

ABSTRACT

PARSONS, ARIELLE WALDSTEIN. Assessment of the Effect of Urbanization on Diversity, Population Dynamics and Wildlife Interactions Using Citizen-Science Camera Ancillary Data. (Under the direction of Dr. Roland Kays and Dr. Krishna Pacifici).

Urban areas have been classically seen as areas of low species diversity, low animal abundance, few native predators, and thus low resilience and ecological function. However, some previously extirpated mammals are returning to cities or colonizing them for the first time, leading to the idea that suburban areas may be more diverse than previously thought. Along with this diversity could come alterations to interspecific interactions which can influence distribution, fitness and persistence. Understanding how animals respond to urbanization and how it shapes their interactions is critical to conservation and management in the Anthropocene. Working with citizen scientist volunteers, I used camera traps to survey mammals across two development gradients in two cities in the eastern United States (Washington, DC and Raleigh, NC). Our objectives were to 1) characterize community-level responses to urbanization (i.e., diversity and relative abundance of mammals) 2) determine the population-level response in terms of distribution and the role of interspecific interactions and 3) determine the population-level response to urbanization in terms of abundance and population dynamics. I found that developed areas had significantly higher or statistically similar mammalian occupancy, relative abundance, richness and diversity compared to wild areas. Using a multispecies occupancy model with four competing predator species (coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*) and bobcat (*Lynx rufus*)) I found interspecific interactions to be key mediators of carnivore occupancy in urban areas. I found that coyotes and gray foxes were more likely to use the same forest patches in suburban areas, suggesting positive spatial interaction. However, gray foxes temporally avoided coyotes in suburban areas by becoming more diurnal,

increasing the potential for human-fox interactions. Using an integrated population model, I found that suburban white-tailed deer (*Odocoileus virginianus*) survival and recruitment were negatively related to coyote density at low levels of development but positively related at high levels of development, consistent with deer exploiting suburban and urban areas for concentrated resources and/or as refuges from coyote predation. Overall, I found that diversity, the frequency of interspecific interactions and prey population dynamics can all be higher in suburban areas. However, as species like coyotes adapt more to suburban landscapes, we might expect changes to their response to urbanization and the dynamics between predator, competitors and prey, leading to consequences unforeseen by our analyses. Although some animals can thrive in suburbia, conservation of wild areas and preservation of green space within cities are needed to protect sensitive species and to give all species the chance to adapt and persist in the Anthropocene.

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Assessment of the Effect of Urbanization on Diversity, Population Dynamics and Wildlife
Interactions Using Citizen-Science Camera Ancillary Data

by
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DEDICATION

To my Dad for his love, support and encouragement throughout my life and who, when I said years ago I wasn't going to pursue my PhD said "Yeah, I bet you will". Well Dad, you bet right.

BIOGRAPHY

Arielle was born in Exeter, New Hampshire and grew up in Vermont. She was exposed from a very young age to wildlife and domestic livestock, developing a love for animals and the outdoors. She got her BSc in Zoology from McGill University in Canada where she gained early research experience studying the breeding biology of eastern loggerhead shrikes. After graduating, she joined the Peace Corps and spent two years in Senegal, West Africa working on the development of sustainable community ecotourism activities. When she returned home, she went to North Carolina State University to pursue her MS studying the ecology of a raccoon population on the Outer Banks. She went on to teach in the NCSU Department of Biology and then became manager of the eMammal project at the North Carolina Museum of Natural Sciences, which gave her the opportunity to further develop her analytical and communication skills to ultimately pursue her PhD.

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I had the good fortune to stumble across a wonderful mentor, Dr. Roland Kays, who taught me how to be a better scientist and science communicator and helped me find confidence in my own abilities. I will always be grateful for the opportunities he has given me and will use his mentorship as a model for my own future students. I am further fortunate in that I have a second mentor in Dr. Krishna Pacifici, who has helped me hone my analytical skills and spent hours patiently helping me work through analytical problems, reassuring me I was on the right track or helping me steer back to that track when I fell off it.

I would also like to thank my other committee members: Dr. Brian Reich, who taught me the wonderful world of Bayesian statistics and is always willing to help me think through the best way to accomplish my analytical goals. Dr. David Cobb, who continues to be the grounding voice in my head, providing the invaluable lesson to constantly think about the limitations of data and statistics, especially in the context of applied science.

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Chapter 1: Mammal communities are larger and more diverse in moderately developed areas

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Introduction

Global loss of biodiversity leads to disruption of ecosystem services around the world, ultimately threatening human well-being (Cardinale et al. 2012). Vertebrate species loss is typically considered to be worst in the most developed landscapes, where urbanization serves as an intense and long-term disturbance that permanently alters habitat and truncates food webs (Mckinney 2006; Lombardi et al. 2017a). However, for some species, urbanization can offer abundant nutrient-rich food that is less ephemeral compared to wild areas (Bateman and Fleming 2012; Wang et al. 2017). Whether this food is enough to counteract the negative effects of disturbance (i.e. higher road mortality, fragmentation) depends on a species' ability to adapt to the stressors of urban living (Witte et al. 1982). Mammal species, especially those with large home ranges, are arguably most at risk from development, leading some to suggest that developed areas have a dearth of predators, and that prey species could benefit by using humans as a shield (Crooks 2002; Ordeñana et al. 2010). Historical studies have shown cities to be depauperate of bird life, supporting the traditional view that development and biodiversity cannot coexist (Keast 1995; Strohbach et al. 2014).

However, recent evidence has shown that some mammal species previously thought mal-adapted to urban landscapes (i.e. mountain lion (*Puma concolor*), fisher (*Martes pennanti*)) are

thriving in them (Bateman and Fleming 2012; Lapoint et al. 2013), suggesting an evolutionary trend that could be important for conservation in the Anthropocene. Existing research on mammal communities across urbanization gradients has focused on single cities, yielding conflicting results, perhaps due to variation in city structure and characteristics (Saito and Koike 2013; Lombardi et al. 2017a). Given the rapid expansion of urban areas worldwide, and the recent case studies of urban adaptations by wildlife (Lapoint et al. 2013; Riley et al. 2014; Wang et al. 2017), more large scale studies are needed to evaluate the response of wildlife communities to urban development if we are to understand urban ecology, conservation, and evolution in the Anthropocene.

Here we present the results of a large-scale mammal survey of two urban-wild gradients. Our objectives were to determine how diversity, richness, detection rate, and occupancy of the mammal community change as a function of human disturbance. We hypothesized that the availability of supplemental food at higher levels of development would positively affect mammalian populations and outweigh the negative effects of disturbance, except for the most sensitive species. Specifically, we predicted that mammalian relative abundance would increase with developmental level but that species richness and diversity would decrease. Furthermore, we predicted that occupancy of the most sensitive species (i.e. large and medium carnivores) would be highest in wild areas both in our study area and around the world.

Materials and Methods

Study sites. Washington, District of Columbia, USA (hereafter DC) is a city of approximately 177 km² with an estimated human population size of 681,000, thus a density of 3,847 people/km². Our study spanned a 56,023.7 km² area around the city with a mean of 4.4

houses/km² and matrix of agriculture (~21.3%) and forest (~54.1%). Raleigh, North Carolina, USA (hereafter Raleigh) is approximately 375 km² with an estimated human population size of 459,000, thus a density of 1,278 people/km². Our study spanned a 66,640 km² area around the city with a mean of 17.7 houses/km² and matrix of agriculture (~24.3%) and forest (~52.3%).

Citizen science camera trap surveys. From 2012-2016, 557 trained volunteers deployed 1427 unbaited camera traps across an urban-wild gradient around Raleigh and DC. Each individual camera was considered a “camera site” and volunteers ran cameras at an average of 2 sites each. Following Hammer et al. (2004), we used the Silvis housing density dataset with 1km grid cells to define five development levels of the gradient for sampling stratification (excluding open water): urban (>1000 houses/km²), suburban (147.048-1000 houses/km²), exurban (12.64-147.047 houses/km²), rural (0.51-12.63 houses/km²) and wild (<0.5 houses/km²). Within those gradient levels, camera placement was also stratified between residential yards, open areas (>0.001 km² absent of trees), small forest fragments (≤1 km²) and large forest fragments (>1 km²) (Table A1). Forest fragment size was verified using the 2006 US National Landcover Dataset (NLCD) and Landscape Fragmentation Tool v2.0 (Vogt et al. 2007) in ArcMap (Version 10.1, ESRI, Redlands, CA, USA) which defines forest fragments by size. Yards were not available for sampling in the urban or wild levels of the gradient. Urban areas were not sampled in Raleigh and open areas were not sampled in DC. All adjacent cameras were spaced at least 200 m apart. Camera placement was randomized as much as possible using ArcMap (Version 10.1) to randomly generate points within polygons while following certain rules. For example, we selected sites within forests that volunteers were permitted to access and were within a reasonable hiking distance (i.e. < 11 km hike round trip) with terrain that was not too steep to

traverse safely (i.e. <45 degree slope). Within yards, cameras were placed as randomly as possible while avoiding the highest human traffic areas (i.e. walkways, doors, gates and driveways).

No explicit power analysis was used to predetermine sample size. Our sample size goal was 20 spatial replicates (equating to ~420 trap nights), which has been found to maximize precision for estimating detection rate (Rowcliffe et al. 2008; Kays et al. 2010b). Camera sites are biological replicates, parallel measurements capturing random biological variation. This study did not include technical replicates.

Volunteers used Reconyx (RC55, PC800, and PC900, Reconyx, Inc. Holmen, WI) and Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS) camera traps attached to trees at 40cm above the ground. Cameras were deployed for three weeks and then moved to a new location without returning, with sampling taking place continuously throughout the year. Cameras recorded multiple photographs per trigger, at a rate of 1 frame/s, re-triggering immediately if the animal was still in view. We grouped consecutive photos into on sequence if they were <60 seconds apart, and used these sequences as independent records, counting animals in the sequence, not individual photos (Parsons et al. 2016). We then collapsed these independent records into daily detection/non-detection for occupancy modeling. Initial species identifications were made by volunteers using customized software (available freely from eMammal.org, source code proprietary) and all were subsequently reviewed for accuracy before being archived at the Smithsonian Digital Repository (Mcshea et al. 2016).

Diversity. We used package iNEXT (Hsieh et al. 2016) in R (Version 3.1.0; R Development Core Team 2008) via R Studio (Rstudio Team 2015) to calculate Hill numbers (i.e. the effective

number of species, incorporating relative abundance and richness) of species richness and Shannon diversity (Chao et al. 2014) between gradient levels (urban-suburban-exurban-rural-wild) and plot types (yard, open, small forest, large forest). iNEXT calculates the Shannon diversity as Hill number $q = 1$, equal to the exponential of Shannon's entropy index, thus the natural log of those results was used for display purposes. We used detection/non-detection data to compute diversity estimates and the associated 95% confidence intervals via rarefaction, plotting the diversity estimates while accounting for sample size. We fit a curve to diversity estimates between gradient levels using a generalized additive model with a polynomial term.

Model covariates. We modeled variation in occupancy (ψ) and detection rate using 13 covariates (Table A2) representing development level, the amount of core forest, small scale forest cover, prey relative abundance and whether hunting was allowed. We added year as a covariate to account for population changes over time. We used the Landscape Fragmentation Tool v2.0 (Vogt et al. 2007) and the NLCD (2006) land use dataset in ArcMap (Version 10.1) to create a landcover layer representing the percent of large core forest (forest patches larger than 1km^2) in a 5km radius around camera locations which we considered best approximated the home range size of our target species (Bekoff 1977; Fritzell and Haroldson 1982; Larivière and Pasitschniak-Arts 1996; Larivière and Walton 1997). Forest patches did not necessarily fall entirely within the buffer. We considered road density as an additional covariate at the 5 km scale but initial evaluations showed it to be highly correlated with housing density (87.1%) so we chose to eliminate it from the analysis. We used a 100 m radius for small scale forest cover to best represent small forest patches within suburban neighborhoods (e.g. small vacant lots with trees, greenways). We represented deer and rodent+lagomorph relative abundance using site-specific

detection rate (the number of detections divided by the total number of camera-nights). We included an indicator (0/1, no hunting/hunting) to categorize whether a site allowed hunting or not. We modeled detection probability (p) using five covariates (Table A2). Because both ambient temperature and undergrowth can affect the camera's ability to detect an animal, we included daily covariates for temperature and NDVI (Moderate Resolution Imaging Land Terra Vegetation Indices 1 km monthly, an average value over the month(s) the camera ran) obtained from Env-DATA (Dodge et al. 2013). To complement NDVI, we also considered site-specific detection distance, a measure of how far away the camera was able to detect a human, which is influenced by both understory and site topography. We included an indicator (0/1, not yard/yard) to categorize whether a site was a residential yard or not. In Raleigh, two different camera models were used (both Reconyx and Bushnell) so we added a 0/1 (Bushnell/Reconyx) covariate to account for potential difference in detection probability between the two brands. We diagnosed univariate correlations between covariates using a Pearson correlation matrix, and used a restrictive prior for beta coefficients for beta coefficients where correlation was >0.60 (i.e. $\text{logistic}(0,1)$; a prior with reduced variance to induce shrinkage, similar to ridge regression; Hooten and Hobbs 2015). All covariates were mean-centered.

Detection rate models. We used a Poisson count model (e.g. Kays et al. 2016) to assess differences in total mammal detection rate (i.e. the intensity with which a site was used, count/day) between the five gradient levels (urban, suburban, exurban, rural, wild) and four plot types (large forest, small forest, open, yard). We fit a curve to total detection rate estimates between gradient levels using a generalized additive model. No other covariates were used in this model. We then ran separate count models for four predator species (coyote (*Canis latrans*),

gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*) and bobcat (*Lynx rufus*)) to evaluate covariates of detection rate, running one fully-parameterized model (Table A2) to evaluate which explained the most variation in detection rate. We assessed model fit with posterior predictive checks (PPC) (Kery and Schaub 2012; Gelman et al. 2014) by calculating the sum of squared Pearson residuals from observed data ($T(y)$) and from data simulated assuming the fully parameterized model was the data-generating model ($T(y_{sim})$). We calculated a Bayesian p -value as $p_B = \Pr(T(y_{sim}) > T(y))$ from posterior simulations and assumed adequate fit if $0.1 < p_B < 0.9$ (Table A3). We fit the detection rate model in OpenBUGS v3.2.3 (Lunn et al. 2009) via R2OpenBUGS v3.2 (Sturtz et al. 2005) in R (Version 3.1.0) via R Studio. We based inference on posterior samples generated from three Markov chains, using trace plots to determine an adequate burn-in phase. All models achieved adequate convergence ($\hat{R} \leq 1.1$) (Gelman et al. 2014) by running for 50,000 iterations following a burn-in phase of 1000 iterations, thinning every 10 iterations. We based significance on whether parameter 95% credible intervals overlapped zero.

Occupancy models. We used the multispecies occupancy model of Rota et al. (2016) to estimate the probability of occupancy of four predator species: bobcat, coyote, red fox and gray fox. Although we are using the term occupancy, because data were collected from camera traps estimates are more analogous to “use” than true occupancy (Burton et al. 2015). This model is distinct from the classic multispecies community models (Dorazio and Royle 2005; Gelfand et al. 2005; Dorazio et al. 2006) and is rather a generalization of the single-season occupancy model (Mackenzie et al. 2002) to accommodate two or more interacting species. It contains single-species (first order) occupancy models for each interacting species alone as well as

pairwise (second order) models for the co-occurrence of each pair of species (Rota et al. 2016). For each species and pairwise interaction, the model estimates detection probability (p), defined as the probability of detecting an occurring species at a camera site, and occupancy (ψ), defined as the probability that a given camera site is occupied, for each species. The latent occupancy state of each species at a site is modeled as a multivariate Bernoulli random variable such that (assuming 2 interacting species):

$$Z \sim MVB(\psi_{11}, \psi_{10}, \psi_{01}, \psi_{00})$$

Where ψ_{11} is the probability that both species occupy a site, ψ_{10} is the probability that only species 1 occupies a site, ψ_{01} is the probability that only species 2 occupies a site and ψ_{00} is the probability that neither species occupies a site. We assumed all species occurred independently and considered the same set of five covariates for the detection probability models and 13 covariates in the occupancy model of each species (Table A2). We considered interactions (i.e. city*covariate) between each occupancy covariate and city (0/1, DC/Raleigh). We estimated occupancy for each species across levels of the development gradient (urban, suburban, exurban, rural, wild) and plot types (yard, open, small forest, large forest) within each city separately by including development level and plot type as categorical covariates in our model.

We fit models in STAN (Version 2.15.1; Stan Development Team 2015b) via the RSTAN (Version 2.15.1; Stan Development Team 2015a) interface in R (Version 3.4.0) via R Studio (Version 1.0.143). We based inference on posterior samples generated from two Markov chains, using trace plots to determine an adequate burn-in phase and subsequently running chains they reached adequate convergence ($\hat{R} > 1.1$) (Gelman et al. 2014). All models achieved adequate

convergence by running for 3000 iterations following a burn-in phase of 1000 iterations. We based predictor significance on whether beta coefficient 95% credible intervals overlapped zero. We assessed model fit with posterior predictive checks (PPC) (Kery and Schaub 2012; Gelman et al. 2014) by calculating the sum of squared Pearson residuals from observed data ($T(y)$) and from data simulated assuming the fully parameterized model was the data-generating model ($T(y_{sim})$). We calculated a Bayesian p -value as $p_B = \Pr(T(y_{sim}) > T(y))$ from posterior simulations and assumed adequate fit if $0.1 < p_B < 0.9$. To our knowledge, the squared Pearson's residual has not been derived in the context of occupancy models, so we present our derivation of this test statistic in Appendix B. We added a random effect on detection/non-detection for the coyote portion of the model since initial assessments of fit for this species were inadequate (i.e. $p_B > 0.9$). We assessed differences in occupancy between gradient levels for each species using overlapping 95% confidence intervals.

Comparison with global occupancy data. We removed omnivores from the dataset of Rich et al. (2017) to better compare with carnivore occupancy from our own dataset. Where species occupancy was estimated from multiple studies in the Rich et al. dataset, we calculated averages to compare to occupancy estimates from our own study. We summarized occupancy estimates of Rich et al. and our own study within each developmental level using a box and whisker plot and assessed statistically significant differences based on whether or not interquartile ranges overlapped.

Data accessibility. Raw detections data have been deposited in Data Dryad, doi:10.5061/dryad.11rf64v. The software used for initial species identifications is available via

eMammal.org. To download and use the software, users must first create an account on eMammal and become associated with an existing project. This can be done by using the 'Join' button on the project's homepage, or by emailing the contact person, also listed on the project homepage. Usually the user will also have to pass an online or in person training, depending on the project requirements, and they will then become approved to download the software.

Results and Discussion

Working with citizen scientist volunteers, we obtained 53,273 detections of 19 mammal species at 1427 sites along an urban-wild gradient in Washington, DC and Raleigh, NC, USA, sampling both private and public lands. In DC, we detected 17 mammal species with mean naïve occupancy of 0.19 (min=0, max=0.93) and mean detection rate of 0.09 detections/day (min=0, max=1.05). In Raleigh, we detected 17 mammal species with mean naïve occupancy of 0.14 (min=0, max=0.79) and mean detection rate of 0.08 detections/day (min=0, max=0.09).

We found no significant decline of species diversity or richness from suburban to wild gradient levels (Figure A1, Figure 2). However, Shannon diversity was significantly lower at the urban level in DC, possibly due to low sampling (Figure 1, Table A1). Diversity in yards was significantly higher or not statistically different from large and small forest fragments in both cities (Figures A2, A3). Most (92.3%) of the 13 mammal species detected >20 times occupied all levels of development below the urban level. Two of the largest predators, coyotes and bobcats, were absent from the highest development level (urban) but were detected at all other levels in both cities. Black bears (*Ursus americanus*), which are actively discouraged from colonizing central North Carolina (North Carolina Wildlife Resources Commission 2011), were not detected in Raleigh and only detected in the DC at the wild level of the gradient. These results indicate

that the extant mammal guild exploits all levels of the urban-wild gradient and that no species are entirely relegated to the wild gradient level. However, some species appear less adapted to habitation in human-dominated areas, spending most of their time at the wild levels of the gradient (i.e. bobcat, bear; Figure 2). We recognize that the current community represents species that survived the initial arrival of high-density human settlement. In particular, two large predators (wolves (*Canis lupus*) and cougars (*Puma concolor*)) were extirpated from our study area a century ago. However, even cougars and wolves have recently shown surprising adaptability in the face of development at other sites (Bateman and Fleming 2012; Wang et al. 2017) suggesting that, given enough time and protection from persecution, many of the most “wild” of species may adapt to human development.

Predators are thought to be the most at risk from urbanization (Crooks 2002), therefore we evaluated predictors for occupancy (Mackenzie et al. 2002) and detection rate (Kays et al. 2016) for four carnivores: coyote, gray fox, red fox, and bobcat. Both of our models fit well, with Bayesian p-values between 0.1 and 0.9 (Table A3). Suburban and urban occupancy probabilities were not statistically different from wild for any of the species (Figure A4) and we noted a decreasing trend in occupancy from urban to wild (Figure 3). We compared the occupancy estimates from our study to those reported for carnivores in protected areas around the world (Rich et al. 2017) and found no significant difference (Figure 3), suggesting that the ecological function of predators in this urban system is not substantially reduced from the current wild state, excepting the historical extirpation of the two largest native predators from the region.

Our occupancy and detection rate models yielded similar results (Tables A4- A6) demonstrating that green space is important to carnivore species that are less-adapted to human-altered landscapes. These models show a greater association of carnivores with green space when

housing density is high (e.g. coyote and gray fox, Tables A4, A5), consistent with other studies finding urban green space important in maintaining biodiversity in cities (Gallo et al. 2017; Lombardi et al. 2017a; Matthies et al. 2017). It is likely that shy species are not avoiding regions of high human density, but require patches of forest to navigate residential areas that are freely used by more commensal species, such as red foxes (Tigas et al. 2002), which we frequently detected in yards. Indeed, we found a gradient of responses in carnivore use of human-dominated environments, from red fox which are the most urban adapted (i.e. negatively associated with local large forest fragments and the only species to have a positive association with yards) to bobcats which appear to be the most human-averse (i.e. they had the lowest occupancy values of any carnivore at the suburban level) (Figures 2, A4).

Contrary to expectations, we found no evidence for a negative impact of suburban and exurban development on extant native mammal diversity, richness, and occupancy and detection rate of carnivores. In fact, all metrics were significantly greater than, or equal to, wild areas. We suspect that developed areas offer good food resources for wildlife through direct and indirect feeding (i.e. bird feeders supplementing prey, pets), accidental feeding (i.e. garbage), and ornamental plantings (for herbivores), but testing this hypothesis will require additional diet studies in urban landscapes (Contesse et al. 2005). Furthermore, the structure of mature suburbia (i.e. older, established neighborhoods with large trees, wooded riparian areas, small parks) contributes to a more diverse and varied landscape than wild areas with more homogenous forest cover, which is potentially beneficial for many generalist species. Developed areas where hunting is limited or prohibited also offer a safe haven for game species, presuming they can navigate the road networks (Collins and Kays 2011) and avoid direct human conflict.

Our discovery of a wild suburbia suggests high levels of adaptation by mammals to developed landscapes over the last few decades, including predators and prey. The resilience of these species gives hope for wildlife in the Anthropocene, but the generality of this pattern needs to be tested in other cities to understand how habitat type, development patterns, apex predators, and hunting regulations influence urban mammal communities, as there are examples of far more drastic impacts of urbanization on other taxa and in other places around the globe (Keast 1995; Mckinney 2008). Indeed, in Tokyo, Japan, the relative abundance of mammals declined with urbanization (Saito and Koike 2013) and avian communities in Quebec, Canada and Rennes, France showed a similar decline in richness (Clergeau et al. 1998; Saito and Koike 2013). This suggests that city structure, size and human density may influence mammalian distribution along urban-wild gradients with large, sprawling New World cities showing different patterns than the smaller more concentrated cities of the Old World. Although our study provides a less dire picture of urban ecosystem function than previously thought, we do not suggest abandoning mitigation of urbanization's negative impacts, or conservation of completely wild areas. Factors such as urban green space, connectivity and availability of completely wild areas give species the time and space to adapt to changing habitats and climates. Further understanding of how urban wildlife navigates human-dominated areas and factors that contribute to the adaptation of species to the Anthropocene will be critical to maintaining diversity in a rapidly urbanizing world.

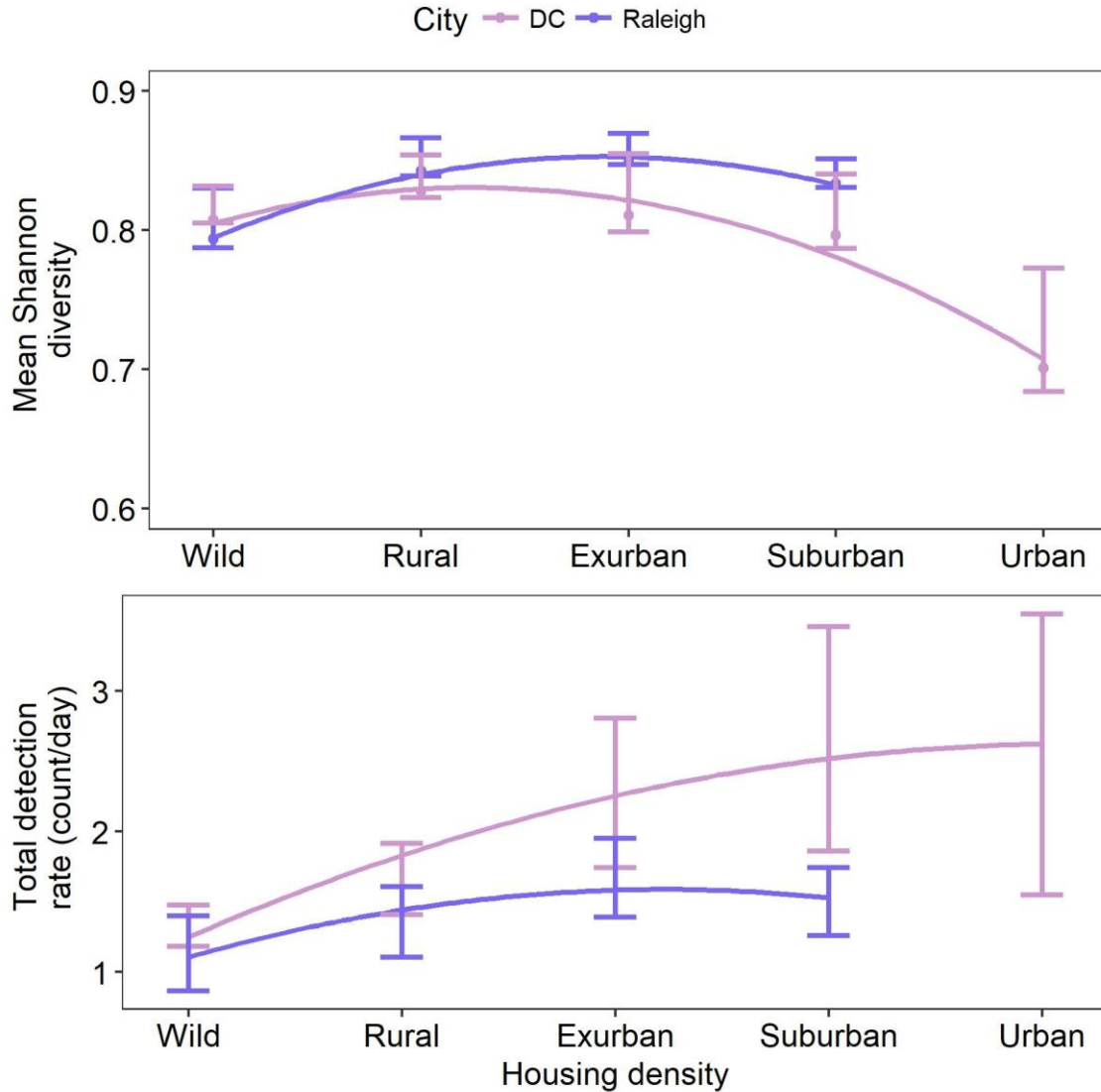


Figure 1: Mean Shannon diversity and total detection rate along a gradient of housing density in two cities, Washington, DC and Raleigh, NC USA taken from camera traps. Bars show 95% confidence intervals, lines are fit using a generalized additive model with a polynomial term. Diversity peaked at intermediate levels of urbanization (exurban in DC and suburban in Raleigh). Total detection rate peaked at the urban level in DC and exurban level in Raleigh.

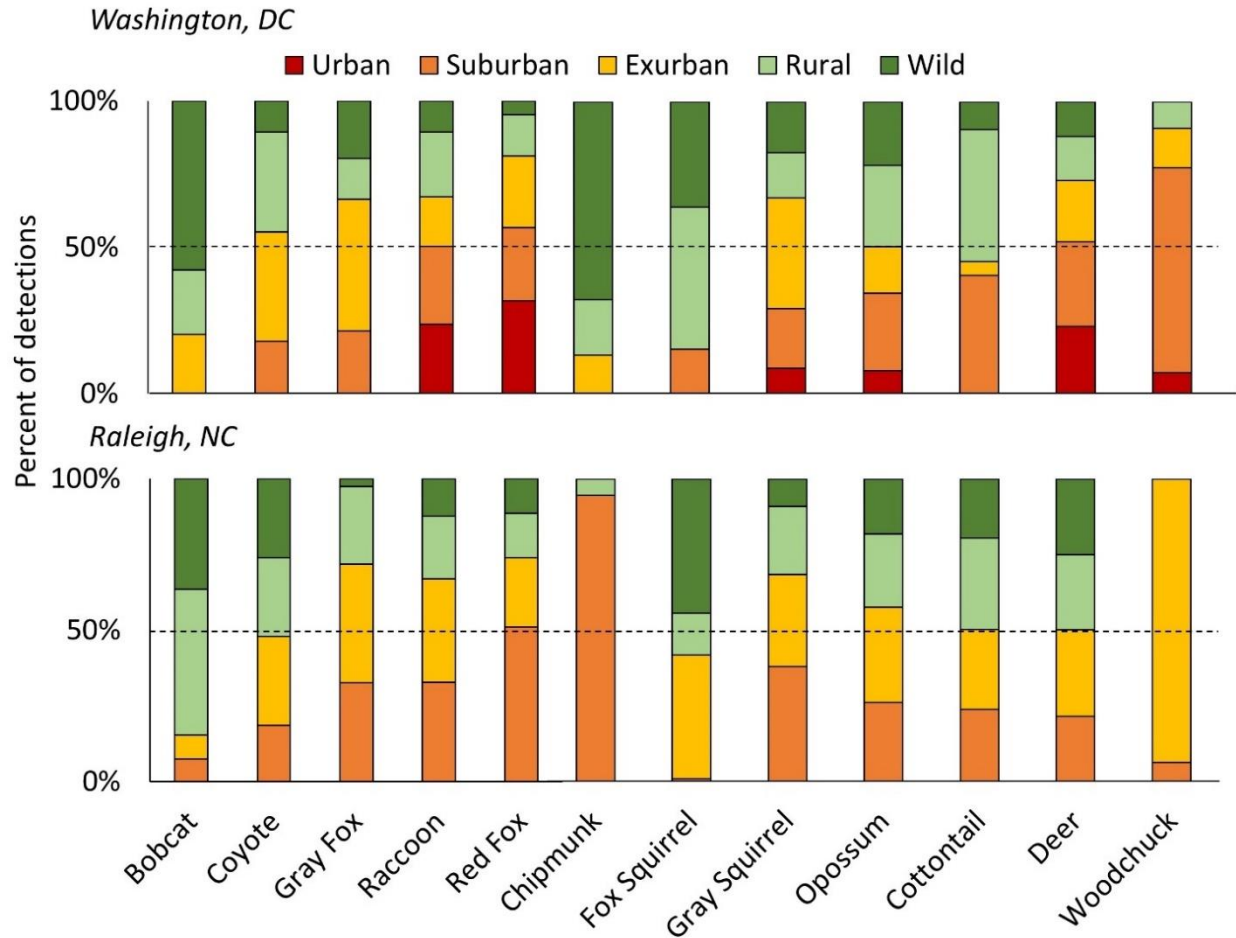


Figure 2: The percent of detections for each species of carnivores (left) and herbivores (right) in each development level along the urban-wild gradient in Washington, DC and Raleigh, NC, USA accounting for the effort (i.e. camera nights) within each level, sorted from lowest to highest proportion urban/suburban in DC. The dashed line shows 50% of total detections. Some species were predominantly rural/wild (i.e. bobcats and fox squirrels) while others were mainly detected in urban/suburban habitats (i.e. red fox, raccoon). Patchy distributions at different gradient levels were seen for species at the edge of their ranges (i.e. chipmunks and woodchucks in Raleigh). Urban habitats were not sampled in Raleigh.

