Spring 2023

Mesopredator Occupancy and Passerine Richness Along an Urbanization Gradient in Central Coastal California

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MESOPREDATOR OCCUPANCY AND PASSERINE RICHNESS ALONG AN URBANIZATION GRADIENT IN CENTRAL COASTAL CALIFORNIA

A Thesis
Presented to the
Faculty of the
Department of Applied Environmental Science
California State University Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Environmental Science

by
Matthew McGee
Term Completed: May 2023

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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Abstract

As anthropogenic activity such as urbanization and agriculture destroys and fragments wildlife habitat, some patches may grow too small or isolated to support apex predators, which may allow mesopredator populations to flourish in the absence of predation and competition pressure. In areas where mesopredator occupancy is high, increased predation pressure may be placed on mesopredator prey species such as songbirds, which are already experiencing declines due to habitat loss. Here I used camera traps to collect occupancy data of the region's most commonly occurring apex predators (coyotes) and three mesopredator species (bobcats, gray foxes, and domestic cats) at 35 sites along an urbanization gradient prominently featuring agriculture in California's Salinas Valley, and I conducted avian point counts to estimate passerine richness at 70 sites along the same gradient. I evaluated the influence of apex predators on mesopredators with single-season occupancy models, and I assessed the potential impact of mesopredators on passerine richness with Random Forest regression analysis. Gray foxes displayed a strong negative relationship with coyote activity and a strong positive relationship with mountain lion presence, while coyotes were negatively associated with mountain lions. Distance to wildland patches was the top predictor for both felid species, neither of which were notably impacted by coyotes. While natural landscape and topography predictors had the greatest explanatory power for passerine richness, domestic cat activity also had a notable adverse effect on passerines, with more explanatory power than all other carnivore and human-related metrics. Agricultural metrics typically displayed only moderate or weak predictive power in all models despite having higher carnivore and passerine richness than all other landscape classes, suggesting that there is greater complexity to how wildlife use agricultural habitat than I captured in this study.

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Introduction

Increasing urbanization results in conversion of wildlife habitat to developed land, fragmenting the natural areas that remain (Saunders et al. 1991). Mammalian carnivores may be particularly sensitive to landscape changes caused by human disturbance due to their large spatial and dietary needs (Crooks 2002). A reduction in habitat due to human alteration may bring apex predators in increasing contact with smaller mesopredators, and as interactions increase, apex predators may reduce or exclude mesopredators from habitat patches through antagonistic actions, predation, and interference competition (Temple et al. 2010, Moll et al .2018). For example, Temple et al. (2010) found gray foxes avoided a natural forest preserve in Georgia with high coyote density, while studies in California found low gray fox occupancy along habitat edges (Kowalski et al. 2015) where coyote occupancy was often high (Ordeñana et al. 2010). Mesopredators may thus seek highly urbanized sites that are unsuitable for large carnivores –the "human shield" effect—to avoid antagonistic interactions (Berger 2007, Moll et al. 2018, Parsons et al. 2019, Gámez and Harris 2021). Habitat fragmentation can also create patches that are too small, isolated, or unproductive to support apex predators (Moll et al. 2018). This may result in mesopredator release, in which mesopredator abundance increases in the absence of top-down control from apex predators (Soulé et al. 1988, Ritchie and Johnson 2009). Urban areas are also the source of a mesopredator often introduced by humans into the ecosystem: the domestic cat, another species that thrives in patches lacking apex predators (Kays et al. 2015).

An increase in mesopredator occupancy may place additional predation pressure on prey species, including many avian species (Crooks and Soulé 1999, Ritchie and Johnson 2009). Bird abundance may decrease in areas with high rates of natural mesopredators such as foxes (Soulé et al. 1992) as well as in areas of human-introduced mesopredators such as domestic cats (Crooks and Soulé 1999). Whereas domestic cats and natural mesopredators exhibit similar responses to apex predators (Cove et al. 2012, Kays et al. 2015), domestic cats may not face the same human persecution or population restraints as natural mesopredators (Kays and Dewan 2004). Domestic cats may thus pose the greatest threat to prey animals such as songbirds in patches without apex predators, and it is estimated that domestic cats kill as many as 4 billion birds in the U.S. each year (Loss et al. 2013). For many avian species, threats due to predation pressure may be compounded by human-driven changes in landscape (Evans et al. 2017). For example, the intensity of human land use may negatively impact bird movement through an urban matrix (Kennedy et al. 2010), and in agricultural habitat, birds responded negatively to monoculture, with decreased avian richness at sites with low habitat heterogeneity (Lee and Martin 2017). Indeed, habitat heterogeneity at microhabitat levels (30x30m) has more predictive power for avian richness at broad spatial scales than other landscape and topographic metrics (Farwell et al. 2020).

In the Salinas Valley of central coastal California, high mesopredator occupancy could have especially damaging effects on local fauna. The Salinas Valley is one of the most productive agricultural centers in the world and an area of relatively little urban development compared to much of the California coast (Monterey County Farm Bureau n.d.). Agriculture separates the urban center of Salinas from the large expanses of native shrublands and woodlands in the upland areas surrounding the valley, as well as the protected coastal habitats of Elkhorn Slough. It is not known if the agricultural mosaic of the Salinas Valley presents suitable connectivity for larger apex predators such as coyotes. If these large carnivores are absent or scarce in the Salinas Valley, mesopredator release could potentially occur in local habitat patches, some of which may have historically offered refuge for the many bird species present in the region. Avian richness is typically high in central coastal California due to the high habitat heterogeneity and the abundant food provided by coastal upwelling, both for resident species and migrants that travel along the Pacific flyway (Roberson 2002). If mesopredator release is occurring in the Salinas Valley, local avian species could be imperiled by increased predation rates.

While many of the individual components of this study have been previously researched, they are rarely encompassed in the same study. The relative scarcity of landscape-level ecology research in central coastal California and the prominence of agriculture along the Salinas Valley urbanization gradient present opportunities to address additional knowledge gaps on how mammalian carnivores use the agricultural matrix in the Salinas Valley, or how different agricultural practices (i.e., ranches vs row crops) in the region could impact mammal and bird occupancy. Both mammalian carnivores and songbirds are typically studied in urban and/or natural habitats; studies on either group are infrequent in agricultural habitat, and even rarer still on a gradient prominently featuring agriculture, urbanization, and natural habitat.

