Human activity	Average number of humans detected per 3-day survey (coyote; range 0–736) or week survey (all other species; range 0–1432)	p
Trail width	Width (m) of trail perpendicular from camera	p
Land type	Public park or private residence	p
Camera type	Bushnell Trophy Cam HD Aggressor, Reconyx Hyperfire, or Reconyx Ultrafire	p

Occupancy Models

I used single-species, single-season occupancy models (MacKenzie et al. 2006) to examine black bear, bobcat, cougar, coyote, opossum, and raccoon occupancy probability as a function of urbanization and human presence. Occupancy models follow a hierarchical framework where temporally replicated surveys are used to estimate the probability of site occupancy, ψ, while simultaneously estimating and accounting for detection probability, p (MacKenzie et al. 2002). For black bears, bobcats, cougars, opossums, and raccoons, I parsed the detection/non-detection data into six week-long surveys. Because of the high number of coyote detections, I parsed the detection/non-detection data for this species into 14 three-day survey periods to improve the fit of the model. Each of the 500 m by 500 m cells was defined as a site. Whereas the area of a site is within the range of published home range sizes of opossums (Wright et al. 2012) and raccoons (Gehrt et al. 2010) in urbanized landscapes, it is significantly smaller than published home range sizes of black bears, bobcats, cougars, and coyotes (Kertson et al. 2013; O'Donnell and delBarco-Trillo 2020). Because these larger-ranging species all have home range sizes that can cover multiple sites, estimates should be interpreted as site use rather than true occupancy (Burton et al. 2015; Tobler et al. 2015). For simplicity, however, I hereafter refer to site use as occupancy.

I used the R package "unmarked" (Fiske and Chandler 2011) to fit a single global model containing all occupancy and detection covariates of interest to the black bear, bobcat, coyote, opossum, and raccoon data. Because cougars were only detected at sites on public land and never at sites that contained buildings, I did not include covariates for building density and land type in the cougar model, but retained all other covariates. Two of the sites located at public parks had an extremely high human presence. Tiger Mountain State Park in Issaquah, WA recorded an average of 326 human detections per day, whereas Lake Hills Greenbelt Park in Bellevue, WA, recorded an average of 352 humans per day; none of the other camera sites averaged more than 84 daily human detections. Given these two sites were such extreme outliers, I examined the effects of removing both sites from all of the species occupancy models but found that doing so only minimally reduced the effect size of the human presence covariate. Because removing these two sites did not affect the results and they provided useful data for the rest of the model covariates, I did not exclude them from the data. I assessed model fit with the MacKenzie-Bailey goodness-of-fit test (MacKenzie and Bailey 2004) using the R package "AICcmodavg." The cougar model showed some evidence of lack of fit ($p = 0.03$, $\hat{c} = 2.6$, $\chi^2 = 211.82$) after 1000 bootstraps. None of the other models showed evidence for lack of fit. My goal was to explore variables affecting occupancy for multiple carnivore species rather than to test specific hypotheses, and as such I report the results of each model and whether covariates were significant at the level of $\alpha = 0.05$.

RESULTS

Camera Trap Survey

During 6,910 cumulative trapnights, cameras recorded 43,595 detections of humans, 10,883 detections of domestic animal species (i.e., dogs, cats, horses, goats, and cows), and 6,096 detections of wildlife. At least 27 non-human animal species were identified from 69,196 image sequences comprising 340,254 total images. Data were only included from 152 of the 175 camera deployments owing to camera theft or damage or from being deployed too close (i.e., < 500 m) to another camera. Humans were present at 90.1% (n = 137) of camera sites with a mean of 318.2 (range = 1–5,258) human detections per site.

Occupancy Models

Black bears were detected at 34.8% of sites (n = 53). The average probability of black bear occupancy (i.e., with all standardized covariates held at their mean) from the occupancy submodel was 0.491 (SE = 0.137). Percent canopy cover was the only significant covariate in the occupancy submodel (p-value = 0.004), with probability of black bear occupancy increasing as percent canopy cover increased (Table 2). The detection submodel contained three significant covariates (Table 3). Black bears more than three times more likely to be detected at sites with Bushnell cameras ($p = 0.321$) or Ultrafire cameras ($p = 0.278$) than at sites with Hyperfire cameras ($p = 0.090$). Black bear detection probability was twice as high at private residences ($p = 0.651$) compared to park sites ($p = 0.321$). As the week of the year increased, detection probability of black bears decreased.