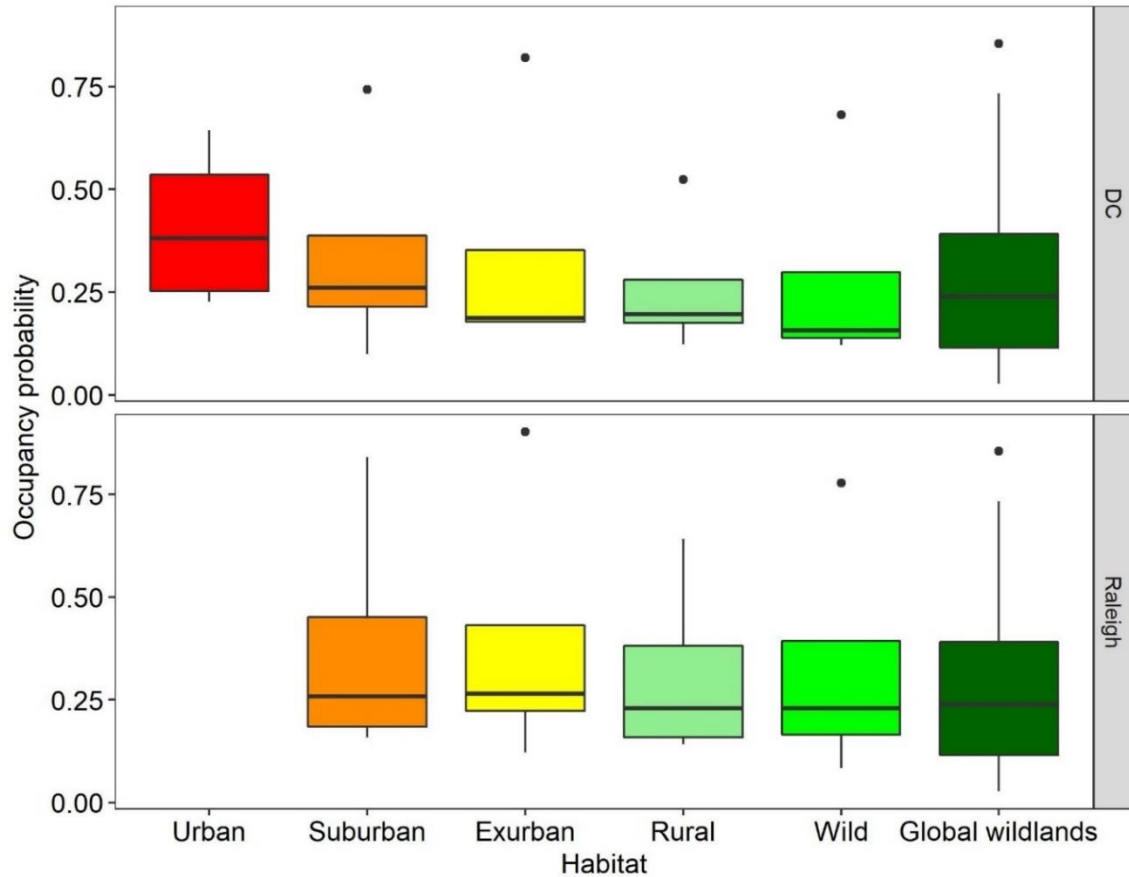


Figure 3: Comparison of carnivore (i.e. bobcat, coyote, gray fox, red fox) occupancy probabilities at each developmental level in two cities with global values from Rich et al. (Rich et al. 2017), representing 93 carnivores from 13 protected areas on five continents (Global Wildlands). Each box for our dataset represents the distribution of marginal occupancy probabilities for each of four carnivore species in that city (i.e. four probabilities). The boxes for Global Wildlands represent the distribution of marginal occupancy probabilities for 93 species. We found no statistically significant differences between any habitat levels in our study or between our study and global wildland occupancy probabilities but noted a decreasing trend in occupancy from urban-wild. We included only predators from Rich et al. 2017 and removed omnivores (i.e. raccoon, coati) to better reflect our data.

Chapter 2: Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions

Parsons, A.W., Rota, C.T., Forrester, T., Baker-Whatton, M.C., McShea, W.J., Schuttler, S.G., Millspaugh, J.J. and Kays, R., 2019. Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, 56(8), pp.1894-1904.

Introduction

Interspecific interactions such as predation, competition, parasitism and mutualism are thought to play critical roles in structuring biotic communities. Antagonistic interspecific interactions can provoke temporal and spatial avoidance, leading to patch exclusion and reduced carrying capacity and population growth rates (Linnell and Strand 2000), with cascading effects on population densities (e.g., Henke and Bryant 1999) and spatial distribution patterns (e.g., Hersteinsson and Macdonald 1992). The ability of species to coexist in the presence of interspecific interactions ultimately contributes to biodiversity and ecosystem stability, where changes to interspecific interactions (i.e., population decline or extirpation of one species) would be expected to have destabilizing consequences such as trophic cascades and local extinctions (Ricklefs 1987).

Competition and predation are interactions common among carnivore species (Palomares and Caro 1999) and thought to play a pivotal role in the structuring and spatial distribution of carnivore communities (Caro and Stoner 2003; Carter et al. 2015; Swanson et al. 2016).

Dominant carnivores are predicted to be distributed according to food availability, while subordinate species select habitats based on both food and safety from dominant carnivore harassment or predation (Heithaus 2001). Avoidance of dominant carnivores may force

subordinate species to use lower quality sites with fewer prey, resulting in lower densities (e.g., Durant 1998). Dominant carnivores can also mediate interactions between competing smaller carnivores by consuming the better competitor, increasing the prey base and enhancing coexistence when present (e.g., St-Pierre et al. 2006), and increasing competition when absent. Despite evidence that interspecific interactions are present among carnivores, their relative importance compared to other ecological factors, and impacts on the broader community, are poorly understood (Gompper et al. 2016).

Changes to carnivore distribution in response to human activity has been of particular interest over the last 20 years (e.g., Randa and Yunger 2006; Lewis et al. 2015b). The dramatic reductions and fragmentation of wildlife habitat associated with human development are thought to be especially problematic for large and wide-ranging carnivores (Muhly et al. 2011), resulting in fewer large carnivores in the most highly developed areas (Bateman and Fleming 2012) and potentially cascading ecological effects. Under this traditional view of carnivore decline in developed areas, we would expect a reduction of competitive interactions between carnivores due to low density and increased prey base (Périquet et al. 2015). However, reductions in populations of large predators in developed areas could actually lead to increases in smaller predator populations (i.e., mesopredator release), resulting in the decline of smaller prey (Crooks and Soulé 1999) and more intense competition between smaller carnivores over increasingly scarce food. When food resources are clumped, as would be expected in urban areas, competition between urban-adapted species can further increase (Macdonald and Johnson 2015). Indeed, prey species in urban areas might be able to use humans as shields, concentrating their activities in the most human-dominated areas to be exploited only by the most urban-adapted predator species (Berger 2007). However, recent evidence has shown that many carnivore species are more

adaptable than previously thought, with some able to thrive in developed areas, presumably habituating to the disturbance of human activity and exploiting anthropogenic food subsidies (Wang et al. 2015), including domestic species (Athreya et al. 2016). The relative ability of some species to exploit human-dominated areas may shift the dynamics between predator species to new competitive advantages based on boldness and adaptation to human disturbance, rather than direct competitive advantage (Geffroy et al. 2015).

Following the historic extirpation of cougars and wolves, extant carnivore communities in the eastern USA have shown little decline in relative abundance or diversity even in the most urban areas (Parsons et al. 2018a), and formerly rare predators are recolonizing suburbia (e.g., fisher *Pekania pennanti* (Lapoint et al. 2015) and mountain lions *Puma concolor* (Bateman and Fleming 2012)). Coyotes (*Canis latrans*) have expanded their geographic range, and are now moving into some of the most populated cities in the US (Weckel et al. 2015; Hody and Kays 2017). Given their use of highly urban areas in their traditional range (Gehrt et al. 2011b), we expect coyotes to become more common in developed areas in the east. Western coyotes impact smaller predators (Fedriani et al. 2000), suggesting that their arrival in eastern cities could have similar cascading effects on resident urban foxes. These dynamic carnivore populations offer an ideal setting to evaluate the impact of human disturbance on species interactions by comparing predator communities along gradients of urbanization.

We used camera traps deployed by citizen-scientists in two cities (Washington, DC and Raleigh, NC) in the mid-Atlantic United States to investigate whether species interactions influence the site occupancy of carnivore species along an urbanization gradient. By sampling not only forested areas, but also residential yards, our study offers a more complete perspective on how animals use developed lands. We tested four hypotheses representing factors that could

influence predator occupancy along the urbanization gradient: forest fragmentation, human influence, prey availability, and interactions between carnivores. We used a multispecies occupancy model with four competing predator species (coyote, bobcat (*Lynx rufus*), grey fox (*Urocyon cinereoargenteus*) and red fox (*Vulpes vulpes*)) to test which hypothesis best explained species occupancy. We predicted that accounting for interspecific interactions would be an important factor in modelling occupancy for all species. If smaller competitors (i.e., grey and red fox) are using humans as shields, we predicted a positive relationship with housing density and less interaction with larger competitors (i.e., coyotes) at higher levels of urbanization. If the clumped distribution of food resources in urban areas is increasing interspecific competition, we predicted that species interactions would be positively mediated by urbanization.

Materials and methods

Study sites – We chose two study sites in the mid-Atlantic United States which varied in size, sprawl and human density. Washington, District of Columbia (hereafter DC) is a city of approximately 177km² with an estimated population size of 681,000, thus 3,847 people/km². Our study spanned a 56,023km² area around the city where surrounding land use was a combination of agriculture (~21%) and forest (~54%) with a mean of 4.4 houses/km². Raleigh, North Carolina (hereafter Raleigh) is approximately 375km² with an estimated population size of 459,000, thus 1,278 people/km². Our study spanned a 66,640km² area around the city where surrounding land use was a combination of agriculture (~24%) and forest (~52%) with a mean of 17.7 houses/km². Forest fragmentation, measured as an index of non-forest to forest pixels (Riitters et al. 2000) within a 100km radius around the city centre, was higher in DC (1.39) than Raleigh (0.94).

Citizen science camera trap surveys – From 2012-2016 (Table C1), 557 trained volunteers (see Parsons et al. 2018c for details) deployed 1,260 unbaited camera traps across urbanization gradients around Raleigh and DC (Figure 4). We used the Silvis housing density dataset (Hammer et al. 2004) and bin levels of Theobald (2005) to define the four levels of the gradient for sampling stratification (excluding open water): suburban (147.05-1000 houses/km²), exurban (12.64-147.06 houses/km²), rural (0.51-12.63 houses/km²) and wild (<0.5 houses/km²). Within gradient levels, camera placement was stratified between residential yards, small forest fragments ($\leq 1\text{km}^2$), and large forest fragments ($>1\text{km}^2$) (Table C2). All adjacent cameras were spaced at least 200m apart. Volunteers used Reconyx (RC55, PC800, and PC900, Reconyx, Inc. Holmen, WI) and Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS) camera traps attached to trees at approximately 40cm above the ground. Trigger sensitivity was set to high for all cameras and we verified that both brands of camera had similar trigger speeds (<0.5s) and randomized placement of the different models to avoid bias due to camera type. Cameras were deployed for three weeks and then moved to a new location. Cameras recorded multiple photographs per trigger, at a rate of 1 frame/s, re-triggering immediately if the animal was still in view. We grouped consecutive photos into sequences if they were <60 seconds apart, counting animals in the sequence, not individual photos, and used these sequences as independent records (see Kays et al. 2016). We collapsed independent records into daily detection/non-detection for occupancy modelling. Initial species identifications were made by volunteers using customized software (eMammal.org) and all were subsequently reviewed for accuracy before being archived at the Smithsonian Digital Repository (as previously described in Mcshea et al. 2016).

Model Covariates – We modelled variation in occupancy using 12 covariates (Table C3) that addressed our hypotheses: housing density and 0/1 indicators of whether a site was hunted, a residential yard and/or had a dog present during the study (humans hypothesis), the amount of forest at the local camera level and at a larger scale around the site (forest fragmentation hypothesis) and prey relative abundance (prey hypothesis). We used the percent tree cover (percent of each 30x30m pixel covered by trees; Hansen et al. 2013) at two scales, a local scale to represent forest cover at the camera site (100m radius around each pixel) and a larger scale (5km radius) to best approximate the home range size of all of our target species (Bekoff 1977; Fritzell and Haroldson 1982; Larivière and Pasitschniak-Arts 1996; Larivière and Walton 1997). We used the Silvis housing density dataset (Hammer et al. 2004) averaged over a 5km radius to represent urban development. We represented prey availability as deer, rodent, and lagomorph relative abundance using site-specific detection rate (detections/day). Because we counted individuals at the sequence level and not in individual photos, we were able to avoid counting high numbers of the same individual(s) within a short period of time (e.g., while foraging in front of the camera). While this measure does not necessarily reflect true prey abundance at a site, it is a proxy for how frequently a site is used by a given prey species and thus relevant to how often a predator may use the same site in response. We added year as a covariate to account for changes in site occupancy over time.

We modelled detection probability (p) using five covariates (Table C3). Because both ambient temperature and undergrowth can affect the camera's ability to detect an animal, we included daily covariates for temperature and NDVI (Moderate Resolution Imaging Land Terra Vegetation Indices 1km monthly) obtained from Env-DATA (Dodge et al. 2013). We also considered site-specific detection distance, a measure of how far away the camera was able to

detect a human, and whether or not a site was a residential yard. In Raleigh, two different camera models were used (Reconyx and Bushnell) so we added a 0/1 covariate to account for potential differences in detection probability between the two brands. We diagnosed univariate correlations using a Pearson correlation matrix, and used a restrictive prior for beta coefficients (Hooten and Hobbs 2015) where correlation was >0.60 . All covariates were mean-centred.

Occupancy Models – We used the multispecies occupancy model of Rota et al. (2016) to assess species interactions of bobcat, coyotes, grey fox and red fox, while accounting for imperfect detection. Although we are using the term occupancy, because data were collected from camera traps, estimates are more analogous to “use” than true occupancy (Burton et al. 2015). This model is a generalization of the single-season occupancy model (Mackenzie et al. 2002) to accommodate two or more interacting species. For each species and pairwise interaction, the model estimates detection probability (p), defined as the probability of detecting an occurring species at a camera site, and ψ which defines the probability of each combination of latent presence/absence. ψ is a function of $(2^S - 1)$ “natural parameters” which can all be modelled as linear functions of covariates and describes the probability a site is occupied by only one species (first order); only two species (second order), and so on up to order S , the number of interacting species (Rota et al. 2016). Species occurrence is assumed independent if all second order and higher natural parameters are fixed at 0, whereas dependence between species can be modelled by estimating parameters associated with second order and higher natural parameters. When second order and higher natural parameters are present, slope coefficients associated with first order natural parameters can be interpreted as log odds ratios of occupancy probabilities (i.e., the

log of the probability a species occupies a site divided by the probability it does not) resulting from a one-unit change in a relevant covariate (Rota et al. 2016).

We calculated absolute log odds ratios to quantify the importance of environmental variables relative to interspecific interactions in influencing the probability of occurrence of each species. Following Rota et al. 2016, we calculated OR_{sp} and OR_h . OR_{sp} is the odds ratio of the predicted probability of occupancy of each species conditional on the presence and absence of each of the other species when covariate (h) (and all other covariates) is held at a baseline level (x):

$$OR_{sp} = \frac{odds(z_1 = 1|z_2 = 1|z_3 = 1|z_4 = 1, h = x)}{odds(z_1 = 1|z_2 = 0|z_3 = 0|z_4 = 0, h = x)}$$

OR_h is the odds ratio of predicted probability of occupancy of each species conditional on the absence of all other species associated with a change in covariate h of x units (Δh) while all other covariates were held at a baseline level:

$$OR_h = \frac{odds(z_1 = 1|z_2 = 0|z_3 = 0|z_4 = 0, h = x + \Delta x)}{odds(z_1 = 1|z_2 = 0|z_3 = 0|z_4 = 0, h = x)}$$

We calculated OR_h for three covariates: housing density, forest at the larger scale and local forest. Since covariates were scaled and centred, we set $\Delta h = 0.5$ units for each.

We fit a set of 25 candidate models that allowed us to test our hypotheses regarding the relative importance of interspecific interactions, forest fragmentation, prey and humans on the

occupancy of each species along the urbanization gradient (Table C4). We considered the same set of five covariates for the detection probability models of each species (Table C3) and chose occupancy covariates to reflect the different hypotheses we were interested in testing (see Table C4). We considered interactions between each occupancy covariate and city. We compared our candidate models with Watanabe–Akaike Information Criterion (WAIC), a fully Bayesian information-criterion which works particularly well with hierarchical models where other model-selection strategies (i.e., DIC, BIC) may not (Gelman et al. 2014; Hooten & Hobbs 2015). We considered the top model to be the one with the lowest WAIC. We fit models in STAN (Version 2.15.1, Stan Development Team 2015b) via the RSTAN (Version 2.15.1, Stan Development Team 2015a) interface in R (Version 3.4.0, R Development Core Team 2008) via R Studio (Version 1.0.143, Rstudio Team 2015). We ran 2 chains for each model, using trace plots to determine an adequate burn-in phase and subsequently running chains until the Brooks–Gelman–Rubin convergence diagnostic indicated adequate convergence ($R\text{-hat} < 1.1$; Gelman et al. 2014). All models achieved adequate convergence by running for 3000 iterations following a burn-in phase of 1000 iterations.

Results

With 1,260 camera sites running a total of 27,379 camera nights we captured 42,814 wildlife detections including 6,413 carnivores across both cities between 2012 and 2016. Detection rate (count/day), an index of relative habitat use, for bobcats and coyotes in suburban and exurban habitats was highest in green space (i.e., forest fragments), but in rural areas was highest in yards (Table C5). All species except bobcat had higher detection rates in suburban green space compared to wild green space (Table C5). Model selection supported the importance of

accounting for multiple interspecific interactions. The top model incorporated interspecific interactions and performed significantly better ($\Delta\text{WAIC} > 10$) than models where interspecific interactions were absent or few (Table C4). While there are no published recommendations for determining significant differences between models based on WAIC, given its similarity to AIC, a conservative cut-off of 10 WAIC points is likely adequate to infer when a model no longer has support relative to the top model (Burnham and Anderson 2003). The top model included a global first order model (i.e., all covariates included) with a global second order model, suggesting that none of the combinations of covariates we examined performed significantly better than any others in isolation. However, the second-best model was not significantly different from the top model ($\text{WAIC} < 10$) and included a global first order model with second order natural parameters related to the interaction of forest fragmentation and housing density, suggesting that the interplay between forest fragmentation and housing density, along with interspecific interactions, are important determinants of carnivore occupancy.

First order occupancy relationships with covariates – Although marginal occupancy for each species showed expected trends along the housing density gradient (foxes and coyote positively associated, bobcat negatively associated) (Figure C1), housing density alone was not a strong first order predictor for any species. Both coyote and grey fox occupancy was different between the cities, being significantly higher in Raleigh.

Second order occupancy: species interactions – We found evidence for multiple pairwise interactions among all four species evaluated. Specifically, the probability of grey fox occupancy was significantly lower in the presence of red fox and vice versa, regardless of city or

habitat, as was the probability of grey fox occupancy in the presence of bobcat and vice versa, and these patterns were reflected in log odds ratios (Figures 6, C2). Additionally, the probability of coyote and grey fox occurring together varied as a function of the housing density/local forest interaction term (Figure 5). We found no evidence of significant interactions between red foxes and either of the two larger species in our top model, however our second-best model showed that in both cities, bobcat and red fox occupancy was lower in sparsely forested areas at high housing density when in the presence of the other species (Table C6). Indeed, log odds ratios from our top model for bobcats and red fox were negative across the gradient in both cities, with the exception of the wild level in DC, further indicating trends towards negative interactions (Figure 6). Most of these ratios were not significant, however, with the exception of the exurban and rural gradient levels in Raleigh. Conversely, log odds ratios indicated positive, but not significant, interactions between coyote and both fox species across the urbanization gradient in both cities, with the exception of grey fox in the suburban and wild levels in DC where interactions were negative (Figure 6). Log odds ratios indicated bobcats were generally less likely to occupy the same sites as coyotes, though ratios were not significant (Figures 6, C2). We did not note any difference in the number of negative log odds ratios between the different gradient levels (Figure 6).

Relative importance of interactions and covariates – The two cities showed similar patterns in the relative importance of forest fragmentation and housing density covariates versus interspecific interactions in determining occupancy, based on absolute log odds ratios. Along both gradients, local forest cover was the most important determinant of occupancy, followed by interspecific interactions (Tables 1, C7). Local forest cover was most important for bobcats in particular in

both cities (Table 1). However, housing density was consistently more important for grey foxes in Raleigh than interactions or other habitat covariates, with the interaction between grey fox and coyote being a more important determinant of grey fox occupancy in DC (Table 1). In both cities, interactions with each fox species were more important determinants of coyote occupancy than any of the habitat covariates. The interaction with coyotes was also the most important determinant of red fox occupancy in Raleigh (Tables 1, C7).

Discussion

Although past studies have examined the distribution of carnivores along an urbanization gradient (Randa and Yunker 2006; Goad et al. 2014; Lewis et al. 2015b; Wang et al. 2015; Moll et al. 2018), this is the first to account for interspecific interactions explicitly within a multi-species occupancy framework, to directly compare two cities, to consider private lands, and to have a larger sample size than most other studies. We found evidence of both positive and negative interactions across the gradient of urbanization with some dependent on available green space, suggesting that fragmentation concentrates carnivores into remaining green space, leading to higher levels of spatial interaction between some species.

Forest fragmentation coupled with housing density was key in mediating species interactions, being in our top model (with all covariates) and also as the only factors in our second-best model, which was not significantly different from our top model in terms of WAIC support. Models incorporating housing density and human-related covariates, prey covariates or forest fragmentation covariates alone received relatively low support (i.e., $\Delta\text{WAIC} > 10$). The relative strength of interactions versus forest fragmentation and housing density was similar

between the cities with forest fragmentation being most important followed by interspecific interactions.

Our prediction that accounting for interspecific interactions would be an important factor in modelling occupancy for all species was supported. Our model selection exercise showed clear support for models including species interactions over models assuming no or few interspecific interactions. The top model incorporated all pairwise interactions between species and performed significantly better than more traditional two-species co-occurrence models (Richmond et al. 2010). Our results suggest that ecological models based solely on habitat without incorporating interspecific interactions may be inaccurate.

Our prediction that housing density (a general measure of development intensity) and other human-related covariates would be strongly associated with the smaller carnivore species was only partially supported. Housing density alone was not a significant predictor in any of our first order models, indicating that all species we modelled use all levels of the urbanization gradient to a similar extent, matching other analyses of these same data (Parsons et al. 2018a). This contrasts other studies of carnivores along urbanization gradients that only considered habitat factors, which typically find significant effects of urbanization on coyote and fox occupancy (Randa and Yunker 2006; Goad et al. 2014). However, when we also considered interspecific interactions, housing density, when coupled with forest fragmentation, became an important predictor in our second order models, supporting our prediction that species interactions would be positively mediated by urbanization. This suggests urban development plays an important role in structuring carnivore communities with available green space (i.e., forest fragmentation) as a mediating factor (Gallo et al. 2017). We interpret this to mean that habitat fragmentation is concentrating the larger, less urban-adapted carnivores (i.e., bobcats,

coyotes) into limited green space, leading to more spatial interactions with urban-adapted species (i.e., grey and red foxes).

Grey foxes were the one species that interacted significantly with every other species included in our model, interacting negatively with both red foxes and bobcats and positively with coyotes. The negative interaction between grey foxes and red foxes and bobcats respectively occurred across all levels of urbanization and forest fragmentation. The diets of both fox species overlap significantly (Cypher 1993) but grey foxes tend more toward omnivory and have been reported to exclude red foxes from some habitats (Carey 1982). The lack of mediation by housing density in interactions between the fox species is consistent with their ability to adapt to urbanization, indeed, both species used yards extensively in this study. Red foxes in particular have been recorded in European cities since the 1930s, and during the past 20 years have colonized additional cities in North America, showing a remarkable ability to thrive and exploit human-dominated landscapes around the world (Wandeler et al. 2003). Grey fox diet tends to overlap less with bobcats than with red foxes (Neale and Sacks 2001) but grey foxes are subject to intraguild predation by bobcats which may account for the negative spatial interaction we observed between these species (Farias et al. 2005). The lack of mediation of this interaction by housing density suggests the risk of intraguild predation is similar across the urbanization gradient.

Grey foxes and coyotes appear to require woodlots to navigate suburban areas and share these spaces without obvious negative consequences, even where those woodlots are rare. Grey foxes are excellent tree climbers, giving them the ability to avoid direct persecution from coyotes which may facilitate coexistence (Terres 1939), as could temporal partitioning. By contrast, red foxes and bobcats, the most and least urban-adapted species respectively, appear to spatially

avoid one another in areas where large tracts of green space are particularly sparse. Where green space is adequate, there appears to be sufficient opportunity for co-existence in an urban landscape between these two species.

Large carnivores typically avoid humans, and smaller carnivores have been shown to reduce agonistic encounters with larger carnivores by living closer to people, a hypothesis known as the “human shield effect” (Berger 2007). Our study design was well suited to test this hypothesis with sampling stratified along the urbanization gradient and small and large interacting carnivores. We found no clear positive association between the smaller carnivores (foxes) and housing density, nor did they appear to spatially avoid some larger carnivores (coyotes) at higher housing densities as would be expected if they were using humans as shields. On the contrary, we found no evidence of a significant interaction between red foxes and coyotes, and grey foxes and coyotes co-occurred at high housing density, suggesting that human-dominated areas do not act as spatial refugia for foxes in these cities. A recent study of urban parks in Cleveland, OH, USA found much stronger evidence of a human shield effect between coyotes and red foxes than we found in our study, noting opposing responses to human development of red foxes and coyotes and avoidance of coyotes by red foxes, supporting the idea that red foxes use humans as shields (Moll et al. 2018). Unfortunately, there are differences in methodology between the two studies that make direct comparisons difficult; Moll et al. (2018) considered temporal dynamics which we did not, while we considered suburban habitats (i.e., yards and small woodlots) and the joint probabilities of occupancy between interacting species. The relative importance of forest fragmentation, housing density and interspecific interactions was similar between the cities with forest fragmentation being the most important determinant of occupancy. These cities are both large and sprawling with high levels of forest fragmentation,

likely causing less urban-adapted carnivores to use patches of forest cover to navigate successfully along the urbanization gradient to exploit the rich resources suburban areas have to offer. Differences in city structure (i.e., sprawl, housing concentration) may be expected to affect how carnivores navigate cities and their success in adapting to urban environments. Whether these results hold in other cities remains to be tested and multi-city comparisons can help us understand how different development patterns influence urban mammal communities to promote conservation in the Anthropocene.

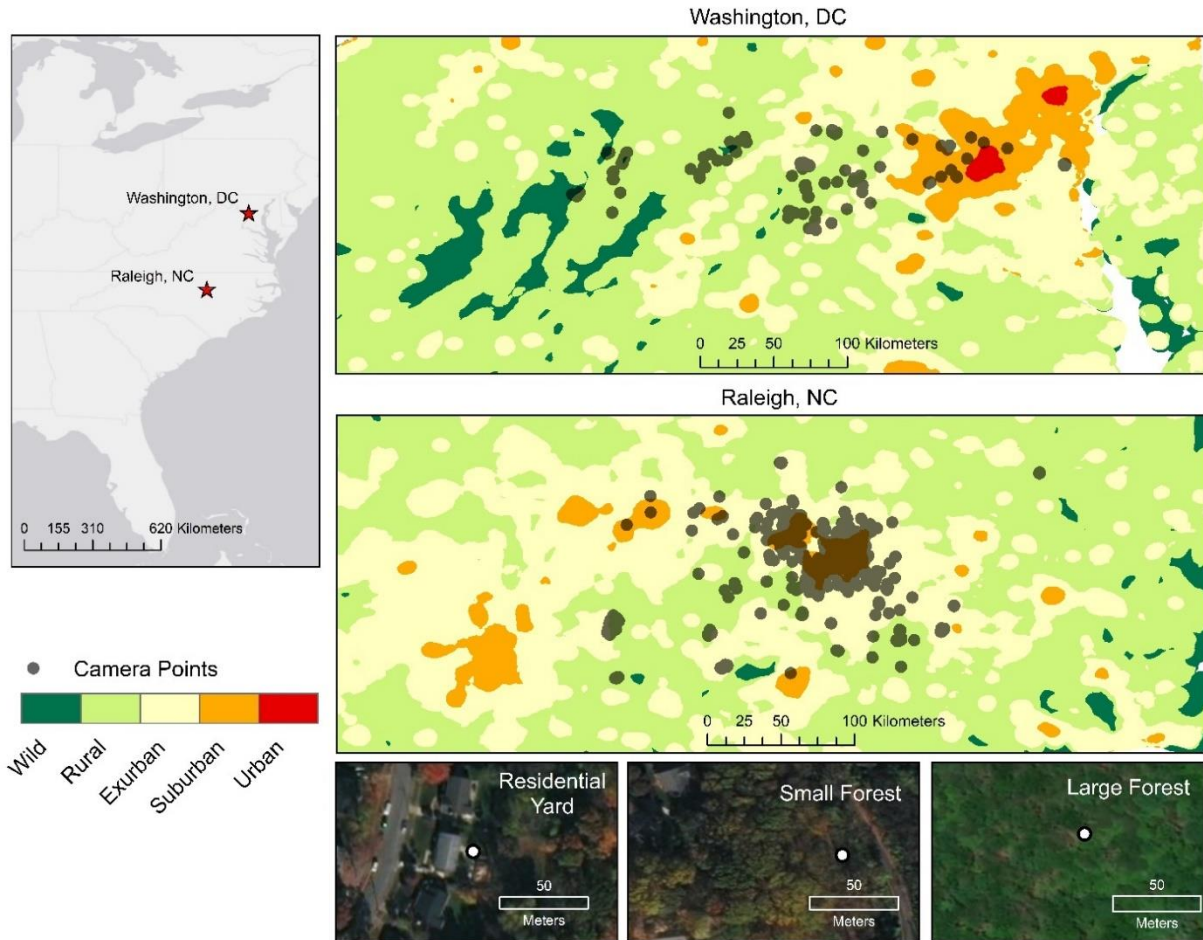


Figure 4: Camera locations in Washington, DC and Raleigh, NC, USA from 2012-2016. The gradient from wild to urban is defined as the average number of houses in a 1km radius (Wild= ≤ 0.5 , Rural=0.51-12.63, Exurban=12.63-147.05, Suburban=147.06-1000, Urban>1000). Examples of the three plot types sampled in each city (residential yard, small forest and large forest) are pictured using satellite imagery.