For this study, I evaluated carnivore occupancy and the impact it may have on local avifauna along an urbanization gradient originating in the city of Salinas, in central coastal California. Through a partnership with the Urban Wildlife Information Network (UWIN; https://urbanwildlifeinfo.org/resources), an international network of urban wildlife researchers created at the Lincoln Park Zoo's Urban Wildlife Institute, I collected mammal occupancy data for the city of Salinas. I used a camera study to assess the occupancies of coyotes, which are the study area's primary apex predator, and three mesopredators known to predate birds (bobcats, gray foxes, and domestic cats) along an urbanization gradient originating in central Salinas. I tested for possible mesopredator release using an occupancy modeling framework with coyote activity as a covariate (Mackenzie et al. 2002). I also conducted avian point counts along the urbanization gradient and evaluated the influence of mesopredators on passerine richness with Random Forest regression analysis (Breiman 2001). As recent studies with a multispecies occupancy modeling approach have demonstrated the importance of interspecific interactions when determining habitat use (Moll et al. 2018, Parsons et al. 2019), I predicted that interspecific dynamics would play a greater role in predicting mesopredator occupancy than environmental attributes. I also predicted that mesopredator occupancy rates would display an inverse relationship with coyote occupancy rates in all habitat types. While I expected that microhabitat-level heterogeneity would be the primary driver of passerine richness, similar to results found by Farwell et al. (2020), I predicted that passerine richness would be lower in patches with higher mesopredator occupancy, most noticeably in patches with higher occupancy rates of domestic cats.

Methods

Study sites

I established three urban-to-wildland transects in the Salinas Valley along which I collected data on mammal occupancy and passerine richness and composition. All transects originated from Big Sur Land Trust's Carr Lake site in central Salinas and extended approximately 15-20 km. I placed 11-13 primary sampling units (hereafter primary sites) along each transect for a total of 35 primary sites (Figure 1). Per UWIN protocols, no primary sites were placed within 1 km of another primary site to maintain site independence. Additionally, I established a secondary sampling unit (hereafter secondary site) 300-500 m from each primary site (Figure 2). I randomized the compass quadrant (e.g., northwest of primary site) in which I placed the secondary site for each primary site. I collected data on passerine composition and richness at all 70 sites (35 primary sites and 35 secondary sites), but mammal data was collected only at the 35 primary sites.

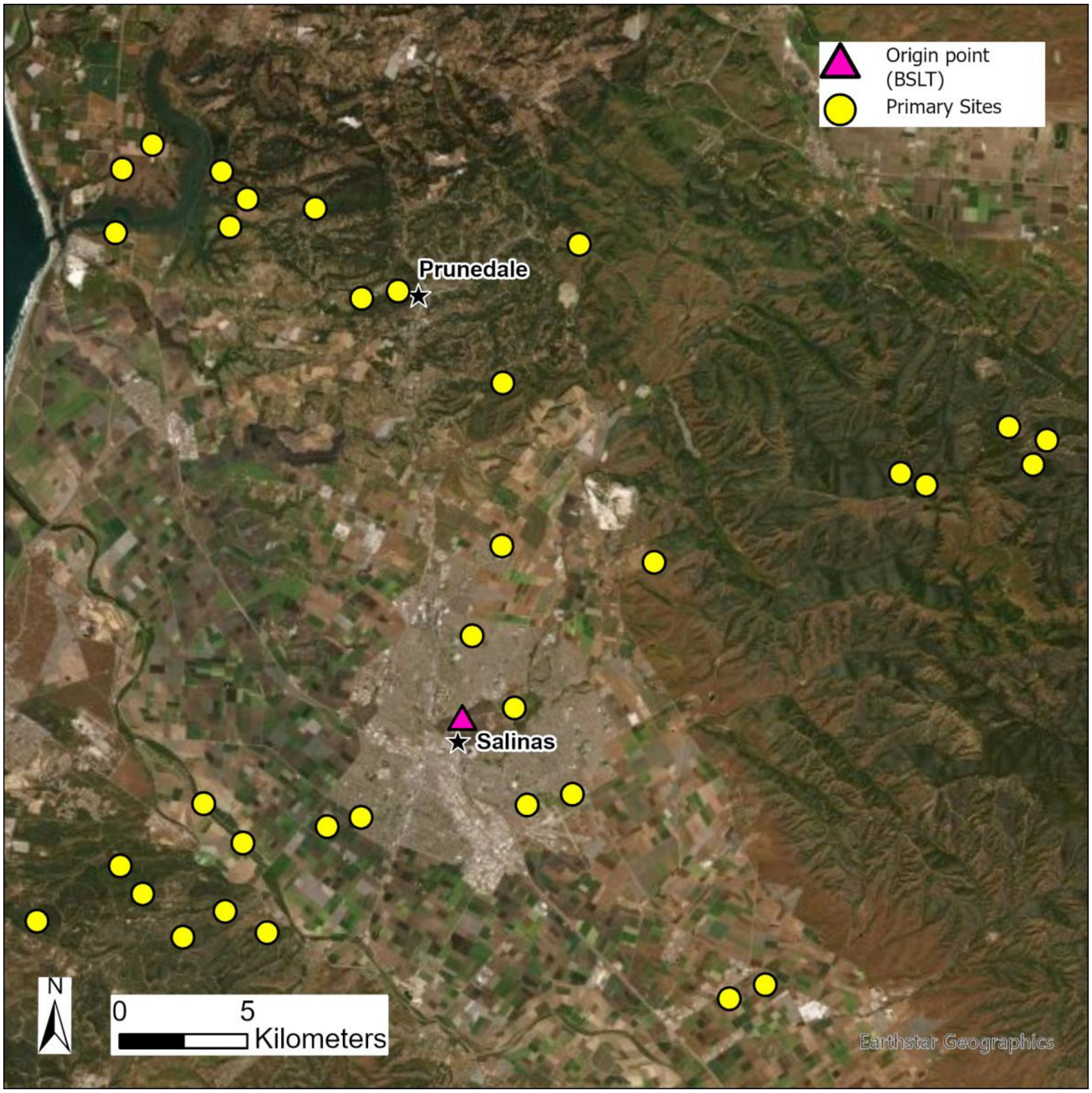

Figure 1. Locations for the 35 primary sites where I collected both mammal and bird data along an urbanization gradient in central coastal California. Sites were placed along transects that originated from the Big Sur Land Trust's (BSLT) Carr Lake property in central Salinas, California.