Bobcats were detected at 55.9% of sites (n = 85), with average probability of occupancy of 0.660 (SE = 0.130). I detected no significant relationships between bobcat occupancy and any of the occupancy covariates (Table 2). There was a strong significant relationship between bobcat detection and trail width (p-value < 0.001), with detection probability increasing as trail width increased (Table 3).

Cougars were the least detected species, recorded at only 9.9% of sites (n = 15). The estimated average probability of cougar occupancy was 0.240 (SE = 0.160). Distance to road was significantly related (p-value = 0.0498) to the probability of cougar occupancy, with occupancy increasing as distance to road increased (Fig. 2a; Table 2). None of the other covariates in the occupancy submodel were significant, nor were any of the covariates in the detection submodel (Table 3).

Coyotes were the most commonly detected species, which was detected at 77% of sites (n = 117). The coyote occupancy submodel estimated that the average probability of occupancy was 0.769 (SE = 0.091). The only significant occupancy covariate was distance to road (p-value = 0.029), with the probability of occupancy decreasing as the distance to the nearest road increased (Fig. 2b; Table 2). Four covariates in the detection submodel had significant relationships with detection (Table 3). Detection probability was greater at sites with Bushnell cameras ($p = 0.471$) than sites with Hyperfires ($p = 0.249$) or Ultrafires ($p = 0.391$). Trail width also had a significant effect, with detection probability increasing as trail width increased. Increasing three-day period of the year resulted in decreasing detection probability.

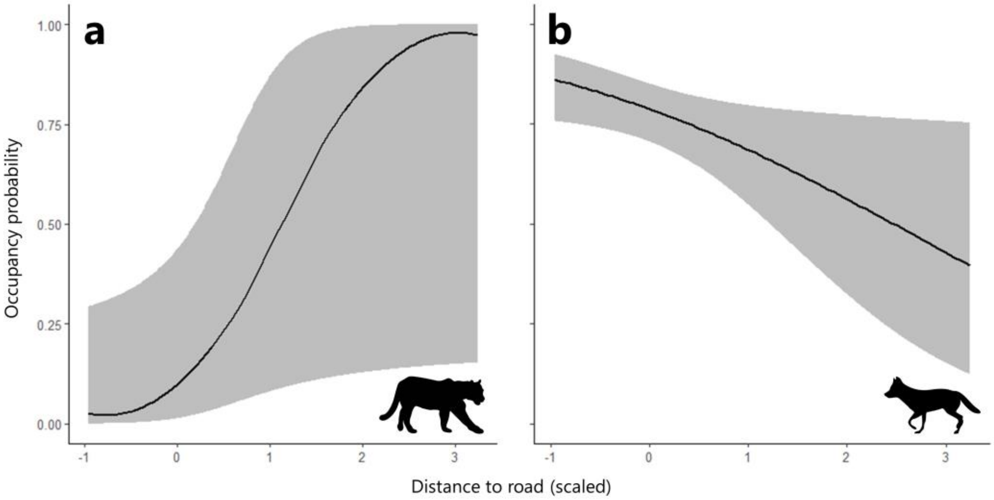

Figure 2. Effects of the distance to the nearest road on occupancy probability for cougars (a) and coyotes (b). Lines are predicted occupancy probability and shaded areas are 95% confidence intervals. Distance to road is scaled to have a mean of 0 and standard devation of 1.

Opossums were detected at 15.8% of sites (n = 24), with an estimated average probability of occupancy of 0.161 (SE = 0.081). Elevation was the only significant occupancy submodel covariate (p-value = 0.005), with probability of occupancy decreasing as elevation increased (Table 2). None of the covariates from the detection submodel were significant (Table 3).

Raccoons were detected at 30.3% of sites (n = 46), with an estimated average occupancy probability of 0.406 (SE = 0.156). None of the covariates in the occupancy submodel were significant (Table 2). Land type was the only significant covariate in the detection submodel (Table 3) and had a strong positive effect, with detection probability at residential sites (p = 0.663) more than three greater than park sites (p = 0.204).

