ABSTRACT

Title of Dissertation:	ANTHROPOGENIC INFLUENCES ON BOTTOM-UP AND TOP-DOWN REGULATION OF ANIMAL DISTRIBUTIONS, POPULATIONS, AND BEHAVIORS IN URBAN ENVIRONMENTS
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Animal populations are simultaneously governed by both bottom-up (e.g., habitat availability) and top-down (e.g., predation) regulation. While ecologists historically sought to differentiate the roles of bottom-up and top-down regulation on ecosystems, the two are not so easily defined in urban ecosystems due to the immense influence humans have on ecological processes in cities. In Chapter One, I present this argument from a philosophical perspective and comment on how this philosophy has shaped my worldview. In Chapter Two, I examine the legacy of historical park planning on urban bird assemblages using archived municipal maps and historical bird data. My analysis found a positive correlation between percent park area and both species richness and functional richness of birds. Additionally, I found the effect size of park area was larger than the effect of certain life history traits thought to facilitate urban exploitation. These results indicate that landscape features and life history traits are equally responsible for the success of synurbic species. Chapter Three explores the effect of urbanization on animal

behavior by analyzing anti-predator behavior of white-tailed deer (*Odocoileus virginianus*) in relation to ambient light, noise, and human activity. Despite negligible predation risk in my study area, deer expressed higher vigilance behavior in dark and noisy conditions, and increased their foraging group size during noisy conditions. These results suggest that anti-predator behaviors are a response to the perception of predation risk rather than a response to the actual presence of predators. Although predation of deer is rare in urban ecosystems, predation of smaller wildlife species by mesopredators, such as non-native domestic cats (*Felis catus*) is common. Chapter Four examines the potential for predation and zoonotic disease transmission between cats and eight native mammals by estimating the spatial and temporal overlap between species. I found that cat distribution was largely driven by anthropogenic features, whereas native wildlife was generally deterred by anthropogenic features and instead occupied forested areas. I also found that cats, as a species, were active on the landscape during the full 24-hour cycle. As a result, while spatial overlap between cats and wildlife varied across the study area, temporal overlap was possible anywhere cats and wildlife co-occurred. Chapter Five expands on Chapter Four and investigates predation directly by using observations of cats carrying prey documented by motion-activated cameras. I found that predation by cats was higher in areas where supplemental cat food was prevalent, but declined near forested areas. Additionally, my results indicate that cats within 250 meters of a forest edge predominantly preyed on native wildlife, whereas cats generally preyed on non-native rats (*Rattus norvegicus*) when greater than 250 meters from a forest edge. Each chapter provides applied recommendations to the management and conservation of urban wildlife, but together, my work demonstrates the entanglement of bottom-up, top-down, and anthropogenic forces in urban ecosystems. In light of these findings, I

advocate for a more nuanced understanding of ecosystem regulation through a socio-ecological lens.

ANTHROPOGENIC INFLUENCES ON BOTTOM-UP AND TOP-DOWN REGULATION OF ANIMAL DISTRIBUTIONS, POPULATIONS, AND BEHAVIORS IN URBAN ENVIRONMENTS

by

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2024

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Dedication

For my incredible wife, Kaitlyn.

For all those who came before us, and all those who will come after.

For the wonderful world that transcends us all - may we never forget its splendor or tire in our work to preserve it.

Acknowledgements

This dissertation would not be possible without the support of my wife, parents, parents-in-law, grandparents, siblings, friends, the URBANxNATURE Lab, and the DC Cat Count team. I am particularly thankful for the support and guidance of my advisor, Dr. Travis Gallo, as well as my committee members at both George Mason University and the University of Maryland. I wish to also thank God for their unconditional love and forgiveness, and for their sublime creation which sustains all.

On a practical level, I would be remise not to acknowledge the bus drivers and train conductors that facilitated my commute; the many public works employees that keep the water running, toilets flushing, electricity flowing, and wifi operational; the facilities and administrative staff at George Mason University, the University of Maryland, and the Humane Rescue Alliance that provided a safe work environment; the public health officials, first responders, and front-line workers that guided us through and out of the COVID-19 pandemic; the medical personnel that care for me; the farmers, fishers, bakers, brewers, and distillers who nourish me; and all other public servants who keep our society functional. If I am able to accomplish even a fraction of the public good that the aforementioned do, I will consider my career a major success.

Preface

The doctoral dissertation is a time-honored tradition in academia, but time has found practicality to be a better companion than tradition. Thus, as time marched on, the dissertation tradition was left behind and has become antiquated. While I am flattered that you wish to read my dissertation in this compiled format, I would suggest that the reader instead read (and cite) the following stand-alone publications for each dissertation chapter:

Chapter 2	Herrera DJ, Fidino M, Luther D, Mullinax JM, Gallo T. 2024. Historical park is associated with modern day patterns of bird diversity in cities. *Landscape and Urban Planning* 249: e105132. DOI: 10.1016/j.landurbplan.2024.105132
Chapter 4	Herrera DJ, Cove MV, McShea WJ, Decker S, Flockhart DTT, Moore SM, Gallo T. 2022. Spatial and temporal overlap of domestic cats (*Felis catus*) and native urban wildlife. *Frontiers in Ecology and Evolution* 10: e1048585. DOI: 10.3389/fevo.2022.1048585
Chapter 5	Herrera DJ, Cove MV, McShea WJ, Flockhart DT, Decker S, Moore SM, Gallo T. 2022. Prey selection and predation behavior of free-roaming domestic cats (*Felis catus*) in an urban ecosystem: implications for urban cat management. *Biological Conservation* 268: e109503. DOI: 10.1016/j.biocon.2022.109503

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Chapter 1: Introduction

1.1 A tail of two cities: Background and motivation

In the late 1850's, Charles Darne slipped from the imaginative mind of Charles Dickens to the pages of a weekly periodical, then to the novel titled *A Tale of Two Cities*, and finally into the canon of literary classics that is widely revered today (Dickens 1987). While Dickens' novel literally takes place in two cities (London, England and Paris, France), its title also alludes to the great disparity between the aristocracy and working class in revolutionary France (Dickens 1987; Britto and Alexander 2021). In this way, readers bear witness to two fundamentally different ways of life within the same great walls – two cities in one. The divided city narrative has since enshrined itself as a familiar paradigm and still persists today (Musterd et al. 2017; Musterd 2020), although Dickens was hardly the first to notice the theme (Marcuse 1993). The glaring flaw that connects each conception of the divided city, however, is that the city is never truly divided. In all cases, members of each class interact to form a transactional system of co-dependence, even if such interactions are lopsided (Kolb 1954). Still, the desire to dichotomize perpetuates an enduring misconception of unreconcilable difference between any two things that, in reality, are only slightly different from each other.

Without exception, everything is interconnected. I remember first being struck by this idea as I learned about the food web in the great prairies of the Midwest, and later recounted it in great detail at the dinner table to my sister's dismay. The idea resurfaced several times between my time in boy scouts, camping with family, and in spirited discussions on runs with my high school cross country team whose coach also happened to be my biology teacher. Although I

could have recited this idea of interconnectedness throughout my childhood, I did not come to fully embrace the idea in my philosophy of life until I attended college. The "liberal arts" label bore little meaning to me as a high schooler, but opened my eyes to a hidden reality as a college student, and eventually formed a personal philosophy that would come to change my understanding of existence. While my friends from high school criticized their gen-ed coursework as an irrelevant waste of time and eagerly anticipated completing this seemingly superfluous aspect of their education, my classmates and I were patiently reminded that the liberal arts curriculum demanded such diversified coursework across all four years. It did not take long for me to see the value of this curriculum. The principles we learned about in my biology classes were complimented by a greater understanding of the social context surrounding scientific discoveries in my history classes, the collective memory of these times in my literature classes, the documentation of these concepts in my art classes, and the ramifications of these concepts in my psychology and policy classes. The intersection of these lessons drove me away from the memorization of isolated facts, and towards a more holistic understanding of nuanced concepts. Eventually, the ties between phenomena which I would have previously declared unrelated became more apparent as I chipped away at the psychological silos that had been enforced throughout my childhood.

To be clear, my previous understanding of a world of silos is neither uncommon, nor anyone's fault in particular. It is human nature to reduce complexity into isolated concepts, no matter how arbitrary such demarcations are (Horst et al. 2005; Clark et al. 2019). But when we hold ourselves to seeing two extremes, we deny ourselves the ability see the important, abundant, and beautiful reality of the middle. Charles Darwin pointed out this tragedy in The Origin of Species, when he uses thirteen chapters to build the case that species slowly enter existence

through a series of gradual advantageous or deleterious mutations over generations, then surprises readers by swiftly changing course and renouncing the concept of species altogether. Darwin argues that the difference between two species is only apparent because the innumerable forms which bridge the two no longer exist (Darwin 1859). If we had the capacity to see every lifeform which has ever existed, and organized them into clusters by degree of relatedness to one another, we would struggle to identify where one species stops and another starts (Figure 1.1A). The brilliance of the middle would overwhelm us and might make us question our most basic understanding of the world. Lacking our capacity to rapidly compartmentalize, we would be forced to shift our cognitive approach from asking "what is this" and instead asking "how is this related to everything else, myself included?"

Perhaps the ultimate fabrication of distance between species is the time-honored tradition of drawing a line between humans and everything else. That is, the tendency for us to see things as being either human or nature (Figure 1.1B; Carter et al., 2014; Hunold, 2019). This contrast is perhaps most readily assumed within the pinnacle of human creation: the city. In reality, cities are a tenuous balance between the desires of humans and both the resources and demands of the natural environment. As such, humans are influenced by ecological factors (e.g., water availability, erosion, zoonotic disease, etc.) and non-human factors are influenced by anthropogenic factors (e.g., pollution, habitat degradation, greenhouse gas emissions, etc.). Thus, considering the city separate from its environment yields a deficient understanding of urbanization since cities are socio-ecological systems (Liu et al. 2007; Evans 2011; Childers et al. 2015; Pickett et al. 2016; Schell et al. 2020). For example, the institutional separation of races and classes during the early days of many US cities was, in part, based on the abundance of greenspace present in a neighborhood since such spaces increased property value and could be

used to prevent the "infiltration of…lower social occupancy…" (Underwriting and valuation procedure under title II of the National Housing Act 1938). Selective investment in already affluent neighborhoods and disinvestment in already disadvantaged neighborhoods resulted in the development of additional greenspaces where they were already prevalent, and thus an unequal distribution of greenspace across the urban landscape. As a result, affluent white neighborhoods now contain the majority of greenspace while neighborhoods with socio-economically disadvantaged and non-white residents have disproportionately less access to greenspace (Nardone et al. 2021). Because wildlife is dependent on habitat availability, the uneven distribution of parks has reorganized wildlife communities to be more prevalent in park-laden areas. Accordingly, greater biodiversity tends to be concentrated in affluent neighborhoods and both lower biodiversity and greater abundance of non-native species are found in socioeconomically depressed neighborhoods (Leong et al. 2018; Magle et al. 2021; Herrera, Michael V. Cove, et al. 2022; Wood et al. 2023). Likewise, the disproportionate heat experienced in sparsely vegetated low-income communities, in combination with increased potential for zoonotic disease transmission from altered wildlife communities, further exacerbates the health disparities already experienced by low-income residents (McDonald and Jones 2018; Schell et al. 2020; Roberts et al. 2022; Fang et al. 2023). Thus, the social components of the urban landscape directly influence its natural components, which in turn creates a feedback loop by further contributing to socioeconomic disparity. This feedback loop, and the many others omitted here, jointly create a system that is neither fully social nor fully ecological, but is instead a socio-ecological system.

Urban wildlife (playfully alluded to here by simply their tails for the sake of literary turn of phrase) are salient examples of socio-ecological systems since these individuals blur the

boundary between the anthropogenic and the natural worlds by literally moving between these two concepts. While society has historically cast humans and nature as two diametric entities, many species make a living by marrying the two. Consider the raccoon (*Procyon lotor*) that lives in forested tracts of a city parkland, but ventures into the surrounding neighborhoods to dine on our discarded leftovers. Likewise, the coyote's (*Canis latrans*) den may epitomize our conception of nature, but she leaves the den nightly to hunt the cats (*Felis catus*) and rats (*Rattus norvegicus*) in our immensely unnatural alleyways. How can we tease apart nature from the city when the two are, in actuality, intertwined? Within this dissertation, I aim to abandon the conventional separation of humans and nature in cities, and instead expound upon the nuanced relationships between society and our non-human neighbors that forms the socio-ecological city. That is, I wish to argue that humans and nature do not comprise a tale of two cities. Instead, humans and nature are inextricably intertwined to the extent that urban wildlife are as much a product of nature as they are a product of society. They are not constrained to one city (i.e., humans) or the other (i.e., nature), but are instead tails of two cities.