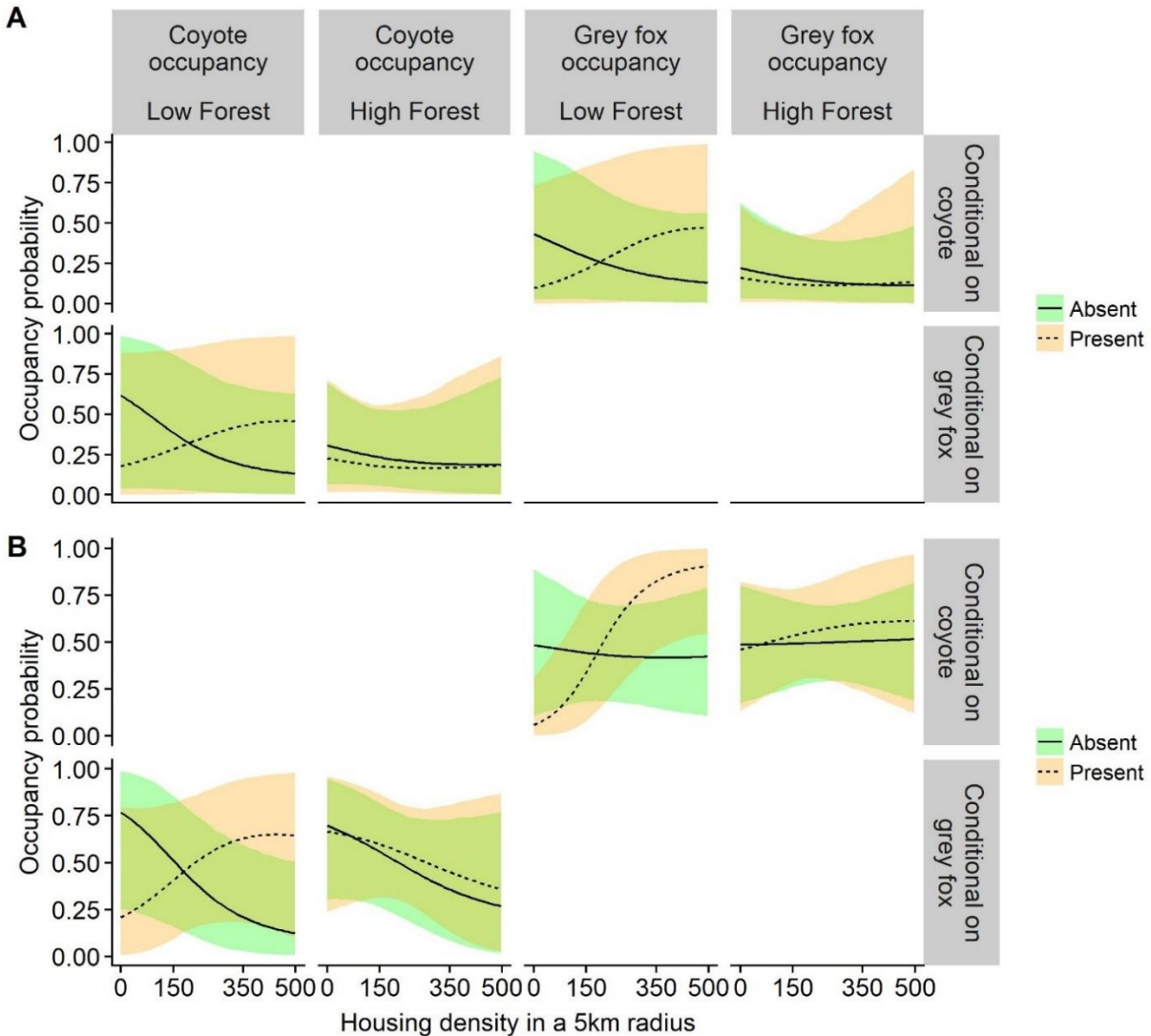


Figure 5: Occupancy for coyote and grey fox in the presence and absence of each other conditional on the absence of bobcat and red fox along a housing density gradient in low (5-50% in a 5km radius) and high percent local forest (51-100% in a 100m radius). Data were taken from camera traps run in Washington, DC (A) and Raleigh, NC, USA (B) between 2012 and 2016. Lines show posterior means and shaded regions are 95% credible intervals. In both cities, coyote and grey fox occupancy was higher in low forest at high housing density when in the presence of the other species.

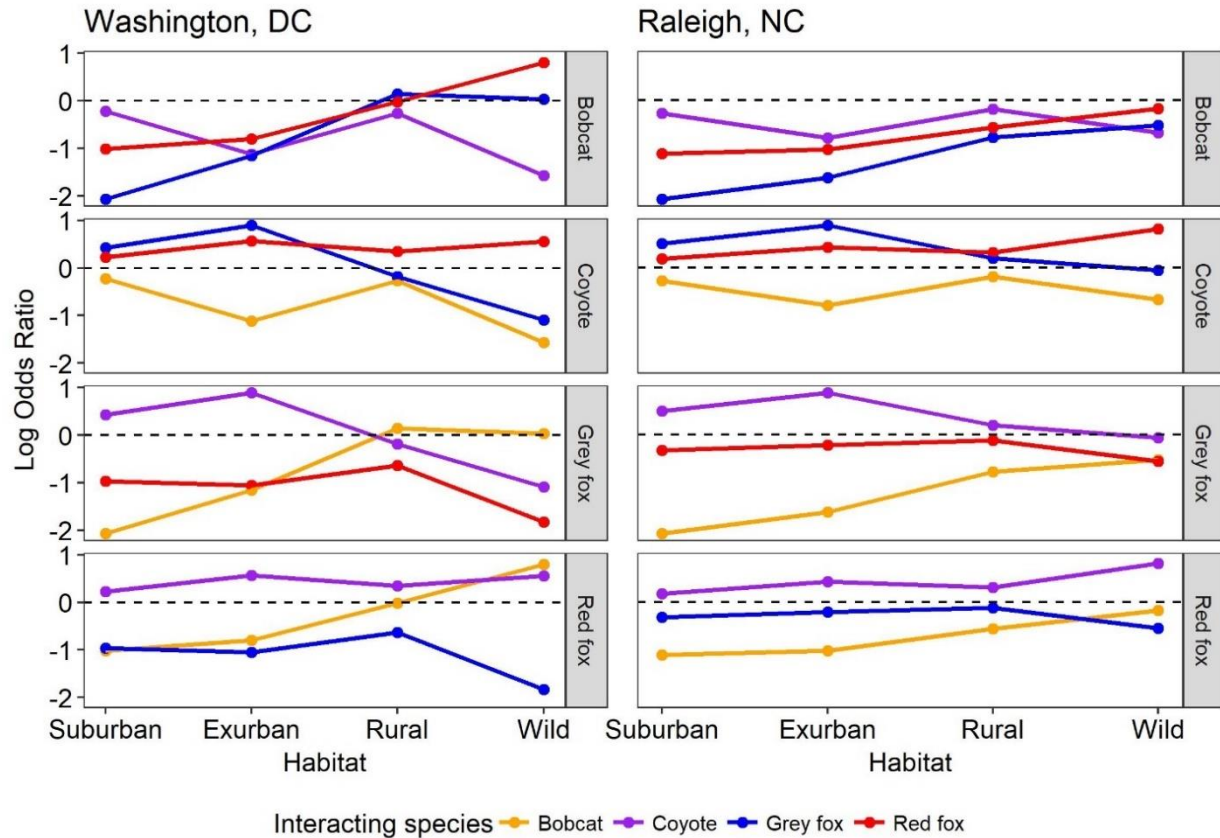


Figure 6: A comparison of log odds ratio for pairwise combinations of species (the log of the probability a species occupies a site divided by the probability it does not, conditional on the presence of an interacting species) in wild, rural, exurban, and suburban gradient levels taken from camera traps run between 2012 and 2016 in Washington, DC and Raleigh, NC, USA. All second order models are conditioned on all other species being absent. Ratios tended to be similar in terms of being positive (co-occurrence) and negative (avoidance) across the gradient levels.

Table 1: The relative importance of environmental covariates versus interspecific interactions in influencing the probability of occurrence for each species. Relative importance was assessed using absolute log odds ratios OR_{sp} and OR_h , associated with the interaction between two species and the change in environmental covariates ($\Delta h=0.5$ units), respectively. Data come from camera trapping in Washington, DC and Raleigh, NC from 2012-2016. All covariates were centered and scaled for easy comparison. Asterisks show the highest ratios for each species. B is bobcat, C coyote, GF grey fox and RF red fox.

| Washington, DC | | | |
|----------------|---------------------|------------|-------------|
| OR_{sp} | OR_h | | |
| | Housing Density 5km | Forest 5km | Forest 100m |
| B*C | | | * |
| B*GF | | | * |
| B*RF | | | * |
| C*B | | * | |
| C*GF * | | | |
| C*RF * | | | |
| GF*B | | * | |
| GF*C * | | | |
| GF*RF | * | | |
| RF*B | | | * |
| RF*C | | | * |
| RF*GF | | | * |
| Raleigh, NC | | | |
| B*C | | | * |
| B*GF | | | * |
| B*RF | | | * |
| C*B | | | * |
| C*GF * | | | |
| C*RF * | | | |
| GF*B | * | | |
| GF*C | * | | |
| GF*RF | * | | |
| RF*B | | | * |
| RF*C * | | | |
| RF*GF | * | | |

Chapter 3: The effect of urbanization on spatiotemporal interactions between gray foxes and coyotes

Introduction

Competition plays a pivotal role in structuring the spatial distribution of many carnivore communities (Caro and Stoner 2003). Dominant predators that have high dietary overlap with smaller predators can suppress the subordinate species through exploitative competition for a shared resource if that resource is in limited supply (Holt et al. 1994). Where resources are abundant and clumped however, such as in urban and suburban areas, subordinate species may not be so easily outcompeted, forming small social groups around rich food patches that are better able to counter competitive advantages of larger species (Macdonald 1981). Smaller carnivores may further reduce agonistic encounters with larger carnivores by living closer to people where larger carnivores tend to be rare due to high fragmentation and persecution (Bateman and Fleming 2012), a hypothesis known as the “human shield effect” (Berger 2007). Competitive dynamics can further change if the largest predators are absent in urban areas, leading to mesopredator release where abundances of small, generalist carnivores like raccoons and foxes increase, leading to potential cascading effects on the abundances of smaller competitors and prey (Ritchie and Johnson 2009).

However, recent evidence has shown that many developed areas are being colonized, or re-colonized, by larger carnivores. For example, mountain lions (*Puma concolor*) have recently recolonized the highly fragmented mountain habitats around Los Angeles (Benson et al. 2019) and increased their use of residential areas in Colorado’s front range (Blecha et al. 2018). The European wolf (*Canis lupus*), long ago eradicated in most of western Europe, has recolonized France, Germany, Switzerland and Denmark, countries densely populated by humans (Mech

2017). Other carnivore species are expanding their ranges for the first time into human-dominated habitats. For example, golden jackal (*Canis aureus*) populations in Europe have been expanding westward since the mid-twentieth century, making regular use of human-dominated habitats (Trouwborst et al. 2015) while in North America, coyotes (*Canis latrans*) have expanded their range east where humans are most concentrated, making increasing use of cities (Hody and Kays 2017). As more carnivore species colonize cities, they are coming into contact with each other and with more established urban dwelling carnivores (e.g., Lewis et al. 2015a). These newer urban carnivores may avoid humans by concentrating their urban activities to green spaces, leading to higher levels of interspecific interaction with smaller species in suburban forests (Parsons et al. 2019). The exact nature of these interactions is still unclear. If interactions are largely agonistic it could lead to patch exclusion, contracted spatial distribution patterns (i.e. Hersteinsson and Macdonald 1992) and lower population densities for subordinate species (i.e. Henke and Bryant 1999). Even if species are spatially tolerant of each other, agonistic interactions could manifest as prey switching and altered activity patterns, having potential consequences for human-wildlife conflict (i.e., Murray et al. 2015).

Measuring interspecific interactions is challenging due to the potential simultaneous spatial and temporal responses they provoke, requiring sophisticated modeling approaches. As a result, although inference on both spatial and temporal processes related to species interactions are frequently of interest in ecology, they are typically treated separately. This becomes problematic if, for example, one species shifts temporal patterns but does not shift space use in response to the presence of another species. Indeed, past analysis of our dataset based solely on spatial interactions found no support for the hypothesis that smaller competitors (i.e., gray fox (*Urocyon cinereoargenteus*)) use humans as shields against larger competitors (i.e., coyotes) at

higher levels of urbanization (Parsons et al. 2019). Here, we take advantage of a new method that integrates a continuous-time detection process into a multi-species occupancy model, allowing inference on spatial co-occurrence and temporal shifts simultaneously (Kellner et al. In Review). This tool represents a new opportunity to simultaneously consider the spatial and temporal nature of species interactions, including the effect of temporally varying factors (e.g., precipitation).

The carnivore guild in the eastern United States has been dynamic over the last century, with the extinction of apex predators (wolves and cougars) and subsequent colonization by coyotes. Coyotes are now present in most or all cities in the eastern United States (Hody and Kays 2017), although not as common in highly urban areas as are western coyotes (Gehrt et al. 2011b). Through interference competition and direct intraguild predation, western coyotes are well known to limit the number and distribution of smaller competitors (Fedriani et al. 2000). The impact of coyotes on smaller competitors is less clear in the east, although recent studies have found evidence for a decline in fox numbers following coyote colonization (Levi and Wilmers 2012), and of foxes becoming relatively more abundant in urban areas to escape coyote competition (Moll et al. 2018). However, other studies have indicated that coyotes and gray foxes are more likely to be detected at the same site in suburban areas, if the site is forested (Parsons et al. 2019), the opposite of what would be expected if coyotes are excluding foxes. By comparing these dynamic eastern communities along a gradient of urbanization and examining spatial and temporal dynamics simultaneously, we can better evaluate the impact of human disturbance on interspecific carnivore interactions.

We used camera traps deployed by citizen-scientists in Raleigh, NC, USA to investigate whether species interactions influence the site occupancy and detection intensity of carnivore species along an urbanization gradient. We hypothesize that although coyotes and gray foxes use

the same sites, they do not use them at the same time. Specifically, we predict that foxes will change their behavior in the presence of coyotes by avoiding a site after the passage of a coyote and/or by changing their daily activity patterns to be active at times coyotes are typically inactive. Scent marking may be key to both partitioning resources and avoidance tactics between species (Apfelbach et al. 2005), but its effectiveness should decrease with precipitation (e.g., Allen et al. 2017). If the species are detecting each other by scent and avoiding areas used recently by the other species, we predict that the time since the last coyote detection will be mediated by precipitation. If smaller competitors (i.e., gray fox) are using humans as shields, we predict a positive relationship between occupancy and housing density and less spatial and temporal interaction with larger competitors (i.e., coyotes) at higher levels of urbanization.

Materials and Methods

Study site – Raleigh, North Carolina is located in the mid-Atlantic region of the United States. It is approximately 375km² with an estimated population size of 459,000, thus 1,278 people/km². Our study spanned a 66,640km² area around the center of the city where surrounding land use was a combination of agriculture (~24%) and forest (~52%) with a mean of 17.7 houses/km².

Citizen science camera trap surveys – From 2012-2016 (Table D1), 336 trained volunteers (see Parsons et al. 2018c for details) deployed 760 unbaited camera traps across an urbanization gradient around Raleigh (Figure 7). We used the Silvis housing density dataset (1km resolution; Hammer et al. 2004) and bin levels of Theobald (2005) to define the four levels of the gradient for sampling stratification (excluding open water): suburban (147.05-1000 houses/km²), exurban (12.64-147.06 houses/km²), rural (0.51-12.63 houses/km²) and wild (<0.5 houses/km²). Within

gradient levels, camera placement was stratified between residential yards, small forest fragments ($\leq 1\text{km}^2$), open areas (at least 0.02km^2 open) and large forest fragments ($>1\text{km}^2$) (Table D2), although we were unable to sample open areas and residential yards in the wild strata due to their rarity. All adjacent cameras were spaced at least 200m apart. Volunteers used Reconyx (RC55, PC800, and PC900, Reconyx, Inc. Holmen, WI) and Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS) camera traps attached to trees at approximately 40cm above the ground. Trigger sensitivity was set to high for all cameras and we verified that both brands of camera had similar trigger speeds ($<0.5\text{s}$) and randomized placement of the different models to avoid bias due to camera type. Cameras were deployed for three weeks and then moved to a new location. Cameras recorded multiple photographs per trigger, at a rate of 1 frame/s, re-triggering immediately if the animal was still in view. We grouped consecutive photos into sequences if they were <60 seconds apart and used these sequences as independent records. We did not bin records into daily or weekly capture histories for occupancy, instead using all independent records for analysis. Initial species identifications were made by volunteers using customized software (eMammal.org) and all were subsequently reviewed for accuracy before being archived at the Smithsonian Digital Repository.

Model Overview – We used a multispecies occupancy model with continuous-time detection process (Kellner et al. In Review) to assess spatial and temporal species interactions of coyotes and gray fox, while accounting for imperfect detection (Figure 8). This model is a generalization of the single-season occupancy model (Mackenzie et al. 2002) to accommodate two or more interacting species, and to allow the detection process to occur in continuous time. The

detections of each species at each site are treated as the realization of a temporal Poisson point process (PPP) with intensity function $\lambda(t)$ evaluated at time t .

The model also estimates the probability of each combination of latent presence/absence for all species, denoted ψ . The probabilities of each combination of latent presence/absence describe the probability a site is occupied by only one species (first order); only two species (second order), and so on up to order S , the number of interacting species. The probabilities of each combination of latent presence/absence are functions of “natural parameters”, denoted f , which can be modeled as linear functions of covariates (Rota et al. 2016). For the two species case, first order f parameters can be denoted f_1 and f_2 , and second order f parameters can be denoted f_{12} . Species occurrence is assumed independent if all second order and higher natural parameters are fixed at 0 (e.g., $f_{12}=0$), whereas dependence between species can be modeled by estimating parameters associated with second order and higher natural parameters (Rota et al. 2016).

Model Covariates – We modeled variation in occupancy using five covariates (Table D3) that were most important in a previous spatial analysis of this dataset (Parsons et al. 2019), applying all five covariates to both first and second order natural parameter models (Table D3). We used percent tree cover (percent of each 30x30m pixel covered by trees; Hansen et al. 2013) at two scales: a local scale to represent forest cover at the camera site (100m radius around each pixel) and a larger scale (5km radius) to best approximate the home range size of our target species (Bekoff 1977; Fritzell and Haroldson 1982). We used the Silvis housing density dataset (Hammer et al. 2004) averaged over a 5km radius to represent urban development.

The detection intensity function can be modeled as a log linear function of covariates, allowing the use of continuously time-varying predictors like precipitation. We modeled detection intensity using nine covariates (Table D3). To account for differences in camera setup, terrain and camera model, we included site-specific detection distance, a measure of how far away the camera was able to detect a human, as a nuisance covariate. To test our hypotheses that coyotes and gray foxes are using the same sites but not at the same time, we used two measures of temporal interaction: activity pattern (detection intensity varied as a function of time of day) and the time since the last coyote detection, the dominant species. We allowed detection intensity for both species to vary by time of day using a Fourier series basis function following Kellner et al. (In Review):

$$\log(\lambda_s(t)) = \frac{\alpha_{s0}}{2} + \sum_{m=1}^M \alpha_{sm} \cos\left(\frac{m\pi t}{L}\right) + \gamma_{sm} \sin\left(\frac{m\pi t}{L}\right)$$

where α_s and γ_s are species-specific regression coefficients to be estimated. We assume a $2L = 24$ -hour period, thus fixing $L = 12$; and fixing $M = 2$ which adequately captures cyclic peaks and troughs in detection intensity. The PPP likelihood requires evaluation of an integral which can be closely approximated with quadrature techniques by dividing the entire sampling interval into arbitrary small time intervals (Kellner et al. In Review). For this analysis, we used 60-minute quadrature intervals for integral approximation.

To address our hypothesis that gray foxes would exhibit altered activity patterns at sites where coyotes were present, we explored potential temporal dependence between gray fox and coyote by comparing models that assumed gray fox detection intensity was independent of latent coyote presence, and models that assumed an interaction between Fourier series coefficients for

gray fox and latent coyote presence. Additionally, we modeled gray fox detection intensity as a function of time since the last coyote detection, conditional on at least one coyote detection at a site. We only considered time since the last coyote detection, assuming that the effect of other species passing between a gray fox and a coyote would be negligible and contribute only to noise in the overall signal of the gray fox-coyote temporal interaction. We used cumulative precipitation readings generated at 30 minute intervals obtained from Env-DATA (Dodge et al. 2013) and interpolated to our detections dataset (ECMWF Interim Full Daily Total Precipitation (mm); European Centre for Medium-Range Weather Forecasts 2019) to test our hypothesis that scent influences the relationship between gray fox detection intensity and the time since the last coyote detection.

We diagnosed univariate correlations using a Pearson correlation matrix ensuring correlation < 0.60 . All covariates were centered and scaled prior to analysis. We compared our candidate models with Watanabe–Akaike Information Criterion (WAIC), a fully Bayesian information-criterion which works particularly well with hierarchical models where other model-selection strategies (i.e., DIC, BIC) may not (Gelman et al. 2014). We considered the top model to be the one with the lowest WAIC. We fit models in STAN (Version 2.15.1, Stan Development Team 2015b) via the RSTAN (Version 2.15.1, Stan Development Team 2015a) interface in R (Version 3.4.0, R Development Core Team 2008) via R Studio (Version 1.0.143, Rstudio Team 2015). We ran three chains for each model, using trace plots to determine an adequate burn-in phase and subsequently running chains until the Brooks–Gelman–Rubin convergence diagnostic indicated adequate convergence ($R\text{-hat} < 1.1$; Gelman et al. 2014). All models achieved adequate convergence by running for 7000 iterations following a burn-in phase of 5000 iterations.

Results

We detected coyotes 347 times and gray foxes 943 times over 908 camera sites running a total of 19,353 traps nights. Our top model included both spatial dependence between the species and temporal dependence in detection intensity that varied by time of day (hereafter “activity pattern”), performing better ($\Delta\text{WAIC} > 10$) than models assuming spatial independence or models assuming spatial dependence but without temporal interactions (Table 2). Our spatial results mirrored a past spatial analysis of this dataset, indicating that these two species are more likely to occupy the same sites where housing density is high and forests highly fragmented (Table 3, Figure 9; Parsons et al. 2019). Our top model indicated important spatial results not detected in our past work which did not account for temporal patterns, showing that coyotes were positively associated with the amount of local forest at low housing densities and most likely to occupy large forests with low housing density regardless of gray fox presence (Table 3). Coyotes were less likely to occupy high housing density sites than gray fox, regardless of forest cover. Gray foxes were negatively associated with the amount of local forest at both low and high housing densities and more likely to occupy small forest fragments regardless of coyote presence (Figures 9, 10).

In addition to patterns of co-occurrence, our spatiotemporal model allowed us to assess patterns of co-detection. Models including activity patterns performed better than models including time since last coyote detection or those without temporal interactions. Models allowing activity patterns to differ based on latent coyote presence/absence performed better than models that did not include a term for latent coyote presence (Table 2). We found that housing density was a significant mediator of activity pattern overlap between gray foxes and coyote. Our top model showed that gray fox expected detections per hour at low housing densities were

highest at night when coyotes were present (Figures 11, D1). At high housing densities however, gray foxes were much more detectable during the day in the presence of coyotes, showing a higher proportion of nocturnal detections when coyotes were absent (Figure 11, D1). Our model of time since coyote detection mediated by precipitation was not supported over a model of unmediated time since coyote detection ($\Delta\text{WAIC} \gg 10$; Table 2).

Discussion

Ecology is defined as “the relations of organisms to one another and to their physical surroundings” (Oxford Collocations Dictionary 2002), yet studying the interactions of highly mobile animals has been challenging because they can behaviorally avoid each other in both space and time. Past work has focused on either the spatial patterns resulting from interspecific interactions (e.g., Grassel et al. 2015), or the temporal patterns (Farris et al. 2015), but seldom the interaction of these two dimensions (but see Moll et al. 2018) and never within a unified framework. Our results represent the first study to consider spatial and temporal interactions of carnivores simultaneously within a unified framework, while accounting for imperfect detection. Accounting for temporal interactions in addition to spatial interactions allowed us to gain more insight into the drivers of occupancy for both species, providing a nuanced picture of how spatiotemporal interactions are mediated by housing density and local forest cover. We found that coyotes and gray foxes both used forest cover and often at the same sites, but generally preferred different amounts of forest. Despite using the same sites as coyotes, gray foxes avoided coyotes temporally by becoming more diurnal, especially where they co-occurred at high housing densities, suggesting the potential for temporal interactions with coyotes to increase human-fox interactions.

We predicted a positive relationship with housing density if smaller competitors (gray fox) are using humans as shields against larger competitors (coyotes). When we look at these data from a simply spatial context, we see a positive relationship between gray fox occupancy and housing density in the presence of coyotes, but only where local forest cover is low. Coyote occupancy was also positively associated with housing density where forest cover was low in the presence of gray fox, suggesting these results are not consistent with gray foxes using humans as shields. However, we noted evidence of gray fox temporal avoidance of human activity through increased nocturnality when coyotes were absent, consistent with a species that has adapted to living around humans and may be using them as shields (e.g., Wang et al. 2017). Wildlife often shift daily activity patterns subtly to avoid humans with nocturnal species becoming more so in areas of high human activity (Gaynor et al. 2018) and carnivores in particular have been shown to alter their daily activity patterns to persist in urban forest fragments (Tigas et al. 2002). Although gray foxes are generally thought to be more urban-adapted than coyotes or bobcats in the east (Kapfer and Kirk 2012), our results suggest that they still consider humans a threat worth avoiding temporally. This may facilitate their ability to occupy high housing density forest fragments, which appear less desirable for coyotes.

We predicted that we would find less interaction of subordinate competitors (gray fox) with larger competitors (coyotes) at higher levels of urbanization if smaller competitors are using humans as shields. Spatially, our results did not support this hypothesis, finding that coyotes and gray foxes were more likely to occupy the same sites at high housing densities where local forest cover was scarce, similar to past studies (Parsons et al. 2019). In the absence of the other species, gray foxes and coyotes were less likely to occupy areas of high housing density where local forest cover was low, but more likely to occupy those same suburban forest fragments

when the other species was present. This supports the idea that remnant forest fragments are necessary for carnivores to occupy suburban environments, but that not all patches are of high enough quality to support carnivores. The patches in which coyotes and foxes co-occurred may represent the only habitat available to carnivores in cities (Parsons et al. 2019). Though these suburban forest fragments are used by both species, we suspect our finding that gray foxes do not show any spatial avoidance of suburban forest fragments used by coyotes is because coyotes are simply passing through these areas and not establishing and defending territories (Kapfer and Kirk 2012). Furthermore, gray foxes are excellent tree climbers and this ability may allow them to avoid predation by coyotes when they co-occur in space and time (Terres 1939). Although gray foxes did not avoid coyotes spatially, they did avoid them temporally at high housing densities, showing increased diurnal activity in the presence of typically nocturnal coyotes. Coyotes have been shown to provoke temporal changes in hunting patterns in gray foxes: gray foxes in California reduced their consumption of nocturnal prey in the presence of coyotes (Smith et al. 2018). This suggests that a shift to greater nocturnality to avoid humans may not be possible at sites where coyotes are present. Indeed, we found foxes shifting to greater nocturnality only at high housing density sites where coyotes were absent. These results show that gray foxes balance the risks associated with human and coyote presence when it comes to temporal partitioning and that alterations in one interaction have the potential to affect the other.

We predicted that if gray foxes are detecting coyotes by scent and avoiding areas used recently, the time since the last coyote detection would be mediated by precipitation. Our model of time since coyote detection mediated by precipitation received little support, suggesting that gray foxes are not using scent to avoid sites recently used by coyotes. Coyotes typically scent mark using urine which decays in the environment more quickly with precipitation, however

subordinate species may avoid a site if marked (and detected) in the past, making this avoidance undetectable on fine temporal scales. Interference in the form of urine scent marking is one possible way to exclude competitors from a resource or territory (Gill 1974), but other signs may alert subordinates to the presence of a dominant competitor that are not as prone to decay by precipitation (Macdonald 1980). When scent is used to detect dominant predators and avoid them, the response of the subordinate competitor should be proportional to the perceived level of threat of the dominant species (Gaynor et al. 2019). Coyotes are more likely to be transients at higher levels of urbanization (Newsome et al. 2015), posing little threat to competitors, which may help explain why our spatial results did not indicate any avoidance of coyotes by gray foxes. Transient coyotes are less likely to scent mark and return to the same site frequently (Gese and Ruff 1997) which may also explain the lack of temporal avoidance response from gray foxes. By using a continuous-time detection process, we were able to test hypotheses related to temporally varying covariates which cannot easily be done with traditional occupancy models that bin detection covariates across days or weeks. While not significant in our study, we think this statistical approach has great potential for testing for interactions between weather and scent communication in other mammal species.

We found that temporal species interactions in this study were important and mediated by spatial factors (i.e., housing density), and this would not have been detected without an explicit spatiotemporal approach. These results show the importance of considering temporal patterns when addressing questions about interspecific interactions mediated by human activities (i.e., Moll et al. 2018). Our study suggests that gray foxes continue to be wary of both humans and coyotes, using temporal partitioning more than spatial partitioning as an avoidance mechanism. Where coyotes are present, gray foxes reduce their nocturnal avoidance of humans, suggesting

avoidance of coyotes has the potential to increase gray fox-human interactions. However, gray foxes do not show a strong spatial response to coyotes moving through the urban matrix, which we suspect are transient animals. Thus, if coyotes adapt further to urbanization and begin establishing territories in more developed parts of cities, we may begin to see further impacts on smaller competitors and their relationship with humans.

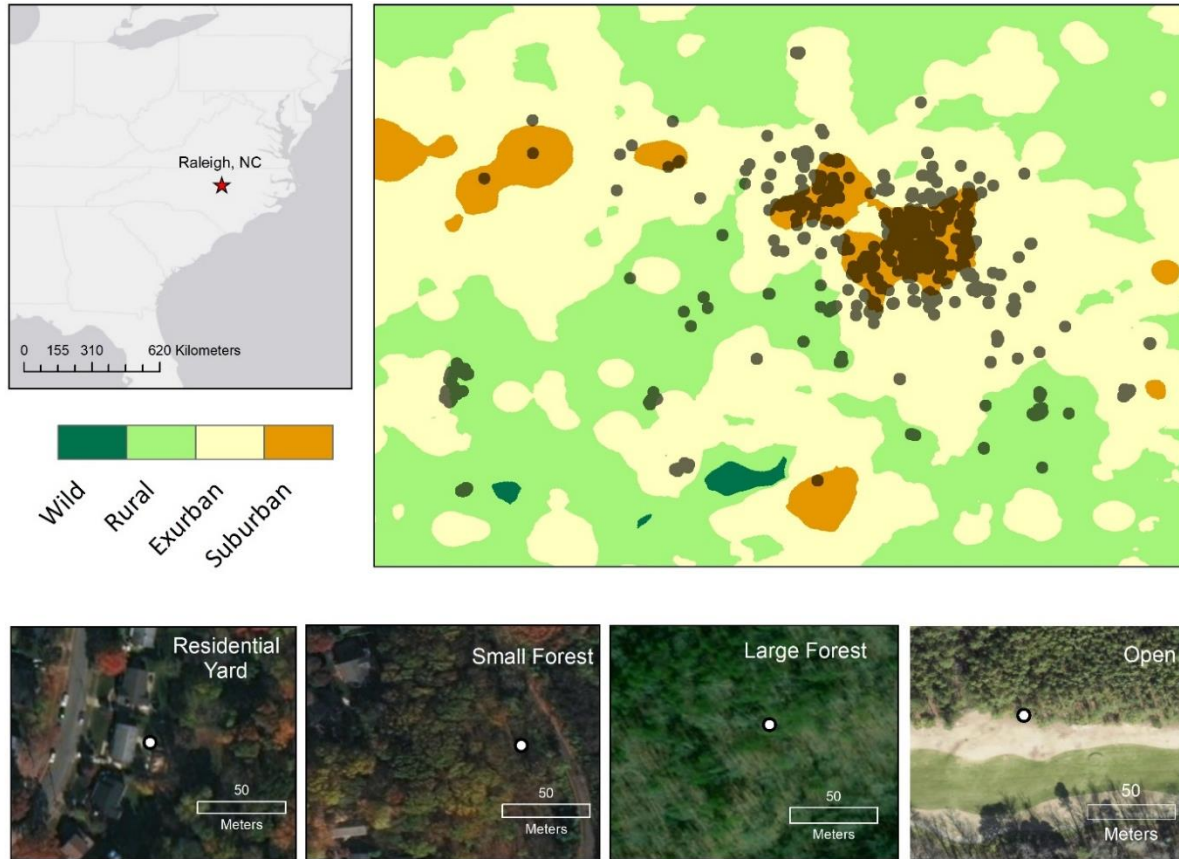


Figure 7: Camera locations in Raleigh, NC, USA from 2012-2016. The gradient from wild to suburban is defined as the average number of houses in a 1km radius (Wild= ≤ 0.5 , Rural=0.51-12.63, Exurban=12.63-147.05, Suburban=147.06-1000). Examples of the four plot types sampled (residential yard, small forest, large forest and open area) are pictured using satellite imagery.