Table 2. Model estimates, standard errors, p-values, and 95% confidence limits of occupancy submodel covariate coefficients for each species. Covariates with p-values < 0.05 are in bold. All values are on the logit scale.

Species	Covariate	$\hat{\beta}$	SE($\hat{\beta}$)	P-value	Lower CI $\hat{\beta}$	Upper CI $\hat{\beta}$
Bear	Intercept	-0.221	0.340	0.516	-0.886	0.445
	Building density	0.346	0.348	0.320	-0.336	1.029
	Trail density	-0.086	0.322	0.789	-0.717	0.545
	Elevation	-0.005	0.419	0.991	-0.825	0.816
	Human presence	-0.560	0.647	0.387	-1.828	0.708
	Edge distance	-0.149	0.320	0.643	-0.777	0.479
	Percent canopy	**1.514**	**0.531**	**0.004**	**0.473**	**2.554**
	Road distance	0.716	0.430	0.095	-0.126	1.559
Bobcat	Intercept	0.661	0.259	0.011	0.153	1.170
	Building density	0.071	0.375	0.850	-0.664	0.806
	Trail density	0.008	0.299	0.979	-0.578	0.594
	Elevation	-0.372	0.266	0.161	-0.893	0.149
	Human presence	-0.749	0.483	0.121	-1.695	0.197
	Edge distance	0.084	0.251	0.739	-0.408	0.575
	Percent canopy	-0.120	0.337	0.721	-0.781	0.540
	Road distance	0.310	0.265	0.242	-0.210	0.830
Cougar	Intercept	-2.263	1.024	0.027	-4.270	-0.255
	Trail density	0.398	0.684	0.560	-0.941	1.738
	Elevation	-1.378	0.756	0.068	-2.860	0.103
	Human presence	-0.289	1.655	0.861	-3.533	2.956
	Edge distance	-0.647	0.976	0.508	-2.560	1.267
	Percent canopy	1.921	1.494	0.199	-1.007	4.848
	Road distance	**2.002**	**1.021**	**0.049**	**0.002**	**4.003**
Coyote	Intercept	1.317	0.222	< 0.001	0.882	1.751
	Building density	-0.456	0.257	0.076	-0.959	0.048
	Trail density	0.066	0.265	0.802	-0.452	0.585
	Elevation	0.444	0.291	0.127	-0.126	1.013
	Human presence	0.313	0.424	0.460	-0.517	1.143
	Edge distance	0.049	0.241	0.839	-0.423	0.522
	Percent canopy	-0.165	0.296	0.578	-0.746	0.416
	Road distance	**-0.534**	**0.245**	**0.029**	**-1.014**	**-0.055**
Opossum	Intercept	-2.666	0.523	< 0.001	-3.691	-1.641
	Building density	0.118	0.323	0.714	-0.515	0.752

Species	Covariate	$\hat{\beta}$	SE($\hat{\beta}$)	P-value	Lower CI $\hat{\beta}$	Upper CI $\hat{\beta}$
	Trail density	0.645	0.362	0.075	-0.064	1.354
	Elevation	**-1.729**	**0.619**	**0.005**	**-2.942**	**-0.516**
	Human presence	-1.399	1.033	0.176	-3.425	0.626
	Edge distance	0.713	0.384	0.063	-0.039	1.465
	Percent canopy	-0.461	0.354	0.193	-1.155	0.232
	Road distance	-0.247	0.505	0.625	-1.237	0.743
Raccoon	Intercept	-0.501	0.370	0.176	-1.225	0.224
	Building density	0.386	0.392	0.325	-0.383	1.155
	Trail density	-0.319	0.341	0.349	-0.989	0.350
	Elevation	0.299	0.410	0.466	-0.505	1.103
	Human presence	0.146	0.487	0.764	-0.808	1.101
	Edge distance	0.441	0.403	0.274	-0.348	1.230
	Percent canopy	-0.268	0.387	0.489	-1.026	0.491
	Road distance	-0.821	0.501	0.101	-1.802	0.161

Table 3. Model estimates, standard errors, p-values, and 95% confidence limits of detection submodel covariate coefficients for each species. Covariates with p-values < 0.05 are in bold. All values are on the logit scale. The intercept coefficient is the reference for both categorical covariates, representing estimated detection probability for both the public land and Bushnell camera categories; estimates for the residential land category and for the Hyperfire and Ultrafire categories are interpretted in relation to the intercept.