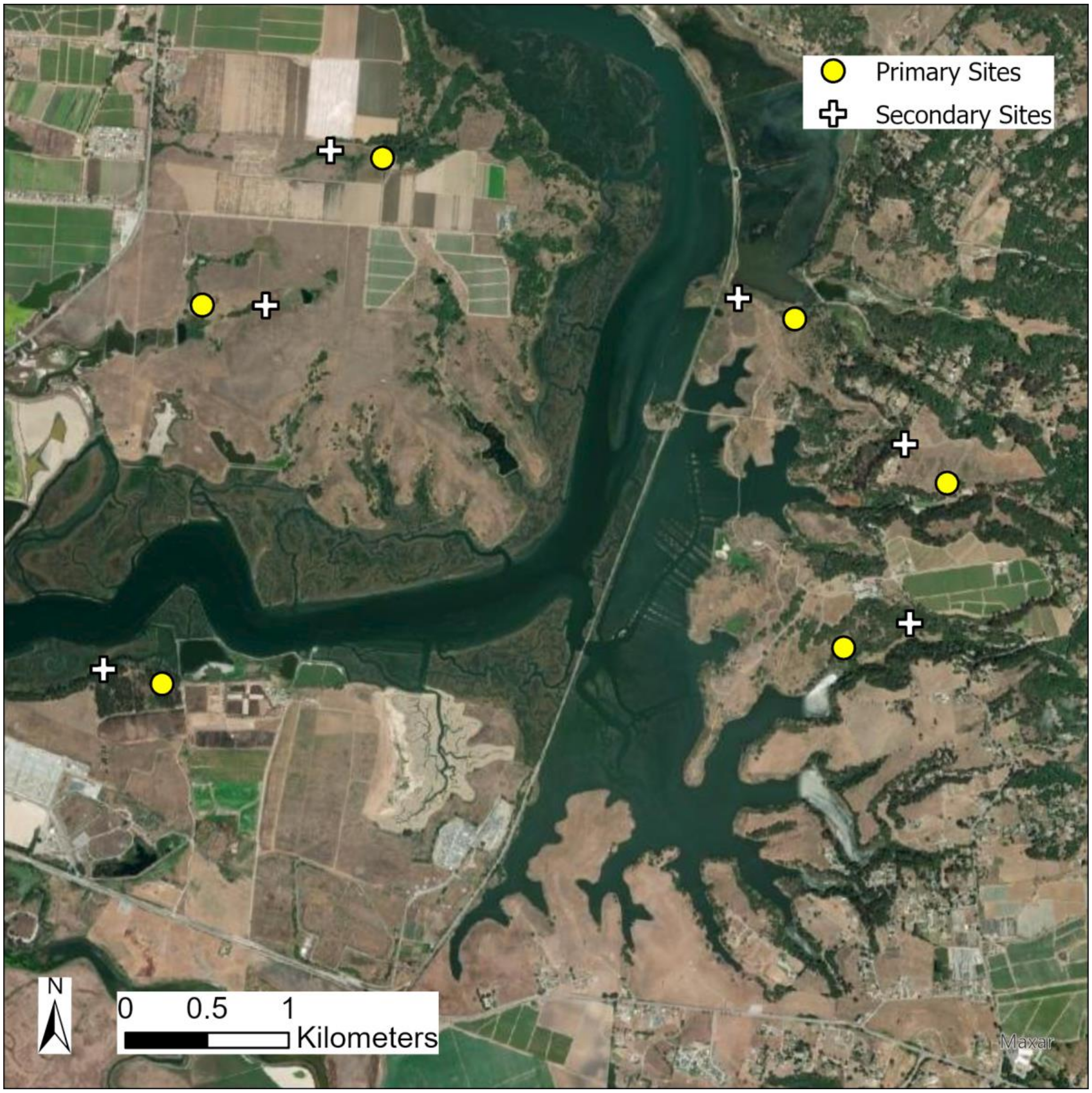

Figure 2. An example of primary and secondary site orientation. I randomized the quadrant (e.g., northwest of primary site) in which each secondary site was placed. All secondary sites are 300-500 m from the primary site.

I identified potential study sites through use of available land cover data from the National Agriculture Imagery Program (NAIP; USDA 2019) and the National Land Cover Dataset (NLCD; Dewitz 2021) in ArcGIS Pro 10.8 in addition to reconnaissance of the study area. I selected a range of sites that reflect the dominant land cover in the study area—urban areas, agriculture, and natural habitat—with additional emphasis on including variations in land use regime (e.g., agricultural land cover included sites in both row crops and ranchland). Final site selection also depended on feasibility of access and safety considerations. I did not consider the likelihood of species occurrence when selecting sites.

Data collection

I used camera surveys to collect data on presence-absence of mammals. At each primary site, I placed one camera (Bushnell Trophy Cam HD) ~0.5 m high on a tree or pole, with a predator survey scent disk (USDA Pocatello Supply) placed within 5 m of the camera in a ziptied mesh pouch. Per UWIN protocols, camera locations within each site were pseudorandomized when possible—I randomly placed a point at each location in ArcGIS before deployment and then placed the camera in the closest suitable location to that point during deployment. All final locations were subject to landowner review, and in some instances, landowners requested camera placement in a specific location. I also attempted to place cameras in locations with limited visibility to the public to reduce potential vandalism or theft. I visited each site approximately twice per month to change batteries, replace memory cards, and ensure the camera station remained operational. I also replaced predator scent disks once per two months or if a scent disk was damaged or missing. I collected data from April 2021 through October 2021 and delineated the duration into 31 7-day sampling periods.

Mammal photos were initially sorted into coarse groupings (i.e., animals, people, vehicles, or empty) with MegaDetector software (Beery et al. 2019). Animal photos were then sorted to species level in TimeLapse Image Analyzer (Greenberg et al. 2019). Any photos that could not be confidently identified to species level were excluded from analysis.

I used point counts to collect data on bird species richness and composition. Surveys with a duration of 8-10 minutes efficiently maximize species detections in chaparral and forest habitats, particularly during the non-breeding season (Dettmers et al. 1999, Shiu and Lee 2003, Crooks et al. 2004); thus, each point count I conducted was 10 minutes in length, following a 1-minute “settling down” period after arriving to the site. I chose a 100-m radius similar to other point count studies conducted in chaparral (Crooks et al. 2004). I recorded all passerine species seen or heard during the 10-minute survey, as a well as the number of individuals detected. I also recorded data on other species with a demonstrated risk of cat attacks (i.e., woodpeckers, hummingbirds, and doves/pigeons) based on a local dataset from the Monterey County Society for the Prevention of Cruelty to Animals (SPCA) (unpublished data; https://www.spcamc.org/). If I detected an individual but could not identify it within the 10-minute survey, I attempted to locate the bird in the field or record the individual's vocalizations for later identification. Only individuals for which I confirmed species identification were included in the final dataset. I omitted any individuals that flew over the site without using the habitat in any way ("fly-overs").

I recorded the weather conditions, temperature, and wind speed at the beginning of each point count, as these can affect bird activity and observer detection ability. I did not conduct point counts in rain or heavy wind, and all point counts were conducted within five hours of sunrise when bird activity is highest (Verner and Ritter 1986). I conducted one point count per month at each of the 70 sites for a total of 7 point counts per site over the duration of the study.