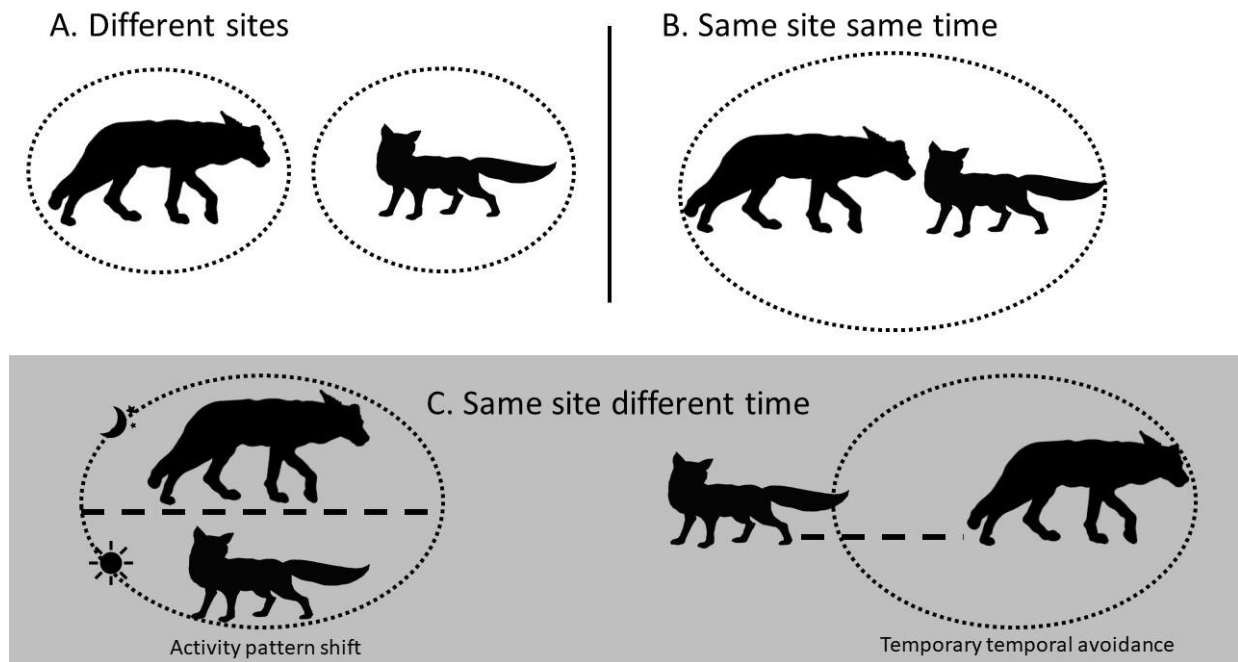


Figure 8: Different potential spatiotemporal interactions between coyotes and gray fox showing

A) spatial avoidance, B) spatial attraction and C) spatial attraction with temporal avoidance.

Spatial attraction with temporal avoidance can take two forms, either avoiding the site during the same time of day as the other species (activity pattern shift) or avoiding the site temporarily after a recent passage of the other species, regardless of the time of day.

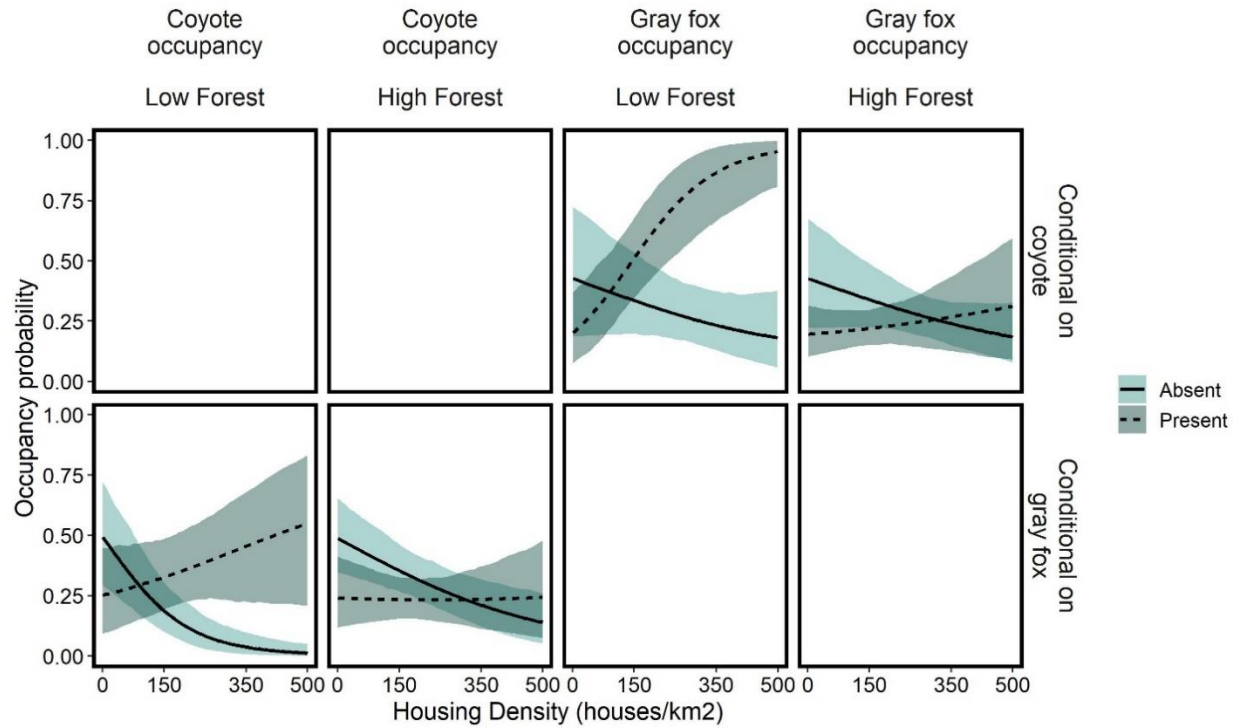


Figure 9: Occupancy for coyote and gray fox in the presence and absence of each other along a housing density gradient in low (13.72% in a 100m radius, 10th quantile) and high (99.36% in a 100m radius, 90th quantile) percent local forest. Data were taken from camera traps run in Raleigh, NC, USA between 2012 and 2016. Lines show posterior means and shaded regions are 95% credible intervals. In both cities, coyote and gray fox occupancy was higher in low local forest cover at high housing density when in the presence of the other species.

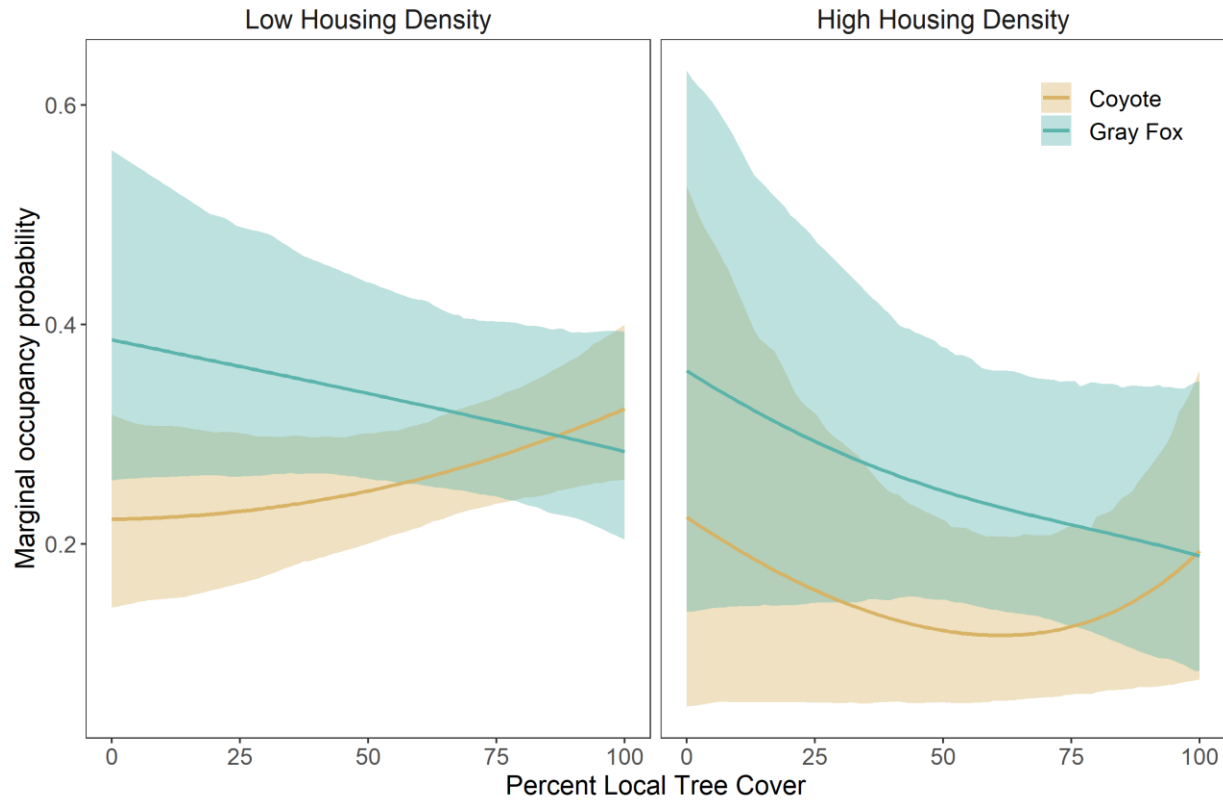


Figure 10: Marginal occupancy results for gray fox and coyote along a gradient of percent local tree cover within a 100m radius of the camera in areas of low (46.78 houses/km² within a 5km radius of the camera, 30th quantile) and high housing density (439.16 houses/km² within a 5km radius of the camera, 90th quantile). Data are taken from camera locations in Raleigh, NC, USA from 2012-2016.

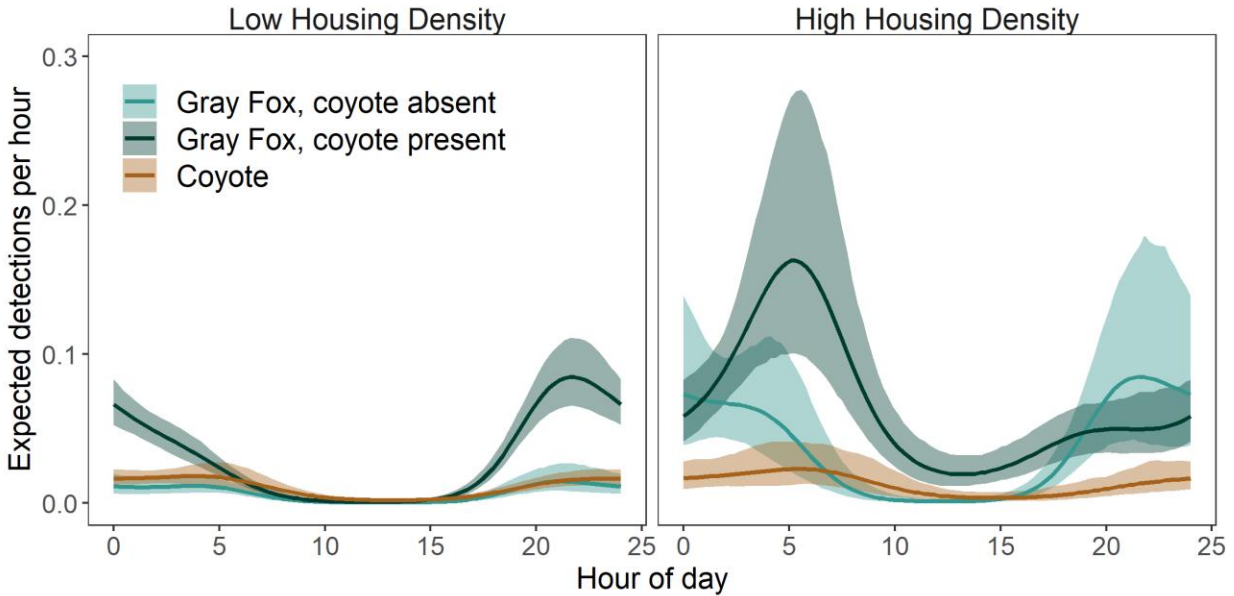


Figure 11: Activity patterns of gray foxes and coyotes from our top spatiotemporal occupancy model in areas of low ($46.78 \text{ houses/km}^2$ within a 5km radius of the camera, 30th quantile) and high housing density ($439.16 \text{ houses/km}^2$ within a 5km radius of the camera, 90th quantile) while accounting for latent coyote site occupancy. Data are taken from camera locations in Raleigh, NC, USA from 2012-2016. At high housing densities, gray foxes were more nocturnal in the absence of coyotes and more diurnal in the presence of coyotes. At low housing densities, gray foxes were more nocturnal in the presence of coyotes.

Table 2: Model selection results for the co-occurrence and co-detection of gray foxes and coyotes along an urbanization gradient.

Data are taken from camera locations in Raleigh, NC, USA from 2012-2016. Models are presented according to the main hypotheses they represent. All first order f parameters were modeled using the linear function

$\sim \text{Forest5} + \text{Forest100} + \text{HDens} + \text{Forest5} * \text{Hdens} + \text{Forest100} * \text{Hdens}$ except in the null models where they were fixed at 1. Those models that allowed for co-occurrence are noted as $f(d)$, meaning that second order f parameters were also modeled using the linear function above. Those models that assume independence between the species (i.e., no co-occurrence) are noted as $f(i)$, meaning second order f parameters were fixed at 0. Detection intensity λ is modeled as a linear function of covariates specific to each hypothesis. Detection covariates included detection distance (DD), a nuisance parameter representing the maximum distance away from the camera that a human can still be detected and photographed, activity pattern (time of day) with latent coyote (activity pattern), activity pattern without latent coyote (activity pattern_NLC), time since the last coyote detection (tsc), average housing density in a 5km radius (Hdens), local tree cover in a 100m radius around the camera site (TC100m), and precipitation (Precip).

| Null spatial models | WAIC | Δ WAIC |
|---------------------|-------|---------------|
| $f(d) \lambda(DD)$ | 20871 | 0 |
| $f(d) \lambda(1)$ | 20999 | 127 |
| $f(i) \lambda(DD)$ | 21012 | 140 |
| $f(i) \lambda(1)$ | 21162 | 291 |

Table 2 (continued)

| Is the interaction between these species spatial, temporal, neither or both? | | |
|---|-------|------|
| f(d) λ (activity pattern, DD) | 20063 | 0 |
| f(d) λ (tsc, activity pattern, DD) | 20176 | 112 |
| f(i) λ (activity pattern, DD) | 20906 | 842 |
| f(d) λ (activity pattern_NLC, DD) | 21548 | 1485 |
| f(i) λ (DD) | 21952 | 1888 |
| f(i) λ (tsc, DD) | 21971 | 1907 |
| f(d) λ (DD) | 22099 | 2035 |
| f(d) λ (tsc, DD) | 22156 | 2092 |
| Do activity patterns (coarse scale temporal) change with habitat? | | |
| f(d) λ (activity pattern, Hdens, activity pattern*Hdens, DD) | 19891 | 0 |
| f(d) λ (activity pattern, DD) | 20063 | 172 |
| f(d) λ (activity pattern, TC100m, Hdens, activity pattern*TC100m, activity pattern*Hdens, TC100m*Hdens, DD) | 21732 | 1840 |
| f(d)p(activity pattern, TC100m, activity pattern*TC100m, DD) | 22478 | 2587 |

Table 2 (continued)

| Does time since detection (fine scale temporal) change with habitat? | | |
|--|-------|-----|
| f(d)p(tsc, TC100m, tsc*TC100m, DD) | 22028 | 0 |
| f(d)p(tsc, DD) | 22156 | 127 |
| f(d)p(tsc, TC100m, Hdens, tsc*TC100m, tsc*Hdens, TC100m*Hdens, DD) | 22157 | 129 |
| f(d)p(tsc, Hdens, tsc*Hdens, DD) | 22245 | 217 |
| Does fine scale temporal interaction change with precipitation? | | |
| f(d)p(tsc, DD) | 22156 | 0 |
| f(d)p(tsc, Precip, tsc*Precip, DD) | 22203 | 47 |
| Does combining all important factors spatial, temporal and covariate factors improve support? | | |
| f(d)p(activity pattern, Hdens, activity pattern*Hdens, DD) | 19891 | 0 |
| f(d)p(tsc, TC100m, tsc*TC100m, activity pattern, Hdens, activity pattern*Hdens, DD) | 19934 | 42 |

Table 3: Predictors used to model 1st (Gray Fox and Coyote) and 2nd (Coyote*Gray fox) order f parameters in a multi-species occupancy model with estimated model coefficients and 95% credible interval, in parentheses. Coefficients for which the 95% credible interval does not overlap zero are shown in bold. Coyotes and gray foxes are more likely to occupy the same site at high housing density (Hdens5km) and low local forest cover (TC100m), shown by the negative Hdens5km*TC100m coefficient.

| Predictor | Gray Fox | Coyote | Coyote*Gray Fox |
|-----------------|-----------------------------|-----------------------------|-----------------------------|
| Intercept | -0.78 (-1.23, -0.29) | -1.14 (-1.47, -0.74) | 0.13 (-0.47, 0.69) |
| TC5km | -0.31 (-0.73, 0.07) | -0.23 (-0.69, 0.18) | 0.28 (-0.39, 0.91) |
| TC100m | 0.01 (-0.31, 0.32) | 0.45 (0.13, 0.78) | -0.68 (-1.2, -0.19) |
| Hdens5km | -0.41 (-0.84, 0.01) | -0.95 (-1.37, -0.58) | 1.1 (0.5, 1.74) |
| Hdens5km*TC5km | 0.18 (-0.15, 0.49) | 0.08 (-0.27, 0.42) | 0.31 (-0.22, 0.86) |
| Hdens5km*TC100m | 0.01 (-0.28, 0.31) | 0.4 (0.02, 0.75) | -0.58 (-1.11, -0.04) |

Chapter 4: Predicting the effect of increasing urbanization on coyotes and white-tailed deer using an integrated population model

Introduction:

White-tailed deer (*Odocoileus virginianus*) are the largest and most common herbivore in the eastern United States (Mcshea 2012). Primarily browsers, deer play an important role in maintaining plant genetic diversity (Parker et al. 2010; Royo et al. 2010) and in forest nutrient cycling (Pletscher et al. 1989). They are also one of the most heavily managed species in the region, relying predominantly on citizen hunters to reduce herds during the annual fall hunting season. Approximately 11.6 million Americans hunt and 16.9 billion dollars are spent each year on deer hunting activities in the United States (Poudel et al. 2016). In the Southeast, hunters and vehicles are the main sources of mortality for deer (e.g., 64%; Kilgo et al. 2016) since the extirpation of their main predators, wolves (*Canis lupus*) and cougars (*Puma concolor*).

However, in the last 3-4 decades, coyotes (*Canis latrans*) have colonized the Southeast (Hody and Kays 2018). Typically larger than their western counterparts, eastern coyotes are capable of depredating large prey species like deer (Kays et al. 2010a). Indeed, there is some evidence to indicate that eastern coyotes occasionally prey upon adult deer (Chitwood et al. 2014) and ample evidence of depredation of fawn neonates, sometimes enough to affect population sizes (Kilgo et al. 2010; Kilgo et al. 2012). Despite this, there is little evidence of declines in deer populations concurrent with coyote range expansion (Bragina et al. 2019) and the effect of coyote predation on deer populations in the Southeast appears variable, with long-term consequences difficult to predict (Mcshea 2012).

Deer may be able to use urban and suburban areas as refuges from coyote predation. Both coyotes and deer use suburban areas regularly but deer appear to use higher levels of urbanization in the Southeast proportionally more than do coyotes, which tend to occupy areas with lower human densities (Parsons et al. 2018b). Furthermore, there is some evidence to suggest that coyotes pose less risk to deer in suburbia than in rural or wild areas, including lower coyote predation rates on fawns (Gulsby et al. 2017) and lower spatial and temporal avoidance responses of deer to coyote presence (Gallo et al. 2019). However, recently coyotes have shown an ability to adapt to urban areas (Gehrt et al. 2011a), suggesting that they could become more common in cities over time (Bateman and Fleming 2012). With urbanization increasing across the country, especially in the Southeast (Sohl et al. 2018), it is important to understand how coyotes will respond and the implications for deer management.

Most data on deer management come from hunter harvest, but hunting is generally prohibited in urban areas (though suburban archery programs exist; Mcshea 2012), thus studying these predator-prey dynamics in urban areas is difficult. Lower rates of predation, the limited hunting, and ample supplemental food (i.e., landscaping) lead to higher density populations of deer living near people (Brown et al. 2000). These large populations result in increased risk of tick-borne infections, vehicle collisions and damage to residential landscaping (Mcshea 2012). This added human element coupled with a lack of data and an adaptable predator make deer management especially challenging in urban areas. Nevertheless, establishing relationships between urbanization and deer and coyote populations is important to the future management of deer in the Southeast.

Predicting trends in deer abundance over time may not be enough to understand the dynamics between predator and prey. Predation can be described on a continuum from

compensatory (not limiting) to additive (limiting), and where predation falls on this continuum determines its effect on prey abundance (Bender 2018). In highly stressed populations, where food is lacking and/or disease present, predation is most likely to be compensatory (Bender 2018). However, in populations in high-quality habitats where individuals attain excellent nutrition, predation is more likely to be additive, with detectable effects on population size more likely (Bender 2018). Thus, if conditions change and populations become more or less stressed by outside factors, whether predation is predominantly compensatory or additive can likewise change. Therefore, it's important to not only monitor abundance, but to determine how predators are affecting key vital rates (i.e., survival and recruitment) under different environmental conditions.

Coyotes could affect deer populations through direct predation on fawns or adults (e.g., Chitwood et al. 2014; Chitwood et al. 2015b), or through indirect effects that increase vigilance (e.g., Lashley et al. 2014; Schuttler et al. 2017) or avoidance behaviors (e.g., Parsons et al. 2016; Gulsby et al. 2017). All of these could lower survival or recruitment and thus affect deer abundance. Estimating survival, recruitment and abundance in free ranging populations is challenging, however, requiring labor-intensive studies which become even more difficult as the geographic scope of inference increases. However, there are many sources of data (e.g., harvest data counts) collected regularly by wildlife managers that are readily available. These datasets are typically indices rather than the robust datasets generated by following individuals through time (e.g., capture-recapture, telemetry). Indices generally correlate to desired quantities, like density or survival, and although they are not providing robust estimates, can nevertheless provide valuable information. Recently developed integrated population models (Schaub and

Abadi 2011) provide a framework for integrating index and more robust datasets from widely varying sources on different spatial scales to estimate survival, recruitment and abundance.

In the last five years, the use of IPMs in ecology has increased seven-fold (2020 Google Scholar search) with managers increasingly using them for joint analysis of survey data commonly collected for managed species (e.g., Mccaffery and Lukacs 2016; Gamelon et al. 2019). The use of state-space models has allowed the flexible IPM framework to incorporate such indices with general success, by allowing observation processes (e.g., detection probability) to be modeled separately from state processes, resulting in parameter estimates similar to those estimated from more robust datasets (e.g., Fieberg et al. 2010). Although state space models can be used outside of IPMs, within an IPM they offer some solutions to estimate confounding quantities like detection probability by informing them with additional datasets (e.g., Hostetler and Chandler 2015). IPMs offer several advantages over the traditional approach wherein different datasets are analyzed separately, and the estimated demographic parameters used as inputs in population projection matrices. IPMs are more efficient, use all available information and allow formal accounting of uncertainty across sub-models (Schaub and Abadi 2011). Furthermore, they may allow estimation of quantities not directly informed by data in the model (i.e., if one parameter is missing data and all others informed by data and linked), and the sharing of parameters between models can increase estimate precision (Schaub and Abadi 2011).

Our first objective was to establish relationships between coyotes and urbanization and their effects on deer survival and recruitment. Our second objective was to predict how deer abundance will respond to increases in urbanization and coyote density. We used camera trap data to measure how coyote density varies with urbanization and to estimate the initial abundance of deer. We used stage-at-harvest data to estimate deer recruitment and annual

survival considering their stage (adult, juvenile) and sex. We used hunter observations of fawn/doe ratios to estimate recruitment and the results of decoy experiments to estimate survival of fawns through the first month of life. We used an IPM to share deer survival and recruitment parameters among camera trap, harvest, hunter observation and fawn decoy experiment data likelihoods in a two-stage, two-sex Lefkovich projection matrix. Survival and recruitment were allowed to vary as a function of urbanization level and predicted coyote density so we could forecast how future changes in those two factors would affect vital rates. We used these relationships to predict deer populations over 10 years in different scenarios of urbanization and coyote density, presuming no immigration.

Studies in urban areas have suggested a predation paradox wherein predator numbers increase with urbanization but predation rates decline (Fischer et al. 2012). Therefore, we hypothesize that the relationship between coyote density and deer population metrics will vary with urbanization. Specifically, we predict that deer recruitment and survival will be lowest where urban landcover is highest. We further predict that the relationship between coyote density and deer abundance will be mediated by urbanization, with higher coyote densities having less effect on deer abundance at high compared to low levels of urbanization.

Methods:

Study area:

The focus of our study was on four counties in central North Carolina (Chatham, Durham, Orange and Wake), located in the mid-Atlantic region of the United States (Figure 12). These counties contain three major cities, Raleigh (area: 375km², population density: 1,278 people/km²), Durham (area: 280km², population density: 811 people/km²) and Chapel Hill (area:

55km², population density: 1,037 people/km²). Surrounding land use of each city is a combination of agriculture (~24%) and forest (~52%).

Data collection:

We used four different datasets to estimate initial abundance, recruitment and survival of white-tailed deer in our study area (Figure 13). We used citizen-science camera trapping to estimate initial abundance of adults of each sex and juveniles (hereafter “fawns”). We used fawn decoy experiments to estimate the survival of fawns through their first month of life. We used harvest data to estimate fecundity and annual survival for adults of each sex and fawns. We used hunter observations of adult females (hereafter “does”) and fawns along with fawn decoy survival and fecundity from harvest data to estimate recruitment.

Citizen science camera trap surveys: From July through December 2017, we worked with 37 trained volunteers to deploy 55 unbaited camera traps across our study area, covering a total of 3,000km² (Figure 12). Camera site selection was chosen to stratify random camera placement among forested, open (>0.02km² treeless) and developed habitat types proportional to their makeup of the study area. Cameras were placed with a minimum spacing of at least 200m from the adjacent camera (mean=2.8km). Volunteers predominantly used Reconyx (PC800, and PC900, Reconyx, Inc. Holmen, WI) with some using Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS), Browning (Strike Force, Browning Trail Cameras Birmingham, AL) and Primos (Proof Cam 01, Primos Hunting Flora, MS). Camera traps were attached to trees at approximately 40cm above the ground. Trigger sensitivity was set to high for all cameras and we verified that all brands of camera had similar trigger speeds (<0.5s). Cameras

were deployed for three weeks and then moved to a new location. Cameras recorded multiple photographs per trigger, at a rate of 1 frame/s, re-triggering immediately if the animal was still in view. We grouped consecutive photos into sequences if they were <60s apart, and used these sequences as independent records for doe, fawn and coyote abundance estimates (as previously described in Kays et al. 2016). We binned captures into six monthly periods for analysis. We fixed capture probability to zero for cameras that were not operational on a given occasion. Initial species identifications were made by volunteers using customized software (eMammal.org) and all were subsequently reviewed for accuracy before being archived at the Smithsonian Digital Repository (as previously described in Mcshea et al. 2016).

Hunter observations:

During the 2017 hunting seasons hunters across the state were asked by the North Carolina Wildlife Resources Commission (hereafter NCWRC) to complete the North Carolina Deer Hunter Observation Survey to document what species they observed on their hunts, given the number of hours they spent hunting, to get an index of abundance. Potential volunteers were recruited through the big game harvest registration database, public news releases, email blasts, and various staff contacts (Fuller et al. 2018). Using a mailed survey form, hunters were asked to record the date they hunted, number of hours, location type (i.e., public or private land), use of bait, species and sex/stage where applicable and the number of animals seen. The location of these observations was known only to the county level, thus estimates in our model were generated at the county level. Hunters were instructed to report their hunting activity even if no wildlife was observed (Fuller et al. 2018). Approximately 1,300 deer hunters participated encompassing 452,429 observation hours. Hunters recorded an average of 19.4 hunts, averaging

3.4 hours per hunt (Fuller et al. 2018). For use in our model, we removed all observations made over bait and averaged observations of hunters that remained in the same hunting stand for multiple days instead of treating those days as independent samples.

Harvest data:

North Carolina requires that all deer harvests be reported using a Big Game Harvest Report Card which is furnished with the issuance of a big game hunting license each season. All harvest data are reported at the county level. The card distinguishes between adult males (hereafter “bucks”), does and button bucks (fawns). Hunters are instructed to carry the card with them on a hunt and punch a hole in the card next to the relevant sex/age class when a kill is made. They then register the kill within 24 hours to the NCWRC. We used deer harvest data from 2012-2017 in our models.

Fawn decoy survival: We used fawn decoys to quantify the rate of mortality for young (<1month) fawns (Boone 2019). We deployed 37 camera-decoy experiments from May to July 2018 in central North Carolina, timed to match the peak of fawn births (Boone 2019). Each location had an initial two-week survey period where two cameras were placed without the decoy or scent lure to habituate predators (Boone 2019). We used Reconyx RC55, PC800, and PC900 and Bushnell Trophy Cam cameras traps with trigger speed set to high, multiple photographs per trigger, re-triggering immediately if the animal was still in view. We stratified camera placement among two land cover groups (open and forest). Cameras were set ~40cm high in pairs (~10m apart), separated from adjacent sites by at least 200m (Boone 2019). Following the initial habituation period, we set inflatable fawn decoys (Frantic Fawn Predator

Decoy; Primos Hunting, Inc) that closely resembled a bedded neonate in front of each pair of cameras, laying it on its stomach and securing it to a metal stake with a rubber band (Boone 2019). We placed a 12- x20-cm piece of carpet lightly sprayed with fawn urine (The Predator bomb – Fawn Urine; Buck Bomb) under the decoy. No vegetation was cleared in front of the cameras or around the decoy (Boone 2019). If a predator (coyote, bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*) or domestic dog (*Canis lupus familiaris*)) approached within 5 meters of the decoy or physically touched it, we considered this to result in a neonate mortality. Any sites without predators approaching the decoy were classified as a surviving neonate. We considered only the first predator “attack” for each decoy to result in its mortality (Boone 2019).

Coyote density estimates:

We used camera trap data (see *Citizen science camera trap surveys*) to estimate coyote density and its relationship with urban land cover. Since we were unable to individually identify coyotes on camera traps, we used camera trap detections and the spatial count model of Chandler and Royle (2013) (hereafter SCM) to estimate their abundance. This model uses the correlation of spatially referenced counts made at closely spaced detectors to infer the number and locations of animal activity centers. The model is analogous to a spatially explicit capture recapture (hereafter SCR) model where the encounter histories are latent. Specifically, the latent encounter data are related to the trap-level count data according to:

$$n_{jk} = \sum_{i=1}^N z_{ijk}$$

Where z_{ijk} represent the latent encounter data for individual i at trap j on occasion k . N represents the total number of individuals in the population and n represents the trap-level count data. We assume:

$$z_{ijk} \sim \text{Poisson}(\lambda_{ij})$$

Where λ_{ij} is the encounter rate of individual i at trap j and is a function of the distance of that individual's activity center from the trap location (D_{ij}), analogous to a SCR model:

$$\lambda_{ij} = \lambda_0 * \exp\left(-\frac{D_{ij}^2}{2\sigma^2}\right)$$

Where λ_0 represents the detection intensity at the location of the activity center. The σ parameter is key since it defines the extent of space use over the period of study (Royle et al. 2013) and the degree of spatial correlation among counts (i.e., large home range = more cameras and less correlation whereas small home range = fewer cameras and more correlation) (Chandler and Royle 2013). This method is an improvement over simple detection rate, which does not account for double-counted individuals or those that remain undetected. The model has been shown to perform best when either ancillary movement data or a subset of marked individuals are available (Chandler and Royle 2013). Since we did not have any ancillary data on coyote movement nor any marked individuals, we used informative priors on the sigma parameter using a study of coyotes in the Southeast (Hinton et al. 2015) to improve precision and reduce the potential of this method for positive bias (Chandler and Royle 2013). We used the detection rate

of coyotes on our cameras (count/day: mean=0.04, SE=0.01) to set a semi-informative, uniform prior on λ_0 .

$$\lambda_0 \sim \text{Unif}(0, 0.2)$$

$$\sigma \sim \text{Unif}(2500m, 3500m)$$

To account for variation in abundance over our study area and predict abundance for regions of our study area that were not sampled, we assumed an inhomogenous point process model where the location of activity centers s_i are not uniformly distributed across the spatial domain (S):

$$[s_i|\beta] = \frac{\mu_p}{\sum_{s \in S} \mu_p}$$

Where μ_p , the intensity parameter which is allowed to vary spatially, is defined at each point s in the spatial domain and modeled as a function of spatially referenced covariates (Royle et al. 2013). To address our hypotheses about the relationship between urbanization and coyote density, we modeled μ_p as a function of urbanization (percent developed land in a 1km radius; Sohl et al. 2018) such that:

$$\log(\mu_p) = \beta_0 + \beta_1 * X_{urbanization}$$

We did not consider other covariates to facilitate interpretation and prediction. This function returns the expected density of activity centers at location s in the spatial domain. We used this

function to predict coyote density statewide in 1km grid cells and averaged over each county for use in our integrated population model.

To mitigate the computational burden of our models, we used a local evaluation of the individual state-space (LESS; Milleret et al. 2019) which creates square evaluation windows that restrict the spatial domain in which an individual's detection probability and activity center location are able to fall. The width of the detection and activity center windows were set to 5σ and 9σ , respectively, as suggested by Milleret et al. (2019), where σ is the upper bound of the σ prior above.