1.2 Overview

Ecosystems are traditionally understood as being driven by a combination of bottom-up (i.e., resource-driven) and top-down (i.e., predator-driven) regulation. Historical interpretations of these phenomena tended to exclude the role of humans, and falsely assumed that both vegetation and predators existed irrespective of anthropogenic actions (Kay 1998; Moll et al. 2021). Over time, however, it became evident that humans play an undeniable role in the distribution and prevalence of predators (Darimont et al. 2015; Suraci et al. 2019; Ordiz et al. 2021). Likewise, human land-management practices control the distribution and diversity of

vegetation (Kay 1998; Fahey et al. 2012; Morris and Rowe 2014). Considered together, the dual control of predators and vegetation indicates that humans govern both top-down and bottom-up regulation in ecosystems, bestowing humans the title of 'hyperkeystone species' (Worm and Paine 2016; Moll et al. 2021). Nowhere is this more apparent than in cities, where humans attempt to exercise intensive control of the landscape and the species present within it. As a result, urban wildlife is uniquely controlled by anthropogenic actions both intentionally and unintentionally. Throughout this dissertation, I explore the entangled roles of bottom-up and top-down regulation on urban wildlife species, and document the ubiquitous influence of humans in both directions of regulation.

Urbanization can act as a filter for wildlife communities by excluding species not pre-disposed to living in disturbed and dynamic environments (Aronson et al. 2016). Intentional urban design may lessen these effects by ensuring sufficient habitats that foster greater biodiversity (Garrard et al. 2018). Land use planning directly governs the location, size, and shape of urban parks, which can act as habitat refuges for wildlife. Thus, land use planning decisions made decades, or even centuries, ago affect modern day habitat availability for wildlife in cities. In Chapter Two, I seek to understand the role of these historical decisions on avian diversity by digitizing historical maps of three mid-sized temperate U.S cities — Washington (DC), Minneapolis (MN) and Pittsburg (PA) — in five-year increments between 1900-2020 and calculating landscape metrics for each city's park system over time. I then used historical Christmas Bird Count data to estimate species and functional diversity metrics over the same 120-year period as a function of historical landscape metrics. My analysis lends support to the species-area relationship, as total greenspace area had the greatest positive relationship with species richness, functional divergence, and observations of species in different functional

groups. Greenspace shape and connectivity also influenced some biodiversity metrics, but to a lesser degree than greenspace area. These findings demonstrate that historical land use decisions have a strong influence on the modern-day patterns of habitat availability, which in turn informs avian diversity. While habitat availability is a decidedly bottom-up regulating feature, the human-centric process that dictates such availability introduces an element of top-down regulation since it derives from actions taken by a species at a higher trophic level. Thus, while the focus of Chapter Two is on bottom-up regulation, the inherently anthropogenic process of filtering species through landscape change highlights subtle traces of top-down regulation.

While Chapter Two explores how human actions influence local species assemblages, Chapter Three focuses on a common artifact of this phenomena: the near-exclusion of apex predators from urban ecosystems. Although non-human apex predators are largely absent from urban landscapes, urban prey species still exhibit anti-predator behavior. Such behaviors are an adaptation that allows prey species to forage while simultaneously avoiding predation, but is only useful if environmental conditions permit the prey to detect potential predators (Quenette 1990; Brown and Kotler 2004). When conditions reduce the prey's predator detection ability, prey may compensate by increasing their anti-predator behavior (Lagory 1986). I tested this hypothesis by recording white-tailed deer (*Odocoileus virginianus*) vigilance behavior and group size alongside ambient light and noise. I used human mobility data to calculate the threat of disturbance by humans, the only potential "predator" of deer in our study system, and combined remotely sensed lidar data and seasonal vegetation intensity data to calculate vegetation complexity. Chapter Three provides support for my hypothesis that deer are more likely to express anti-predator behaviors when ambient conditions inhibit them from detecting potential predators, even when actual risk of predation is low. However, immediate risk – defined as the

number of human visitors mediated by the complexity of the habitat – had no significant impact on anti-predator behavior. While top-down regulation is undoubtably the ultimate cause of anti-predator behavior, these findings suggest that abiotic bottom-up factors act as proximate causes. That the societal afterthoughts of light and noise pollution so alter animal behavior to provoke a fear of non-existent predators further exemplifies the entanglement of society and nature.

While light and noise from anthropogenic development prompts behavioral shifts within wildlife in adjacent habitat patches, it can also deter species from using such patches and thus influence how species are distributed across the city. Ecological traps may occur where habitat availability lures individuals into an area which appears to be viable habitat, but is actually plagued with attributes which decrease fitness, such as heightened predation risk. Free-roaming domestic cats are a non-native predator and are well adapted to urban living (Kays et al. 2020; Herrera, Michael V. Cove, et al. 2022). Although cats are abundant in urban areas, little is known about how these prolific predators are distributed across urban landscapes, and even less is known about the extent to which they overlap with urban wildlife (e.g., Gehrt et al. 2013). Chapter Four analyzes presence-absence data from domestic cats and eight native wildlife species to understand their individual distributions across DC, as well as how cats overlap with wildlife both spatially and temporally. Notably, cats had a positive association with human population density and a negative association with canopy cover, while other species were found to have negative associations with humans and positive associations with canopy cover. As a result, overlap between cats and native wildlife was relatively low within forested parks, but higher in developed areas of DC. While habitat selection is typically informed by bottom-up processes, Chapter Four demonstrates that bottom-up regulation can mediate the risk of top-down regulation by simultaneously governing where predators and prey are distributed, which

impacts the degree to which the two overlap and thus the risk of one depredating the other. This becomes especially apparent when such predators are released and sustained by humans, further blurring the line between natural and anthropogenic.

Analyzing predation risk by examining prey behavior (Chapter Three) and predator-prey overlap (Chapter Four) offer great insight into urban predation dynamics, but fall short of studying the actual predation that drives top-down regulation. The fifth and final chapter overcomes this shortcoming by analyzing predation behavior and prey selection of domestic cats. Cats are often allowed outside as a means of non-native rodent control. However, cats do little to control the non-native rodent population and instead reduce native biodiversity by preying on native species (Glass et al. 2009; Loss et al. 2013; Doherty et al. 2016; Parsons et al. 2018). Chapter Five investigates the prevalence of predation by free-roaming domestic cats, as well as the factors contributing to their predation of native vs non-native species. I found that the probability of predation by cats had a positive association with the availability of cat food, and a negative association with the distance to a forest edge. Crucially, I also found that the probability of a prey being a native species declined as cats moved away from the forest edge. Although predation is unequivocally a top-down force, these findings again illuminate the role that habitat availability – in this case, distance to forest edge – plays in mediating such pressures. Once again, the unilateral influence of either top-down or bottom-up regulation is marred by their interwoven effects, and is further muddied by the direct involvement of humans via supplementally feeding predators.

Taken together, it is my hope that this body of work advances our understanding of urban ecological pressures for wildlife by exploring human influences on a blurred gradient of bottom-

up and top-down regulating features common in the urban environment (Figure 1.1C). In our crusade to exercise control in urban areas, we craft a specific set of circumstances in which nature carries out its processes. Similar to how an author declares a story's setting and characters before detailing the predictable course of events that would follow, society engineers cities that inherently lend themselves to specific species and the logical associations between them. All the while we observe and document such phenomenon with curious bewilderment as if we had not produced the situation or guided the direction in which it progressed. This sentiment is not intended to be cynical, but is instead intended to elicit reassuring, albeit cautious, optimism. By reconciling that human have an outsized influence on both the top-down and bottom-up regulation present in urban ecosystems, we can take ownership of our actions and instead create cities that promote biodiversity rather than decimate it. Through thoughtful urban design and regulation, we can transform cities into productive socio-ecological systems that live in harmony with the natural world (Rosenzweig 2003; Ives et al. 2016; Garrard et al. 2018). In short, recognizing the omnipresent intervention of humans in urban ecosystems can allow us to capitalize on our influence and empower us to instead make decisions that position cities as a part of, not apart from, nature. Tails of two cities no longer.

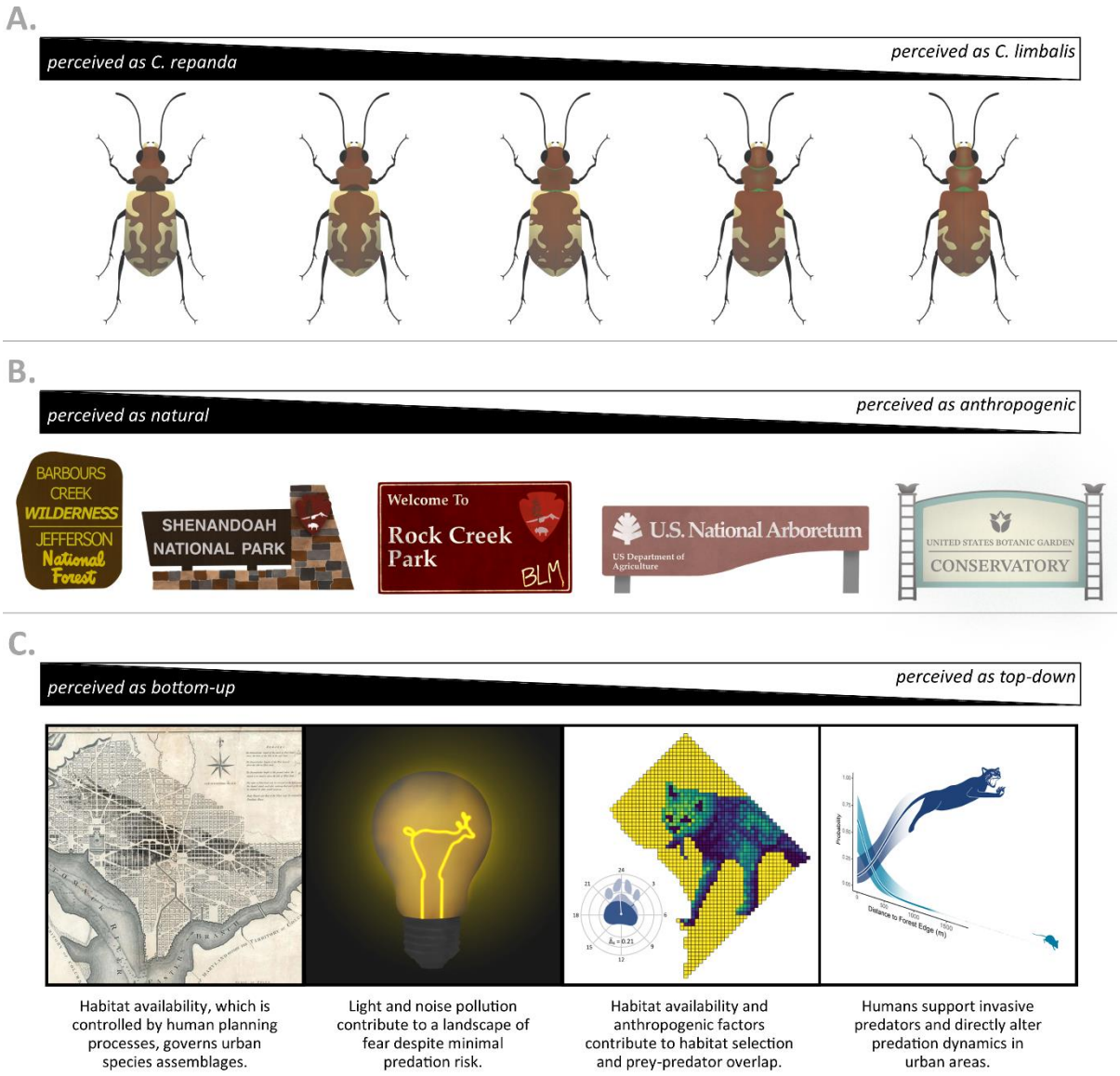


Figure 1.1 Conceptual figure depicting the difficulty of demarcating two extremes when the various forms bridging such extremes are also considered. Specifically, the figure uses (A) the first animals I ever researched, tiger beetles (*Cicindela spp.*), to demonstrate Charles Darwin's point that the species concept breaks down if all evolutionary links between modern species are considered. The middle panel (B) extends this concept to depict the gradient between what is conventionally perceived as nature and a similarly vegetated space which is conventionally perceived as anthropogenic. Although wilderness areas are generally categorized as being natural and conservatories are undeniably anthropogenic, it is difficult to identify when greenspaces cease to be nature and instead become products of human design. Finally, the bottom panel (C) depicts the chapters of my dissertation in a gradient between bottom-up and top-down regulation, noting that humans are implicated across this gradient.