Occupancy Modeling

I examined potential factors influencing habitat usage of target carnivore species with single-season occupancy models. A site was considered occupied by a species if the species was detected on camera at least once during each 7-day sampling period. If a species was not detected during a sampling period, the site was considered unoccupied by that species for that sampling period even if it had been detected in a previous sampling period. I created a detection matrix for each species over the 31-week study period, with a "1" indicating detection of the species in a given sampling period, a "0" indicating a lack of detection, and a "–" indicating that the camera was not active during a given sampling period. Since it is unlikely that a species will always be detected during sampling periods even when occupying a site, I included covariates to model imperfect detection. Mean NDVI (Normalized Difference Vegetation Index) was used as a proxy for undergrowth, as dense vegetation may trigger cameras more frequently and conceal wildlife. I quantified the size of potential movement corridors along each camera placement with a site type covariate categorized as none (0), game trail (1), established trail (2), or road (3). Vehicle and human detection rates were calculated from the number of detections of motorized vehicles and pedestrians, respectively, divided by the number of days each camera was active in the field.

I selected a separate suite of covariates representing habitat conditions and interspecific interactions to model the occupancy of each species. Distance to wildland indicates each site's position along the urbanization gradient, with "wildland" defined as patches of natural habitat greater than 1 km^2 in size. To represent the three dominant land covers in the study area, I included the percentage of natural habitat, agriculture, and urban land cover within a 500-m radius circle (0.79 km^2) surrounding each camera trap. I chose this size to capture the macrohabitat surrounding each camera site while remaining within the mean home range size of all four target species (Sawyer and Fendley 1990, Chamberlain and Leopold 2000, Gehrt et al. 2009, Temple et al. 2010, Horn et al. 2011, Deuel et al. 2017). This size also allowed me to avoid predictor overlap with adjacent sites. All land cover percentages were derived using 2019 NLCD data. To address potential variations in habitat and anthropogenic intensity among different agricultural practices, I also considered the dominant agricultural land use regime at each site, defined as either none, ranchland, or row crops. As the presence of mountain lions—the largest carnivore that occurs in the study area—could impact the activity of smaller carnivores, I used 1/0 indicators to represent whether a mountain lion was detected at least once at a given study site over the duration of the study period. Additionally, I calculated the daily rate of coyote detections at each camera site and used this as a covariate in the models for the three mesopredator species (bobcat, gray fox, and domestic cat). All spatial analysis for calculating covariates was conducted in ArcGIS Pro 10.8.

I evaluated all covariates for collinearity using Pearson's correlation coefficients (Puth et al. 2014) and did not include covariates with significant correlations ($r \geq 0.349, df = 33$) in the same models, with the exception of mean NDVI, which had significant correlations with all other covariates. I assessed the occupancy of target species using single-season occupancy models in package "unmarked" (Fiske and Chandler 2011) in R statistical software (v4.2.2, R Core Team 2022) by running detection-only models and then using the top detection model for each species while building occupancy models. In addition to running models with each individual occupancy covariate, I included the following candidate models:

$$Percent\ agriculture + Percent\ urban$$

$$Distance\ to\ wildland + Percent\ agriculture$$

$$Distance\ to\ wildland + Dominant\ agriculture$$

$$Distance\ to\ wildland + Mountain\ lion\ presence$$

I chose the first three models to provide a more nuanced assessment of carnivore relationships with human disturbance, particularly to examine how carnivores use agricultural habitat at different proximities to large natural areas. The distance to wildland and mountain lion model tests for a possible human-shield effect if smaller carnivores are choosing patches closer to the urban center and farther from natural habitat patches with mountain lion activity. No other sensible combinations were possible due to correlations between covariates. For the three mesopredator species, I also included a model with coyote detection rate, as well as models with coyote detection rate and each of percent natural habitat, percent agriculture, percent urbanization, distance to wildland, and mountain lion presence.

All model comparisons were conducted with the corrected version of Akaike's Information Criterion for smaller sample sizes (AICc) in package "AICcmodavg" (Mazerolle 2020).

Passerine Analysis in randomForest

I used regression analysis to model the influence of environmental attributes and carnivore occupancy on the passerine richness of each site. For the context of this model, I defined site richness as the total number of permanent or seasonally resident passerines detected over the duration of the sampling period. Total site richness provides a more accurate representation of site composition than mean site richness (Gotelli and Colwell 2011), particularly given the detection limitations of a ten-minute survey (e.g., randomness in bird activity and detection capabilities of the observer). Primary and secondary sites were considered unique sites in the model for a total of 70 sites.

I chose covariates representing a range of categories that could impact passerine occupancy and detection at sites in the study area: survey-specific conditions, topography, natural landscape factors, habitat heterogeneity, anthropogenic land use, and carnivore activity (Table 1). Survey-specific conditions were averaged across the seven surveys conducted at each site. I calculated the mean value for non-survey-specific covariates within the 100-m radius circle surrounding each point, where applicable. Due to the close proximity of sites and the coarseness of available datasets, some covariate values were shared between primary and secondary sites. Covariates derived from camera detections were also shared between primary and secondary sites. While carnivore occupancy could vary between primary and secondary sites, particularly in cases with potential movement barriers between sites, each secondary site was within the home range of all target carnivore species, and habitats were typically similar between paired primary and secondary sites. All spatial analysis was conducted in ArcGIS Pro 10.8.

Table 1. Covariates used in passerine richness randomForest model. Data sources are listed in the Source column. NLCD is the National Landcover Dataset (https://www.mrlc.gov/data), USDA is the United States Department of Agriculture (https://datagateway.nrcs.usda.gov/), and USGS is the United States Geological Survey (https://www.usgs.gov/). Data from the U.S. Census Bureau is available at https://www.census.gov/programs-surveys/popest/data/data-sets.html. Habitat heterogeneity metrics were taken from publicly available data from the Silvis lab at the University of Wisconsin-Madison (https://silvis.forest.wisc.edu/). "" indicates that the covariate was derived from a separate dataset taken from the listed source. Data collected in the field is represented with "-".*

Category	**Covariate**	**Source**
Survey-specific	Wind speed	-
	Temperature	-
	Fog/cloud cover	-
	Time after sunrise (TAS)	-
Climate and Topography	Elevation	USDA
	Slope	USDA*
	Aspect	USDA*
	Topographic Roughness Index (TRI)	USDA*
	Mean historic temperature	USDA
	Mean historic precipitation	USDA
Natural landscape	Percent natural habitat	NLCD
	Tree canopy	NLCD
	Distance to water	USGS
	Distance to wildland	NLCD
	Mean NDVI	USGS
Habitat heterogeneity	Dissimilarity	Silvis lab
	Entropy	Silvis lab
	Contrast	Silvis lab
Anthropogenic land use	Percent agriculture	NLCD
	Dominant agriculture type	-
	Percent urbanization	NLCD
	Housing density	U.S. Census Bureau
	Impervious surface	NLCD
Carnivore activity	Coyote detection rate	-
	Bobcat detection rate	-
	Gray fox detection rate	-
	Domestic cat detection rate	-

I evaluated the factors influencing passerine richness using randomForest (RF) regression analysis (Breiman 2001). RF is a powerful machine learning algorithm that has been successfully used in a number of practical problems (Biau and Scornet 2016), including predicting species distributions (Evans et al. 2011, Kosicki 2020). RF allows for a large suite of predictors and it has demonstrated high performance in models with relatively small sample sizes (Biau and Scornet 2016). While it is not often used in avian models, Kosicki (2020) found high predictive power when bird distributions were driven by multiple predictors, as RF was better at finding nuance and complex interplay between predictors than other modeling approaches. RF also allows for a much larger suite of covariates than standard regression analysis. I ran all passerine richness models in package "randomForest" (Liaw and Wiener 2002).