Species	Covariate	$\hat{\beta}$	SE($\hat{\beta}$)	P-value	Lower CI $\hat{\beta}$	Upper CI $\hat{\beta}$
Bear	Intercept	-0.748	0.273	0.006	-1.283	-0.214
	Week of year	**-0.566**	**0.287**	**0.048**	**-1.128**	**-0.005**
	Human activity	-0.400	0.316	0.206	-1.021	0.220
	Trail width	-0.153	0.152	0.316	-0.451	0.146
	Residence	**1.370**	**0.553**	**0.013**	**0.286**	**2.455**
	Hyperfire	**-1.571**	**0.467**	**0.001**	**-2.485**	**-0.656**
	Ultrafire	-0.208	0.377	0.580	-0.947	0.530
Bobcat	Intercept	-0.473	0.178	0.008	-0.823	-0.124
	Week of year	0.078	0.133	0.558	-0.182	0.338
	Human activity	0.122	0.198	0.537	-0.265	0.510
	Trail width	**1.116**	**0.159**	**0.000**	**0.805**	**1.427**
	Residence	-0.608	0.494	0.218	-1.576	0.360
	Hyperfire	0.551	0.354	0.119	-0.143	1.245
	Ultrafire	-0.365	0.298	0.221	-0.948	0.219
Cougar	Intercept	-3.823	1.205	0.002	-6.184	-1.461
	Week of year	-0.180	0.308	0.559	-0.784	0.424
	Human activity	-4.800	3.331	0.150	-11.329	1.729
	Trail width	0.162	0.341	0.635	-0.507	0.831
	Hyperfire	0.078	0.766	0.919	-1.424	1.580
	Ultrafire	0.914	0.714	0.201	-0.486	2.314
Coyote	Intercept	-0.118	0.083	0.158	-0.281	0.046
	Three-day period	**-0.211**	**0.059**	**< 0.001**	**-0.327**	**-0.096**
	Human activity	0.022	0.046	0.635	-0.068	0.111
	Trail width	**0.212**	**0.063**	**0.001**	**0.088**	**0.336**
	Residence	0.025	0.209	0.906	-0.386	0.435
	Hyperfire	**-0.984**	**0.162**	**< 0.001**	**-1.301**	**-0.667**
	Ultrafire	**-0.325**	**0.139**	**0.020**	**-0.599**	**-0.052**
Opossum	Intercept	-0.575	0.337	0.088	-1.236	0.085
	Week of year	-0.392	0.221	0.076	-0.825	0.041
	Human activity	0.153	0.453	0.735	-0.734	1.040
	Trail width	0.304	0.434	0.483	-0.546	1.154

Species	Covariate	$\hat{\beta}$	SE($\hat{\beta}$)	P-value	Lower CI $\hat{\beta}$	Upper CI $\hat{\beta}$
	Residence	1.228	1.024	0.230	-0.778	3.234
	Hyperfire	0.532	1.487	0.720	-2.383	3.448
	Ultrafire	-1.072	0.990	0.279	-3.012	0.868
Raccoon	Intercept	-1.364	0.284	< 0.001	-1.920	-0.808
	Week of year	-0.149	0.162	0.358	-0.467	0.169
	Human activity	0.111	0.151	0.464	-0.185	0.407
	Trail width	0.102	0.200	0.610	-0.290	0.494
	Residence	**2.040**	**0.523**	**< 0.001**	**1.015**	**3.066**
	Hyperfire	-0.987	0.511	0.054	-1.988	0.015
	Ultrafire	-0.961	0.501	0.055	-1.942	0.021

DISCUSSION

As the reach of urbanization and human activity continues to expand, there is increasing need to understand the impacts of these forces on wildlife and ecosystems. Here, I used occupancy models to examine how human infrastructure and the presence of humans affected six carnivore species in western Washington, USA. I found that no one covariate explained occupancy across all six species, and no species responded significantly to more than one covariate. Only two species, cougars and coyotes, exhibited significant relationships with human impacts (i.e., distance to road), and their responses were different. These findings add to a growing literature revealing that spatial wildlife responses to human infrastructure and activity in urban landscapes are species-specific and can be limited, while also shedding new light on carnivore occupancy dynamics in a system that has not previously been scrutinized.