Chapter 2: Historical park planning is associated with modern-day patterns of bird diversity in cities

2.1 Introduction

Urbanization acts as a filter for species assemblages such that some species adapt to urban living with relative ease while others are extirpated (McKinney and Lockwood 1999; Aronson et al. 2016). Traits which accommodate the demands of urbanization have been proposed as the mechanism behind this phenomenon (Santini et al. 2019; Weiss et al. 2023). While life history and morphological traits may 'pre-dispose' a species to urban living, the traits themselves are not filters. Instead, the physical form of an urban area interacts with these traits in ways that encourage the success of some species and limit the success of others (Tratalos et al. 2007; Andersson and Colding 2014; Aronson et al. 2016). Because the configuration of urban habitat (e.g., parks, cemeteries, natural areas, and other forms of green space) is driven by human development policies (e.g., planning, zoning, design) rather than ecological processes (e.g., natural disturbances or ecological succession), the availability and configuration of urban habitat can be disproportionately attributed to contemporary and historic development decisions (Faeth et al. 2011; Fahey et al. 2012; Lowry et al. 2012; Aronson et al. 2016; Norton et al. 2016; Roman et al. 2018; Schell et al. 2020; Dunn et al. 2022). In this way, humans implicitly design landscape-level filters which control species diversity in urban areas via the structure of the city and its green spaces.

While urban green spaces have always been preserved for human benefit, they have inadvertently benefited wildlife through the creation of habitat. Park systems may be especially beneficial since they have relative permanence and are distributed across the city regardless of

development density, unlike other green spaces such as private yards (Nielsen et al. 2014; Fahey and Casali 2017). However, park systems differ between cities, and thus, may filter species differently. The theories of island biogeography and species-area relationship would suggest that systems with large parks (Rosenzweig and Ziv 1999) or systems comprised of numerous small parks (Simberloff and Abele 1982) would contain greater biodiversity than systems with small or few parks. An analysis of historic records affords a 'natural' experiment in which the relationship between the design of urban park systems and biodiversity can be assessed.

This study uses archived maps and historic bird surveys to study the relationship between park system design and species diversity for three US cities: Washington (DC), Minneapolis (MN), and Pittsburgh (PA). These cities share a similar development age (≥200 years old), area (<180 km^2), and human population density (~2,000-4,000 people/km^2; United States Census Bureau, 2020). Additionally, they all contain at least one large river but are not coastal cities, and experience seasonality (Lisovski et al. 2017). Studying current ecological trends through a longitudinal lens – rather than a cross-sectional study – allows for the identification of park attributes that have promoted biodiversity without disregarding the unique historic and geographic context that have also contributed to biodiversity (Lindenmayer et al. 2011). Such an approach offers insight into urban planning practices that foster biodiversity, which will be increasingly important in a rapidly urbanizing world (Magle et al. 2012; Garrard et al. 2018; Collins et al. 2021; Kay et al. 2022).

2.1.1 Urban beginnings

An extensive network of cities and towns existed across North America for at least 3,000 years prior to European settlement (Griffin 1967). The design of these indigenous settlements

varied according to local geography and cultural values (McGuire and Schiffer 1983). Unfortunately, little is known about the layout of the indigenous settlements preceding Washington, Pittsburgh, and Minneapolis. In all three cities, indigenous populations were extirpated and their urban infrastructure was ignored in the next phase of urban development.

The Seneca village of Diondega is believed to have existed in the modern-day Golden Triangle district of Pittsburgh prior to French military development, followed then by English and then American military expansions (Sipe 1930). However, archeological evidence cannot confirm permanent settlement of the site prior to colonization (Swauger 1977). The Lenape settlement of Shannopin's Town was located 3 km upriver in the modern-day neighborhood of Lower Lawrenceville (Sipe 1930; Swauger 1977). While the location of Shannopin's Town is well documented, the archeologic record is sparse regarding its urban form (Lombardi et al. 2013).

The city of Nacochtank, located between the Benning and Congress Heights neighborhoods of modern-day Washington, DC, was home to the Nacotchtank people (Burr 1920; Humphrey and Chambers 1977; McFadden-Resper and Williams 2005). Archeological evidence suggests a portion of the city was fortified with dispersed dwellings and agricultural fields beyond the city walls, but little information exists regarding the physical layout of the city (Humphrey and Chambers 1977). Eventually, the Nacochtank were forcefully relocated to what is now called Theodore Roosevelt Island , but archeological excavations offer no insights about the layout of the village built there (Smith 1624; Burr 1920; Theodore Roosevelt Island cultural landscape report 2018).

Modern-day Minneapolis resides in the ancestral homeland of the Dakota People, whose tradition holds that the epicenter of creation is just beyond the Minneapolis border (Carlson and John 2015; Gould and Rock 2016; Gould and Rock 2016). The Dakota's semi-nomadic lifestyle resulted in frequent encampments in the sacred region, but little permanent development until the agricultural village of Ȟeyáta Othúŋwe was established in the present-day neighborhood of Uptown in 1829 (Carlson 2012; Beane 2014; Carlson and John 2015). Notions of the village's form are limited to two conflicting sources: a letter describing fenced paths between corn fields (Pond 1835; as cited in Beane 2014), and a painting depicting a cluster of dwellings surrounded by open prairie (Catlin 1835). The village was later relocated, but recent land disputes indicate that elements of Dakota development have inconspicuously endured within Minneapolis until at least 1999 (Wainwright and Robertson 2003; Beane 2014; Gould and Rock 2016).

2.1.2 Post-colonial urbanization

Urban development progressed along rectilinear street grids following European colonization as a means of both fostering economic growth and structuring cities around the symbolic ideals of order and influence (Loughran 2020; Boeing 2021). As grid systems expanded, streets often encountered non-rectilinear geographic features like rivers or valleys (Crawford 1905; Ignatieva et al. 2011). Such was the case in Pittsburgh, whose rivers and hills kept neighborhoods relatively isolated. As a result, numerous independent street grids developed simultaneously. A unifying plan was eventually proposed to bridge these isolated developments, and the connecting of non-aligned street systems resulted in irregular junctions and oddly shaped parcels that, despite their inconvenient shape, were nonetheless built upon (Pittsburgh Department of City Planning 2012).

Conversely, misshapen parcels were the desired outcome of Washington, DC's urban design. Under the direction of Pierre Charles L'Enfant, Washington's street system was intentionally planned to include both rectilinear and diagonal streets whose intersections would form triangular parcels that would serve as civic space (Crawford 1905; Berg 2008). These small greenspaces were prolific throughout the city and created an early park system that was intended to be accessible by all residents of the US capital (Berg 2008; Schroder 2021). Still, L'Enfant's plan largely respected the impositions presented by the natural environment. After extensive surveys from Andrew Ellicott and Benjamin Banneker, Washington was planned to incorporate local geography (Bedini 1969; Berg 2008). By siting the Capitol building atop Jenkins' Hill (now called Capitol Hill) and by placing the Executive Mansion (now called the White House) on the edge of the Potomak (now spelled Potomac) River, the local geography contributed to the urban design rather than detracted from it (*note that the Potomac River has since been dredged and the White House no longer sits on the riverbank as a result*; Hines 1991; Berg 2008).

In Minneapolis, urban planners incorporated the natural shape of the Mississippi River into the city's design expressly to avoid misshapen parcels. Land adjacent to the river was almost exclusively used for industrial purposes. Development of the river corridor was thus organized for maximum economic efficiency, which avoided irregular grids and thus undeveloped land (John O. Anfinson et al. 2003). Despite being separate municipalities at the time, land east and west of the Mississippi River were surveyed by the same crew and the two road systems were purposefully designed to align where neighboring grids met. Between business interests and cohesive survey efforts, Minneapolis developed into a city of regularly shaped and sized blocks, with relatively little designated open space (Atwater 1893).

2.1.3 The American Parks Movement

The Industrial Revolution prompted a mass-migration to cities by jobseekers, which caused US cities to become overcrowded in the latter half of the 1800's (Hirschman and Mogford 2009; LaGrand 2020). To compensate, parks were formally introduced to urban landscapes to allow residents a place to relax outside of their homes (LaGrand 2020; Loughran 2020). Additionally, urban elites felt that physical and social reform were intrinsically tied, and thought that the creation of parks would advance their ideals of morality and civic-mindedness (Rosenzweig 1984; Taylor 1999). Although common spaces have always existed in urban areas — and were often vegetated to accommodate grazing livestock — the Parks Movement shifted these spaces from places of utility to places of leisure and social enlightenment (Taylor 1999; Brinkley and Vitiello 2014; Brinkley 2020). Minneapolis responded to the movement by formally designating its Board of Park Commissioners in 1883 (History of the Grand Rounds 1999), and Pittsburgh formalized its own Committee on Parks six years later (Maxwell 1985). Being under federal control, Washington's park system was governed by various federal agencies until local governance was obtained nearly 100 years later (Capital Space: A park system for the nation's capital 2010).

As urban park systems grew, prominent urban planners such as Fredrick Law Olmstead exercised outsized influence on the design of greenspaces of many major US cities, including Minneapolis and Washington (Crawford 1905; Ignatieva et al. 2011; Eisenman 2013). Olmstead's son, Fredrick Law Olmstead Jr., eventually also entered the profession and contributed to the urban design of Pittsburgh, and later improved upon his father's work in Washington (Klaus 1991; Peterson 1991) When siting new parks, the Olmsteads and other urban

planners prioritized the creation of sizable parks in already affluent neighborhoods – largely inaccessible to those of lower economic means (Maxwell 1985; Loughran 2020). At the same time, romanticized notions of spacious rural living captivated the minds of overcrowded urbanites, which prompted a transformation of urban green spaces from their native habitats to a picturesque and idealized imitation of country pasture (Crawford 1905; Maxwell 1985; Gobster 2007; Ford 2015).

While Pittsburgh's parks embraced this bucolic aspiration, Washington and Minneapolis both represent notable exceptions to the trend. In Minneapolis, Olmstead planned a novel linear park system (Crawford 1905; Ignatieva et al. 2011). As a result, Minneapolis' park system slowly moved towards a greenway network rather than a collection of isolated parks (History of the Grand Rounds 1999; Ford 2015). Olmstead Jr. sought to create a similar greenway in Washington, which was juxtaposed by an 1890 act of congress that authorized the establishment of Rock Creek Park in the center of the city (Finnigan 2012). Uniquely, the 7 km^2 park was established with a mandate that management must preserve its native flora, as opposed to being solely managed for recreation as other parks had been (Rock Creek Park Enabling Act 1890; Carruthers et al. 2009).

2.1.4 The City Beautiful Movement

The late 1800s bore witness to rampant poverty, disease, and civil unrest in cities (LaGrand 2020). The City Beautiful movement aimed to alleviate these issues by enhancing urban aesthetics – namely through municipal art and thoughtful landscaping (Peterson 1976; Szczygiel 2003; Freestone 2011; LaGrand 2020). The new style of city was showcased at the 1893 World's Columbian Exposition in Chicago, and quickly became the pinnacle of urban

design (Hines 1991). The preservation of existing urban forests and increased planting of urban trees ensued as increasing attention was given to semi-natural and beautified landscapes in urban parks (Peterson 1976). By 1900, the City Beautiful movement was fully realized and public parks were considered synonymous with urban improvement (Peterson 1976; Szczygiel 2003).

As urban park systems grew, some cities shifted their efforts from establishing new parks to connecting existing parks (Crawford 1905; Ignatieva et al. 2011). The structure of Minneapolis' park system became decidedly linear as it grew into an early example of a municipal greenway system (Fábos 2004). Meanwhile, Pittsburgh's park system focused on developing small neighborhood parks and improving access for residents, which was becoming a growing focus of cities across the country (Maxwell 1985; Freestone 2011).

While Washington's planned park system was revolutionary, it went largely unrealized until the City Beautiful Movement (Hines 1991; Berg 2008; Dickey 2014; Vernon 2014). In 1901, Congress commissioned Fredrick Law Olmstead Jr. to improve upon city's park system, which ultimately transformed DC into its modern aesthetic via an enlargement of the National Mall and the creation of the Mall's iconic memorials and museums (Peterson 1976; Hines 1991; Peterson 1991; Witt 2005; Finnigan 2012; Vernon 2014). Olmstead Jr. also established a plan to create a greenway system connecting the abandoned Civil War battlements to bolster park space beyond the National Mall. Although the greenway was never completed, the parcels acquired for the plan remain as parks today (Peterson 1991; Finnigan 2012).

2.1.5 Modern history of urban parks

Critics of the City Beautiful movement accused it of doing little to actually improve urban life at a great economic expense. In response, supporters of the movement claimed that

urban beautification brought about "moral environmentalism," the notion that urban aesthetics fostered an environment of societal improvement (Mackintosh 2005; Freestone 2011). True environmentalism, however, was largely absent from park planning until well after the desire for a practical city replaced that of a beautiful one (Daniels 2009; Freestone 2011).