Results

Camera trapping

I ran 35 camera stations from April 2021 to October 2021 for a total of 4,678 trapping nights. Among the four target carnivore species, domestic cats were the most frequently detected (3,099 detections among 11 sites), although over half of the detections (1,565) were from one site. Coyotes were the most widespread of all target carnivores and had the second highest number of total detections (1,843 detections, 25 sites), followed by gray foxes (1,725 detections, 9 sites) and bobcats (423 detections, 20 sites). Similar to domestic cats, the majority of gray fox detections (1,527) were from only 2 sites.

Coyotes were the only target carnivore species detected in all three of the dominant land cover types. Gray foxes and bobcats were not detected at urban sites, while domestic cats were not detected at natural habitat sites. All four species were detected at agricultural sites.

Avian point counts

I conducted 490 avian point counts from April 2021 to October 2021 across 70 sites (35 paired primary and secondary sites). I detected 96 unique species of passerine, woodpecker, hummingbird, and dove across the study range, excluding migratory visitors. Total site richness ranged from 5 species to 40 species, with a mean site richness of 22.4 species. Species detections at primary sites and secondary sites were almost equal (782 total species detections at primary sites versus 785 at secondary sites), although between individual site pairs, secondary sites averaged five more species than their paired primary site. Avian richness was highest at agricultural sites (mean= 25.1 species), followed by natural habitat and urban sites (23.2 and 15.9 species, respectively).

Carnivore occupancy modeling

I assessed which covariates most strongly influenced the detection and habitat use of each target carnivore species with single-species occupancy models. Top detection-only models were similar among all species (Table 2). Detection probabilities decreased with increasing rates of pedestrian activity for all species, while denser undergrowth also decreased detection probabilities for coyotes and domestic cats. Vehicular activity was present in top detection models for foxes, cats, and bobcats, although trends differed among species: fox detection probability decreased with increasing vehicular activity, while both bobcat and domestic cat detection probability increased with increasing vehicular activity. Both foxes and bobcats were also more likely to be detected at sites with larger movement corridors.

Table 2. Beta estimates (β) with 95% confidence intervals of detection covariates in top detection-only models for each target species. Human represents daily pedestrian activity, vehicle represents daily vehicular activity, site type represents the size of potential movement corridors at each camera, and NDVI represents a proxy for undergrowth. Models were ranked with Akaike's Information Criterion corrected for small sample sizes (AICc). Covariates that were not present in the top detection model for a given species are indicated with "–"

	Human	**Vehicle**	**Site Type**	**NDVI**
Coyote	-0.66 (-1.02 - -0.31)	–	–	-0.55 (-0.74 - -0.32)
Gray Fox	-5.12 (-7.12 - -3.11)	-2.00 (-3.91 - -0.09)	1.50 (0.96 – 2.04)	–
Bobcat	-3.32 (-5.63 - -1.00)	0.55 (0.34 – 0.75)	0.50 (0.22 – 0.78)	–
Domestic Cat	-0.57 (-0.79 - -0.36)	0.54 (0.23 - 0.84)	–	-0.62 (-0.91 - -0.33)

The most supported occupancy models (ΔAICc < 2.00; Table 3) suggest that habitat use by canids in the study area is largely influenced by the presence of larger carnivores, while habitat use by felids is more dependent on the site's location along the urbanization gradient. Top canid models indicate that coyote occupancy decreases at sites where mountain lions are present (β= -0.842, 95% CI: -1.59 – -0.09; Figure 3) while fox occupancy increases with mountain lion presence (β= 3.62, CI: -13.5 – 20.75) and decreases with increased coyote activity (β= -4.07, CI: -9.3 – 1.17; Figure 4a). Confidence intervals for top fox models overlap zero, however, suggesting that support is not as robust for these models. Distance to wildland was a strong predictor for both bobcats and domestic cats (Figure 5); with bobcat occupancy decreasing with distance from natural areas (β= -2.7, CI: -5.05 – -0.34; Figure 5a) and cat occupancy increasing with distance from natural areas (β= 3.4, CI: 0.93 – 5.87; Figure 5b). Although coyotes also displayed a negative relationship with distance to wildland in several top models, this trend was weaker than it was for felids (β=-0.76) and confidence intervals overlapped zero (CI: -1.66 – 0.14), indicating less substantial support.

Table 3. Summary of top models (ΔAICc < 2.00) for each target species, where ψ represents occupancy covariates and p represents detection covariates. Models were evaluated with Akaike's Information Criterion corrected for small sample sizes (AICc). ΔAICc is the difference between a given model and the top model, w is the weight (out of 1.00) of each individual model, and K is the number of parameters in each model.

Species	**Top Model(s)**	**AIC_c**	**ΔAIC_c**	**w**	**K**
Coyote	ψ (Mountain Lion), p (NDVI+Human)	895.96	0.00	0.25	5
	ψ (Mountain Lion+ Distance to Wildland), p (NDVI+Human)	896.00	0.04	0.24	6
	ψ (Percent Ag), p (NDVI+Human)	896.67	0.91	0.16	5
	ψ (Percent Ag + Distance to Wildland), p (NDVI+Human)	897.11	1.16	0.14	6
Gray Fox	ψ (Mountain Lion), p (Human+Vehicle+Site Type)	352.94	0.00	0.38	6
	ψ (Coyote+ Percent Urban), p (Human+Vehicle+Site Type)	354.57	1.62	0.17	7
	ψ (Coyote + Mountain Lion), p (Human+Vehicle+Site Type)	354.58	1.64	0.17	7
Bobcat	ψ (Distance to Wildland), p (Human+Vehicle+Site Type)	542.80	0.00	0.58	6
Domestic Cat	ψ (Percent Ag+ Distance to Wildland), p (Human+Vehicle+NDVI)	391.68	0.00	0.47	7
	ψ (Distance to Wildland), p (Human+Vehicle+NDVI)	392.84	1.16	0.27	6