Integrated population model:

An integrated population model has two main components, a vector of initial abundance estimates for each stage and sex and a projection matrix populated with survival probabilities for each stage and sex and a recruitment rate. We used a Lefkovich matrix with two sexes and two stages (fawn and adult) linking initial abundance of each stage and sex to survival and recruitment (Figure 14). Initial abundances, survival and recruitment were estimated from different data sources using separate likelihoods and the components of these likelihoods shared some parameters in common (Figure 14). Specifically, we were interested in estimating annual survival of bucks and does for which we had very little data, and recruitment which is an important metric for managers to set harvest rates (e.g., Skalski and Millspaugh 2002). We allowed all survival and recruitment rate parameters to vary as functions of covariates and were interested in estimating the relationship between survival/recruitment, urbanization and coyote density. We estimated initial abundance for bucks, does and fawns from camera trap data. We estimated fawn survival through the first month of life using fawn decoy experiments. We

estimated annual survival and fecundity (a component of recruitment) using stage-at-harvest data. Finally, we estimated recruitment using hunter observation data.

Initial buck abundance: We used camera trap data to estimate initial buck abundance for our population model. We identified individual bucks based on their antler pattern (i.e., Parsons et al. 2017). We constructed encounter histories for each individual and analyzed them within a spatially explicit capture recapture framework (Royle et al. 2013). In SCR, the spatial encounter histories at a set of detectors are used to estimate the latent locations of individual activity centers. They are hierarchical state-space models that combine a spatial point process model describing the spatial distribution of individual activity centers, and an observation model, describing the relationship between an individual's detection probability and distance to its activity center. We used a Poisson observation model with a half-normal detection function which assumes that the probability p of detecting individual i at detector j decreases with distance between the detector and the activity center (D_{ij}):

$$p_{ij} = \lambda_0 * \exp\left(-\frac{D_{ij}^2}{2\sigma^2}\right)$$

Where λ_0 represents the baseline encounter frequency at the location of the activity center and σ is the scale parameter (i.e., extent of space used over the period of study) (Royle et al. 2013).

We used uninformative, uniform priors on λ_0 and σ with the σ prior representing the range of home range radius values for resident bucks in the literature (Stewart et al. 2011).

$$\lambda_0 \sim \text{Unif}(0, 1)$$

$$\sigma \sim \text{Unif}(500m, 2000m)$$

Just as for the coyote density model, we assumed an inhomogenous point process model where the location of activity centers s_i were not uniformly distributed across the spatial domain (S). Instead, we allowed abundance to vary as a function of percent tree cover (percent of each 30x30m pixel covered by trees; Hansen et al. 2013) and average housing density (Silvis housing density dataset, houses/square km; Hammer et al. 2004) in a 5km radius and the interaction between the two which have been shown to be important predictors of deer occupancy (Kays et al. 2016). We used a local evaluation of the individual state-space (LESS; Milleret et al. 2019) to improve computation time. The width of the detection and activity center windows were set to $5*\sigma$ and $9*\sigma$, respectively where σ is the upper bound of the σ prior above.

Initial doe abundance: We used camera trap data to estimate initial doe abundance for our population model. Since we were unable to individually identify does on camera traps, we used camera trap detections and SCM to estimate their abundance analogous to our coyote density model. Since we did not have any ancillary data on doe movement nor any marked individuals, we used informative priors on the sigma parameter using a telemetry study of does in the Southeast (D'angelo et al. 2005). We also used an informative, uniform prior on λ_0 by using the estimated λ_0 from the buck SECR submodel (λ_{0Buck}) as a maximum bound.

$$\lambda_0 \sim \text{Unif}(0, \lambda_{0Buck})$$

$$\sigma \sim \text{Unif}(400m, 500m)$$

Just as for the buck SCR model, we assumed an inhomogenous point process, allowing abundance to vary as a function of percent tree cover and average housing density in a 5km radius and the interaction between the two. We used a local evaluation of the individual state-space (LESS; Milleret et al. 2019) to improve computation time. The width of the detection and activity center windows were set to 5000 and 9000, respectively.

Initial fawn abundance: We used camera trap data to estimate initial fawn abundance for our population model. Although we were able to individually identify fawns from camera traps, our traps were spaced too widely to recapture individuals on different cameras, preventing analysis by SCR. Similar to does and coyotes, we used camera detections with SCM and informative priors to account for our lack of information about σ and λ_0 (Epstein et al. 1985).

$$\lambda_0 \sim Unif(0, \lambda_{0Buck})$$

$$\sigma \sim Unif(200m, 300m)$$

Just as for our other abundance models, we assumed an inhomogenous point process and allowed abundance to vary as a function of percent tree cover and average housing density in a 5km radius and the interaction between the two. We used a local evaluation of the individual state-space (LESS; Milleret et al. 2019) to improve computation time. The width of the detection and activity center windows were set to 5000 and 9000, respectively.

We were concerned that because sigma was so small relative to the average spacing of our cameras, we might further bias our estimates (Chandler and Royle 2013). Therefore, we conducted simulation studies to quantify the level of bias we could expect in our estimates due to

large camera spacing relative to sigma, even with the use of highly informative priors. We simulated a dataset with a true sigma of 300m and N=30 randomly distributed individuals. We simulated a random array of cameras throughout the landscape under three different maximum allowed spacings: 200m (“good spacing”), 1km (“okay spacing”), 2km (“bad spacing”). We ran 50 simulations under each spacing scheme and used the results to adjust the uncertainty in our abundance estimates based on the model.

Fawn first month survival: Fawn survival has been shown to be lowest during the first month of life (Kilgo et al. 2012) and fawns typically do not move and are not harvested during that first month (Chitwood et al. 2017). Therefore, we estimated fawn survival for the first month separately from fawn survival to adulthood, which we considered to be the end of their first year, considering only fawns surviving this first month as “recruits” in our model. We used “survival” data from fawn decoy experiments to estimate fawn survival from predation through the first month of life using a logistic exposure model (Shaffer and Thompson 2007). Binary successes (survival, 1) and failures (predation, 0) for each decoy i each day of risk j were modeled as Bernoulli random variables with daily survival probability η_i .

$$y_{ij} \sim \text{Bernoulli}(\eta_i * y_{ij-1})$$

The daily survival probability (η_i) was allowed to vary on the logit scale as a linear function of covariates with uninformative β priors:

$$\text{logit}(\eta_i) = \beta_{0Fawn} + \beta_{1Fawn} * X_1 + \beta_{2Fawn} * X_2 \dots$$

$$\beta_{Fawn} \sim Unif(-5, 5)$$

Specifically, we modeled η_i as a function of site-level urbanization and average coyote density in a 1km radius (see *Coyote density estimates*). We then predicted η_c , the average daily survival rate for each county, using county-level averages for each covariate. Average county-level survival of fawns in the first month of life (29 days) was then given by:

$$\omega_{3m,c} = (\eta_c^{29} * 0.79)$$

Where the 0.79 represents a correction of estimated decoy survival to include additional 21% mortality from other sources (e.g., starvation/abandonment: Saalfeld and Ditchkoff 2007; Kilgo et al. 2012; Chitwood et al. 2015b).

Annual survival: We used the dynamic N-mixture model of Zipkin et al. (2014) to estimate stage and sex-based annual survival rates from stage-at-harvest data collected statewide from 2012-2017 over all 100 counties of North Carolina. Although our initial abundance data were collected in 2017 over four counties of the state, in order to estimate stage-based survival and recruitment from stage-at-harvest data, we needed multiple years of count data. We wanted to use many sites (i.e., counties) to better establish relationships between survival/recruitment and predictors for projection. Furthermore, we felt it was important to incorporate as much information about potential annual fluctuations in these rates, thus we chose to model six years of harvest data to generate estimates for 2017 survival and recruitment that incorporated uncertainty due to annual variation for our projections. The statewide harvest data are collected

by county each year for two stages for male deer (adults and fawns about to transition to adulthood (i.e., button bucks)) and does. We assumed that all button bucks were fawns and all females were adults. The observed harvest count (n_{ict}) of individuals in stage/sex i recorded in each county c during year t is distributed as:

$$n_{ict} \sim \text{Bin}(N_{ict}, \varepsilon_{ict})$$

where ε_{ict} is the stage/sex-specific harvest rate for a given county in a given year. We estimated the harvest rates in our study area outside of our model by dividing the stage/sex-specific harvest counts by their respective abundance estimates (50%, 50% and 14% for bucks, does and fawns, respectively) and added them as data, assuming all counties in all years were harvested at the same rate.

We assumed the initial (year 1 = 2012) population size for each stage/sex in each county (N_{ic1}) is a Poisson random variable with mean (λ_{ic}), using an informative prior to limit it to a 10,000 individual upper bound:

$$N_{ic1} \sim \text{Pois}(\lambda_{ic})$$

$$\lambda_{ic} \sim \text{Unif}(0, 10000)$$

Subsequent years are modeled by allowing transitions between stages by considering the number of individuals that survive (S) and are gained through recruitment (G) in the population as follows:

$$S_{1ct} \sim \text{Bin}((N_{1ct-1} + N_{3ct-1}), (\omega_{1c} * \varepsilon_{1ct}))$$

$$S_{2ct} \sim \text{Bin}((N_{2ct-1} + N_{3ct-1}), (\omega_{2c} * \varepsilon_{2ct}))$$

$$S_{3ct} \sim \text{Bin}(G_{3ct}, (\omega_{3c} * \varepsilon_{3ct}))$$

$$G_{3ct} \sim \text{Poisson}(\gamma_c * \omega_{3mc} * N_{2ct-1})$$

where stage/sex 1, 2 and 3 are bucks, does and male fawns respectively. We assumed that male and female fawns have equal recruitment rates and survival to adulthood (Denicola et al. 2008) and that all does breed each year. We assumed that immigration and emigration were compensatory and did not estimate them under the model. The number of adults surviving of each sex in each county each year is determined by the number of adults and transitioning fawns of a given sex in the previous year and the product of respective annual survival (ω_{ic}) and harvest rates (ε_{ict}). The number of male fawns surviving is determined by the number of recruits (G_{3ct}), average county-level annual fawn survival (ω_{3c}) and the annual county-level harvest rate of button bucks (ε_{3ct}). Stage/sex specific survival rates in each county each year are allowed to vary as a function of average urbanization (percent developed land in a 1km radius; Sohl et al. 2018), average coyote density within each county and their interaction.

$$\begin{aligned} \text{logit}(\omega_{ict}) = & \beta_{0i\text{Survival}} + \beta_{1i\text{Survival}} * X_{\text{urbanization}} + \beta_{2i\text{Survival}} * X_{\text{coyote}} \\ & + \beta_{3i\text{Survival}} * X_{\text{coyote} * \text{urbanization}} \end{aligned}$$

With an uninformative prior on the β parameters to bound ω_{ict} between 0 and 1 on the probability scale.

$$\beta_{Survival} \sim Unif(-1,1)$$

The number of male fawns gained in each county in each year (G_{3ct}) is determined by the fecundity rate (γ_c ; the average number of male fawns produced by each doe in county c) and the probability of survival past the first month of life (ω_{3mc} ; see *Fawn first month survival*) multiplied by the number of does in the county population in the previous year. Note that by incorporating ω_{3mc} into the equation governing the number of recruits in each year, the meaning of annual fawn survival (ω_{3c}) changes to be fawn survival from month 2-12, though we will continue to refer to it as fawn annual survival. The average number of male fawns produced by each doe in county c was allowed to vary as a function of average urbanization (percent developed land in a 1km radius; Sohl et al. 2018) and average coyote density within each county and their interaction.

$$\begin{aligned} \log(\gamma_c) = & \beta_{0Recruit} + \beta_{1Recruit} * X_{urbanization} + \beta_{2Recruit} * X_{coyote} \\ & + \beta_{3Recruit} * X_{coyote*urbanization} \end{aligned}$$

With an informative prior on the β parameters to bound γ_c between 0 and 1.5 male fawns per doe (Witham and Jones 1992).

$$\beta_{Recruit} \sim Unif(-0.3, 0.3)$$

Since our census took place right before fawns transitioned to adulthood and we considered all fawns to reach adulthood at one year of age, we did not model a transition probability. Our goal

was to estimate the county-level annual survival parameters ω_{ic} , which requires estimation of the true abundance of each stage/sex i in county c in year t (N_{ict}). The stage-specific abundances in a given county c in year t are then determined by:

$$N_{1ct} = S_{1ct} + S_{3ct}$$

$$N_{2ct} = S_{2ct} + S_{3ct}$$

$$N_{3ct} = G_{3ct}$$

Recruitment: We estimated average recruitment from hunter observation data statewide in 2017 using a generalized linear model with a log-link to predict doe counts. We assumed that the count of does in each county c was distributed as a Poisson random variable with mean $\lambda_{dc} * p_{dc}$ and that the count of fawns was distributed as a Poisson random variable with mean $(2\gamma_c * \lambda_{dc} * \omega_{3mc} * p_{fc})$:

$$C_{dc} \sim \text{Poisson}(\lambda_{dc} * p_{dc})$$

$$C_{fc} \sim \text{Poisson}(2\gamma_c * \lambda_{dc} * \omega_{3mc} * p_{fc})$$

where γ_c and ω_{3mc} are the number of male fawns produced by each doe in county c , estimated from harvest data (see *Annual survival*), and fawn survival probability in the first month of life in county c , estimated from fawn decoys (see *Fawn first month survival*), respectively. To account for differences in detection probability between does and fawns, we added county-specific detection probability terms to each likelihood (p_{dc} and p_{fc} , respectively). To estimate detection probabilities, we summed the hunter observation counts over our four focal counties

and used our estimates of doe (N_2 ; see *Doe initial abundance*) and fawn (N_3 ; see *Fawn initial abundance*) abundance within the model to link abundance, counts and detection probabilities:

$$C_{dFocal} \sim \text{Poisson}(N_2 * p_{dFocal})$$

$$C_{fFocal} \sim \text{Poisson}(N_3 * p_{fFocal})$$

We then used p_{dFocal} and p_{fFocal} as informative priors for p_{dc} and p_{fc} , respectively:

$$p_{dc} \sim \text{Normal}(p_{dFocal}, 0.1) T(0,1)$$

$$p_{fc} \sim \text{Normal}(p_{fFocal}, 0.1) T(0,1)$$

We modeled λ_{dc} as a function of average urbanization (percent developed land in a 1km radius; Sohl et al. 2018) and average coyote density within each county and their interaction.

$$\log(\lambda_{dc}) = \beta_{0Doe} + \beta_{1Doe} * X_{urbanization} + \beta_{2Doe} * X_{coyote} + \beta_{3Doe} * X_{coyote*urbanization}$$

With an uninformative prior on the β parameters.

$$\beta_{Doe} \sim \text{Normal}(0, 0.01)$$

We considered county-level recruitment (ρ_c) to be the product of $2\gamma_c$ and ω_{3mc} since we considered true “recruits” to be those fawns that were born and survived the risky first month of life:

$$\rho_c = 2\gamma_c * \omega_{3mc}$$

By sharing the γ_c and ω_{3mc} parameters between models, we are able to fully integrate the three likelihoods, increasing our ability to precisely and accurately estimate these parameters (Zipkin and Saunders 2018).

Population projections:

Key quantities of coyote density, recruitment and stage/sex-specific survival and harvest rates were modeled as linear functions of covariates, allowing us to predict changes in these quantities given changes in the covariates used to model them. To test our hypotheses about the potential effects of increases in urbanization on coyote density and deer abundance, we predicted deer survival and recruitment as functions of low, medium and high levels of urbanization (10, 49, 90% in a 1km radius) and coyote density (0.03, 1.18, 2.7 coyotes/km²), respectively. We predicted each quantity for each combination of urbanization and coyote density using the β coefficient estimates from 2017 associated with each submodel. For each combination of urbanization and coyote density, we populated our projection matrix with predicted survival and recruitment vital rates and projected our model forward 10 years using:

$$N_{1y} = (N_{1y-1} * \omega_{1y} * (1 - \varepsilon_{1y})) + ((\frac{N_{3y-1}}{2}) * \omega_{3y} * (1 - \varepsilon_{3y}))$$

$$N_{2y} = (N_{2y-1} * \omega_{2y} * (1 - \varepsilon_{2y})) + ((\frac{N_{3y-1}}{2}) * \omega_{3y})$$

$$N_{3y} = N_{2y-1} * \rho_y$$

Where N_{1y} , N_{2y} and N_{3y} are the predicted abundances of bucks, does and fawn (of both sexes combined), respectively, in our four focal counties for each year of projection, with N_{11} , N_{21} and N_{31} being the initial abundances in 2017 estimated from camera trap data. Buck, doe and fawn average annual survival probabilities over our focal counties are given by ω_{1y} , ω_{2y} and ω_{3y} , respectively. Buck, doe and male fawn average harvest rates over our focal counties are given by ε_{1y} , ε_{2y} and ε_{3y} , respectively, and were assumed constant based on rates in our focal counties in 2017. Finally, ρ_y is the average recruitment of fawns (of both sexes combined) per doe in our four focal counties for each year of projection. Note that ρ_y represents the number of fawns produced by each doe that survive the risky first month of life.

Immigration and harvest rates can have profound effects on abundance projections (i.e., whether they are increasing, decreasing or stable) but estimating these rates are challenging. We tested three scenarios of immigration and harvest rates for our four focal counties to demonstrate the sensitivity of projections to changes in these rates. We tested harvest levels of 2%, 5% and 50% for adult males and females, with juvenile harvest rates being 28% of adult harvest rates (i.e., 0.006, 0.01 and 0.14, respectively) based on relative harvest rates calculated from initial abundance estimates and harvest count data. We tested immigration levels of 0, 1000 and 1500 adult male and adult female annual immigrants to the population.

We used USGS landcover projections (Sohl et al. 2018) to predict what we might expect for the deer population in our study specific to actual predicted increases in urbanization over the next 10 years, rather than theoretical levels of each covariate. We first predicted coyote density

using the beta coefficient values estimated under our coyote density model (see *Coyote density estimates*) and the amount of urbanized landcover predicted in each year by the USGS. We then generated predictions each year for deer survival and recruitment by using the β coefficient estimates from 2017 associated with each submodel and predicted values of urbanization and coyote density each year. We averaged survival and recruitment estimates each year over our four counties to generate a single yearly estimate of recruitment and annual survival for each stage and sex to use in our projection matrix. We then projected buck, doe, fawn and the total population abundance forward over the 10-year period using the survival and recruitment rates predicted for each year.

Parameter sharing test:

To determine if the sharing of parameters in an integrated population modelling framework improved estimate precision, we also ran our submodels separately, with no sharing of parameters or integrated framework. Our separate submodels were structurally the same as their counterparts in our model with parameter sharing, except for the lack of shared parameters. Specifically, for our annual survival model (see *Annual survival*), instead of sharing fawn probability of survival past the first month of life, (ω_{3mc} ; see *Fawn first month survival*) with the fawn decoy and hunter observation likelihoods, it was simply given an uninformative prior:

$$\omega_{3mc} \sim \text{Unif}(0,1)$$

Additionally, in our recruitment model we removed the sharing of γ and ω_{3mc} (see *Recruitment*) and instead assumed that the count of does in each county c was distributed as a Poisson random

variable with mean $\lambda_{dc} * p_{dc}$ and that the count of fawns was distributed as a Poisson random variable with mean $\lambda_{fc} * p_{fc}$:

$$C_{dc} \sim \text{Poisson}(\lambda_{dc} * p_{dc})$$

$$C_{fc} \sim \text{Poisson}(\lambda_{fc} * p_{fc})$$

Where p_{dc} and p_{fc} are county-level doe and fawn detection probabilities, respectively. Since we did not share parameters in this model, detection probabilities were not modeled using initial abundance estimates, instead they were simply given uninformative priors:

$$p_{dc} \sim \text{Unif}(0,1)$$

$$p_{fc} \sim \text{Unif}(0,1)$$

We modeled λ_{dc} and λ_{fc} as functions of urbanization (percent developed land in a 1km radius; Sohl et al. 2018) and average coyote density within each county (N=100).

$$\log(\lambda_{dc}) = \beta_{0Doe} + \beta_{1Doe} * X_{urbanization} + \beta_{2Doe} * X_{coyote} + \beta_{3Doe} * X_{coyote*urbanization}$$

$$\log(\lambda_{fc}) = \beta_{0FawnC} + \beta_{1FawnC} * X_{urbanization} + \beta_{2FawnC} * X_{coyote} + \beta_{3FawnC} * X_{coyote*urbanization}$$

We calculated a county-level recruitment parameter (ρ_c) for use in our projection matrix as the ratio of fawn to doe counts:

$$\rho_c = \lambda_{fc}/\lambda_{dc}$$

Since fawns are bedded and not likely to be detected during the first month of life, this measure also represents true “recruits” (i.e., those fawns that were born and survived the risky first month of life).

Model fitting: We fit our models in JAGS (Plummer 2003) via the runjags (Denwood 2016) interface in R (Version 3.4.0, R Development Core Team 2008) via R Studio (Version 1.0.143, Rstudio Team 2015). We ran three chains, using trace plots to determine an adequate burn-in phase and subsequently running chains until the Brooks–Gelman–Rubin convergence diagnostic indicated adequate convergence ($\hat{R} < 1.1$; Gelman et al. 2014). All models achieved adequate convergence by running for 200,000 iterations following a burn-in phase of 5000 iterations. Methods for assessing goodness-of-fit for integrated population models have not been established, so we assessed the fit of each submodel separately using posterior-predictive checks (PPC) (Schaub and Abadi 2011). We calculated a Freeman-Tukey statistic from observed data T_y and from data simulated assuming a given submodel was the data-generating model ($T_{y_{sim}}$). We calculated a Bayesian P -value as:

$$P_B = \Pr(T_{y_{sim}} > T_y)$$

from posterior simulations and assumed adequate fit if $0.1 < P_B < 0.9$. For buck initial abundance, our PPC critical values were assessed based on expected and observed individual encounter frequencies at each detector. These critical values have been assessed by other authors and found to be meaningful for SCR models (Royle et al. 2013). For initial fawn and doe abundance, our PPC critical values were assessed based on expected and observed trap frequencies on each occasion, analogous to SCR.

Results:

All models fit well with Bayesian p values $0.1 < p < 0.9$ except the doe and fawn initial abundance models for which $p=0$, indicating poor model fit. This is not surprising given the large camera spacing relative to the expected sigmas, especially for fawns. Our simulations indicated that we could expect a 26% positive bias on our fawn abundance estimates using the Chandler-Royle method due to large camera spacing. To account for this, we added a 26% lower bound to our estimate of uncertainty for initial fawn abundance in the fawn abundance submodel.

Density, survival, fecundity and recruitment estimates generally aligned well with other studies of deer and coyotes in urban/suburban/exurban areas, although recruitment tended to be high (Table 4). Our estimate of doe annual survival was similar to estimates from a recent telemetry study in Cumberland County, NC, however fawn 1-month survival was high (Table 3; Chitwood et al. 2015a; Chitwood et al. 2015b).

Submodel results

Initial abundance and covariate relationships

Over 1101 trap nights at 55 camera sites over four counties, we detected coyotes on the camera traps 53 times and estimated average coyote density in 2017 to be 1.01 (95% CI: 0.43, 2.55) individuals/km². Our models estimated a positive but weak relationship between coyote density and urbanization (Table 6). We captured bucks 351 times, does 535 times and fawns 108 times on our cameras. We identified 61 individual bucks an average of 1.8 times (SE=0.17) each. Estimated population sizes for bucks, does and fawns in 2017 were 7687 (95% CI: 2035, 19880), 4056 (95% CI: 1979, 11860) and 5080 (95% CI: 1549, 14070), respectively, corresponding to densities of 2.56 (95% CI: 0.68, 6.63), 1.35 (95% CI: 0.67, 3.95) and 1.69 (95% CI: 0.52, 4.69) individuals/km². The estimated total deer density in our study area was 5.61 (95% CI: 1.85, 15.27) individuals/km².

Survival, recruitment and covariate relationships

Survival and recruitment for both sexes and stages of white-tailed deer were significantly associated with both the percent of developed land (i.e., urbanization) and coyote density, and their relationship with coyote density varied with urbanization (Table 6). Estimates were generally highest in areas of high urbanization or showed a positive relationship with coyote density in areas of high urbanization (Figure 15). We found that annual survival for all stages and sexes had a positive or neutral relationship with coyote density in areas of high urbanization, a neutral or negative relationship with coyote density at medium levels of urbanization and a consistent negative relationship at low levels of urbanization (Figure 15). Fecundity had a negative relationship with coyote density at high and medium levels of urbanization with a

neutral relationship at low levels of urbanization (Figure 15). Recruitment and fawn first month survival were positively associated with coyote density at low levels of urbanization and showed a negative or neutral association at high levels of urbanization (Figure 15). Recruitment estimates were significantly higher compared to a model with parameter-sharing that assumed equal detection probability of does and fawns in the hunter observation data (Table 7).

Integration test

Abundance estimates from our model without parameter-sharing tended to be higher and more uncertain than parameter-sharing estimates, but 95% credible intervals from both models overlapped substantially (Table 8). Estimates for shared parameters (fawn 1-month survival, fecundity and recruitment) were more precise or equally precise when estimated within a parameter-sharing framework than when they were estimated separately, without parameter sharing (Figure 16). However, the adult survival parameters were more precise when the stage-at-harvest data were analyzed separately, without sharing the fecundity and fawn 1-month survival parameters with their respective data likelihoods (Figure 16). This is most likely a result of the annual survival model being overfit when run separately, so that distinguishing between fecundity, fawn 1-month survival and annual survival becomes impossible without additional data, resulting in overly precise and potentially biased estimates (Hooten and Hefley 2019).

10-year projection

We used different levels of urbanization and coyote density to predict new recruitment and survival rates, then projected the deer population forward 10 years. Assuming compensatory immigration/emigration and homogenous adult harvest rates at 50% (juveniles 14%), we found

that the population projections declined at all levels of urbanization and coyote density. Increases in net immigration of 1000 adult males and females per year stabilized the population and 1500 adult males and female net yearly immigration resulted in an increasing population (Figure 17). Likewise, decreases in average harvest rate from 50% to 5% stabilized the population, and harvest rates of 2% resulted in an increasing population, assuming compensatory immigration and emigration (Figure 18). Regardless of the trajectory, relative changes in abundance over time showed significantly lower deer abundance in areas of low urbanization compared to high (i.e., $\geq 90\%$) and medium (i.e., $\geq 49\%$) levels, except where coyote densities are high (i.e., ≥ 2.7 coyotes/km²). Where coyote densities are high, our model predicted that deer abundance in areas of low urbanization would be significantly lower than areas of high urbanization, but statistically similar to areas of medium urbanization (Figure 19). We used USGS landcover projections (Sohl et al. 2018) to predict what we might expect for the deer population in our study area given projected increases in urbanization over the next 10 years. The USGS predicts that the average amount of developed land in a 1km radius in our study area will increase by 11% from 2017 to 2026 (Sohl et al. 2018). In response to that increase, we predicted an increase in coyote density of 1% over the same period. Projections of the deer population into the future based on those predicted increases showed trends consistent with what we would predict for a medium-development, medium-coyote density area (Figures 17, 18).

Discussion:

Our model differs from many other recent IPMs in that we used predominantly “low quality” datasets (i.e., harvest and count data) that are not considered as robust as capture-recapture, telemetry or distance-sampling data in estimating population parameters. Nevertheless, harvest

and count datasets are often the only datasets available for large-scale management of species in the United States and we are not the first to use them within an IPM framework. Indeed, past studies have shown good success using harvest and count data within an IPM, in terms of estimates aligning with those from more robust datasets (e.g., Fieberg et al. 2010). To our knowledge, however, this is the first published application of an IPM to white-tailed deer. Our estimates of abundance, survival and recruitment, when compared to other studies of white-tailed deer population metrics in developed areas using more robust datasets, were generally similar, falling within or overlapping the ranges estimated by other studies. Indeed, when we compared our estimates of doe annual survival to a recent telemetry study in Cumberland County, NC (Chitwood et al. 2015a), we found good agreement, showing how commonly collected data requiring less effort can yield similar results. However, our estimate of fawn 1-month survival in Cumberland County, NC was significantly higher than estimates from a recent telemetry study in the same county (Chitwood et al. 2015b). It's possible that the broad scale covariates we used to predict fawn 1-month survival were not sufficient to capture variation in this metric over space, lead to an overestimate of fawn 1-month survival. However, it's also possible that the habitat (e.g., low nutritional value and extensive edge, ideal for coyote hunting behavior) of our comparison study site contributed to increased predation and starvation rates over what is found in the rest of the county (Ncwrc 2018).

Benefits and drawbacks of using an IPM for white-tailed deer management

We show that integration of harvest, count and capture-recapture datasets can not only provide similar results to more robust datasets, but can be more precise and potentially provide less biased estimates than if any of those were used on their own (Maunder and Piner 2017; Saunders

et al. 2019). For example, our recruitment estimates tended to be higher than comparable studies, including estimates from the NCWRC. This is most likely because we corrected for differences in detection probability in our fawn and doe counts where other studies did not. Our estimates of detection probability were higher for does than fawns, as is expected based on fawn small body size and cryptic coloration, resulting in significantly higher recruitment estimates than if detection probability had been assumed equal. This shows how leveraging the parameter-sharing ability of an integrated population model can improve estimates by adding additional data to estimate each parameter, giving critical insights important to management.

When abundance, survival and recruitment are estimated separately and means used to populate a projection matrix, there is no formal way to account for estimate uncertainty (variances and covariances) and so population abundances and changes over time will appear overly precise. This is especially problematic for cases where a management decision could be made with a narrowed view of potential outcomes. By using an integrated population model, all sources of uncertainty arising from each component dataset are adequately included (Schaub and Abadi 2011), giving a more realistic accounting of possible projection outcomes.

Integrated population models can offer potential solutions to problems of difficult to estimate quantities. Using stage-at-harvest data to estimate survival and fecundity simultaneously resulted in overparameterization (i.e., not enough data to estimate both; Hooten and Hefley 2019). This likely contributed to the high precision in our survival estimates for our model without parameter sharing. By using an integrated population model, we were able to combine harvest data with hunter observations and fawn decoy experiments to provide more information to estimate fecundity, which allowed our stage-at-harvest model to estimate annual survival with a more realistic measure of uncertainty.

Although integrated population models offer a flexible framework to combine many disparate datasets of different spatial and temporal scales, if integrated data sources conflict (i.e., show different trends or give wildly different estimates) population inference may be misleading. This is particularly problematic when there is feedback between the demographic processes, common with parameter-sharing models (Saunders et al. 2019). The integrated population modelling framework can be leveraged to address these issues of conflicting data, but the problem must first be recognized. Another drawback of integrated population models is that they are complex and can be difficult to fit. They may require more computation time than running each model component separately. Given enough data, the simple approach might provide the required answers just as well as a fully integrated approach for less time and computational effort.

Urbanization mediates how deer survival and recruitment are related to coyote density

Past studies have suggested that coyotes play an important role in regulating prey species in urban/suburban habitats where hunting is prohibited (Jones et al. 2016). We found that deer survival and recruitment rates were significantly related to coyote density and the relationship depended on the amount of urban development. This supports our hypothesis that the deer population would respond to changes in coyote density, but that the effect would vary with urbanization. Our survival and recruitment estimates were generally highest in areas of high urbanization, supporting our prediction that the effect of coyotes would be lowest where urban landcover was highest. This is likely due to highly productive habitats with low predation rates, consistent with other studies of deer in urban areas (Denicola et al. 2008). Although recruitment and fawn survival through the first month of life were significantly lower at low levels of

urbanization, they showed a positive, though highly uncertain, relationship with coyote density. This suggests a saturating effect wherein, at a certain point at low urbanization, more coyotes do not necessarily equate to higher predation rates on fawns (Solomon 1949). We also noted a significant negative relationship between fecundity and coyote density at high levels of urbanization. This could be due to deer being more stressed at high housing densities, increasing vigilance rates and decreasing feeding rates, which is compounded in the presence of a high concentration of coyotes (e.g., Boonstra et al. 1998). This result requires more study and would benefit from the addition of direct fecundity data to interpret.

Dynamics between coyotes and deer are more complicated than simply “more coyotes=fewer deer”

High coyote densities (i.e., 2.7 coyotes/km²) are predicted to decrease deer abundance at low (i.e., 10%) and medium (i.e., 49%) levels of urbanization. However, at high levels of urbanization, our projections suggest that a high coyote density will have less effect on deer abundance. This supports our prediction that the relationship between coyote density and deer abundance is mediated by urbanization and shows that the predation dynamics between coyotes and deer are more complicated than simply “more coyotes=fewer deer”, consistent with a “predation paradox” in urban areas. For example, although coyote density may be high, predation rates on deer could be low due to predator saturation or if coyotes are exploiting other concentrated urban food sources (i.e., abundant rodents/lagomorphs, pets, other anthropogenic food sources) (Poessel et al. 2017). The complex relationship between these two species and humans deserves more research to better predict population dynamics and mitigate associated human-wildlife conflict. Furthermore, our projections assume that the relationship between

coyotes and urbanization will be the same in 2026 as it was in 2017. Increasingly, studies are considering the concept of non-stationarity when estimating relationships in time and space (e.g., Miller 2012; Pease et al. In Prep). As coyotes adapt more to suburban landscapes (Bateman and Fleming 2012) we might expect larger increases in density and levels of predation, leading to consequences we are unable to predict.