Species-specific responses to anthropogenic disturbances in urbanized landscapes appears to be the norm. Multi-species studies in Texas (Lombardi et al. 2017), Colorado (Goad et al. 2014), and California (Wang et al. 2015; Nickel et al. 2020) have all reported varying species responses to human infrastructure for carnivore species including American black bear, bobcat, cougar, coyote, Virginia opossum, and raccoon. Research on the effects of human presence in Colorado (Lewis et al. 2021) and California (Reilly et al. 2017) has similarly found that responses varied across these six carnivore species. My study suggests that this pattern of variability also extends to carnivores in urbanized areas in Washington.

Overall, we were able to detect few apparent effects of urbanization on carnivore occupancy, with only two species (cougars and coyotes) responding significantly to any of the covariates representing anthropogenic infrastructure. Not unexpectedly, cougar occupancy increased with increasing distance to roads. Paved roads are a major source of cougar mortality (Hornocker and Negri 2009; Thompson et al. 2014) and cougars often avoid them (Dickson et al. 2005). By contrast, coyote occupancy decreased as distance to roads increased. Roads do not appear to act as a barrier to coyotes, as they are known to travel on lightly-used roads (Bandak et al. 2020) and frequently cross even major roads despite a relatively high risk of mortality (Tigas et al. 2002; Gehrt et al. 2010). Prey availability may also explain why coyotes in this system were more likely to occupy areas in closer proximity to roads, as coyotes frequently use the easements along major roads to hunt small mammals (Gehrt et al. 2009). Whereas none of the models indicated a significant relationship between building density and occupancy for any of the species in this study, cougars were not detected at any camera sites that had buildings within a 250 meter radius. This result suggests cougars may avoid using sites in such close proximity to buildings. Kertson et al. (2011) found that cougars fitted with GPS telemetry collars in the same area of western Washington predominantly used wildland areas; however, 12.15% of GPS relocations occurred $\leq$ 500 meters from a residential structure, indicating that cougars will use developed areas provided they offer abundant native cover, sufficient prey availability, and allow cougars to minimize their exposure to anthropogenic disturbance. I detected black-tailed deer (*Odocoileus* *heminous columbianus*), the cougar's preferred prey in western Washington (Kertson et al. 2011), at 84% (n = 127) of sites, including the site that had the maximum measured building density (6.3 buildings per ha). Thus, prey availability is likely not the factor causing the absence of cougars in developed areas. Although all of the sites had some canopy cover (range = 12.4-84.0%, mean = 66.0%), these values represent average canopy cover over the buffer area and may not accurately describe the amount of available ground cover suitable for concealment. Therefore, whereas it is unlikely that all sites where cougars were not detected lacked suitable ground cover, it is possible that this may be the case at some sites. Another possible reason cougars were not detected within 250 meters of any structures may be the inherent limitations of my study design. Namely, I was limited to deploying cameras either at private residences or on trails in public parks. Cougars that use residential areas still attempt to minimize their exposure to anthropogenic disturbance (Kertson et al. 2011), including noise (Suraci et al. 2019), and with most cameras at residences deployed within ~50 meters of a building, it may be that cameras were too close to constant sources of disturbance. Similarly, buildings may also have been too close to cameras deployed on park trails for a cougar to use.