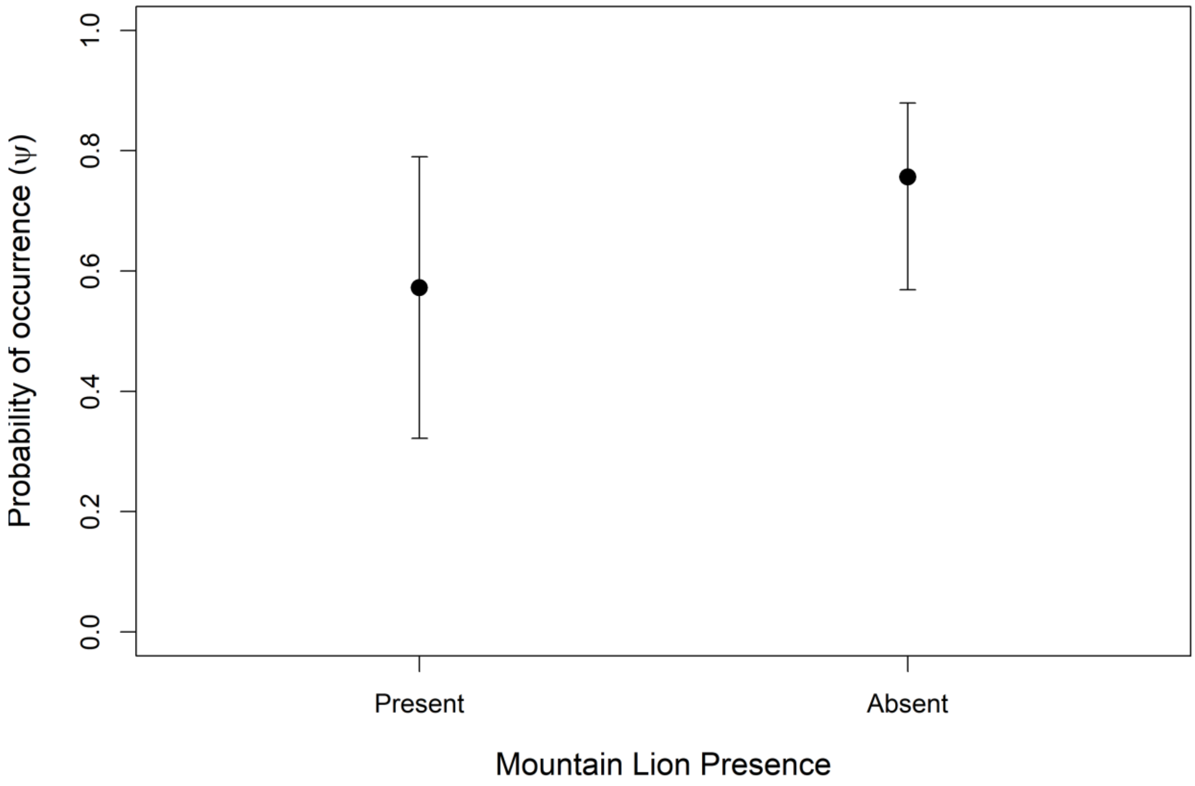

Figure 3. Likelihood of coyote occupancy at sites where mountain lions were and were not detected. Arrows represent 95% confidence intervals.

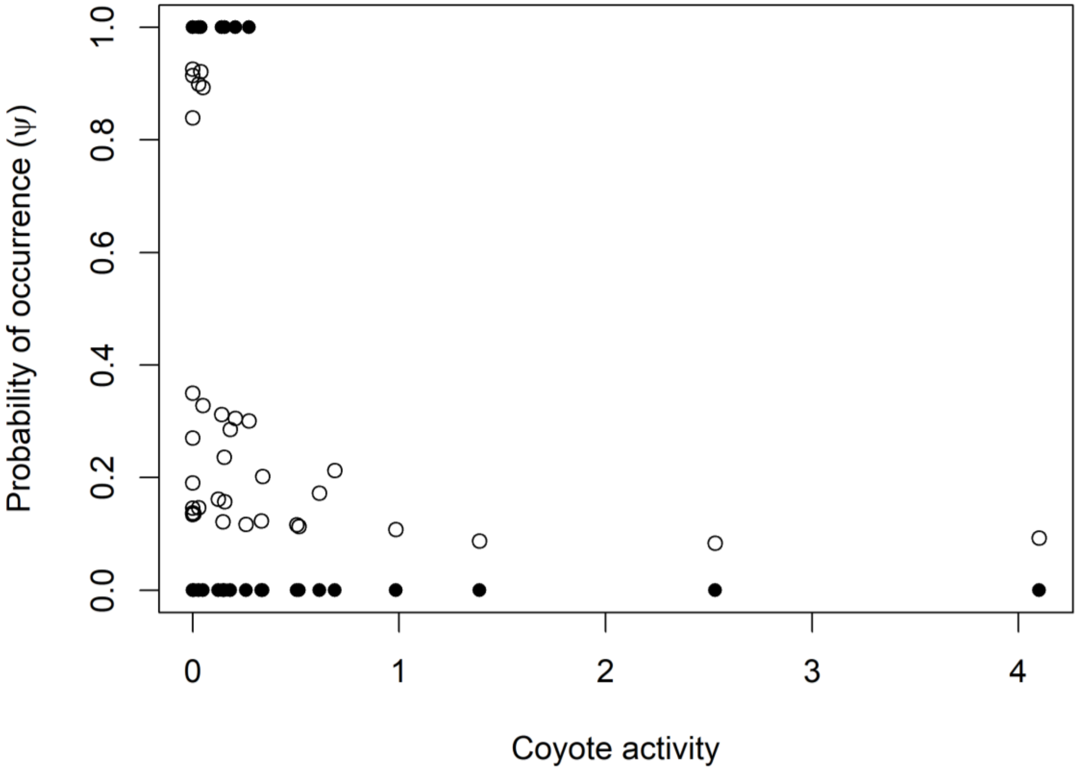

Figure 4. Relationship of occupancy probabilities for gray fox with increasing daily coyote detections. Open circles represent the occupancy probability at each site. Closed circles represent detection (1) or non-detection (0) of gray foxes.