Model assumptions and limitations

Our modeling results are conditional on a number of assumptions: 1) we assumed density-independence, 2) we assumed all does bred at the same rate each year 3) we assumed the amount of urban landcover was the only driver of deer and coyote populations 4) we assumed compensatory immigration and emigration and 5) we assumed harvest rates were constant across counties and years. We believe density dependence is not a critical factor driving deer population dynamics in our study given that even at densities far exceeding our estimates (e.g., 25-60 deer/km²), density-dependence has been difficult to confirm in deer populations (Deyoung et al. 2008). However, the addition of density-dependence into IPMs is an area of active research (Schaub and Abadi 2011) and will be key to improving the applicability of this modeling technique for urban wildlife populations. We assumed that all does bred at the same rate each year which is reasonable for highly productive habitats like urban areas (e.g., Denicola et al. 2008), however studies have shown that yearling does tend to be less productive than older does (e.g., Fortin et al. 2015) which could have biased our fecundity estimates high. To isolate our inference to the effect of urbanization, we did not consider other factors that could influence coyote and deer populations which could have oversimplified our inference. For example, forest cover and hunting rates are important predictors of coyote and deer occupancy (e.g., Kays et al.

2016). Although they are generally correlated with urbanization (i.e., where urban landcover is high, forest cover and hunting rates are low), they could induce additive effects which, when ignored, produce homogenous estimates of abundance and/or bias estimates low.

Our assumptions of compensatory immigration/emigration and homogenous harvest rates across counties and years are key drivers of abundance projection trends. By increasing either net immigration or decreasing harvest rates, our projections change from decreasing to stabilizing to increasing. These two factors are critical to providing realistic population projections yet are notoriously difficult to estimate. Absent direct data on harvest rates, we inferred them from our initial abundance estimates and harvest counts and assumed they were constant over time and space which is unrealistic given known heterogeneity in harvest regulations and hunter population size (Winkler and Warnke 2013). Furthermore, our homogenous harvest rates were high and resulted in declining projections. True mean heterogenous harvest rates are likely substantially lower since ~24% of land in our study area prohibits hunting. A lower mean harvest rate would result in a stable or growing population, which better reflects what is already known about deer populations in our study area (Bragina et al. 2019; Ncwrc 2019).

In addition to the population model itself, each submodel has its own assumptions, which, when violated, can affect estimates of shared parameters and parameters not directly informed by data (Riecke et al. 2019). Key assumptions of our submodels were 1) demographic closure 2) 1:1 fawn sex ratio at birth 3) harvest reporting rates were 100%. Our capture-recapture and initial abundance counts spanned six months through the rut period when males are especially mobile, making it likely that dispersal and long-distance movements took place during our study. Although these scenarios violate the closure assumption, estimators remain unbiased if movements in and out of the study area are completely random (Kendall 1999). If movements

are not random, our abundance estimates could be biased high. Although studies have shown variability in the sex ratio of fawns based on doe age (Verme 1983), on average across the populations, the sex ratio of produced fawns should be balanced (e.g., Ebersole et al. 2007; Denicola et al. 2008). Harvest reporting rates are an important source of error in stage-at-harvest models that we ignored due to a lack of data to estimate these rates. This could have resulted in actual harvest rates being higher than the harvest counts indicated, which would result in our annual survival and fecundity estimates being biased high.

Future directions

There are a number of pieces of data that would help improve our model for management purposes. First, other important landscape factors should be added as predictors (e.g., the amount of agricultural land, hunting, road density) to improve estimates of coyote density and deer survival, recruitment and abundance. Second, explicit data on fecundity, age distribution and harvest reporting rates would help better parameterize our annual survival model. Third, harvest rates are known to vary spatially and temporally (Norton et al. 2012) and estimates can have considerable influence on abundance projections (Collier and Krementz 2007) thus, heterogeneity in harvest over space and time should be explicitly modeled to provide more realistic abundance projections. Fourth, data on immigration and emigration rates should be explicitly modeled, or estimates used from the literature, to allow some level of net immigration. Fifth, more robust initial abundance and survival data would be beneficial, especially for fawns where capture-recapture is possible with a targeted sampling design (e.g., Chandler et al. 2018). Finally, a more explicit estimation of transient behavior could be incorporated into the model using Pollock's robust design to relax the assumption of closure in initial abundance estimates.

Conclusions

Several recent studies have looked at the link between coyote predation and deer vital rates in the Southeast (e.g., Kilgo et al. 2012; Chitwood et al. 2015a; Bragina et al. 2019), concluding that large-scale coyote effects on prey in the region remain small. However, as urbanization in the region increases and coyotes respond positively, there is potential for coyote predation to affect deer abundance, even in suburban areas. Since the effect of predation on prey populations can vary due to a number of factors (e.g., land cover, density, hunting, other mortality factors), simply monitoring trends in coyote and deer abundance over time may not be enough to predict long-term effects, especially under changing conditions. There is a consensus that coyotes could have an impact in the future (Bragina et al. 2019) and a model-based approach that considers all of these factors can help managers understand how best and when to adapt harvest regulations in the face of growing coyote populations. White-tailed deer are one of the most data-rich species in the world, with wildlife agencies throughout the region collecting harvest data, observational data, fecundity data, camera-trap data and age distribution data regularly. Recently developed tools such as integrated population models provide a framework through which we can leverage and use these disparate datasets, providing the potential for a more detailed understanding of population dynamics to better address the complex questions facing wildlife managers in a rapidly changing world.

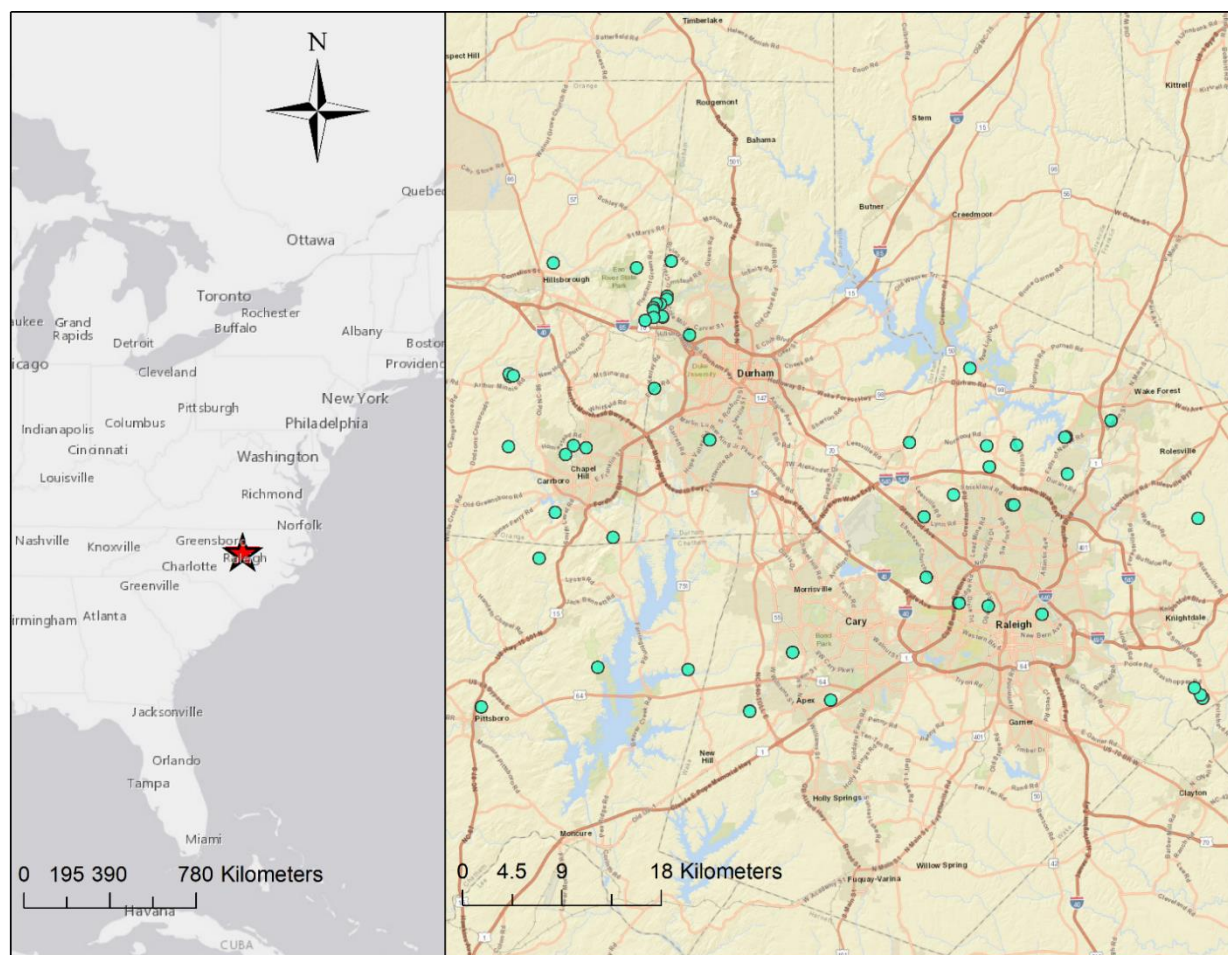


Figure 12: A map of camera locations in central North Carolina, located over four counties with three major cities. Cameras were set by citizen scientists and run from July-December 2017.

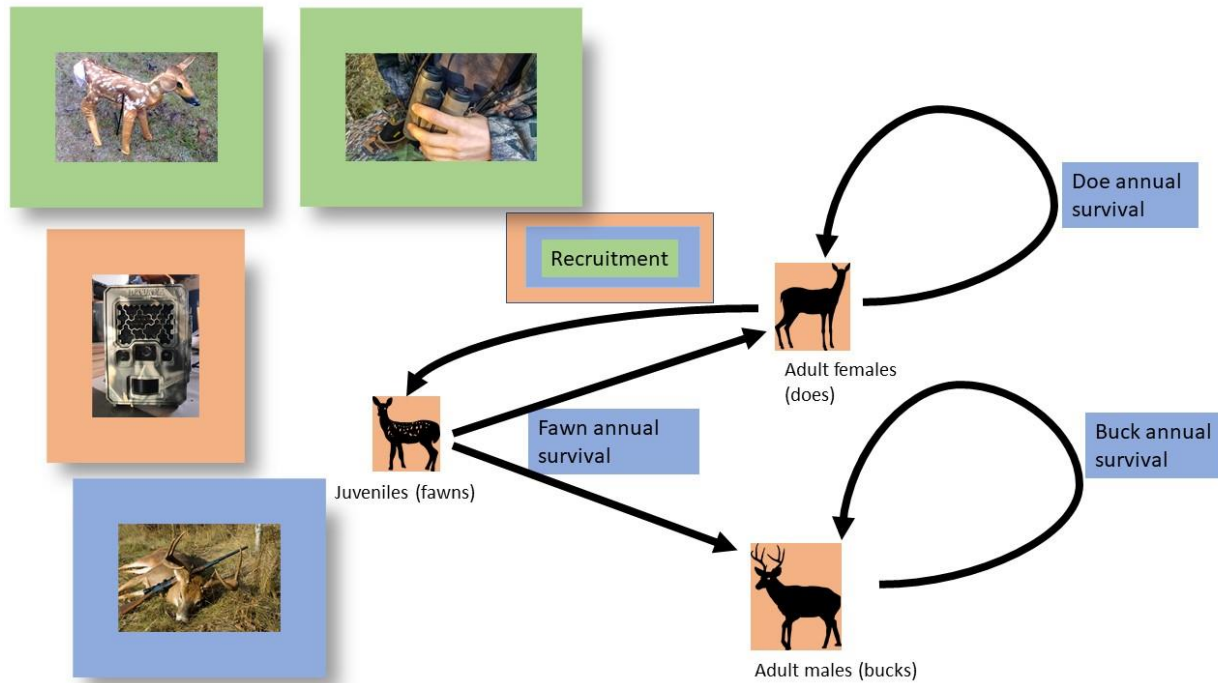


Figure 13: White-tailed deer life cycle diagram highlighting the data sources used to estimate each element for a population of white-tailed deer across four counties in North Carolina. Initial abundance for adults of each sex and fawns were estimated using citizen-science camera trapping (orange highlight). Annual survival of adults and fawns and fecundity were estimated using harvest data (blue highlight). Recruitment was estimated using hunter observations of does and fawns and fawn decoy experiments (green highlight) which allowed us to correct fecundity estimates from harvest data (blue highlight) to account for survival over the risky first month of life. Those fawns born that survived the risky first month of life were considered recruited into the population. Recruitment from hunter observations was further corrected for detection probability differences using initial abundance estimates (orange highlight).

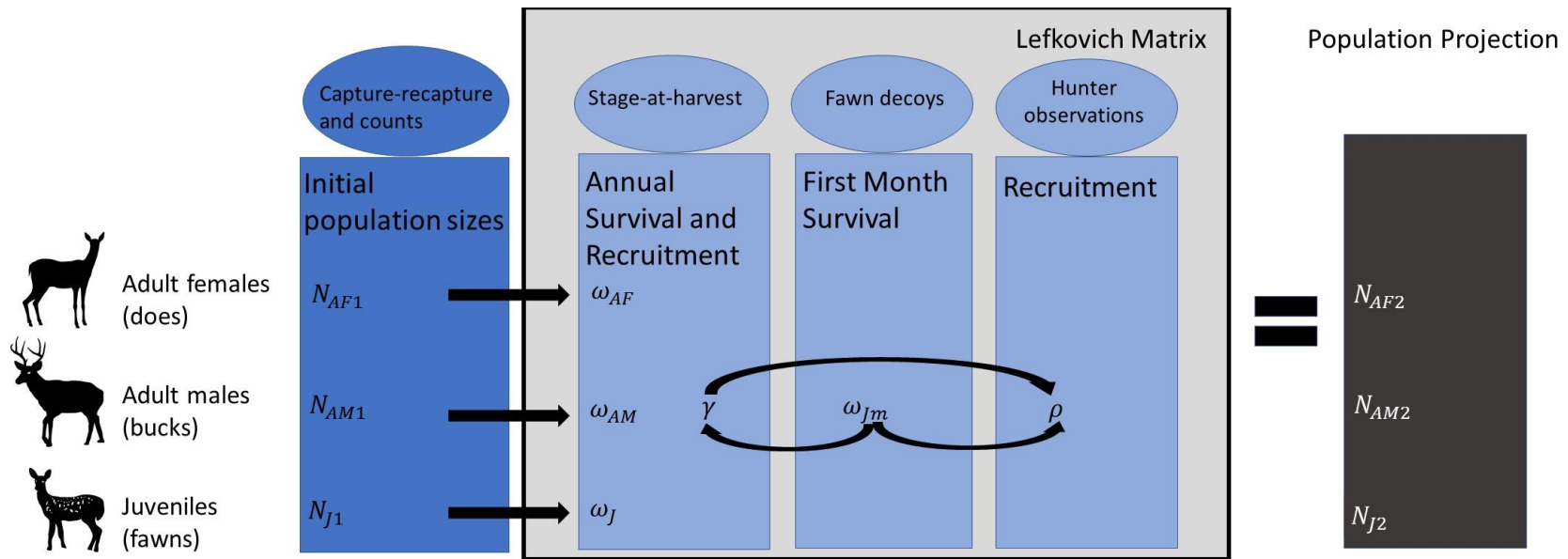


Figure 14: Model structure and integration for white-tailed deer across four counties in North Carolina. Initial abundance estimates for each sex and stage were estimated from camera trap data from July-December 2017. The core of the model is a Lefkovich projection matrix with two sexes and two stages (fawn and adult), survival parameters for each sex/stage and a recruitment parameter. Annual survival (ω) and fecundity (γ) were modeled from stage-at-harvest data collected between September-January over six years (2012-2017). The survival of fawns in the first month of life (ω_{Jm}) was estimated using fawn decoy experiments from predation and was shared with the annual survival model. The recruitment parameter (ρ) was modeled as the ratio of fawn:doe counts from hunter observation data, incorporating both fecundity (γ), survival of fawns in the first month of life (ω_{Jm}) and an estimate of detection probability informed by initial abundance estimates (black arrows).

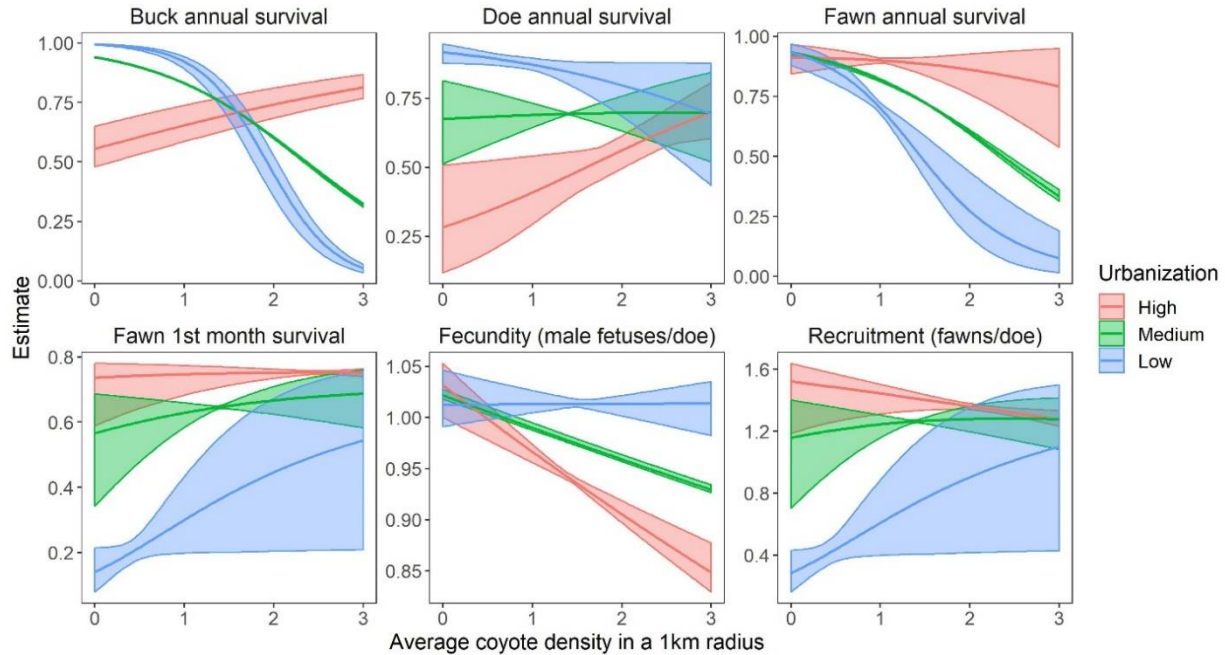


Figure 15: Relationships between deer vital rates and coyote density across three levels of urbanization. Predictions apply to four counties of central North Carolina in 2017 at high (80%), medium (40%) and low (10%) levels of anthropogenic development. Lines are posterior means and shading shows 95% credible intervals. Recruitment represents the number of fawns produced by a doe that survive the first month of life. All vital rates except doe annual survival and fecundity were lowest at low levels of urbanization and highest at high levels of urbanization. Annual survival had a negative relationship with coyote density in rural areas but a positive or neutral relationship at higher levels of urbanization. However, fawn survival through the first month showed the opposite relationship, being positively associated with coyote density in rural areas. Recruitment and fecundity also had a positive or neutral relationship with coyote density at low and a negative relationship with coyote density at high levels of urbanization.

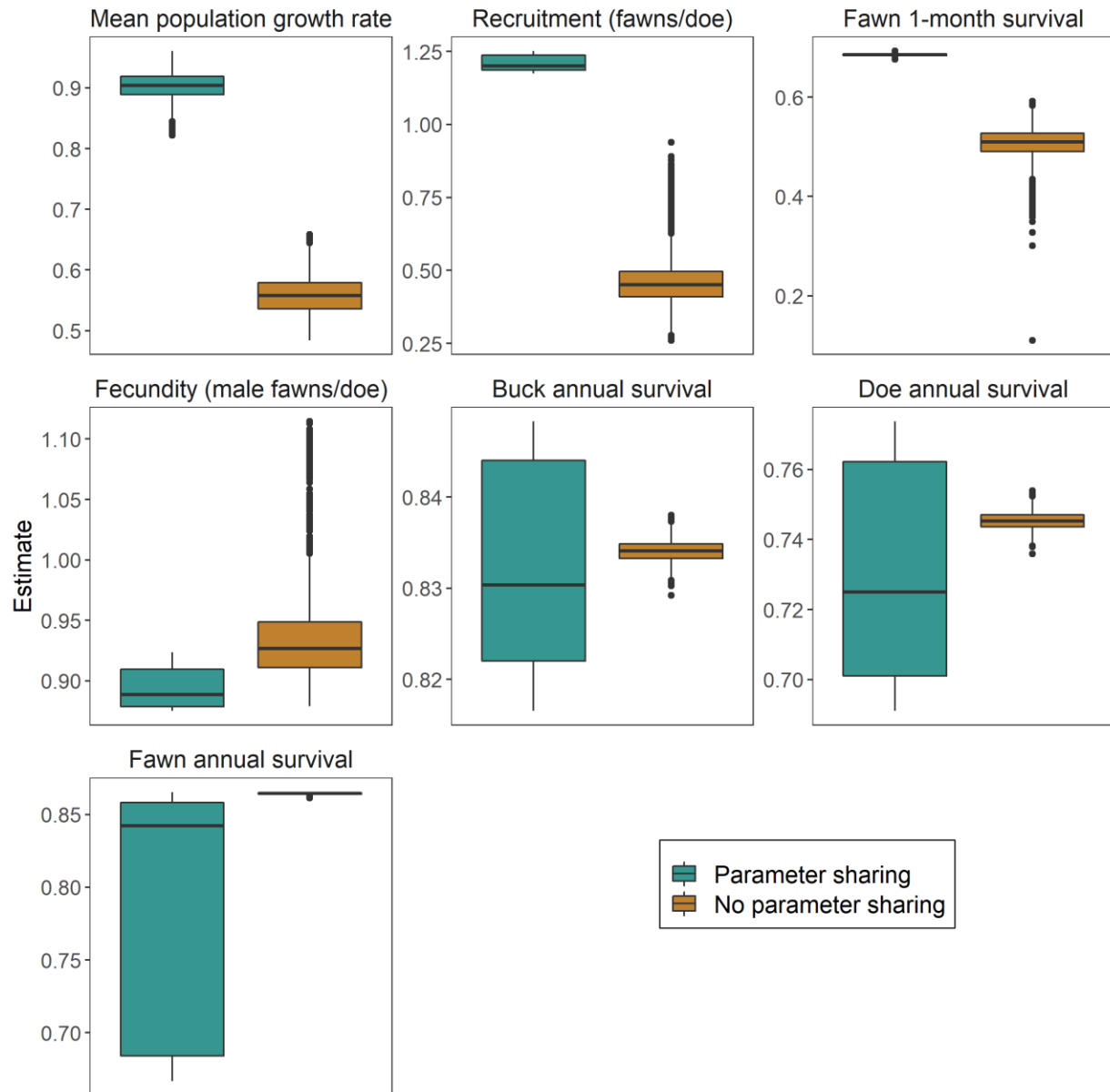


Figure 16: Parameter estimates for a white-tailed deer population in four counties of central North Carolina in 2017. Estimates are compared between an integrated population model with parameter sharing between submodels with three submodels estimating annual survival and fecundity, fawn 1-month survival and recruitment, respectively. This is compared to estimates where submodels were run separately and without parameter sharing.

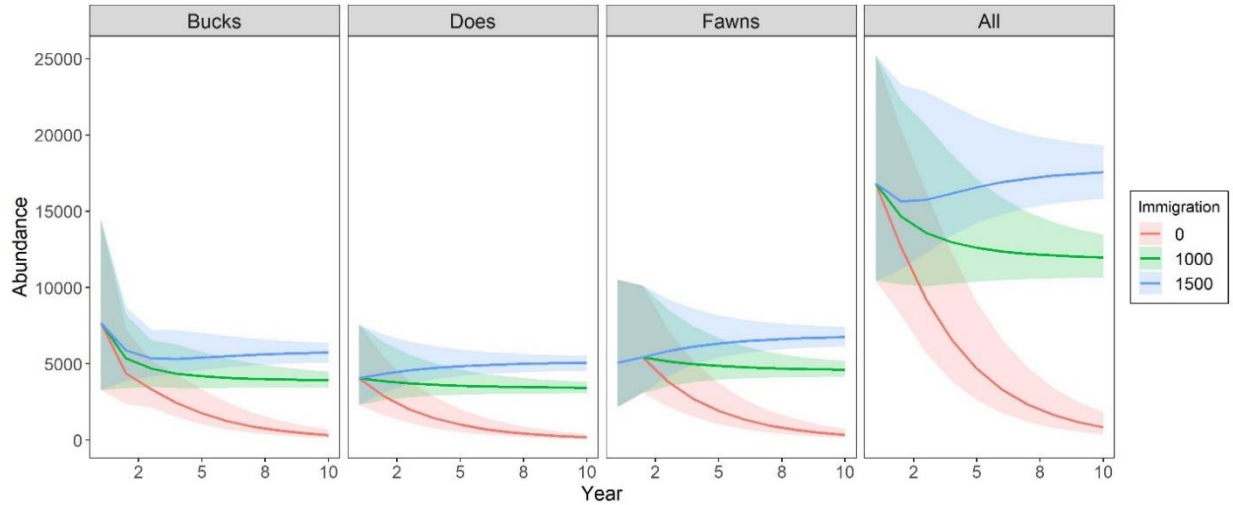


Figure 17: Abundance projections for a white-tailed deer population in four counties of central North Carolina from 2017-2026 using actual landcover projections from the USGS Sohl et al. (2018). Colors show how different levels of net immigration (number of adult males and females entering the population each year) change projections from declining, to stable, to increasing given homogenous harvest rates. We predicted expected coyote density changes based on an estimated relationship between coyotes and urbanization. We then used predicted covariates to predict survival and recruitment each year. We used survival and recruitment estimates to populate a stage (fawn, adult) and sex-based Lefkovich matrix for each year of projection. We then multiplied initial abundance estimates through the matrix to generate population projections for each year.

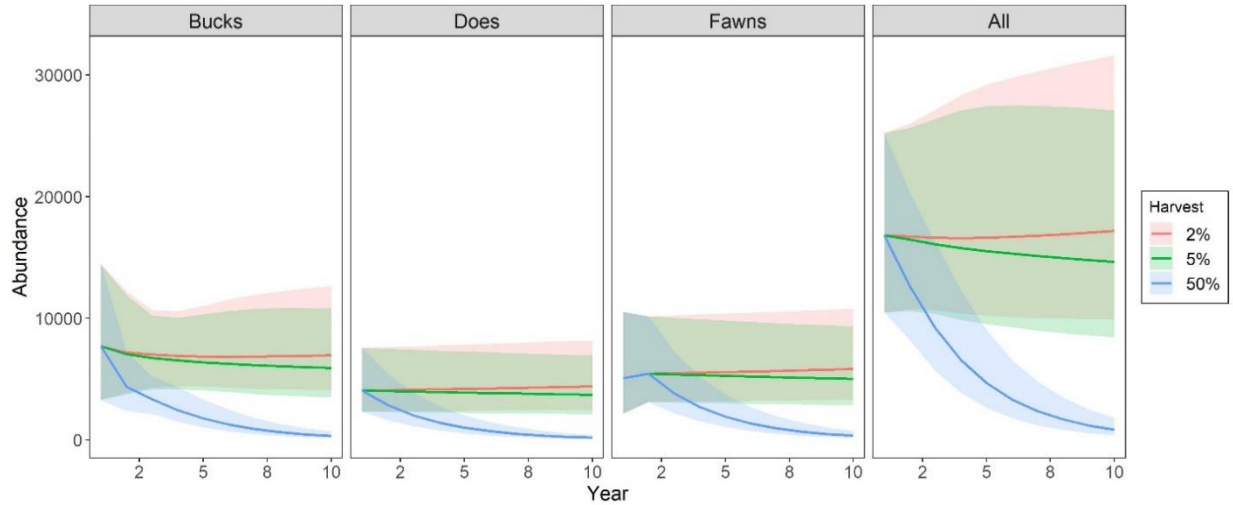


Figure 18: Abundance projections for a white-tailed deer population in four counties of central North Carolina from 2017-2026 using actual landcover projections from the USGS Sohl et al. (2018). Colors show how different levels of harvest (percent of population harvested each year) change projections from declining, to stable, to increasing given compensatory immigration and emigration. We predicted expected coyote density changes based on an estimated relationship between coyotes and urbanization. We then used predicted covariates to predict survival and recruitment each year. We used survival and recruitment estimates to populate a stage (fawn, adult) and sex-based Lefkovich matrix for each year of projection. We then multiplied initial abundance estimates through the matrix to generate population projections for each year.

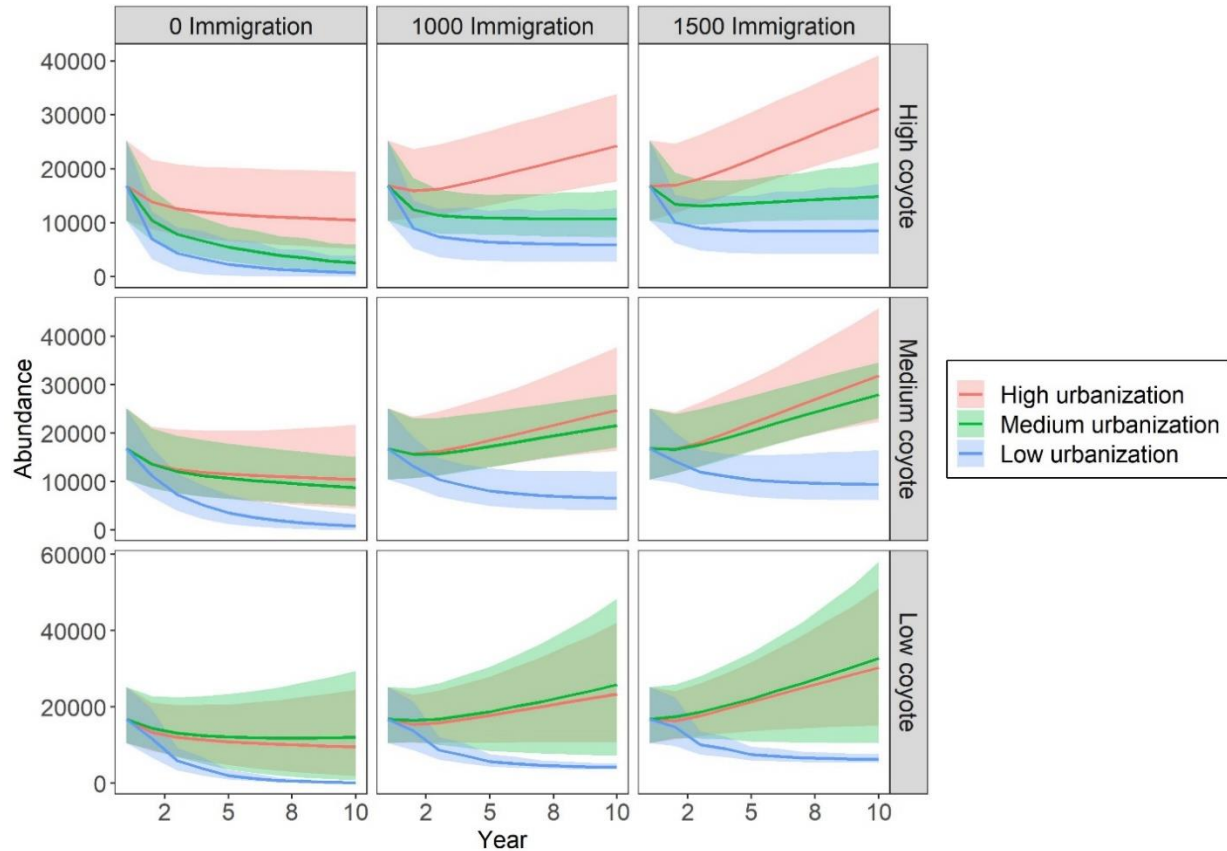


Figure 19: Abundance projections for a white-tailed deer population in four counties of central North Carolina. Survival and recruitment rates were modeled as functions of the amount of local anthropogenic development and coyote density. Beta coefficients were used to predict vital rates at three categorical levels of each covariate under three scenarios of net immigration (0, 1000 and 1500 adult males and females/year) with harvest rates held at 50%. Low, medium and high levels of development correspond to 10, 49 and 90% respectively. Low, medium and high levels of coyote density correspond to 0.03, 1.18 and 2.7 coyotes/km² respectively. Predicted survival and recruitment were used to project abundance forward 10 years by multiplying the initial stage and sex-specific abundances through the projection matrix.