Pittsburgh was an early adopter of ecological panning in its parks. A 1947 report assesses the ecological condition of Pittsburgh's Frick Park for the first time (Maxwell 1985), whereas Washington did not systematically consider the ecological state of its parks until 20 years later (The nation's capital: Policies plan for the year 2000 1961; Maxwell 1985; Gobster 2007; Capital Space: A park system for the nation's capital 2010). After an additional 20 years, Minneapolis also adopted an ecological approach to park planning and began removing invasive species (Ford 2015), then began reintroducing native plants in the 1990's (Friborg 1998).

National trends in urban planning have helped shape the park systems of Minneapolis, Pittsburgh, and Washington. However, local nuances in the cities' histories and designs have contributed to three distinct park systems in structure, and presumably function. Until recently, humans have been the sole consideration when planning park systems. Yet the physical structure of these park systems has influenced both the quality and quantity of wildlife habitat present. Thus, the legacy of historic land use and urban planning is likely responsible for the ecological communities present in each of these cities today (Tratalos et al. 2007; Parker et al. 2010; Fahey et al. 2012; Lowry et al. 2012).

In this study I use historical bird surveys and municipal maps to perform a longitudinal assessment of the relationship between urban park configuration and avian diversity over the last 120 years. Understanding these relationships can increase our understanding of the mechanisms

that contribute to the filtering of urban species and inform park planning efforts to maximize biodiversity conservation. With this knowledge, my aim is to encourage vibrant and biodiverse cities which afford ample green space for humans and wildlife alike.

2.2 Methods

2.2.1 Historical bird data

I queried historical bird observations from Christmas Bird Count survey records (National Audubon Society 2020). The Christmas Bird Count, an annual survey of birds between December 14 and January 5, has taken place in each study city (at least intermittently) since 1901 (DC), 1907 (PA) and 1941 (MN). Christmas Bird Count records contain the number of individuals observed of each species detected during each survey year and the survey effort (people per survey). The Christmas Bird Count is volunteer-driven, and thus likely biased towards conspicuous species. Additionally, the survey is biased towards granivorous and frugivorous species, since insectivorous species migrate to warmer regions during the survey period. Likewise, Christmas Bird Count surveys occur within a 12-km radius of a center point, which expands the possibly surveyed area beyond the boundaries of my study cities. It is possible that these bird data, despite being centered in my study cities, contain records from neighboring suburbs whose landscape metrics are not captured in this analysis. Despite these limitations, the longevity of the Christmas Bird Count provides an invaluable record of resident bird species since 1900. Because surveys do not overlap in space, concurrent surveys from cities which contain multiple surveys were collapsed into a single dataset with combined effort. Similarly, I combined data from each annual survey within each five-year period to achieve city-

specific cumulative species counts for every five-year period. The periods used to coalesce these surveys match those used in the collection of historical maps.

While numerous diversity indices are available, I chose to use species richness, species diversity (Shannon-Wiener Index), functional richness, and functional divergence, which is an index of functional diversity and describes the dissimilarity of traits present in a community. I did not analyze species or functional evenness since this measure is already considered in measures of species diversity and functional divergence. While species richness and functional richness were positively correlated, I analyzed them separately to differentiate the impacts of historical variables on various biological levels. Species richness was calculated by summing the number of unique species observed during each survey period in each city. Shannon's Diversity Index was calculated using the 'vegan' package (Oksanen et al. 2022). Functional richness and functional divergence were each calculated using the 'FD' package (Laliberté and Legendre 2010). The 'FD' package uses continuous life history traits to compute functional indices in multidimensional space using a distance-based framework. Under this framework, functional richness is defined as the volume of the convex hull formed by the species' points in trait-space. Functional divergence, which represents the magnitude of dissimilarity of traits across the community, is contrived from the distribution of functional units in multi-dimensional trait-space irrespective of the number of dimensions (i.e., species and traits) of the community's total niche space (Petchey and Gaston 2002; Laliberté and Legendre 2010; Mouchet et al. 2010). I chose to use these measures of functional richness and divergence because they are not linearly correlated with species richness and do not require the arbitrary categorization of species into discrete functional groups. I used the following life history traits to calculate functional richness and divergence: diet breadth, foraging breadth, range size, body mass, and clutch size (trait

justifications provided in Appendix B). Trait data for each species was obtained from Wilman, et al. (2014) and Tobias and Pigot (2019), and was accessed using the 'traitdata' package (RS-eco 2022). These traits were also used to categorize species into trait-specific functional groups to assess the dual roles of life history traits and environmental characteristics on species persistence. To do so, I first scaled all traits to have mean of 0 and standard deviation of 1 to allow for direct comparison of model results. Following this, I labeled any species whose trait value was within one standard deviation of the mean as having an average trait value. Species whose trait values differed from the mean trait value by more than one standard deviation were labelled as belonging to a functional group whose trait value is greater or less than average, respectively. This categorization resulted in three groups per functional trait: less than average (e.g., dietary specialists, small-ranged species, etc.), average, and greater than average (e.g., dietary generalists, large-ranged species, etc.). To create trait-specific survey data I summed observations of all species in each trait-specific functional group.

I accounted for variation in survey effort by including the number of Christmas Bird Count participants as an additional parameter in each model. Survey participants were summed across all surveys within each five-year period. When participant data was missing, the arithmetic mean of the nearest two surveys was used to impute this missing value. All independent variables were scaled by subtracting each value by the city-specific mean, then dividing by the dataset-wide standard deviation (Gallo et al. 2022).

2.2.2 Historical landscape and independent variables

I obtained park system maps between 1900 and 2019 for Washington (DC), Pittsburgh (PA), and Minneapolis (MN) from historical archives, libraries, and online databases (Appendix

A). A single park system map was obtained for every five-year period for each city and was assumed to be representative of the park system during this timeframe. When multiple maps were available for the same city during the same period, the map with higher resolution (digital) or smaller scale (print) was selected to obtain the most accurate park shapes. I scanned and imported maps to ArcMap 10.8 (*ESRI*, 380 New York Street, Redlands, CA 92373). Once imported, I overlaid historical city maps on the current street grid of each respective city and georeferenced the historical map using major intersections that existed over the entire study period. Once georeferenced, the greenspaces were digitized by manually drawing polygons over land that was identified as park space, cemeteries, golf courses, and all other public lands (Figure 2.1). Military bases and educational campus were not included as greenspaces as they were not consistently labeled over the years. Individual structures within these lands were not always represented and are thus not identified in this dataset. Similarly, because some maps did not depict street width, all parks with a linear orientation that were bisected by streets were drawn as if the street was not present and the park was continuous.

I imported completed park shapefiles into v 4.2.2 of R (R Core Team 2021) and converted polygons to 20x20 m rasters with the 'sf' and 'raster' packages (Figure 2.1; Hijmans, 2023; Pebesma, 2018). I used a 20x20 m resolution for two reasons. First, larger resolutions are not sufficient to detect changes in urban park systems over time (Qian et al. 2015). Second, the varying resolutions of historical landscape data may bias year-to-year changes in metrics due to varying degrees of cartographic detail indicating changes in greenspace shape which were actually present in previous years but not documented under a coarser scale. Although I included any park that was depicted in the historical maps, I was beholden to the inclusion criteria of the

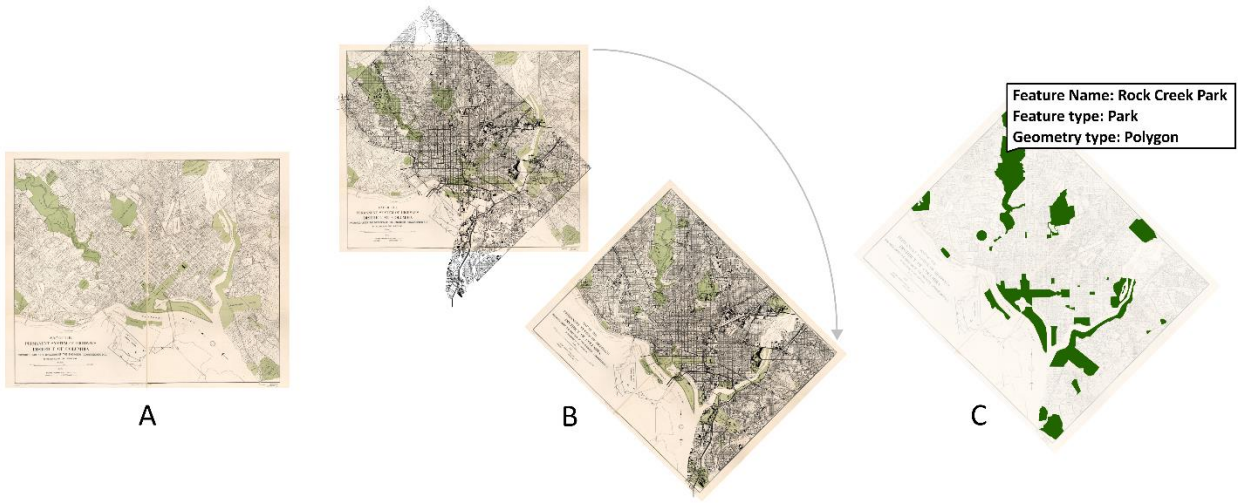


Figure 2.1 Visualization of the map digitization process, including (A) obtaining the map, (B) georeferencing the map by aligning it with the current street grid, and (C) tracing each park to create a digital polygon shapefile. Map reprinted from the United States Library of Congress, Geography and Map Division.

cartographers of the era, and thus cannot report a consistent minimum mapping unit. I used the 'landscapemetrics' package (Hesselbarth et al. 2019) to calculate various landscape metrics which described the total area of greenspace and average shape and connectivity of patches within each city during each time period (Table 2.1). Pair-wise Pearson correlation coefficients were calculated for all variables, and variables with $r \geq |0.70|$ were removed (Wei and Simko 2021). After removing colinear landscape variables, the following variables remained: proportion of the city which is greenspace, representing habitat availability; mean greenspace edge-interior ratio, representing the edge-effect imposed by complexity of shape; and clumpiness index of greenspaces, representing habitat connectivity.

Table 2.1 Potential landscape variables considered for analysis. Traits were ultimately selected for parsimony and lack of collinearity.

Variable	Justification	Metric	Unit	Used in final analysis?
Area of greenspace	Species-area relationship states that spaces with more habitat area will support more species	Proportion of greenspace	percent	yes
		Greenspace area	m^2	no
		Mean greenspace area	m^2	no
Shape of greenspace	The *single-large or several-small* (SLOSS) debate suggests that intact systems will support more species than fragmented systems	Edge-interior ratio	unitless	yes
Configuration of greenspaces	Theory of island biogeography states that patches with greater connectivity (less isolation) will support more species	Clumpiness index	unitless	yes
		Mean nearest neighbor	m	no
		Effective mesh size	m^2	no

To control for additional factors that may impact avian diversity, I included survey year to reflect the passing of time (Fernández-Juricic, 2000; Nielsen et al., 2014), human population density (Fontana et al. 2011; Gagné et al. 2016), and mean winter temperature (Reif et al. 2010; Lehikoinen et al. 2016) as continuous variables. Human population density was calculated by dividing each city's population by its area using data from the US Census Bureau archives (specific publications are listed in Appendix A). Because the US census is only conducted every ten years, no census records existed for survey periods which did not include a decadal year (e.g., 1945-1949). In these instances, I averaged the census counts before and after the survey. Mean winter temperature was calculated by taking the mean daily temperature between the months of December through February of all weather stations within a 50-km buffer of each city center.

Temperature readings were obtained using the ‘rnoaa’ package (Chamberlain 2023) and were averaged so a single value was representative of each five-year survey period’s mean winter temperature.

2.2.3 Analysis

I fit a series of generalized linear mixed models in a Bayesian framework to assess how species richness, species diversity, functional richness, and functional divergence (dependent variables) varied as a function of the various covariates I calculated. These models estimated each of these dependent variables as a function of survey year, survey effort, human population density, mean winter temperature, and all landscape metrics. Local species pools govern the species available, and differ between cities. I accounted for this in my models by including a random intercept for each city. This approach allowed the assumption that birds across all three cities share similar responses to the independent variables, but the intercept value for each dependent variable (e.g., species richness, functional divergence, etc.) differs between cities. I modeled species richness using Poisson regression because the data consisted of species count data, and used a linear model with the dependent variables logged to model species diversity and functional richness because the data consisted of positive non-integers. Functional divergence values were bounded between 0 and 1, which necessitated the use of a beta regression model.