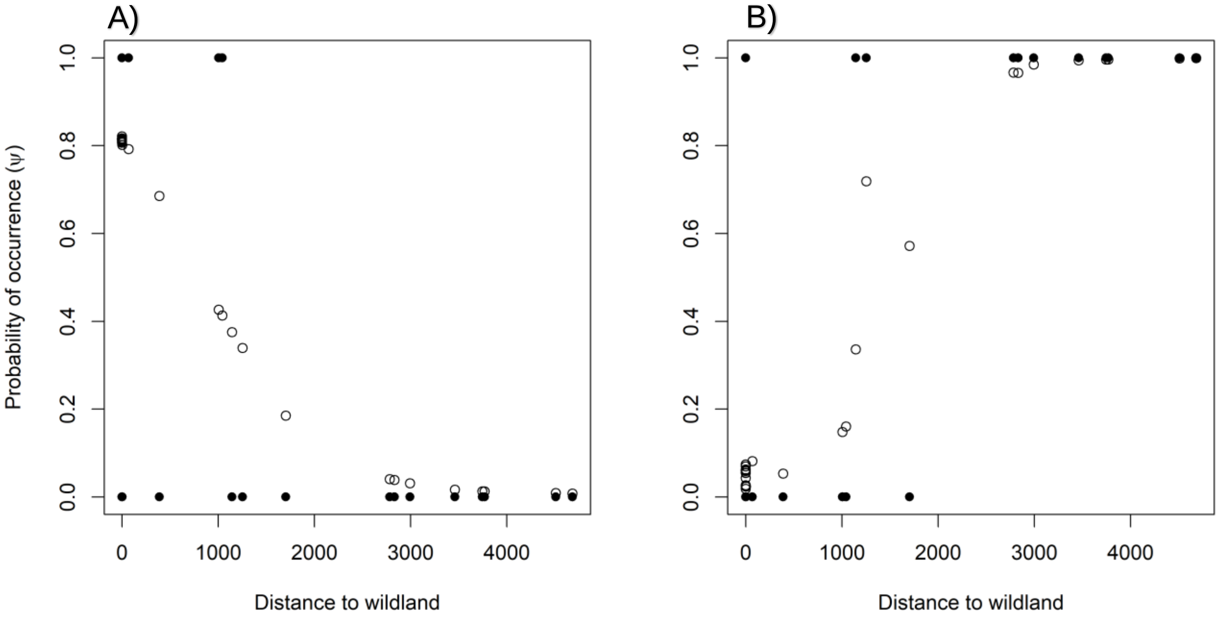

Figure 5. Occupancy probabilities for bobcats (A) and domestic cats (B) with increasing distance from wildland patches. Open circles represent the occupancy probability at each site. Closed circles represent detection (1) or non-detection (0) of gray foxes.

Regression analysis on passerine richness

Almost half the variance (47.93%) in passerine richness among sites was explained by the final randomForest model. Natural landscape and topographic covariates are the most important predictors of passerine richness in the study area—six of the seven predictors with greater than 10% explanatory power fell into this category (Figure 5). Distance to wildland (19.54%) and percent natural habitat (19.01%) showed the most explanatory power in the model, with passerine richness decreasing with distance from natural areas and with lower percentages of natural habitat. Passerine richness also declined sharply at sites with higher rates of domestic cat activity, which was the only top predictor (11.07% explanatory power) not categorized as topography or natural landscape (Table 1). Domestic cats were the only carnivore with substantial influence on passerine richness in the model. While anthropogenic predictors typically showed only moderate explanatory power, there was still a discernible trend of high passerine richness at sites with 20-50% agricultural or urban land cover. Survey conditions were notably weak predictors, with only two covariates (cloud cover and time after sunrise) in the final model and both with less than 5% explanatory power.

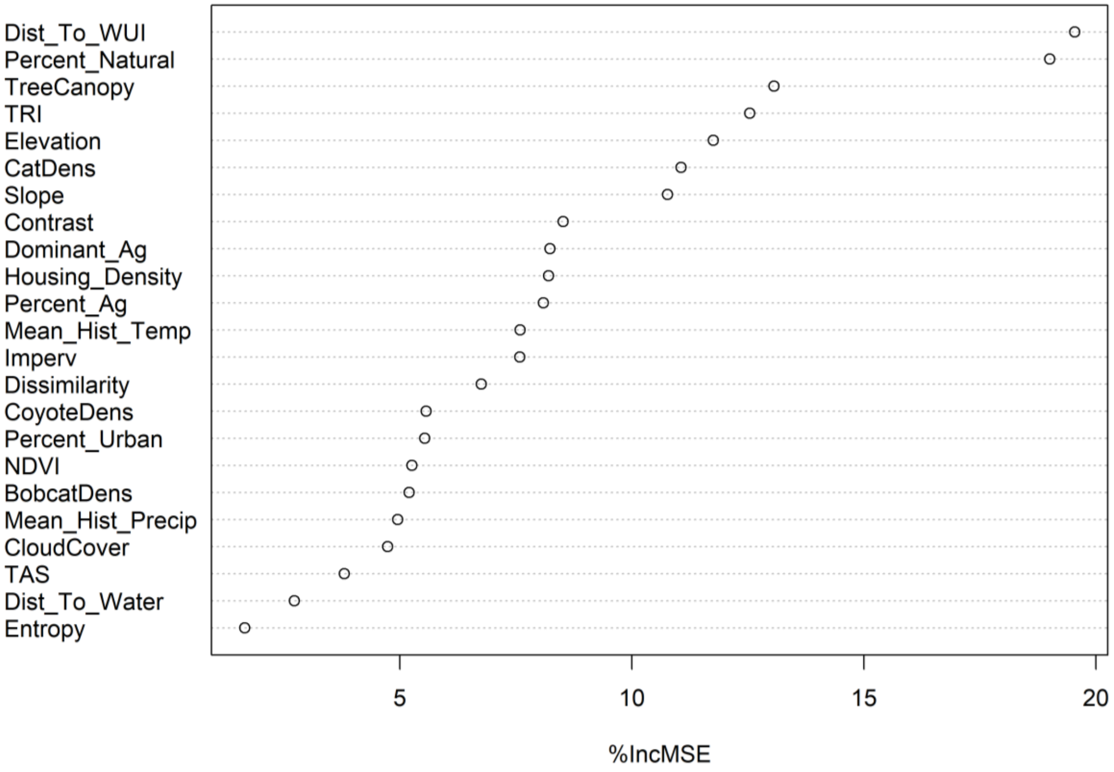

Figure 6. Ranked list of predictor importance on passerine richness, where open circles represent the explanatory power (out of 100%) of each predictor.

Discussion

This study investigated the influences of interspecific interactions and land-use patterns along an urbanization gradient on carnivore occupancy and passerine richness, with particular emphasis on testing for possible mesopredator release. Few other studies have simultaneously examined the relationships of mesopredators with their potential predators, competitors, and prey, particularly along a gradient that prominently features urban, agricultural, and natural habitats. Gradient-related metrics were important predictors in nearly all models, demonstrating the influence of the human footprint on carnivore and passerine habitat selection and the complex relationship between wildlife and agriculture. While I did not observe widespread mesopredator release occurring in the study area, results from this study do highlight the significance carnivores may have on community dynamics.