Table 4: Comparisons of our density, survival and recruitment estimates for white-tailed deer to previous studies. We focused on studies that used robust methods (i.e., capture recapture, telemetry, distance sampling) and were conducted in urban, suburban or exurban study sites.

| Parameter | Estimate | Study | Location |
|---|-------------------|---------------------------|------------------|
| Doe annual probability of survival | 0.73 (0.70, 0.77) | This study | Raleigh, NC |
| Doe annual probability of survival | 0.65 (0.49, 0.79) | (Ebersole et al. 2007) | Cecil Co., MD |
| Doe annual probability of survival | 0.80 (0.52, 1.00) | (Witham and Jones 1992) | Chicago, IL |
| Doe annual probability of survival | 0.82 (0.70, 0.96) | (Etter et al. 2002) | Chicago, IL |
| Doe annual probability of survival | 0.86 (0.59, 0.97) | (Clevinger 2017) | Bloomington, IN |
| Buck annual probability of survival | 0.83 (0.82, 0.85) | This study | Raleigh, NC |
| Buck annual probability of survival | 0.76 (0.42, 0.87) | (Witham and Jones 1992) | Chicago, IL |
| Buck annual probability of survival | 0.83 (0.63, 1.00) | (Etter et al. 2002) | Chicago, IL |
| Buck annual probability of survival | 0.70 (0.31, 0.93) | (Clevinger 2017) | Bloomington, IN |
| Buck annual probability of survival | 0.72 (0.30, 1.00) | (Mcdonald Jr et al. 2011) | Carlisle, MA |
| Coyote density (individuals/km ²) | 1.01 (0.43, 2.55) | This study | Raleigh, NC |
| Coyote density (individuals/km ²) | 2 (1.6, 3.0) | (Fedriani et al. 2001) | Santa Monica, CA |

Table 4 (continued)

| | | | |
|---|---------------------|-------------------------------|-----------------|
| Coyote density (individuals/km ²) | 1.4 (0.4, 3.5) | (Gehrt et al. 2011a) | Chicago, IL |
| Coyote density (individuals/km ²) | 1.38 (0.82, 1.94) | (Lombardi et al. 2017b) | Nacogdoches, TX |
| Deer density (individuals/km ²) | 14.47 (4.80, 39.40) | This study | Raleigh, NC |
| Deer density (individuals/km ²) | 12 (2.93, 23.33) | NCWRC | Raleigh, NC |
| Deer density (individuals/km ²) | 23 (14, 40) | (Williams et al. 2008) | N. Branford, CT |
| Deer density (individuals/km ²) | 22 (13, 39) | (Urbanek et al. 2012) | Chicago, IL |
| Deer density (individuals/km ²) | 11.2 (8.6, 14.7) | (Otto 2014) | Oxford, OH |
| Deer density (individuals/km ²) | 4.2 (3.21, 5.51) | (Kilheffer 2014) | Syracuse, NY |
| Fawn annual probability of survival | 0.80 (0.67, 0.86) | This study | Raleigh, NC |
| Fawn annual probability of survival | 0.87 (0.66, 1.00) | (Grund 2011) | Bloomington, MN |
| Fawn annual probability of survival | 0.85 (0.72, 1.00) | (Etter et al. 2002) | Chicago, IL |
| Fawn annual probability of survival | 0.94 (0.13, 1.00) | (Piccolo et al. 2010) | Chicago, IL |
| Fawn annual probability of survival | 0.76 (0.64, 0.90) | (Kennedy 2015) | Cleveland, OH |
| Fawn first month probability of survival | 0.69 (0.68, 0.69) | This study | Raleigh, NC |
| Fawn first month probability of survival | 0.56 (0.48, 0.64) | (Saalfeld and Ditchkoff 2007) | Auburn, AL |

Table 4 (continued)

| | | | |
|--|-------------------|----------------------------------|-----------------|
| Fawn first month probability of survival | 0.95 (0.91, 0.99) | (Kennedy 2015) | Cleveland, OH |
| Fawn first month probability of survival | 0.40 (0.22, 0.58) | (Chitwood et al. 2015b) | Fort Bragg, NC |
| Recruitment (number of fetuses/doe) | 1.78 (1.38, 2.00) | This study | Raleigh, NC |
| Recruitment (number of fetuses/doe) | 1.57 (1.20, 1.85) | (Denicola et al. 2008) | Iowa City, IA |
| Recruitment (number of fetuses/doe) | 1.63 (1.38, 1.79) | (Ebersole et al. 2007) | Cecil Co., MD |
| Recruitment (number of fetuses/doe) | 1.53 (0.5, 2.60) | (Witham and Jones 1992) | Chicago, IL |
| Recruitment (number of fetuses/doe) | 1.65 (1.52, 1.76) | (Grund 2011) | Bloomington, MN |
| Recruitment (fawn:doe ratio) | 1.21 (1.18, 1.25) | This study | Raleigh, NC |
| Recruitment (fawn:doe ratio) | 0.55 (0.34, 0.85) | NCWRC | Raleigh, NC |
| | | | Omaha-Bellevue, |
| Recruitment (fawn:doe ratio) | 0.95 (0.40, 1.50) | (Vercauteren and Hygnstrom 2000) | NE |
| Recruitment (fawn:doe ratio) | 0.89 (0.84,0.94) | (Ebersole et al. 2007) | Cecil Co., MD |
| Recruitment (fawn:doe ratio) | 1.00 (0.66, 1.61) | (Denicola et al. 2008) | Iowa City, IA |

Table 5: Estimates of doe annual survival and fawn 1-month survival for Cumberland County, NC using an integrated population modelling approach with harvest, decoy, camera trap and hunter observation data. Estimates are compared to estimates derived from telemetry data from Fort Bragg in Cumberland County 2011-2012 (Chitwood et al. 2015a, Chitwood et al. 2015b).

| Parameter | Estimate | Study |
|-----------------------|-------------------|-------------------------|
| Doe annual survival | 0.69 (0.61, 0.78) | This study |
| Doe annual survival | 0.79 (0.68, 0.87) | (Chitwood et al. 2015a) |
| Fawn 1-month survival | 0.61 (0.60, 0.62) | This study |
| Fawn 1-month survival | 0.40 (0.22, 0.58) | (Chitwood et al. 2015b) |

Table 6: Beta coefficient estimates for the relationship between survival and fecundity vital rates with the percent of developed land, coyote density and their interaction from an integrated population model. Beta coefficient estimates for the relationship between the percent of developed land and coyote density are also shown. Quantities in parenthesis show 95% credible intervals. Quantities in bold are those with 95% credible intervals that do not overlap 0. Recruitment is modeled as the product of 2*fecundity*fawn first month survival, thus does not have specific beta coefficient estimates associated.

| Parameter | % Developed in 1km radius | Coyote density (1km) | % Developed x Coyote Density |
|---------------------------|-----------------------------|-----------------------------|------------------------------|
| Coyote density | 0.04 (-0.18, 0.19) | | |
| Fecundity | -0.03 (-0.03, -0.03) | -0.03 (-0.03, -0.03) | -0.02 (-0.03, -0.01) |
| Buck annual survival | -0.1 (-0.32, 0.18) | -0.99 (-1, -0.97) | 1 (0.99, 1) |
| Doe annual survival | -0.63 (-0.86, -0.38) | 0.05 (-0.39, 0.5) | 0.36 (0.33, 0.39) |
| Fawn annual survival | 0.78 (0.47, 0.99) | -0.94 (-0.99, -0.85) | 0.52 (0.05, 0.92) |
| Fawn first month survival | 0.98 (0.4, 1.42) | 0.26 (-0.23, 0.9) | -0.19 (-0.22, -0.16) |

Table 7: Estimates of detection probability used to correct counts from hunter observations to estimate recruitment (fawns/doe) within an integrated population model for white-tailed deer in four focal counties of North Carolina. The resulting recruitment estimate is shown under the "Counts corrected" column. This is compared to a model where doe and fawn detection probabilities were assumed equal (i.e., no correction of counts for detection probability: Counts uncorrected).

| Estimate | Counts corrected | Counts uncorrected |
|----------------------------|-------------------|--------------------|
| Doe detection probability | 0.45 (0.12, 0.78) | |
| Fawn detection probability | 0.19 (0.04, 0.42) | |
| Recruitment (fawns:doe) | 1.21 (1.18, 1.25) | 1.08 (1.07, 1.09) |

Table 8: Abundance estimates for a white-tailed deer population over four focal counties in North Carolina in 2017. Estimates come from spatially explicit capture recapture (bucks) or spatial count (does and fawns) models using camera trap data. Estimates are either generated from submodels within an integrated population model with parameter sharing or through separate models, without parameter sharing.

| Estimate | Parameter sharing | No parameter sharing |
|-----------------|---------------------|----------------------|
| Buck abundance | 7687 (2053, 19880) | 7556 (2010, 19765) |
| Doe abundance | 4056 (1979, 11860) | 7107 (2169, 16442) |
| Fawn abundance | 5080 (1549, 14070) | 6734 (1712, 18810) |
| Total abundance | 16823 (5581, 45810) | 21397 (5891, 55017) |

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APPENDICES

Appendix A: Chapter 1 supplementary information

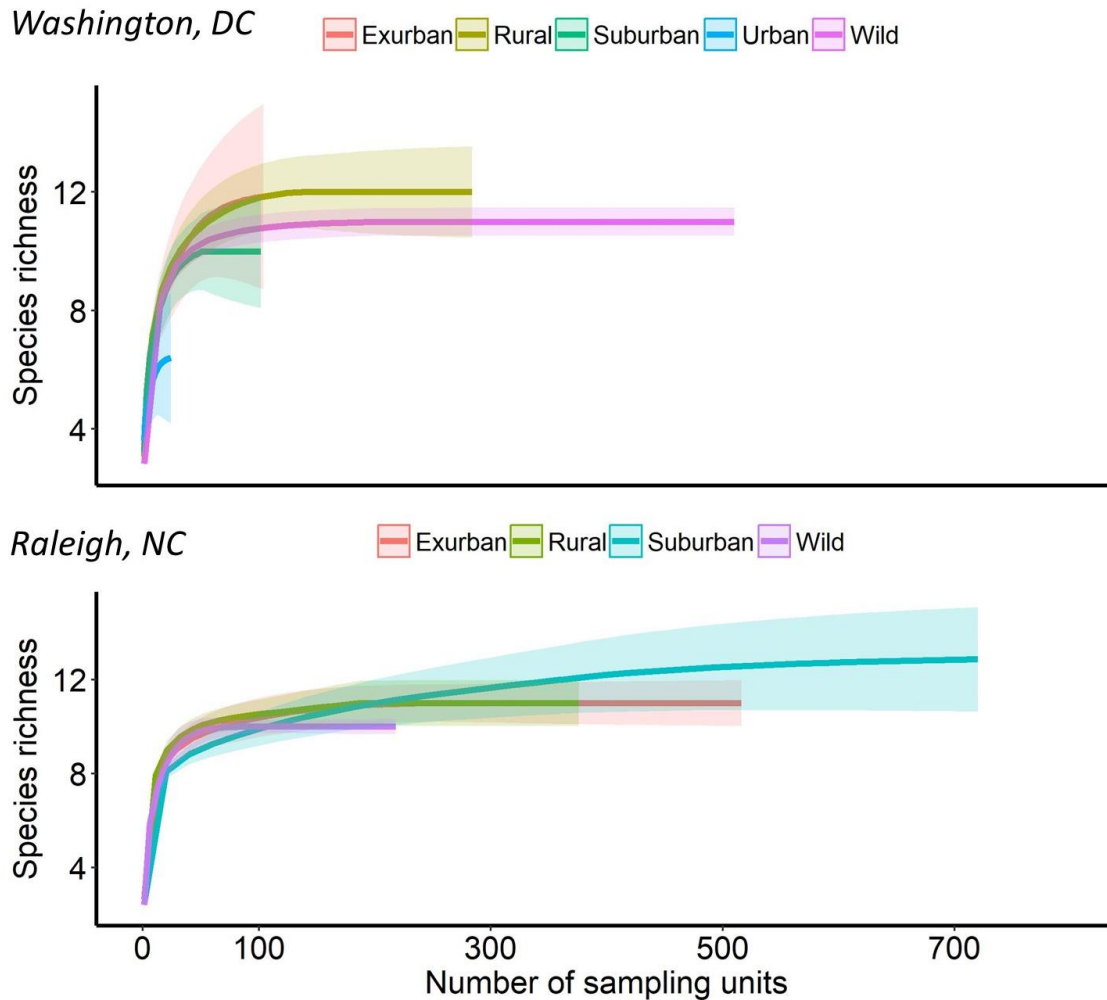


Figure A1: Rarefaction curves estimating species richness in five development levels (urban, suburban, exurban, rural, wild) in two cities, Washington, DC and Raleigh, NC, USA, using camera traps between 2012 and 2016. Shaded areas represent 95% confidence intervals.

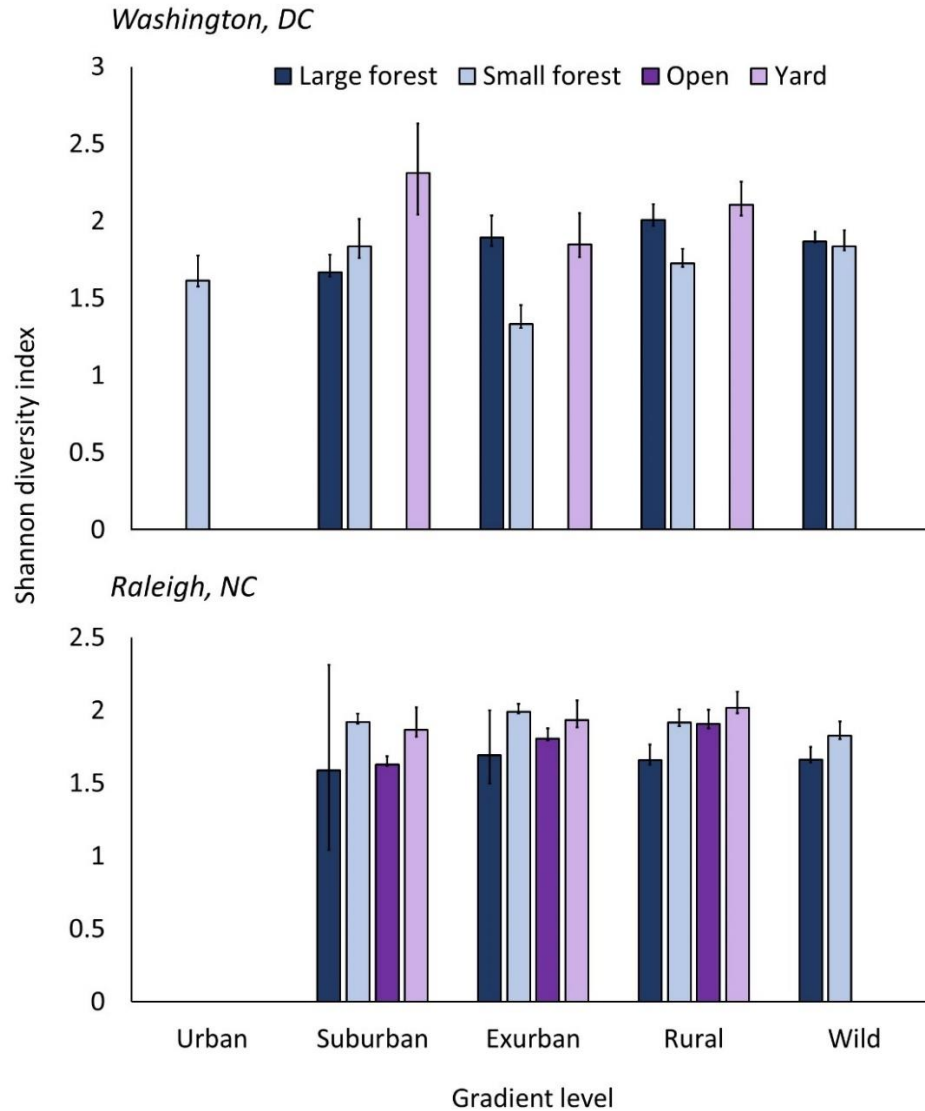


Figure A2: Shannon diversity index estimates from camera trapping in two cities, Washington, DC and Raleigh, NC, USA, across five development levels (urban, suburban, exurban, rural, wild). Diversity is separated by four plot types: large forest, small forest, open and residential yard. Data were collected using camera traps between 2012 and 2016. Bars show 95% confidence intervals. Urban small forests were not sampled in Raleigh, open areas were not sampled in DC and urban/wild yards, urban open areas and urban large forests were not sampled in either city.

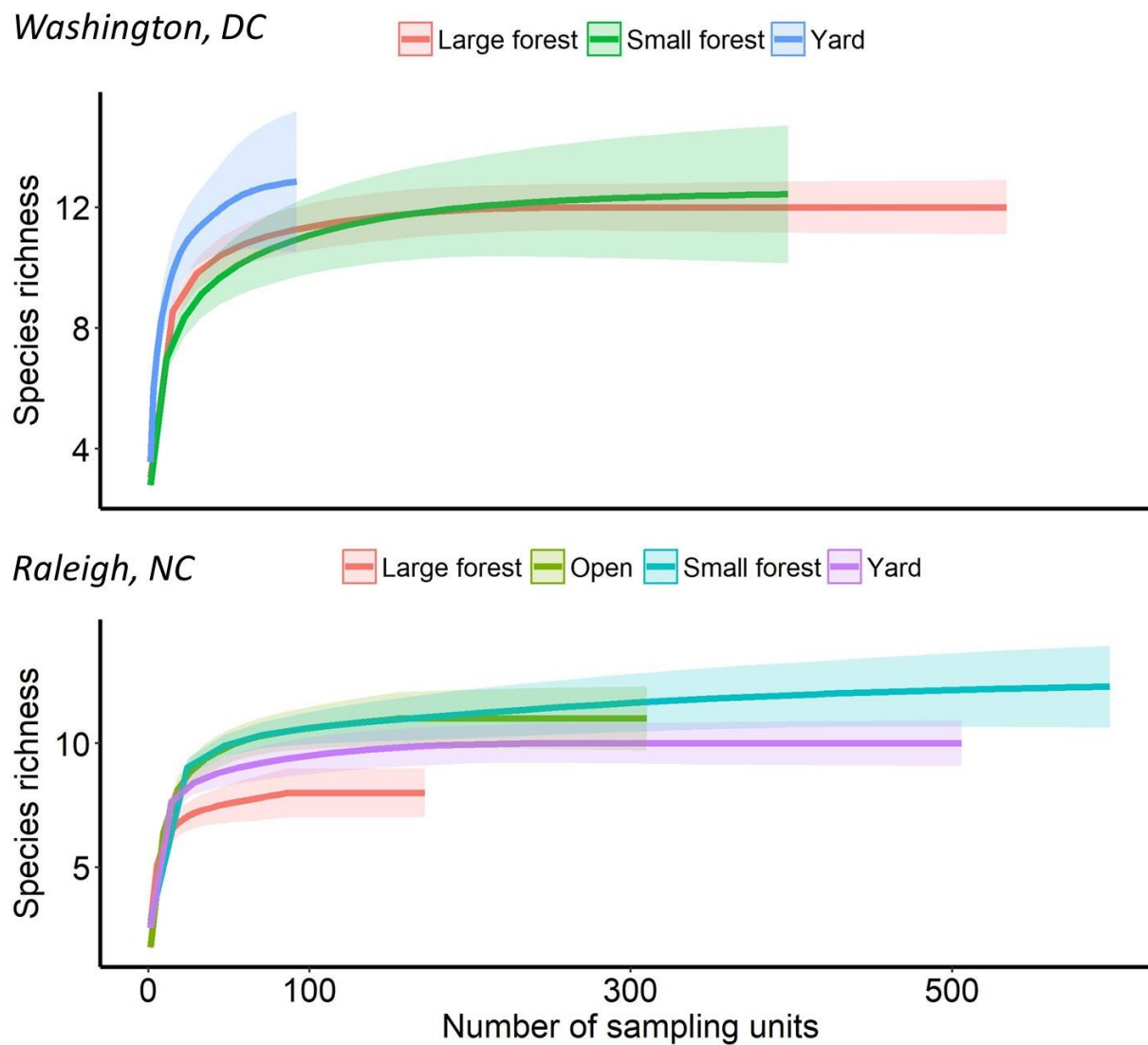


Figure A3: Rarefaction curve estimating species richness in three plot types (residential yard, small forest, large forest) in two cities, Washington, DC and Raleigh, NC, USA, using camera traps between 2012 and 2016. Shaded areas represent 95% confidence intervals.

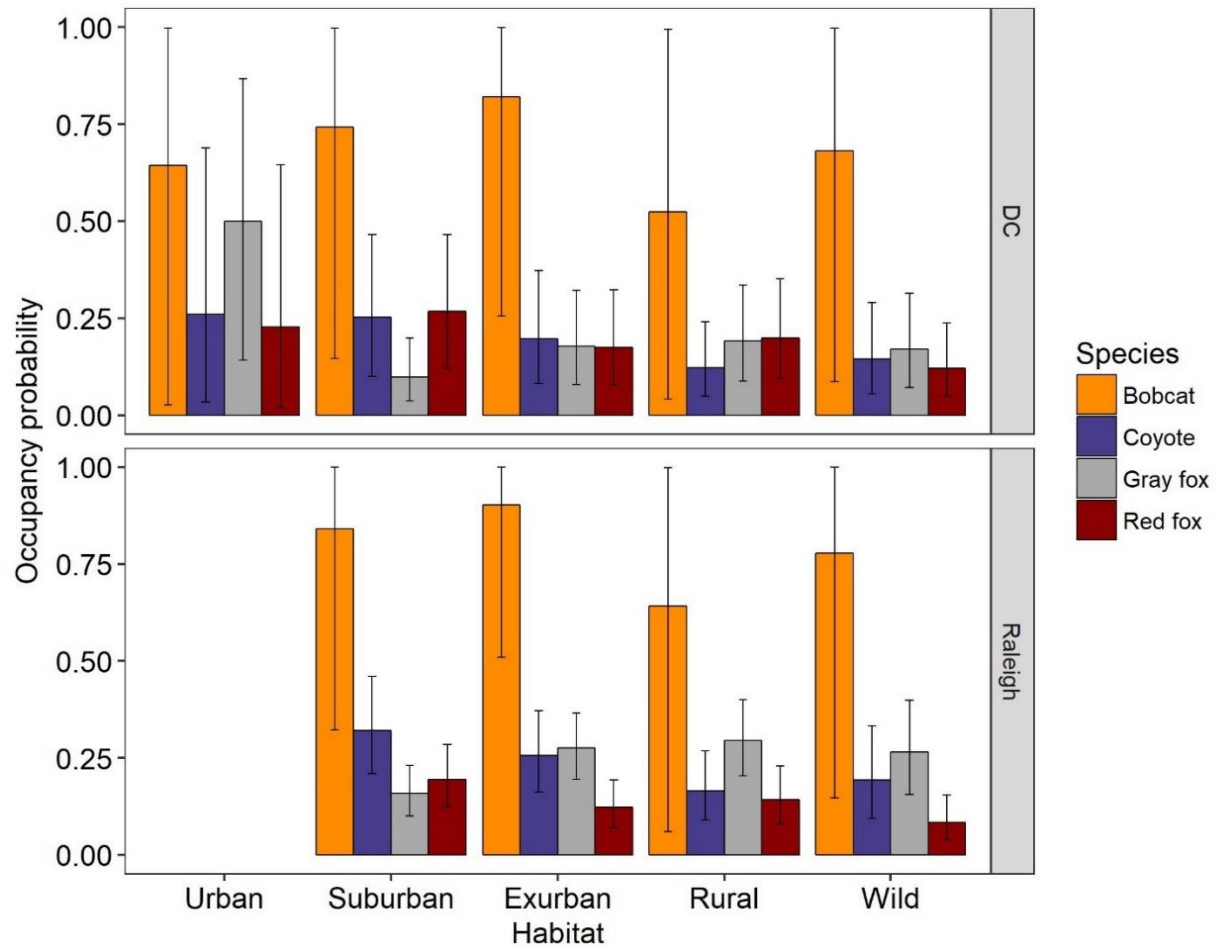


Figure A4: Occupancy estimates from single season occupancy model for four carnivore species (bobcat, coyote, gray fox and red fox) in five development levels (urban, suburban, exurban, rural, wild) in two cities, Washington, DC and Raleigh, NC, USA, using camera traps between 2012 and 2016. Bars represent 95% credible intervals. Uncertainty was high with no significant differences between the habitats for any species.

Table A1: Effort expressed as camera nights with spatial replicates in parentheses for camera traps run in Washington, DC and Raleigh, NC from 2012-2016 between different levels along the urban-wild gradient around each city.

| Washington, DC | | | | | |
|----------------|-------------------------------------|-------------------------------------|--------------|--------------|---------------|
| Gradient Level | Large Forest >10 km ² | Small Forest ≤10 km ² | Yard | Open | Total |
| Urban | 0 (0) | 430.3 (12) | 0 (0) | 0 (0) | 430.3 (12) |
| Suburban | 517.4 (25) | 530 (21) | 109.4 (5) | 0 (0) | 1156.8 (51) |
| Exurban | 671.8 (31) | 150.5 (7) | 281 (14) | 0 (0) | 1103.3 (52) |
| Rural | 737.4 (35) | 1699 (80) | 598.3 (27) | 0 (0) | 3034.7 (142) |
| Wild | 4076 (176) | 1720.6 (79) | 0 (0) | 0 (0) | 5796.6 (255) |
| Total | 6002.6 (267) | 4530.3 (199) | 988.8 (46) | 0 (0) | 11521.6 (512) |
| Raleigh, NC | | | | | |
| Suburban | 105.9 (4) | 3346 (152) | 2981.9 (149) | 1070.3 (55) | 7504.2 (360) |
| Exurban | 251.5 (12) | 2673.6 (120) | 1545.9 (77) | 956.1 (49) | 5427.1 (258) |
| Rural | 603.2 (27) | 1801.4 (83) | 637.1 (27) | 1059.9 (51) | 4101.5 (188) |
| Wild | 987.7 (43) | 1322.7 (66) | 0 (0) | 0 (0) | 2310.3 (109) |
| Total | 1948.4 (86) | 9143.6 (421) | 5164.9 (253) | 3086.3 (155) | 19343.1 (915) |

Table A2. Covariates used in the detection rate and occupancy analyses.

| Covariate | Description | Type | Model |
|------------------------------------|---|-----------------|-----------|
| City | 0/1 Washington, DC or Raleigh, NC. Interactions between this term and all other covariates were tested. | Camera site | Ψ |
| Large Forest | % Large core (cont. forest frag >5 acre) in 5 km radius | GIS 5 km | Ψ |
| Small Tree Cover | % tree cover in 100 m radius (Sexton et al. 2013) | GIS 100 m | |
| Housing Density | Average Housing Density (houses/km ²) in 5km radius (Hammer et al. 2004) | GIS 5 km | Ψ |
| Large Forest x Housing Density | Interaction of large core forest and housing density in a 5 km radius | Interaction | Ψ |
| Small Tree Cover x Housing Density | Interaction of small scale (100 m) tree cover and housing density in a 5 km radius | Interaction | Ψ |
| Rolag Rate | Site-specific detection rate (count/day) of rodents and lagomorphs | Camera site | Ψ |
| Deer Rate | Site-specific detection rate (count/day) of white-tailed deer | Camera site | Ψ |
| Hunting | Categorical covariate for hunting or no hunting is permitted at the site (0,1) | Camera site | Ψ |
| Year | Year sampled | Camera site | Ψ |
| Dog | 0/1 variable representing if a dog is located at the site (yards only) | Camera site | Ψ |
| Dog x Yard | An interaction term between dog presence and whether or not a site is a yard | Interaction | Ψ |
| Yard | 0/1 variable representing if the camera was located inside or outside of a residential yard | Camera site | Ψ, p |
| NDVI | Moderate Resolution Imaging Spectroradiometer Land Terra Vegetation Indices 1 km monthly NDVI (Dodge et al. 2013) | Camera site/Day | p |
| Temperature | ECMWF Interim Full Daily SFC Temp (2m above ground) (Dodge et al. 2013) | Camera site/Day | p |
| Camera (Raleigh) | 0/1 variable representing the type of camera used (0=Bushnell, 1=Reconyx) | Camera site | p |
| Detection distance | Maximum distance at which camera detects animals (m) | Camera site | p |

Table A3: Results of goodness-of-fit tests for occupancy and Poisson count models assessed by posterior predictive check with adequate fit if $0.1 < pB < 0.9$.

| Species | Occupancy | Count Model |
|----------|-----------|-------------|
| Bobcat | 0.32 | 0.28 |
| Coyote | 0.24 | 0.5 |
| Gray Fox | 0.26 | 0.34 |
| Red Fox | 0.30 | 0.5 |

Table A4: Results of Poisson regression for single species using camera trapping over two cities between 2012-2016. Posterior mean and posterior standard deviation for each predictor are shown with bold entries indicating predictors with 95% credible intervals that did not overlap zero. Predictors in bold were used for modeling occupancy for that species. Housing density was used as a predictor in all occupancy models, regardless of whether it was significant in the preliminary count analysis.

| Covariate | Bobcat | Coyote | Gray Fox | Red Fox |
|--|---------------------|--------------------|---------------------|--------------------|
| Intercept | -12.31(2.14) | -7.61(0.88) | -10.08(1.63) | -4.14(0.64) |
| Hunting | -1.09(0.83) | 1.43(0.4) | -1.54(1.31) | 0.35(0.33) |
| Yard | -3.03(3.92) | 0.24(1.09) | -2.8(3.2) | 1.54(0.65) |
| Dog | 3.45(4.11) | -0.37(1.44) | 7.71(3.27) | 0.32(1.18) |
| Year | -0.85(0.53) | -0.57(0.24) | 0.71(0.75) | 0.26(0.19) |
| Forest | 1.34(1.13) | 0.88(0.33) | 1.27(0.92) | -0.68(0.29) |
| Housing Density | -2.85(2.93) | 1.26(0.53) | 1.69(0.77) | 0.6(0.49) |
| Large Forest x Housing Density | 1.32(1.26) | 0.81(0.31) | 0.97(0.35) | 0.39(0.29) |
| Rolag Rate | -2.64(4.13) | -1.99(2.69) | -1.23(5.16) | 3.16(1.95) |
| Deer Rate | -2.17(1.92) | -2.3(1.47) | -2.47(1.51) | -2.25(1.2) |
| Small Tree Cover Housing Density x Small Tree Cover | -0.05(1.12) | -0.06(0.37) | -0.68(0.69) | -0.09(0.26) |
| Yard*Dog | 1.09(1.33) | 0.37(0.22) | 0.12(0.22) | -0.1(0.14) |
| City | 1.04(2.07) | 0.66(0.71) | -0.28(0.69) | -1.21(0.87) |
| City x Hunting | 2.27(1.76) | 2.23(0.86) | 4.27(1.62) | -3.9(0.7) |
| City x Yard | 2.78(1.16) | -0.45(0.49) | 1.9(1.39) | -0.66(0.67) |
| City x Dog | 1.82(3.89) | -1.37(1.16) | 2.88(3.22) | -0.19(0.79) |
| City x Year | -3.3(4.09) | 0.24(1.39) | -7.24(3.24) | 0.94(1) |
| City x Large Forest | 0.77(0.68) | 0.64(0.28) | -1.48(0.77) | -0.03(0.3) |
| City x Housing Density | -2.67(1.02) | -0.56(0.38) | -0.71(0.96) | 1.12(0.54) |
| City x Rolag Rate | -0.42(2.61) | -0.95(0.57) | 0.02(0.78) | 0.06(0.75) |
| City x Deer Rate | 2.61(4.15) | 2.13(2.69) | 1.4(5.16) | -3.06(1.95) |
| City x Small Tree Cover | 5.34(5.48) | 11.63(2.59) | 9.22(3.21) | 1.3(4.9) |
| | 0.68(0.83) | 0.16(0.38) | 0.38(0.71) | 0.11(0.33) |

Table A5: Beta coefficients and 95% credible intervals (parentheses) for an occupancy model based on camera trapping data in Washington, DC, USA and Raleigh, NC, USA from 2012-2016. Those coefficients with 95% CIs not overlapping zero are shown in bold.