I used the same model structure to model life history traits, but used the number of observations of individuals from each functional group as the dependent variable. Data from all three trait-specific functional groups (e.g., dietary specialist, average dietary breadth, and dietary generalist) were included in the same model with a categorical variable to identify the functional group each data point belonged to. I used the average group (e.g., average dietary breadth) as the

reference category for this analysis, comparing the number of observations of birds from less than average and greater than average functional groups to the number of observations of birds with the average value for the respective functional trait.

I assigned each intercept term and all parameters vague normal priors with a mean of zero and a standard deviation of 1,000. Hyperpriors were similarly assigned the same vague normal priors when possible or were otherwise assigned uniform priors between 0 and 100 if the term was constrained to positive values (e.g., variance terms). Each model was fit using the 'runjags' package (Denwood 2016) and consisted of 4 MCMC chains of 500,000 iterations and a 250,000-iteration burn-in. To reduce autocorrelation within each chain, every fifth iteration was retained. Upon convergence, each MCMC chain's Gelman-Rubin statistic was checked to ensure it was less than 1.10, and each chain's traceplot was visually inspected for adequate mixing (Gelman et al. 2000). Additionally, a visual inspection of posterior predictive plots was made to ensure that estimated results generally matched those of the actual dataset indicating a proper model fit, and visual inspections of residual plots were made to ensure that residuals did not present obvious patterns such as regular oscillation, etc. (Kruschke 2015). I considered a variable to have a significant effect if its 95% credible interval did not overlap zero. All diagnostic tests indicated adequate model fit.

2.3 Results

2.3.1 Summary statistics of survey and city data

Christmas Bird Count surveys during my time periods yielded a total of 4,555,450 observations of 235 species across a total of 268 survey years. Survey effort increased substantially in all three cities between the first and last survey period (DC = 7 – 905 people; MN

= 22 – 328; PA = 7 – 806), and consequentially so did the number of species (DC = 48 – 147 species; MN = 38 – 82; PA = 10 – 101) and individual birds observed (DC = 1,445 – 165,122 individuals; MN = 2,665 – 53,335; DC = 379 – 153,809). Most birds fell within 1 standard deviation of the mean for each functional trait (Table 2.2).

I obtained 22 historical landscape records for DC (18 maps, 4 shapefiles), 19 records for Minneapolis (10 maps, 9 shapefiles) and 16 records for Pittsburgh (14 maps, 2 shapefiles; Appendix A). Together, these yielded a sample size of 55 data points for models assessing diversity indices, and a minimum of 150 data points for each model assessing functional traits. Over time, all three cities increased their proportional park area (Figures 2.2 & 2.3; DC = 9.48% - 19.29%; MN = 6.65% – 11.01%; PA = 5.35% - 12.91%). In addition to increased park area, parks in all three cities became more convoluted in shape (Figure 2.2; DC = 0.05 – 0.11 change in edge-interior ratio; MN = 0.03 – 0.07; PA = 0.01 – 0.11) and more evenly distributed across the city (Figure 2.2; DC = 0.97 – 0.90 change in clumpiness index; MN = 0.93 – 0.89; PA = 0.97 – 0.91). Washington and Minneapolis experienced warmer winters since the surveys began (DC = 1.75 – 3.87 ^{o}C; MN = -7.47 - -6.98 ^{o}C), but Pittsburgh's mean winter temperature has decreased (-0.23 - -0.72 ^{o}C).

2.3.2 Avian richness and diversity

Avian species richness was most strongly positively correlated with survey year (β = 0.20, 95% BCI = 0.11 – 0.29), followed by greenspace area (β = 0.18, 95% BCI = 0.10 – 0.27) and survey effort (β = 0.12, 95% BCI = 0.04 – 0.19). Species richness was strongly negatively correlated with mean winter temperature (β = -48.3, 95% BCI = -70.74 – -25.95). Credible intervals for greenspace edge-interior ratio (β = 0.01, 95% BCI = -0.06 – 0.06), greenspace

Table 2.2 Summary of functional trait groups for the 235 species detected during Christmas Bird Counts in Washington DC, Pittsburg, and Minneapolis between 1900 and 2019. Each species belongs to either the below-average, average, or above-average functional group for each of the five functional traits.

Trait	Mean value and standard deviation	Number of species with value lower than one standard deviation from mean	Number of species with value within one standard deviation from mean	Number of species with value greater than one standard deviation from mean
Diet breadth	2.85 (SD = 1.21)	28	186	18
Foraging breadth	2.19 (SD = 0.91)	51	163	18
Mass	605.46 (SD = 1350.23)	0	218	14
Clutch size	1.53 (SD = 0.42)	31	163	38
Home range size	15.73 (SD = 0.89)	29	166	37

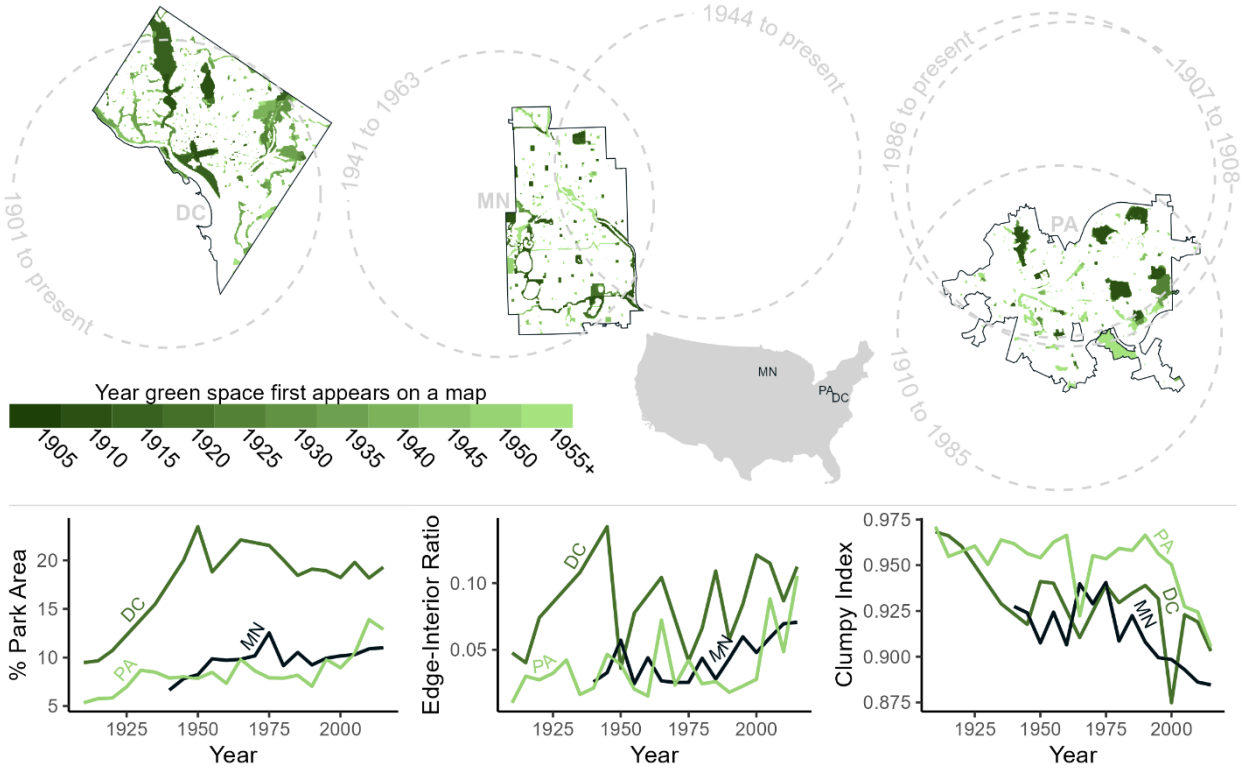


Figure 2.2 (Top) Growth of park systems over time, where a greenspace's color represents the first year it appears on a map. Grey circles around the cities indicate the spatial extent of the bird surveys. Each survey circle has a radius of 12-km. (Bottom) Graphs of change in greenspace area, shape, and distribution over time. Initials signify the District of Columbia (DC), Pittsburgh (PA) and Minneapolis (MN).

clumpiness (β = 0. 06, 95% BCI = -0.02 – 0.14), and human population density (β = -5.08, 95% BCI = -13.28 – 3.19; Table 2.3) all contained zero. Intercept values — which indicate what each city's dependent variable value would be if all independent variables were held at their mean value, here representing differences in each city's unique initial species pool — were similar across the three cities, but were slightly higher in DC (β_0 = 4.59, 95% BCI = 4.54 – 4.65) compared to Minneapolis (β_0 = 4.23, 95% = 4.16 – 4.30) and Pittsburgh (β_0 = 4.02, 95% BCI = 3.97 – 4.08).

Shannon's diversity index, which describes the degree to which species are evenly represented in the community by considering both species richness and evenness, was most strongly positively associated with human population density (β = 15.56, 95% BCI = 5.09 – 25.93) followed by survey year (β = 0.19, 95% BCI = 0.08 – 0.30). Diversity was negatively associated with greenspace area (β = -0.15, 95% BCI = -0.27 – -0.02). Greenspace edge-interior ratio (β = -0.02, 95% BCI = -0.11 – 0.07), and clumpiness (β = 0.06, 95% BCI = -0.05 – 0.17), mean winter temperature (β = -11.34, 95% BCI = -38.95 – 16.56), and survey effort (β = 0. 07, 95% BCI = -0.02 – 0.16; Table 2.3) all had credible intervals which overlapped zero. Estimated intercepts were similar across all three cities (DC β_0 = 0.87, 95% BCI = 0.81 – 0.94; MN β_0 = 0.85, 95% BCI = 0.78 –0.92; PA β_0 = 0.85, 95% BCI = 0.80 – 0.90).

2.3.3 Functional richness and diversity

Avian functional richness, which represents the quantity of functional groups present in the community, was positively associated with survey year (β = 0.81, 95% BCI = 0.34 – 0.1.28). Greenspace area (β = -0.02, 95% BCI = -0.50 – 0.46; Figure 2.3), edge-interior ratio (β = 0.12, 95% BCI = -0.27 – 0.51), clumpiness (β = 0.29, 95% BCI = -0.17 – 0.76), mean winter

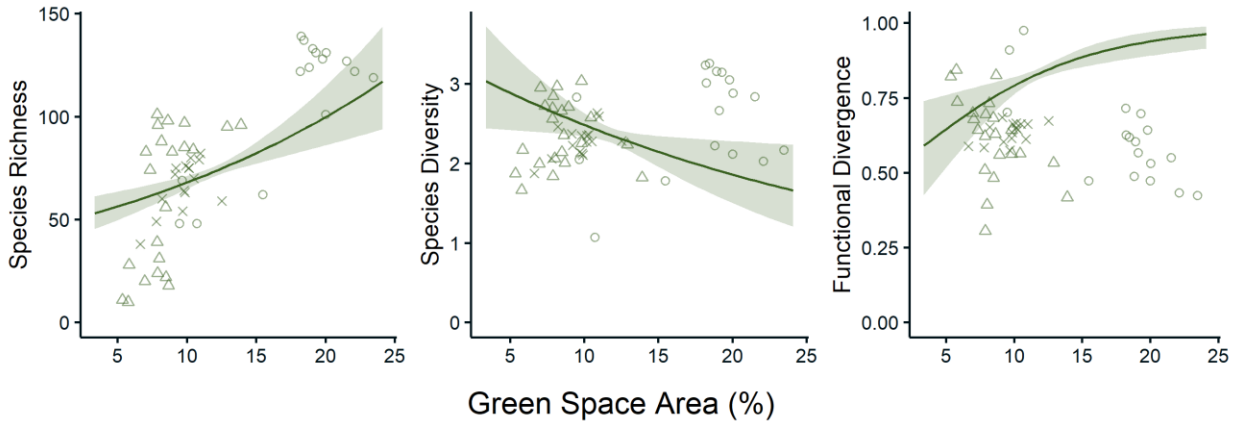


Figure 2.3 Effect of proportional park area on species richness, species diversity, and functional divergence. Mean predicted value is depicted as a dark line, while 95% credible intervals are depicted as a shaded polygon. Points depict observed data from the three study cities, where circles represent data from Washington (DC), x's represent data from Minneapolis (MN), and triangles represent data from Pittsburgh (PA). Note that y-axes differ between graphs.

temperature (β = -13.83, 95% BCI = -69.61, 34.64) and survey effort (β = 0. 07, 95% BCI = -0.34 – 0.47; Table 2.3) all contained zero in their 95% credible intervals. Estimated intercepts were similar, but highest for DC (β_0 = 3.72, 95% BCI = 3.39 – 4.05) compared to Minneapolis (β_0 = 3.47, 95% BCI = 3.13 – 3.82) and Pittsburgh (β_0 = 2.90, 95% BCI = 2.64 – 3.17).