Due to limited capture rates, I was not able to fully test my hypothesis that interspecific interactions would typically outrank habitat variables when determining carnivore occupancy. My hypothesis that coyotes would negatively impact the occupancy of all three mesopredator species was only partially supported, as coyote presence had a negligible impact on bobcat and domestic cat occupancy. Gray foxes, however, displayed a strong negative association with coyote presence, possibly due to predation and competition pressure. Coyotes are a potential source of antagonistic interactions for gray foxes (Temple et al. 2010, Moll et al. 2018), and coyotes in the western United States have been documented to kill gray foxes at high enough rates to potentially alter fox habitat selection (Fedriani et al. 2000). Interestingly, coyote populations that have expanded into the eastern United States do not always display similar trends—Parsons et al. (2019) found a positive relationship between coyote and gray fox occupancy along urbanization gradients on the East Coast, perhaps because of limited habitat space due to more widespread fragmentation. While fox detections were positively skewed by two sites, potentially causing higher rates of error in the fox-specific occupancy model, there was little observed spatial overlap between gray foxes and coyotes. The two species also displayed inverse trends with mountain lions—foxes were positively associated with mountain lion presence, while coyotes were negatively associated. This may speak more to the exclusion of coyotes from certain sites by mountain lions than the impact of coyotes on gray foxes, as a study in the nearby Santa Cruz mountains found that gray fox occupancy was negatively associated with coyote occupancy specifically in areas where mountain lions were present (Wang et al. 2015). Indeed, mountain lion presence was the top predictor of occupancy for both coyotes and gray foxes in my study, presenting compelling evidence that community dynamics can be greatly influenced by the presence of large carnivores.

I did not find evidence supporting the human-shield effect, in which species at risk of predation or competition from large carnivores seek out smaller, less productive patches near humans that large carnivores typically avoid (Berger 2007, Moll et al. 2018). While gray foxes and coyotes rarely overlapped at study sites, foxes were never detected at urban sites, and they displayed more sensitivity to urbanization than the other three carnivore species. It is notable that foxes are considered the more urban-adapted species in the eastern United States (Parsons et al. 2019), whereas coyotes have shown greater urban adaptation in the west (Fedriani et al. 2001, Gehrt et al. 2011). Coyotes were the only target carnivore detected in all three landscape classes, and the only species other than domestic cat detected in urban areas, so perhaps the ubiquitousness of coyotes in the Salinas Valley helps deter smaller carnivores from urban areas where they may already face human persecution. Although it may be plausible that coyotes, considered an apex predator in this study, are more likely to frequent urban areas to avoid mountain lions in some of the large upland reserves, there was no discernible difference in how coyotes responded to urbanization in models with and without mountain lions.

My hypothesis on the impact of carnivore activity on passerine richness in the Salinas Valley also received mixed support. I predicted that passerine richness would negatively correlate with higher rates of mesopredator activity, but there was no clear trend between bobcat activity and passerine richness. Bobcats are known to predate birds, albeit much less frequently than bobcats predate other mammals (Tewes et al. 2002), and some bobcats in California have exhibited diets that consist almost entirely of lagomorphs and small mammals (Fedriani et al. 2000), so perhaps the large populations of species like ground squirrels in the study area helps insulate birds from bobcat predation. Gray foxes in California have displayed more diverse diets than bobcats (Fedriani et al. 2000) and I documented a predation event from a gray fox on a spotted towhee at one of my study sites, but gray fox activity had no explanatory power for passerine richness and was excluded from the final model. While coyote activity displayed moderate explanatory power, trends between coyote activity rates and passerine richness were unclear, in contrast to previous research in California that found higher avian richness at sites with coyote presence (Crooks and Soulé 1999). As expected, domestic cat activity had a substantial negative impact on passerine richness, showing more explanatory power than all other anthropogenic and carnivore-related metrics. The adverse impact that cats have on avian populations has been well documented (Loss et al. 2013), although other studies have found evidence for a predation paradox in urban areas where both domestic cats and avifauna thrive in high numbers (Shochat 2004, Sims et al. 2009, Fischer et al. 2012, Seress and Liker 2015). Indeed, passerine richness positively correlated with moderate amounts of urbanization in this study. While the model was possibly influenced by two sites with exceptionally high cat detection rates, and thus should be interpreted with caution, models omitting the outlier sites still displayed a strong negative trend between cat activity and passerine richness, although with marginally less predictive power. Sims et al. (2009) noted that the true impact of domestic cats on bird populations may not be realized without studies in areas of both high and low cat density, potentially lending further credence to my observations. A more targeted study on cats and their avifauna prey species in a variety of habitats could provide additional clarity.

Contrary to my prediction, habitat heterogeneity metrics were not strong predictors of passerine richness. While Farwell et al. (2020) found microhabitat-level habitat heterogeneity as an effective predictor of avian richness, that study took place at a much larger spatial scale (the coterminous U.S.) and found that habitat heterogeneity textures had only weak correlations with grassland specialists and negative correlations with shrubland specialists. Given the relatively high abundance of shrubland and grassland cover in the study area, perhaps it is not surprising that habitat heterogeneity had only marginal predictive power. Natural habitat and topographic factors were the leading predictors of passerine richness in the model, similar to results found from similar studies on passerines (Kosicki 2017, Kosicki 2020).

While many of the trends I observed for both carnivores and passerines were expected (e.g., passerine richness increased with increasing tree canopy), microhabitat metrics had less predictive power than the location of each site along the urbanization gradient. Distance to wildland was the top predictor for passerines, bobcats, and domestic cats, and the second-best predictor for coyotes, potentially indicating insufficient connectivity between the large habitat patches at the end of each gradient. Even though the abundance of agriculture in the Salinas Valley could possibly provide more accessible dispersal routes than an area with greater urban landcover, I did not observe evidence of this for most species. Bobcats and domestic cats were rarely detected farther than 1 km from natural habitat patches and urban areas, respectively, and passerine richness also began declining at patches farther than 1 km from large wildland patches. All mammal species were detected at agricultural sites, but only coyotes were detected frequently at both ranch and row crop sites. Mesopredator occurrence was typically limited to only one agricultural land use regime: gray foxes and bobcats were primarily observed at the partially unmanaged ranches closer to natural habitat on the gradient, while domestic cats favored the row crop parcels closer to the urban center. I observed a similar discrepancy in agricultural habitat use by passerines—among all land cover types, I found the highest number of passerine species at ranches and the lowest number in row crops. Despite the seeming importance of agricultural regimes, agricultural metrics were not strong predictors for either carnivores or passerines. There is likely more complexity to wildlife's habitat use of agriculture in the Salinas Valley than captured in this study.

Results from this study should be interpreted with caution. It was difficult to gain access to potential urban and agricultural sites during the COVID-19 pandemic, skewing sites toward natural habitat and often creating uneven gaps between sites on transects. The pandemic also delayed the start of the project, thus shortening its duration. Social distancing protocols prevented participation of field assistants, which also prevented me from checking cameras as frequently as planned. Despite these setbacks, many of the trends observed here are consistent with previous studies, particularly those from nearby locations such as the Santa Cruz mountains (Wang et al. 2015). Those studies generally lack the emphasis on agriculture that I included in this study, however. Given the high agricultural productivity in central California and the rising demand for agricultural products globally, additional studies that specifically address the complexities with which wildlife use agricultural cover will be essential to understanding and maintaining wildlife populations in an increasingly fragmented biosphere.

Appendix I: Literature Cited

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