Human presence was not a significant predictor of occupancy for any species, suggesting that carnivores in the study area are not spatially altering site use in response to humans. This finding is consistent with the results of Reilly et al. (2017), who found that carnivore habitat use was not significantly affected by human presence in the San Franscisco Bay ecoregion. A similar study in central California, however, found that while human presence did not significantly influence coyote, opossum, and raccoon occupancy, bobcat and cougar occupancy were positively related to human presence, most likely owing to consistently high recreation throughout the study area that made spatial avoidance of humans too costly for species with larger home ranges (Nickel et al. 2020). Instead of avoiding areas used by humans, Nickel et al. (2020) found that bobcats, cougars, and coyotes became more nocturnal to avoid times of higher human activity, a behavioral response consistently found in other studies of those species (George and Crooks 2006; Wang et al. 2015; Reilly et al. 2017; Moll et al. 2018; Bandak et al. 2020). The temporal responses of opossums and raccoons are more inconsistent, with some studies finding that these synanthropic species did not change their temporal activity patterns in response to human presence (Reilly et al. 2017), whereas other studies have documented minor changes in temporal activity patterns and foraging behavior (Wang et al. 2015; Suraci et al. 2019). This variability in response might by explained by differences in baseline temporal activity patterns for opossums and raccoons. Whereas several studies found that opossums and raccoons were almost exclusively nocturnal (Gehrt et al. 2010; Wang et al. 2015; Reilly et al. 2017) and therefore already most active outside of periods of high human activity, Mims et al. (2022) found that raccoons in Seattle, Washington, were also active during crepuscular periods and thus more likely to encounter humans. Similarly, black bears also display varied responses to human presence, with bear populations in southern British Columbia, Canada, Colorado, USA, and Massachusetts, USA, becoming more nocturnal in response to increasing human activity (Zeller et al. 2019; Lewis et al. 2021; Procko 2022) but those in Alberta, Canada showing no change (Ladle et al. 2018). The spatial resilience many carnivore species exhibit as a result of temporal activity shifts suggests that temporal avoidance may allow many species to persist in urbanizing landscapes without having to spatially avoid humans.

Only two species, black bears and opossums, exhibited significant relationships with the habitat covariates included in the models. Unsurprisingly, black bear occupancy probability was positively associated with increasing canopy cover. Black bears have been found to select for forested habitat across varying levels of development along urban-wildland gradients (Obbard et al. 2010; Karelus et al. 2016; Zeller et al. 2019), as forested areas provide rest and denning sites, food via hard and soft mast (Karelus et al. 2016; Welfelt et al. 2019), and thermal and escape cover (Rogers 1993). Opossum occupancy was negatively correlated with increasing elevation, a result also reported by Reilly et al. (2017). Increasing elevation generally corresponded with decreasing levels of urbanization in my study area, and given the opossums preference for developed areas elsewhere (Bateman and Fleming 2012), lower elevation sites most likely provided more of the anthropogenic resources opossums excel at exploiting (Gehrt et al. 2010).

Whereas camera trap surveys are a powerful tool for sampling wildlife, careful consideration must be given to a study’s design and how it may influence results (Burton et al. 2015). I measured landcover features using a 250 meter radius because previous research (Kelly and Holub 2008) suggested smaller carnivores (such as raccoons and opossums) select habitat at that scale. Recent research by Moll et al. (2020), however, found that many carnivore species respond to urbanization at much larger scales (i.e., radii in the thousands of meters) irrespective of species’ body mass, suggesting that the scale at which I was attempting to measure species’ responses to landscape-level characteristics may have been too small for all species of interest in this study. I also only examined spatial responses to anthropogenic disturbances; with many studies finding that carnivores avoid human infrastructure and presence temporally rather than spatially (George and Crooks 2006; Wang et al. 2015; Reilly et al. 2017; Moll et al. 2018; Nickel et al. 2020; Bandak et al. 2020), it is possible that carnivores in the study system may similarly shift their temporal activity patterns in response to anthropogenic disturbance, or already occupy temporal niches that are relatively free from human disturbance, and thus have little need to alter patterns of space use. Small sample size may also have been a factor; both cougars and opossums had a low number of detections (n = 29 and n = 154), resulting in lower power for the models for these species to detect a relationship with the covariates.

Overall, the results of this investigation suggest that most carnivore species in the study area are tolerating anthropogenic disturbances, both in terms of infrastructure and activity, at least spatially and at small spatial scales. Carnivore responses to human infrastructure were minimal, and a common measure for the intensity of landscape development, building density (Theobald 2005), had no significant effect on carnivore occupancy. Carnivores also seemed unaffected by human presence on trails and did not change their spatial patterns to avoid areas of higher human use. Given what has been found in other urban landscapes, the next steps for better understanding this system are to evaluate relationships among landcover characteristics and carnivore occupancy at larger and varied scales, and to examine how human presence affects carnivore temporal activity patterns. Notably, the responses to urbanization that I did observe varied among the six focal species. More broadly, then, my findings underscore the need for additional work exploring the generality of spatial resilience to urbanization in carnivore guilds as well as the biotic and abiotic drivers that shape variation in wildlife responses to anthropogenic infrastructure and activity.

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