Functional divergence, which describes the variation in functional traits across the community, was positively associated with greenspace area (β = 0.72, 95% BCI = 0.32 – 1.12; Figure 2.3) and negatively associated with human population density (β = -43.14, 95% BCI = -72.58 – -13.61). Greenspace edge-interior ratio (β = 0.03, 95% BCI = -0.28 – 0.35) and clumpiness (β = 0.01, 95% BCI = -0.36 – 0.38), mean winter temperature (β = -21.75, 95% BCI = -73.25 – 30.24), survey year (β = 0.01, 95% BCI = -0.34 – 0.36) and survey effort (β = -0.23, 95% BCI = -0.51 – 0.06; Table 2.3) all had 95% credible intervals which contained zero. The estimated intercept was highest in DC (mean = 1.88, 95% BCI = 1.61 – 2.15), but values for

Minneapolis (mean = 1.44, 95% BCI = 1.20 – 1.69) and Pittsburgh (mean = 1.44, 95% BCI = 1.25 – 1.62) were similar.

2.3.4 Life history traits

Regarding the life history models, model coefficients for non-trait variables were the same across all functional trait models (Table 2.4), and indicated a positive correlation, regardless of trait group, with greenspace area (β = 0.72, 95% BCI = 0.722 – 0.727), survey year (β = 0.42, 95% BCI = 0.419 – 0.425), survey effort (β = 0.19, 95% BCI = 0. 187 – 0. 192), and park clumpiness (β = 0.10, 95% BCI = 0.096 – 0.100), and a negative correlation with mean winter temperature (β = -52.099, 95% BCI = -52.841 – -51.355), human population density (β = -11.210, 95% BCI = -11.520 – -10.900), and edge-interior ratio (β = -0.056, 95% BCI = -0.057 – -0. 054; Table 2.4).

The analysis of dietary functional groups revealed a strong negative correlation between the number of observations of a species and both dietary specialization (*less than average group* β = -4.558, 95% BCI = -4.570 – -4.545) and dietary generalization (*greater than average group* β = -0.028, 95% BCI = -0.030 – -0.026), when compared against the average dietary breadth. Similarly, birds were less likely to be observed if they had either larger (β = -2.851, 95% BCI = -2.855 – -2.847) or smaller (β = -3.418, 95% BCI = -3.423 – -3.413) foraging breadths, relative to species with an average foraging breadth. Species with above-average dispersal capabilities were less likely to be observed (β = -0.232, 95% BCI = -0.233 – -0.230), as were species with below-average dispersal capabilities (β = -2.638, 95% BCI = -2.642 – -2.633). Birds with clutch sizes above (β = -1.828, 95% BCI = -1.831 – -1.825) and below (β = -1.356, 95% BCI = -1.359 – -1.354) the average clutch size were also less likely to be observed. Finally, species with greater

Table 2.3 Parameter estimates and 95% credible intervals for models predicting diversity indices. Parameters whose credible intervals do not overlap zero are bolded.

Dependent variable	Parameter	Mean	95% Credible Interval	
			Lower	Upper
Species richness	Percent park area	**0.19**	0.10	0.27
	Edge-interior ratio	0.01	-0.06	0.07
	Clumpiness index	0.06	-0.02	0.14
	Regional temperature	**-48.35**	-70.74	-25.95
	Population density	-5.08	-13.28	3.20
	Year	**0.20**	0.11	0.29
	Survey effort	**0.16**	0.04	0.19
Species diversity	Percent park area	**0.87**	0.81	0.94
	Edge-interior ratio	**0.85**	0.78	0.92
	Clumpiness index	**0.85**	0.80	0.90
	Regional temperature	**-0.15**	-0.27	-0.02
	Population density	-0.02	-0.11	0.07
	Year	0.06	-0.05	0.17
	Survey effort	-11.34	-38.95	16.56
Functional richness	Percent park area	**3.72**	3.39	4.05
	Edge-interior ratio	**3.48**	3.14	3.82
	Clumpiness index	**2.90**	2.64	3.17
	Regional temperature	-0.02	-0.50	0.46
	Population density	0.12	-0.27	0.51
	Year	0.29	-0.17	0.76
	Survey effort	-13.83	-69.61	42.14
Functional divergence	Percent park area	**0.72**	0.32	1.12
	Edge-interior ratio	0.03	-0.28	0.35
	Clumpiness index	0.01	-0.36	0.38
	Regional temperature	-21.75	-73.25	30.24
	Population density	**-43.14**	-72.58	-13.61
	Year	0.01	-0.34	0.36
	Survey effort	-0.23	-0.51	0.06

than average body mass were less likely to be observed (β = -2.899, 95% BCI = -2.903 – -2.895; Table 2.4) when compared to the average body mass. No birds had a body mass which was one standard deviation less than average.

2.4 Discussion

Cities, and the species which inhabit them, change over time as a function of urban planning and land use decisions (Fahey et al. 2012; Roman et al. 2018; Dunn et al. 2022; Fidino et al. 2022). This analysis sought to understand how these land use decisions impact avian diversity in cities. Overall, increased greenspace was associated with greater species richness and greater numbers of observations of birds regardless of their functional traits. Yet, while richness and abundance increased, the proportion of park area in a city was negatively correlated to species diversity, which indicates that some species disproportionately increased in abundance and drove species evenness down (La Sorte et al. 2023). Park connectivity and shape were also associated with abundance but the magnitudes of these relationships were considerably less than that of park area. Likewise, park area had a larger effect than some functional traits, suggesting that habitat availability may filter even the most urban-adapted species. Because these findings corroborate the validity of the species-area relationship within urban areas (Rosenzweig and Ziv 1999; Nielsen et al. 2014), I echo calls for continued creation and preservation of urban greenspace to achieve species conservation in cities (Rosenzweig 2003; Garrard et al. 2018; Apfelbeck et al. 2020).

Table 2.4 Parameter estimates and 95% credible intervals for models predicting observations of individuals from functional groups. Parameters whose credible intervals do not overlap zero are bolded.

Dependent variable	Parameter	Mean	95% Credible Interval	
			Lower	Upper
All functional group models	Percent park area	**0.72**	0.72	0.73
	Edge-interior ratio	**-0.06**	-0.06	-0.05
	Clumpiness index	**0.10**	0.10	0.10
	Regional temperature	**-52.10**	-52.84	-51.36
	Population density	**-11.21**	-11.52	-10.90
	Year	**0.42**	0.42	0.42
	Survey effort	**0.19**	0.19	0.19
Functional group: clutch size	Clutch size above the mean value	**-1.83**	-1.83	-1.83
	Clutch size below the mean value	**-1.36**	-1.36	-1.35
Functional group: diet breadth	Diet breadth above the mean value	**-0.03**	-0.03	-0.03
	Diet breadth below the mean value	**-4.56**	-4.57	-4.54
Functional group: foraging breadth	Foraging breadth above the mean value	**-2.85**	-2.86	-2.85
	Foraging breadth below the mean value	**-3.42**	-3.42	-3.41
Functional group: body mass	Body mass above the mean value	**-2.90**	-2.90	-2.90
Functional group: home range size	Home range size above the mean value	**-0.23**	-0.23	-0.23
	Home range size below the mean value	**-2.64**	-2.65	-2.63

The species-area relationship posits that patches with greater area will contain a greater number of species compared to smaller patches (Williams 1943; Macarthur and Wilson 1967; Rosenzweig and Ziv 1999). This concept similarly applies to urban habitats, indicating that cities with greater cumulative habitat will contain more species than cities with less cumulative habitat (Davis and Glick 1978; Beninde et al. 2015; Dunn et al. 2022). The distribution of habitat within a city can further impact biodiversity, with systems comprised of fragmented and isolated patches tending to have lower biodiversity due to reductions in core habitat, genetic flow, and probability of recolonization after local extinction (Nielsen et al. 2014; Haddad et al. 2015). Habitat fragmentation, understood here as patch edge-interior ratio, and lack of connectivity between patches are common features of urban park systems and threaten urban biodiversity (Nielsen et al. 2014; Norton et al. 2016). However, my analyses revealed that park fragmentation and connectivity were not significant predictors of any avian diversity metric. Furthermore, the effect of total habitat area was notably larger than connectivity or fragmentation for all avian functional groups (7 and 12 times larger, respectively). These findings further support the notion that habitat availability, not configuration, drives urban avian assemblages (Dale 2018).

While increasing overall park area had a positive correlation with species richness and functional divergence, this analysis revealed a negative correlation between park area and species diversity. Because diversity indices consider both richness and evenness, the addition of a low-abundance species will increase richness but lower diversity if the site is still dominated by individuals of only a few species (Morris et al. 2014). Furthermore, greenspaces vary widely in both form and function, and the species supported by greenspaces differ based on how the space is managed (Sandström et al. 2006; Aronson et al. 2017; Gallo et al. 2017). I suggest that future

studies explore species turnover and beta diversity in response to a changing park system to better understand changes in community composition over time (Fidino et al. 2022).

Particular traits (Evans et al. 2011; Santini et al. 2019), or flexibility within particular traits (Weiss et al. 2023) can pre-dispose a species for success in urban environments. These findings support the notion that specific traits confer an advantage to some species and demonstrate that species were observed less frequently if their traits deviated from the average trait value, even if the deviation is conventionally considered advantageous (e.g., dietary generalism). This is likely because the mean trait values in my analysis were derived from species assemblages that have endured generations of anthropogenic pressures and whose traits may already reflect urban optimality. In this way, my analysis supports previous claims that ideal trait combinations can contribute to urban exploitation. These findings further suggest, however, that such traits do not exclusively determine urban success.

Traits such as dietary generalism and large dispersal ability are generally considered helpful to species persistence in urban areas (Santini et al. 2019; Cove and Pease 2021; Penteado 2021; Neate-Clegg et al. 2023). Yet, this analysis found these traits to be disadvantageous to birds and the strengths of effect for these traits (β = -0.03 and -0.23, respectively) were less than that of greenspace area (β = 0.72), and for diet generalists, less than that of greenspace clumpiness (β = 0.1). These findings indicate that landscape features have an equal, if not greater, effect on filtering urban species compared to life history traits – further indicating that thoughtfully planned networks of urban greenspace have the potential to overcome inherent self-limiting factors for some species.

In addition to functional traits and landscape features, these findings emphasized the role of time in the formation of avian communities. Avian species richness and diversity, functional richness, and total observations of birds in every functional group each had a positive association with the survey year. One possible explanation for these phenomena is that the rise of environmental awareness has produced greater environmental regulations which have positively benefited bird communities (Taylor et al. 2005; Wood et al. 2019). Simultaneous increased survey efforts have also likely contributed to a larger, and thus more representative sample in later years, although this was controlled for in my analysis. An ecological explanation for the relationship between survey year and avian diversity and abundance is that habitats take decades to mature into a complex state that can support a greater breadth of ecological niches (Roman et al. 2017; Gilhen-Baker et al. 2022). Again, future studies should explore species turnover and beta diversity to identify any changes in species assemblages across time or seasons (e.g., La Sorte et al., 2023).

There are undoubtably limitations to using historical bird data and historical maps. First, the historical park data relied on the judgments of cartographers, who depicted park systems to differing degrees of detail depending on the purpose of the map or their perceptions of the greenspace (Monmonier 1991). Additionally, my model investigated changes in greenspace availability, but I could not assess greenspace composition or quality. Changes in landscaping trends or temporary repurposing of parks would likely impact wildlife communities, but those changes were not reflected on maps of the era. Furthermore, my analysis assumed that designated greenspace was the only available urban habitat. This assumption is false, as birds regularly make use of private greenspaces, abandoned lots, etc. However, historical records offer

little insight into the availability of privately-owned urban habitat and limit any insight into the contribution of these habitats over time.

An additional constraint imposed by my historical data is that the Christmas Bird Count occurs during the winter and at a spatial scale larger than my study cities. Winter conditions in temperate regions greatly reduce resource availability, prompting many bird species to migrate in search of food. While supplemental resources and the urban heat island effect have encouraged some species to remain in cities through the winter (Bonnet-Lebrun et al. 2020), urban avian species richness and functional divergence have still been found to decline in winter months (La Sorte et al. 2023). By using data collected in the winter, this dataset likely underrepresents species from functional groups which cannot sustain themselves in temperate winters such as insectivores. Furthermore, the tendency for some species to form larger flocks during the winter (e.g., South and Pruett-Jones, 2000) may increase their visibility to observers and cause them to be disproportionately represented in the data. However, these trends may not hold true in the less-temperate cities which host migrating birds or otherwise do not encourage seasonal flock behavior. Finally, Christmas Bird Counts take place within a circle with a ~12-km radius. While survey circles were approximately centered on each of the study cities, some observations were made from outside city boundaries and were influenced by neighboring landscapes that were not accounted for in my analysis. Despite these limitations, I believe that this approach provides strong insight into historical trends in urban biodiversity and the legacies of park planning.