| | Bobcat | Coyote | Gray Fox | Red Fox |
|------------------------------------|------------------|------------------|---------------------|--------------------------|
| Intercept | 1.1 (-1.5, 4.5) | -1.3 (-2.8, 0.1) | -1.2 (-2.7, 0.2) | -1.3 (-2.8, 0.2) |
| Housing Density | -1.8 (-5.4, 1.4) | -0.1 (-1, 0.8) | 1 (0.2, 1.8) | 0.2 (-0.7, 1) |
| Large Forest | 0.6 (-1.7, 3.3) | 0.3 (-0.2, 0.9) | 0.4 (-0.1, 0.9) | 0.5 (0, 1) |
| Housing Density x Large Forest | -0.4 (-3.4, 1.9) | -0.1 (-0.6, 0.4) | 0.6 (0.1, 1) | 0.1 (-0.3, 0.6) |
| Hunting | 0.4 (-2.3, 3.7) | 0.1 (-0.5, 0.7) | -0.4 (-1.1, 0.2) | 0.6 (0.1, 1.2) |
| Yard | 0.7 (-2.4, 4.1) | -0.7 (-2.2, 0.8) | 0.2 (-1.3, 1.6) | 0.4 (-1.1, 1.8) |
| Dog | -0.8 (-3.9, 2) | -0.8 (-3, 1.2) | 0.3 (-1.6, 2.2) | -0.1 (-2, 1.9) |
| Rolag Rate | -0.2 (-3.8, 3.5) | -0.9 (-4, 1.9) | -0.4 (-2.7, 2.3) | -1.9 (-5.9, 0.7) |
| Deer Rate | -0.7 (-2.9, 1.5) | -0.2 (-0.6, 0.1) | -0.1 (-0.4, 0.3) | 0 (-0.4, 0.3) |
| Year | 0.2 (-3.4, 3.8) | 0.5 (-0.2, 1.3) | 0.4 (-0.1, 0.9) | 0.2 (-0.3, 0.8) |
| Dog*Yard | 0.5 (-2.8, 4.2) | 0.5 (-0.7, 1.7) | -0.7 (-1.6, 0.3) | 0.3 (-1, 1.6) |
| Small Tree Cover | -1.4 (-4.5, 1.1) | 0.2 (-0.3, 0.8) | 0.4 (-0.2, 1.1) | -0.1 (-0.6, 0.4) |
| Housing Density x Small Tree Cover | 0 (-2.9, 2.7) | 0.1 (-0.2, 0.4) | -0.2 (-0.4, 0.1) | 0.1 (-0.1, 0.4) |
| City | 0.9 (-1.7, 3.9) | 0.4 (-0.4, 1.3) | 0.6 (-0.2, 1.4) | -0.4 (-1.2, 0.4) |
| City x Large Forest | -0.1 (-2.9, 2.5) | 0.1 (-0.6, 0.8) | 0.2 (-0.5, 0.8) | -0.7 (-1.3, 0) |
| City x Hunting | -0.8 (-4.4, 2.7) | -0.1 (-1, 0.8) | 0.4 (-0.5, 1.2) | 0 (-0.9, 0.9) |
| City x Year | 0.1 (-2.9, 3.8) | 0.3 (-0.2, 0.8) | -0.1 (-0.6, 0.3) | 0.1 (-0.4, 0.5) |
| City x Deer Rate | 0 (-3.7, 3.5) | -0.3 (-3.6, 2.9) | 1 (-1.8, 4.1) | -1.2 (-5.1, 2) |
| City x Dog | 0.2 (-3.1, 3.8) | -0.1 (-1.5, 1.3) | 0.1 (-1.2, 1.5) | -1.4 (-2.7, -0.2) |
| City x Housing Density | 0.6 (-2.5, 3.9) | 0.7 (-0.3, 1.7) | 0.4 (-0.5, 1.3) | -0.5 (-1.4, 0.4) |
| City x Yard | -0.8 (-3.8, 2.2) | 0.8 (-1.2, 3) | -0.3 (-2.2, 1.5) | 0 (-2, 1.9) |
| City x Rolag Rate | -1.1 (-4.5, 1.7) | 0 (-0.6, 0.6) | -0.1 (-0.8, 0.6) | 0 (-0.5, 0.5) |
| City x Small Tree Cover | -0.1 (-3.8, 3.6) | 0 (-1.9, 2) | 1.2 (-0.7, 3.2) | -0.2 (-2.5, 1.8) |

Table A6: Results of a Poisson regression to determine differences in detection rate between the wild gradient level (reference level) and all other levels of the development gradient (above dotted line). Also presented are results of a separate Poisson regression to determine differences in detection rate between yards and all other plot types. Significant results (95% CIs not overlapping zero) are in bold.

| Washington, DC | | | | |
|----------------|--------------|------|-------|-------|
| Predictor | Mean | SD | 2.5% | 97.5% |
| Intercept | -0.07 | 0.06 | -0.18 | 0.06 |
| Rural | 0.25 | 0.1 | 0.06 | 0.45 |
| Exurban | 0.51 | 0.13 | 0.25 | 0.77 |
| Suburban | 0.69 | 0.13 | 0.44 | 0.96 |
| Urban | 0.72 | 0.27 | 0.16 | 1.22 |
| Intercept | 0.54 | 0.15 | 0.26 | 0.83 |
| Large Forest | -0.46 | 0.17 | -0.77 | -0.13 |
| Small Forest | -0.42 | 0.17 | -0.77 | -0.11 |
| Raleigh, NC | | | | |
| Intercept | -0.51 | 0.13 | -0.77 | -0.28 |
| Rural | 0.15 | 0.17 | -0.18 | 0.46 |
| Exurban | 0.32 | 0.16 | 0.02 | 0.67 |
| Suburban | 0.07 | 0.15 | -0.21 | 0.34 |
| Intercept | -0.37 | 0.09 | -0.56 | -0.2 |
| Large Forest | 0.05 | 0.17 | -0.3 | 0.35 |
| Small Forest | 0.15 | 0.12 | -0.09 | 0.38 |
| Open | -0.42 | 0.15 | -0.68 | -0.13 |

Appendix B: Calculating goodness of fit statistics

Pearson residuals

The squared Pearson residual is defined as:

$$r_P^2 = \frac{(y - \mu)^2}{V(\mu)}$$

where y is an observed response variable, $E(Y) = \mu$, and $V(\mu)$ is the variance function (McCullagh and Nelder 1989, equation 2.11).

Occupancy Models

Occupancy models (sensu Mackenzie et al. 2017) are defined by the following joint distribution of z , the partially observed latent state, and y , detection / non-detections of the underlying state:

$$z \sim \text{Bernoulli}(\psi)$$

$$y \sim \text{Bernoulli}(zp)$$

This can alternatively be written as:

$$f(z, y) = \psi^z (1 - \psi)^{1-z} (zp)^y (1 - zp)^{1-y}$$

Since we only fully observe y , we marginalize over z to obtain the distribution of y :

$$f(y) = \psi p^y (1 - p)^{1-y} + (1 - \psi) 0^y$$

To calculate squared Pearson's residuals, we first obtain $E(y)$ as:

$$\begin{aligned} E(Y) &= \sum_y y f(y) \\ &= \psi p \end{aligned}$$

To obtain $V(\mu)$, we first obtain the variance of y as:

$$\begin{aligned}
 Var(Y) &= E(Y^2) - E(Y)^2 \\
 &= \sum_y y^2 f(y) - (\psi p)^2 \\
 &= \psi p - (\psi p)^2 \\
 &= \psi p(1 - \psi p)
 \end{aligned}$$

Since $E(Y) = \mu = \psi p$, $V(\mu) = \mu(1 - \mu) = \psi p(1 - \psi p)$ we can now write a squared Pearson's residual as:

$$r_P^2 = \frac{(y - \psi p)^2}{\psi p(1 - \psi p)}$$

Appendix C: Chapter 2 supplementary information

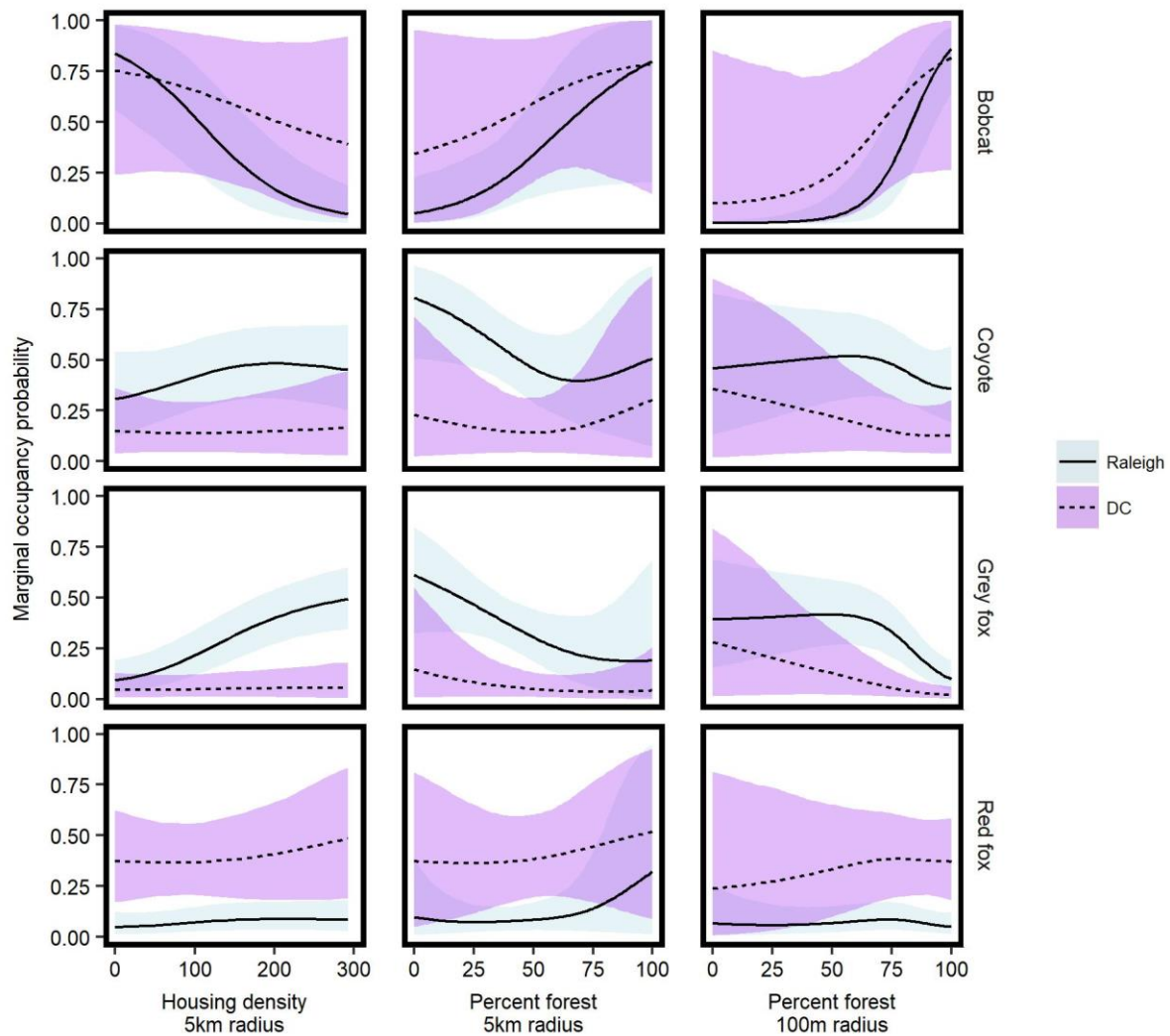


Figure C1: Marginal occupancy plots for each species along a gradient of housing density, percent forest cover in a 5km radius and 100m radius taken from camera traps run between 2012 and 2016 in Washington, DC and Raleigh, NC, USA. Lines show posterior means and shaded regions are 95% credible intervals.

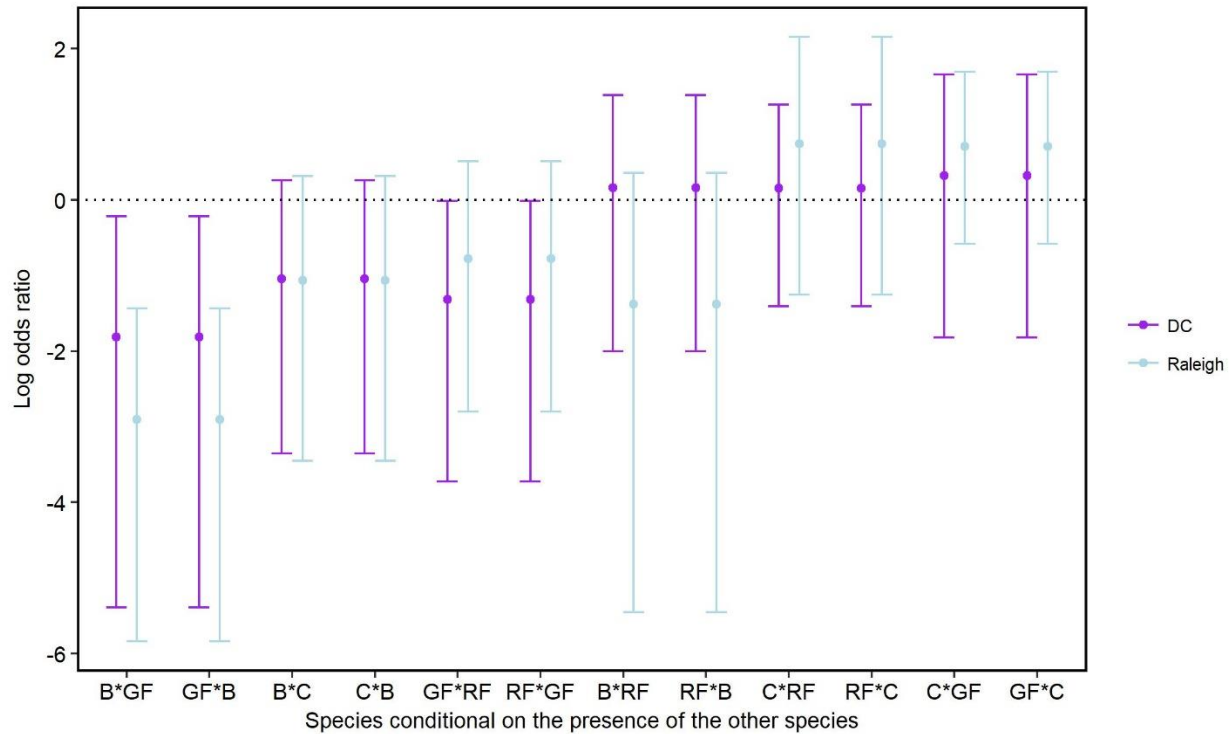


Figure C2: A comparison of log odds ratios (i.e., the increase in log odds of occurrence of species 1 when species 2 is present) taken from camera traps run between 2012 and 2016 in Washington, DC and Raleigh, NC, USA. RF is red fox, GF is grey fox, C is coyote and B is bobcat. All pairwise comparisons are conditioned on all other species to be absent. Bars represent 95% CI. The ratios trended negative for most species pairs except coyote and red fox and grey fox respectively, indicating trends towards avoidance between most species. Grey fox interactions with bobcat were significant and negative in both cities.

Table C1: Camera effort in terms of camera nights for camera traps run in Washington, DC and Raleigh, NC in each year from 2012-2016.

| Washington, DC | | | |
|----------------|-------------------|---------------------|------------------------|
| Year | Months | Total Camera Nights | Number of Camera Sites |
| 2012 | July-November | 2975 | 139 |
| 2013 | March-November | 3253 | 137 |
| 2014 | April-December | 1293 | 61 |
| 2015 | March-November | 3364 | 153 |
| 2016 | April-June | 206 | 10 |
| Raleigh, NC | | | |
| 2012 | January-July | 998 | 69 |
| 2013 | February-December | 2673 | 116 |
| 2014 | January-December | 5177 | 237 |
| 2015 | January-December | 4062 | 188 |
| 2016 | January-September | 3346 | 150 |

Table C2: Effort in terms of camera nights for camera traps run in Washington, DC and Raleigh, NC from 2012-2016 between different habitat types along the urbanization gradient around each city.

| Habitat | Large Forest >1km ² | Small Forest ≤1km ² | Yard | Total |
|----------------|--------------------------------|--------------------------------|---------|----------|
| Washington, DC | | | | |
| Suburban | 517.42 | 529.97 | 109.41 | 1156.8 |
| Exurban | 671.78 | 150.48 | 281.01 | 1103.27 |
| Rural | 737.36 | 1698.95 | 598.34 | 3034.65 |
| Wild | 4076.02 | 1720.62 | 0.00 | 5796.63 |
| Total | 6002.58 | 4530.29 | 988.76 | 11521.63 |
| Raleigh, NC | | | | |
| Suburban | 105.94 | 3345.99 | 2981.9 | 6433.83 |
| Exurban | 251.54 | 2673.56 | 1545.9 | 4471.01 |
| Rural | 603.21 | 1801.37 | 637.06 | 3041.65 |
| Wild | 987.69 | 1322.65 | 0.00 | 2310.34 |
| Total | 1948.39 | 9143.58 | 5164.86 | 16256.82 |

Table C3: Covariates used in the occupancy analyses. Each occupancy covariate is categorized according to our main hypotheses.

| Hypothesis | Covariate | Description |
|---------------------------------|------------------|---|
| Forest fragmentation | Forest5 | % tree cover in 5km radius ³ |
| Forest fragmentation | Forest100 | % tree cover in 100m radius ³ |
| Humans | Hunt | Hunting permitted at the site (0=No,1=Yes) |
| | Year | Year sampled |
| Humans | Dog | Dog is located at the site (0=No,1=Yes), yards only |
| Humans | Yard | Site is a yard (0=No,1=Yes) |
| Humans | HDens | Average Housing Density (houses/km ²) in 5km radius ² |
| Forest fragmentation and Humans | Forest5* HDens | Interaction term between large forest patches and housing density |
| Forest fragmentation and Humans | Forest100* HDens | Interaction term between local tree cover and housing density |
| Prey | Rolag | Detection rate (count/day) of rodents and lagomorphs |
| Prey | Deer | Detection rate (count/day) of white-tailed deer |
| | City | 0/1 Washington, DC or Raleigh, NC |
| | NDVI | Moderate Resolution Imaging Spectroradiometer Land Terra Vegetation Indices 1km monthly NDVI daily ¹ |
| | Temp | ECMWF Interim Full Daily SFC Temp (2m above ground) ¹ |
| | Camera (Raleigh) | Camera type (0=Bushnell, 1=Reconyx) |
| | Det_dist | Maximum distance at which camera detects a human (m) |

1 EnvData (Dodge et al. 2013)

2 Landscape and Urban Planning 69 (2004) 183-199 (Hammer et al. 2004)
(<http://silvis.forest.wisc.edu/old/Library/HousingData.php>)

3 Percent Tree Cover, Global Forest Change Dataset (Hansen et al. 2013)

Table C4: Model selection results for a multi-species occupancy analysis from camera traps run in Washington, DC and Raleigh, NC from 2012-2016. All no-interaction models set pairwise interaction components to zero (i.e., effectively removed second order models).

Global models refer to those where all covariates in Table 1 were included.

| Single Species Models | Pairwise Models | Hypothesis | WAIC | Delta WAIC |
|---|---|---|--------|------------|
| Global | Global | Interactions Global | 9865.9 | 0.0 |
| Global | HDens+Forest5+Forest100+HDens*Forest5+HDens*Forest100 | Interactions, Humans and Forest Fragmentation | 9869.9 | 4.0 |
| Global | HDens+Yard+Dog+Rolag+Deer+Hunt+Yard*Dog | Interactions, Humans and Prey | 9880.4 | 14.5 |
| Global | Rolag+Deer | Interactions and Prey | 9884.7 | 18.8 |
| Global | Forest5+Forest100 | Interactions and Forest Fragmentation | 9892.9 | 27.0 |
| Global | HDens+Yard+Dog+Yard*Dog | Interactions and Humans | 9893.9 | 28.0 |
| Global | Global: Bobcat*Gray fox, all others 0 | One pairwise interaction | 9895.3 | 29.4 |
| Global | Global: Bobcat*Coyote, all others 0 | One pairwise interaction | 9901.1 | 35.2 |
| Global | 1 | Unmediated Interactions | 9903.4 | 37.5 |
| Global | Global: Bobcat*Red fox, all others 0 | One pairwise interaction | 9912.1 | 46.2 |
| Global | Global: Coyote*Red fox, all others 0 | One pairwise interaction | 9921.0 | 55.1 |
| Global | 0 | No interactions | 9923.6 | 57.6 |
| Global | Global: Gray fox*Red fox, all others 0 | One pairwise interaction | 9925.8 | 59.9 |
| Global | Global: Coyote*Gray fox, all others 0 | One pairwise interaction | 9930.2 | 64.2 |
| HDens+Yard+Dog+Rolag+Deer+Hunt+Yard*Dog | 0 | Humans and Prey without Interactions | 9934.0 | 68.1 |

Table C4 (continued)

| | | | | |
|---|---|--|---------|-------|
| HDens+Yard+Dog+Rolag+Deer+Hunt+Yard*Dog | 1 | Humans and Prey with Unmediated Interactions | 9934.1 | 68.2 |
| HDens+Yard+Dog+Yard*Dog | 0 | Humans without Interactions | 9941.9 | 76.0 |
| HDens+Yard+Dog+Yard*Dog | 1 | Humans with Unmediated Interactions | 9943.2 | 77.3 |
| HDens+Forest5+Forest100+HDens*Forest5+HDens*Forest100 | 1 | Forest and Humans with Unmediated Interactions | 9952.0 | 86.0 |
| HDens+Forest5+Forest100+HDens*Forest5+HDens*Forest100 | 0 | Forest and Humans without Interactions | 9958.8 | 92.9 |
| Forest5+Forest100 | 1 | Forest with Unmediated Interactions | 9964.0 | 98.1 |
| Forest5+Forest100 | 0 | Forest without interactions | 9969.0 | 103.1 |
| Rolag+Deer | 1 | Prey with Unmediated Interactions | 9991.0 | 125.1 |
| Rolag+Deer | 0 | Prey without Interactions | 9992.5 | 126.6 |
| 1 | 0 | Null model | 10128.5 | 262.6 |

Table C5: Average detection rate (count/day) for four competing carnivore species from camera traps run in Washington, DC and Raleigh, NC from 2012-2016 between green space and yards in suburban, exurban and rural habitats. Standard error is shown in parentheses. Bobcat and coyote detection rates were higher in green space in suburban and exurban habitats, and higher in yards in rural habitats. All species except bobcat had higher detection rates in suburban green space compared to wild green space.

| | Suburban | | Exurban | | Rural | | Wild |
|----------|-----------------------|-----------------------|-----------------------|-----------------------|----------------|-----------------------|----------------|
| Species | Green Space | Yard | Green Space | Yard | Green Space | Yard | Green Space |
| Bobcat | 0.02 (0.01) | 0.00 (0.00) | 0.02 (0.01) | 0.00 (0.00) | 0.03 (0.01) | 0.06 (0.03) | 0.06 (0.01) |
| Coyote | 0.41 (0.09) | 0.05 (0.03) | 0.65 (0.13) | 0.26 (0.10) | 0.23 (0.08) | 0.31 (0.11) | 0.25 (0.04) |
| Grey Fox | 0.74 (0.16) | 1.53 (0.63) | 1.00 (0.32) | 1.26 (0.62) | 0.28 (0.07) | 0.61 (0.33) | 0.04 (0.02) |
| Red Fox | 0.51 (0.16) | 0.21 (0.13) | 0.30 (0.09) | 0.64 (0.21) | 0.36 (0.08) | 1.02 (0.31) | 0.24 (0.04) |

Table C7: OR_{sp} associated with the presence of absence of species 2 on the occupancy of species 1 and OR_h associated with the change in covariates of 0.5 units based on camera trapping data in Washington, DC and Raleigh, NC from 2012-2016. All covariates were centered and scaled for easy comparison. B is bobcat, C coyote, GF grey fox and RF red fox. For OR_h , the occupancy of species 1 is conditioned on the absence of species 2 and all other species.

| Species | OR_{sp} | OR_h | | | City |
|---------|-----------|------------------------|---------------|-------------|---------|
| | | Housing Density 5km | Forest 5km | Forest 100m | |
| B*C | 0.35 | 0.60 | 1.56 | 3.13 | DC |
| B*GF | 0.16 | 0.61 | 1.59 | 3.28 | DC |
| B*RF | 1.17 | 0.65 | 1.56 | 3.72 | DC |
| C*B | 0.35 | 0.86 | 0.99 | 0.94 | DC |
| C*GF | 1.38 | 1.01 | 0.94 | 0.90 | DC |
| C*RF | 1.17 | 0.98 | 0.97 | 0.88 | DC |
| GF*B | 0.16 | 0.83 | 0.91 | 0.87 | DC |
| GF*C | 1.38 | 1.20 | 0.89 | 0.83 | DC |
| GF*RF | 0.27 | 1.24 | 0.86 | 0.89 | DC |
| RF*B | 1.17 | 1.32 | 1.04 | 1.33 | DC |
| RF*C | 1.17 | 1.04 | 1.08 | 1.20 | DC |
| RF*GF | 0.27 | 1.06 | 1.02 | 1.33 | DC |
| B*C | 0.34 | 0.19 | 1.59 | 5.88 | Raleigh |
| B*GF | 0.05 | 0.26 | 1.90 | 5.89 | Raleigh |
| B*RF | 0.25 | 0.23 | 2.19 | 5.91 | Raleigh |
| C*B | 0.34 | 0.71 | 0.69 | 1.10 | Raleigh |
| C*GF | 2.03 | 1.53 | 0.77 | 1.04 | Raleigh |
| C*RF | 2.11 | 1.67 | 0.66 | 1.08 | Raleigh |
| GF*B | 0.05 | 1.31 | 0.80 | 1.06 | Raleigh |
| GF*C | 2.03 | 2.49 | 0.93 | 0.98 | Raleigh |
| GF*RF | 0.46 | 2.75 | 0.80 | 1.10 | Raleigh |
| RF*B | 0.25 | 0.78 | 1.05 | 1.09 | Raleigh |
| RF*C | 2.11 | 2.08 | 0.91 | 1.02 | Raleigh |
| RF*GF | 0.46 | 1.85 | 1.33 | 1.56 | Raleigh |

Appendix D: Chapter 3 supplementary materials

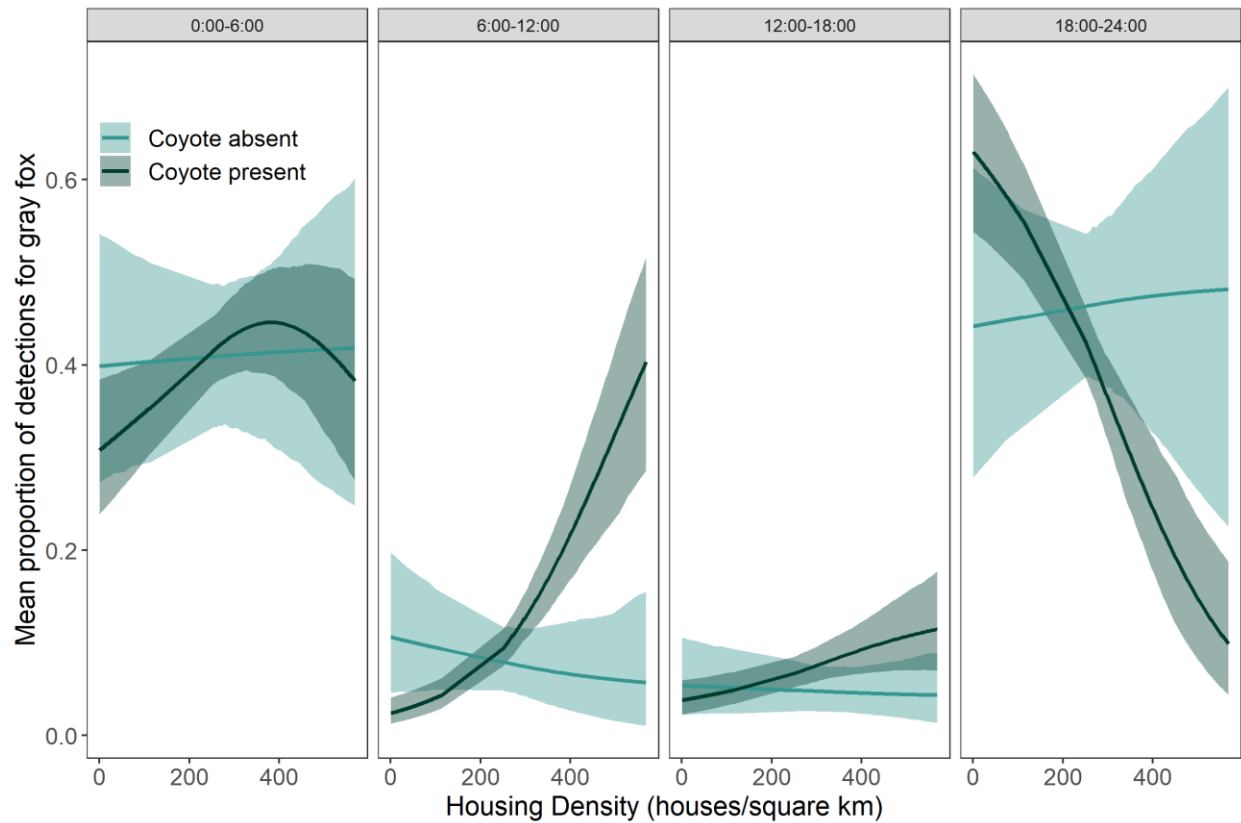


Figure D1: The change in the average proportion of gray fox detections within each of four time periods (0:00-6:00, 6:00-12:00, 12:00-18:00, 18:00-24:00) as housing density increases in the presence and absence of coyotes. Data are taken from camera locations in Raleigh, NC, USA from 2012-2016. Gray foxes were more diurnal at high housing densities in the presence of coyotes and more nocturnal in the absence of coyotes.

Table D1: Camera effort in terms of camera nights for camera traps run in Raleigh, NC in each year from 2012-2016.

| Year | Months | Total Camera Nights | Number of Camera Sites |
|------|-------------------|---------------------|------------------------|
| 2012 | January-July | 998 | 69 |
| 2013 | February-December | 2673 | 116 |
| 2014 | January-December | 5177 | 237 |
| 2015 | January-December | 4062 | 188 |
| 2016 | January-September | 3346 | 150 |

Table D2: Effort in terms of camera nights for camera traps run in Raleigh, NC from 2012-2016 between different habitat types along the urbanization gradient around each city.

| Habitat | Large Forest $>1\text{km}^2$ | Small Forest $\leq 1\text{km}^2$ | Open | Yard | Total |
|----------|------------------------------|----------------------------------|---------|---------|----------|
| Suburban | 105.94 | 3345.99 | 1070.32 | 2981.90 | 6433.83 |
| Exurban | 251.54 | 2673.56 | 956.15 | 1545.90 | 4471.01 |
| Rural | 603.21 | 1801.37 | 1059.90 | 637.06 | 3041.65 |
| Wild | 987.69 | 1322.65 | 0.00 | 0.00 | 2310.34 |
| Total | 1948.39 | 9143.58 | 3086.37 | 5164.86 | 16256.82 |

Table D3: Covariates used in the occupancy analyses. Each covariate is categorized by whether it was used in the spatial model, temporal model or both.

| Interaction Type | Covariate | Description | Type | Model |
|----------------------|--|---|--------------------------|-----------|
| Spatial | Forest5 | % tree cover in 5km radius ¹ | GIS 5km | ψ |
| Spatial | Forest5* HDens | Interaction term between large forest patches and housing density | Interaction | ψ |
| Spatial and Temporal | Forest100 | % tree cover in 100m radius ¹ | GIS 100m | ψ, p |
| Spatial and Temporal | HDens | Average Housing Density (houses/km ²) in 5km radius ² | GIS 5km | ψ, p |
| Spatial and Temporal | Forest100* HDens | Interaction term between local tree cover and housing density | Interaction | Ψ, p |
| Temporal | Det_dist | Maximum distance at which camera detects a human (m) | Camera site | p |
| Temporal | Precip | ECMWF Interim Full Daily Total Precipitation (mm) | Temporal and camera site | p |
| Temporal | Time since last coyote detection | The length of time since the last detection of a coyote at a given site (hours) | Temporal and camera site | p |
| Temporal | Activity pattern | Fourier series basis function | Temporal and camera site | p |
| Temporal | Latent coyote occupancy | Model-estimated latent indicator of whether coyote occupied the site or not | Camera site | p |
| Temporal | Activity pattern*Latent coyote occupancy | Interaction | Temporal and camera site | p |

1. Percent Tree Cover, Global Forest Change Dataset (Hansen *et al.* 2013)

2. Landscape and Urban Planning 69 (2004) 183-199 (Hammer *et al.* 2004)

3. EnvData (Dodge *et al.* 2013)