Urbanization has contributed to substantial habitat degradation and destruction globally (Haddad et al. 2015; Liu et al. 2016). However, urbanization also has the potential to slow or reverse the global extinction crisis if cities are planned with conservation in mind (Ives et al.

2016; Soanes and Lentini 2019). Research shows that urban form has consequences on biodiversity, and can thus be planned to accommodate human needs while minimizing habitat and species loss (Andersson and Colding 2014; Lynch 2019; Tratalos et al. 2007; Humphrey et al. 2023). I acknowledge that the establishment of large new nature reserves and corridors in urban areas are not likely, at least immediately. Rather, systems of preserved greenspace are more likely to grow incrementally as property becomes available (Qian et al. 2015). I recommend that urban planners do not discount this method of park system growth, as my analysis suggests that the total area of greenspace has a greater impact on the conservation of species than greenspace connectivity or fragmentation, and that the incremental growth of park systems in my study cities (mean growth of 0.16 km^2 per year) contributed to long-term gains in biodiversity. I do, however, still recommend that connectivity be maintained and fragmentation and edges minimized when possible – especially for the sake of species with lower dispersal abilities (Elliot et al. 2014; Beninde et al. 2015; Lynch 2019). Similarly, it is important to recognize that cities are different from one another in form, and presumably function. As such, further investigations into landscape-level differences between cities may further illuminate mechanisms of urban biodiversity and contribute to biophilic cities.

Habitat availability in urban areas is dictated by human decisions, and is the product of the urban planning processes (Fahey et al. 2012; Roman et al. 2018). While some life-history traits clearly advantage certain species in urban areas, this analysis found that the physical landscape plays just as large a role in filtering species. Here, I demonstrated that urban planning decisions which maximize the area of greenspace will have an outsized effect on avian richness and diversity, with greenspace shape and connectivity having less of an effect. Although minimizing the edge-interior ratio and maintaining connectedness between greenspaces are of

obvious importance, my results demonstrate that the addition of any greenspace will contribute to a biophilic city. Modern park systems are the manifestation of historical urban planning efforts that were meant to benefit humans but have inadvertently benefited wildlife. Contemporary urban planners can continue this legacy by expanding systems of greenspace to further serve humans and wildlife alike.

Chapter 3: Landscapes of perception: Inability to detect predators still prompts anti-predator behavior in a relatively predator-free environment

3.1 Introduction

Anti-predator behaviors, such as vigilance and grouping behavior, are common adaptations that allows an individual to continue feeding while avoiding predation by either periodically pausing to scan the landscape for potential threats, or by surrounding themselves with other vigilant eyes to aid in predator detection (Quenette 1990; Brown and Kotler 2004; Creel et al. 2014; Olson et al. 2015). Although these behaviors reduce the overall calories consumed by an individual via decreased foraging time or intraspecific competition, they ultimately increase individual fitness since such actions allow the individual to survive another day (Dehn 1990; Lind and Cresswell 2005; Olson et al. 2015; Gaynor et al. 2019). While animals clearly benefit from such behaviors in the presence of predation risk, individuals can maximize their caloric intake by foraging alone and reducing vigilance behavior in situations where predation is unlikely (Quenette 1990; Sirot et al. 2021). Animals are thus presented with a tradeoff: trust environmental cues that predation risk is low and reduce anti-predator behaviors to maximize food intake, or continue to exhibit anti-predator behaviors and suffer reduced food intake but hedge against the unlikely event that a predator appears (Lind and Cresswell 2005).

In order for anti-predator behaviors to be effectively employed, prey species must be able to perceive the incoming predator or threat (Jordan and Ryan 2015; Gaynor et al. 2019). Prey species rely on a combination of visual, audio, and olfactory cues to detect potential predators and formulate their perceived landscape of fear (Grostal 1999; Hartman and Abrahams 2000;

Laundré et al. 2001; Hermann and Thaler 2014; Lynch et al. 2015; Arteaga-Torres et al. 2020). When environmental conditions preclude the use of these senses, animals may face greater predation risk and compensate by increasing their anti-predator behavior (Lagory 1986; Lynch et al. 2015). For instance, individuals foraging with high levels of background noise are less capable of hearing an approaching predator, and therefore may favor vigilance behavior over food consumption (L. Quinn et al. 2006; Evans et al. 2018; Giordano et al. 2022). Likewise, the intensity of light can also alter vigilance behavior. Light presents greater ecological nuance as visual information is altogether limited in low-light conditions, whereas increased light may allow prey to gather visual cues but simultaneously exposes prey through increased visibility to predators. As a result, some species are shown to increase their vigilance behaviors under brightly lit conditions (Fernández-Juricic and Tran 2007; Zhang et al. 2020), while other species reduced vigilance behavior under such conditions (Lashley et al. 2014).

The landscape of fear can track fluctuating environmental conditions such as light and noise (Gaynor et al. 2019), but it can also be influenced by the physical environment surrounding the individual (Laundré et al. 2014). Animals often mitigate predation risk by selecting habitat patches with ample refugia in which to hide (Heithaus et al. 2009; Palomo-Munoz et al. 2024). Refugia which offer greater habitat complexity (e.g., variation in stand height, variation in vegetation density) may offer more opportunities to hide, and thus offer greater protection for many prey species (Schmidt and Kuijper 2015; Atuo and O'Connell 2017). If increased vegetation complexity offers increased safety for prey, prey may perceive these environments as lower-risk and relax their anti-predator behavior (Schmidt and Kuijper 2015). Alternatively, prey in complex stands may not moderate their anti-predator behavior since their own sight lines are obscured and their capacity to flee predators may be compromised (Lagory 1986). Because

vegetation is known to both protect from and conceal predators, the structural environment alone is not a reliable indicator of safety. Thus, wildlife must rely on other, non-structural environmental cues to accurately assess predation risk.

In addition to the protection provided by aspects of the environment, social prey species are capable of directly influencing their predation risk by altering the size of their foraging group. Some relatively social species, such as ungulates, reduce their individual vigilance behavior when with other conspecifics - presumably because the collective benefit of increased attentive eyes relieves any one individual's responsibility to remain vigilant (Lagory 1986; Beauchamp 2003; Lashley et al. 2014; Olson et al. 2015). If no predators are present, however, larger groups may prove disadvantageous since individuals will experience interference competition but gain no safety benefits (Beauchamp 2003; Creel et al. 2014; Olson et al. 2015). Thus, in the absence of predators, group size does not mediate predation pressure and may have little impact on vigilance behavior. Instead, fluctuating environmental conditions that impact an individual's ability to perceive an incoming predator may play a larger role in regulating vigilance behavior than does group size.

Historically, research on anti-predator behavior and landscapes of fear have occurred within regions where substantial predation risk exists (Ciuti et al. 2012). As a result, our understanding of the roles predation risk and environmental cues play in anti-predator behavior may be confounded since it is impossible to isolate the roles of either factor if both are present (Maurer et al. 2022). Urban ecosystems often exclude apex predators but maintain environmental conditions that prevent prey from being certain of predators' absence, such as intense noise and light pollution (Lowry et al. 2013; Schirmer et al. 2019; Ordiz et al. 2021; Nelson-Olivieri et al.

2023). Thus, cities offer a unique environment to study prey reacting to a landscape of fear that they assume contains non-negligible predation risk, but which actually carries relatively little predation risk relative to undeveloped areas (Fischer et al. 2012).

Although apex predators are generally excluded from urban ecosystems (Prugh et al. 2009; Fischer et al. 2012; Ordiz et al. 2021), humans are hyperabundant and represent the primary source of disturbance for many wildlife species in urban landscapes (Frid and Dill 2002). Indeed, humans have been recognized as global super-predators due to harvest rates that far exceed natural predation (Darimont et al. 2015), and frequent disturbances that prompt changes in wildlife behavior and activity patterns (Suraci et al. 2019; Gaynor et al. 2020; Palmer et al. 2023). Similar to apex predators, the formative influence of the human super-predator is not limited to predation events. Non-hunting humans still pose a threat to wildlife directly (e.g., wildlife-vehicle collisions, etc.; McCance et al., 2015) and indirectly (e.g., window strikes, introduction of invasive predators or competitors, etc.; Doherty et al., 2016; Loss et al., 2012), and still contribute to an environment saturated with cues of risk (Frid and Dill 2002; Smith et al. 2021). As a result, urban prey may be unknowingly safe from predation by non-human apex predators, but still reside within a novel landscape of fear crafted by humans (Frid and Dill 2002; Ciuti et al. 2012; Smith et al. 2021; Palmer et al. 2023).

Within urban areas, white-tailed deer (*Odocoileus virginianus*; here after ‘deer’) are an ideal organism to study anti-predator behavior. Deer are common in many American cities (Magle et al. 2019), too large to be predated upon by most synurbic mesopredators (~55kg; Faurby et al., 2018), and conspicuously communicate their vigilance through obvious changes in posture (e.g., Gallo et al., 2019; Lashley et al., 2014). Additionally, the size and abundance of

deer in urban settings allows for easy and ample data collection, as opposed to other less-abundant or more cryptic prey species such as cottontails (e.g., Lima et al., 2021). Although deer are often used to investigate anti-predator behavior in undeveloped landscapes, few studies have examined their vigilance or grouping behavior in urban systems (e.g., Gallo et al., 2019). While deer are notoriously tolerant of humans in cities, urban deer still exhibit anti-predator behavior despite the lack of apex predators (Ciach and Fröhlich 2019; Maurer et al. 2022), allowing the opportunity to investigate the non-consumptive mechanisms that influence such behavior.

A possible explanation for continued anti-predator behavior despite the lack of non-human predators is that deer are not reacting to a perceived imminent attack, but rather they are compensating for features of the urban environment that lower one's ability to perceive their surroundings. If this explanation were true, urban light and noise may offer deer a human shield from their natural predators, but do not produce a stress-free environment since these disturbances limit their ability to confirm the predators' absence (Collins et al. 2020). To test if vigilance behavior in urban deer is associated with ambient conditions which inhibit the perception of potential predators, I measured vigilance behavior and foraging group size, ambient noise and light, and the potential for human disturbance at each sample site. I hypothesized that anti-predator behaviors are a reaction to the perception of potential threats, as opposed to the threat itself. As such, I predicted that loud and dark conditions hinder a deer's ability to detect potential threats, and therefore deer would increase vigilance behavior and foraging group size in darker and/or louder environments. I also predicted that deer would relax anti-predator behaviors when relative risk of encountering humans is low. In this study, I define relative risk as a combination of structural complexity of the habitat and the number of humans present (see Equation 3.5). By exploring the mechanisms behind anti-predator responses in a

system with reliably low predation pressure, I hope to gain a better understanding of fear responses in wildlife and to provide better insight into the mechanisms that govern landscapes of fear.

3.2 Methods

3.2.1 Study area

The Washington, DC, metropolitan region is home to roughly 6.3 million people with a mean density of 375.4 people/km^2 (United States Census Bureau 2020). Approximately 155 km^2 (~21% of landcover) of managed non-residential greenspace is distributed across the region and is primarily either landscaped park space or beech-oak upland forest (Ossi et al. 2015). The region receives roughly 106 cm of precipitation annually, and experiences mean temperatures ranging from 3.1 to 27.2 ^{o}C across four distinct seasons (US National Oceanic and Atmospheric Administration 2024). The DC metropolitan region resides in the ancestral homeland of the Nacotchtank and Piscataway People (Tayac 2014).

3.2.2 Site selection

Sampling sites consisted of a stratified random sample from an existing array of 75 trail cameras used for long-term wildlife monitoring in the region (Magle et al. 2019; Collins and Gallo 2024). I selected a subset of 24 sites from this larger camera array to represent a gradient of development intensity by identifying the percent impervious surface within 500 m of each camera, and the distance between each camera and the nearest major roadway. Both metrics were then binned to reflect three equally-sized categories per metric (i.e. high, moderate, and low). Both binned metrics were then combined to create nine unique classifications from all possible

combinations of the two metrics (e.g., high impervious near major roadway, moderate impervious far from a major roadway, etc.). Predictably, no sites were categorized as 'high impervious surface and high distance from roadway,' so this category was removed. Some categories were only sparsely represented in this array ($n \leq 5$ sites), and thus all sites representing those categories were retained. For categories represented by more than five sites, I randomly selected 4-5 sites within each classification (Figure 3.1). The bin widths for each metric, and the number of sites representing each category are available in Appendix C.

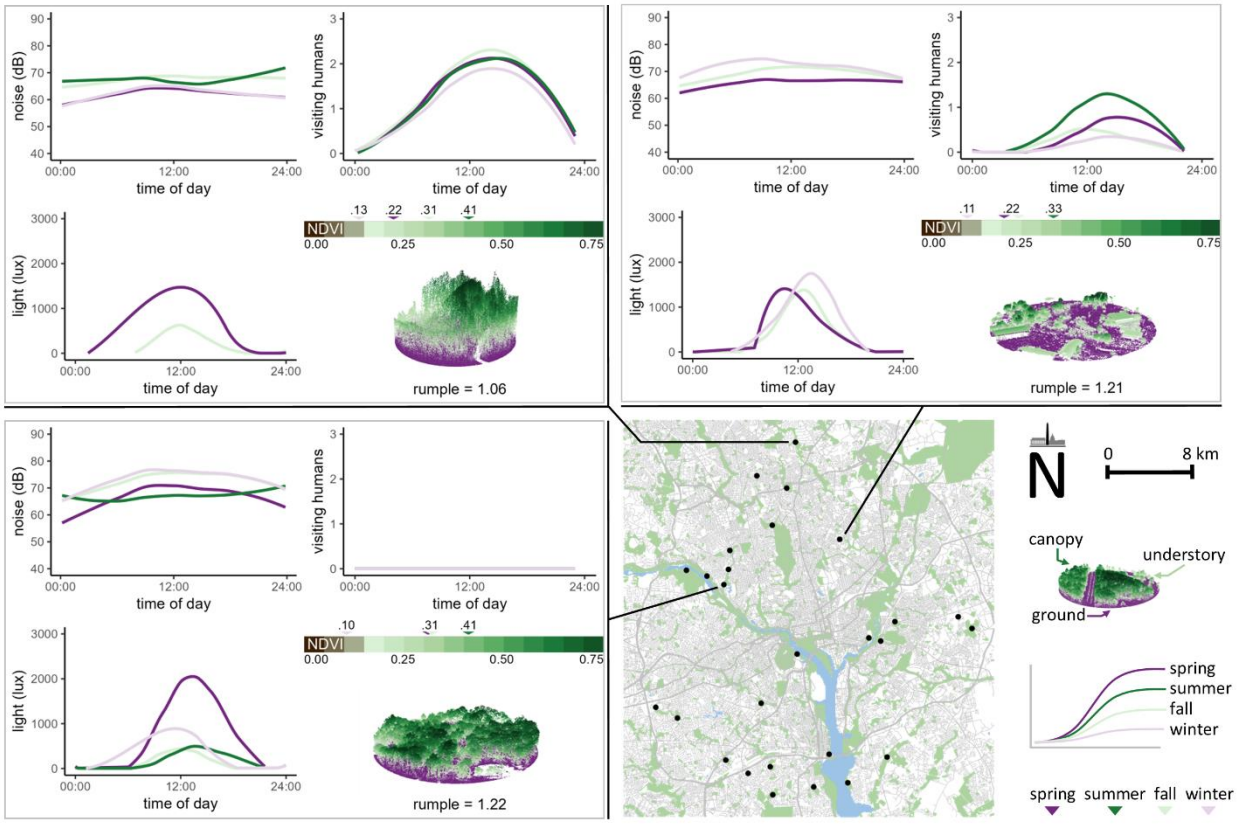


Figure 3.1 Map of cameras deployed with audio recorders for this analysis across the Washington, DC, metropolitan area with insets visualizing the ambient noise and light conditions per hour, the number of human visitors within one deer home range per hour, the vegetative intensity per season, and the three-dimensional rendering of the habitat structure within one deer home range of the camera. Insets are only shown for specific sampling sites to demonstrate the heterogeneity of variables across sites.

3.3.3 Deer observations and behavioral coding

At each sampling site, I deployed a single Reconyx Hyperfire 2 infrared flash trail camera (Reconyx Inc., 3828 Creekside Ln, Ste 2, Holmen, WI 54636). Each camera was set to take a single photograph per trigger with a 15-second delay between triggers. All cameras were fixed to a tree at a height of less than 1-meter off the ground and were aimed at game trails. Prior to deployment, the firmware of each camera was updated to enable relative light levels to be recorded in the metadata of each photograph. Cameras were deployed for four weeks during July and October of 2021, and January and April of 2022.

Two trained individuals reviewed each photograph independently to numerate and identify each animal to species. If the two reviewers disagreed on an identification, a third reviewer was used to settle the discrepancy. Photographs of white-tailed deer then underwent additional review to determine if the deer was vigilant or non-vigilant. I defined vigilant as a body posture in which the deer's head was held above its body, whereas non-vigilant behavior consisted of the deer holding its head below its body, laying its head on the ground, or engaging in grooming behavior (Appendix D). I excluded photographs from analysis if the deer's head was not visible or if the head was even with its body. The number of deer in each photograph were counted regardless of whether their heads were visible. To account for the fact that each photograph provides an instantaneous record of group size, but the foraging group may be larger than those documented in a single photograph, I assigned the maximum number of individuals observed within 30 minutes of time t at site i as the observation-specific group size ($s_{i,t}$).

3.3.4 Calculating ambient light levels

Ambient light in lux, $l_{i,t}$, was obtained using the unitless relative light values, *C0DATA* and *C1DATA*, recorded by the camera with each trigger and stored in the photograph's metadata. Photograph metadata were accessed using the 'exifr' package (Dunnington and Harvey 2021). These values were converted to lux using the following equations provided by the camera manufacturer and the larger of the two quotients was retained as the lux value provided it is greater than zero:

$$Lux1_{i,t} = \frac{(C0DATA - 2 \times C1DATA)}{CPL} \qquad \textit{Equation 3.1}$$

$$Lux2_{i,t} = \frac{(0.6 \times C0DATA - C1DATA)}{CPL} \qquad \textit{Equation 3.2}$$

$$l_{i,t} = \max(Lux1_{i,t}, Lux2_{i,t}, 0) \qquad \textit{Equation 3.3}$$

Counts per lux, *CPL*, was calculated using the following set of constants specific to this model of tail camera (Reconyx Hyperfire 2, LED-flash): $ATIME_{MS}$ = 27.2, *AGAINx* = 16, and *GA* = 21.4.

$$CPL = \frac{(ATIME_{MS} \times AGAINx)}{(GA \times 53)} \qquad \textit{Equation 3.4}$$

3.3.5 Calculating ambient noise

In addition to a camera, I also deployed an AudioMoth acoustic recording device (Hill et al. 2019) at each site to record one minute of audio every ten minutes. Due to equipment limitations, I rotated 12 acoustic recorders between the 24 sites such that each acoustic recorder was active for approximately two weeks at one site before moving to another site. While cameras were active for four-week sampling periods, this analysis only uses photographs taken during the two-week period in which an acoustic recorder was active at the respective site. Acoustic recorders had a sampling rate of 32KHz and a medium gain, and were affixed to a tree roughly 1.5-meters from the ground within 10 meters of the camera.

Ambient noise, $s_{i,t}$, was characterized using median sound pressure level (SPL) calculated using the PAMGuide processing techniques provided in Merchant, et al. (2015) in R version 4.2.0. When calculating SPL, I used the technical specifications provided by Open Acoustic Devices: transducer sensitivity = -18; gain = 15; zero-to-peak voltage = 3.3, analysis type = broadband. An SPL was calculated for each half-second of each one-minute recording period, resulting in 120 SPL's per recording. The median of those 120 values was then used to represent the ambient noise present at the site for that ten-minute period. I then associated each SPL value with any deer observations made in the following ten minutes of the respective recording. I chose to associate deer observations with the closest preceding audio recording since I assumed deer would be responding to conditions which have already occurred rather than anticipating future noise levels (i.e., SPL readings that occurred after the deer observation).

3.3.6 Quantifying relative risk

Because our study design does not permit us to measure risk directly, we instead consider the relative risk of human encounter based on the prevalence of both humans and habitat complexity (i.e., abundance of refugia in which to hide). To account for the relative risk of encountering humans, $r_{i,t}$, I multiplied a metric of habitat openness by the number of humans visiting the site, $h_{i,t}$.

$$r_{i,t} = o_{i,t} \times h_{i,t} \qquad \textit{Equation 3.5}$$

Where $h_{i,t}$ is the cumulative number of humans within one urban deer home range (17.3 hectares ; Roden-Reynolds et al., 2022) around site *i* during hour *t*. My study design rarely captures photographs of humans since cameras are purposefully located away from human trails. Instead of using photographic observations to quantify human activity at each site, I used human mobility data from ADVAN Research (https://advanresearch.com/) via the Dewey platform (www.deweydata.io). ADVAN Research uses cell phone data to aggregate human foot traffic information at specific Points of Interest (POI's) in the US. I used the weekly patterns dataset to retrieve the number of raw visits per hour at each POI within my study area between 2021-06-28 and 2022-05-08. Because POI's are stored as points, I created a Voronoi polygon around each POI that retained the hourly foot traffic data from the respective POI point. Around each sampling site, I created a 235-m fixed radius buffer to correspond with an urban deer home range. I then calculated the mean number of hourly visits for each Voronoi polygon that intersected the deer home range buffer to obtain the human activity variable, $h_{i,t}$.

Habitat openness, $o_{i,t}$, was calculated by subtracting the mean vegetative intensity within the home range buffer, $v_{i,t}$, from one and dividing the resulting value by the structural complexity of the understory within the same buffer, c_i.

$$o_{i,t} = \frac{1 - v_{i,t}}{c_i} \qquad \textit{Equation 3.6}$$

Here, $v_{i,t}$ is the normalized difference vegetation index (NDVI) and is calculated using remotely sensed near-infrared (b_{IR}) and red (b_r) spectral bands obtained from Landsat 8 (United States Geological Survey). Remotely sensed data were processed using the 'sf,' 'raster,' and 'terra' packages in R (Pebesma 2018; Hijmans 2023b; Hijmans 2023a).

$$v_{i,t} = \frac{b_{IR} - b_r}{b_{IR} + b_r} \qquad \textit{Equation 3.7}$$

I used rumple to characterize vegetative complexity, c_i, at each site, which is the ratio of the three-dimensional (SA_{3D}) and two-dimensional (SA_{2D}; i.e., footprint) space that vegetation occupies created using remotely sensed lidar points. Due to the multi-jurisdictional nature of the study area, lidar data are housed across multiple repositories, which are listed in Appendix E.

$$c_i = \frac{SA_{3D}}{SA_{2D}} \qquad \textit{Equation 3.8}$$

Thus, more complex and heterogenous three-dimensional surfaces yield higher ratios and simpler three-dimensional surfaces yield smaller ratios since they more closely resemble their two-dimensional footprint. Because this analysis was concerned with the understory, I only used lidar points within two meters of the forest floor. Rumple was calculated using the 'lidR' package in R (Roussel et al. 2020).

Vegetated regions in my study area never experience NDVI values of exactly 1, but are always greater than 0 (Equations 7). As a result, the numerator of Equation 6 is always positive and less than or equal to 1. Likewise, c_i is a ratio and is always positive (Equation 8). As a result $o_{i,t}$ is always positive and less than 1 (Equation 6). Because the value of habitat openness, $o_{i,t}$, (Equations 6) is always between zero and one, Equation 5 allows habitat complexity to govern the effect of humans since complex habitats ($o_{i,t}$ approaching 0) with ample refugia artificially reduce the number of humans observed at the site (effect of humans), while simple habitats ($o_{i,t}$ approaching 1) with few places to hide permit the full effect of humans at the site to be felt.

3.3.7 Model formulation and fitting

Finally, I constructed a global logistic regression model for vigilant behavior at site i during time t consisting of relative risk ($r_{i,t}$), documented herd size ($s_{i,t}$), ambient light ($l_{i,t}$), and ambient noise ($n_{i,t,}$):

$$vigilance \sim Bernoulli(p_i) \qquad \textit{Equation 3.9}$$

$$logit(p_i) = \beta_0 + \beta_1 \times r_{i,t} + \beta_2 \times s_{i,t} + \beta_3 \times l_{i,t} + \beta_4 \times n_{i,t} \quad \textit{Equation 3.10}$$

To model group size, I constructed a similar Poisson regression model, but excluded documented herd size ($s_{i,t}$) as an independent variable since this became the dependent variable:

$$group\ size \sim Poisson(\lambda_i) \quad \textit{Equation 3.11}$$

$$log(\lambda_i) = \beta_0 + \beta_1 \times r_{i,t} + \beta_2 \times l_{i,t} + \beta_3 \times n_{i,t} \quad \textit{Equation 3.12}$$

Each independent variable was scaled to have mean of zero and standard deviation of one. Prior distributions for the intercept term and all coefficients were normally distributed with a mean of zero and standard deviation of 100. To estimate the coefficient values, I ran four 100,000-iteration MCMC chains with a 50,000-iteration burn-in period using NIMBLE version 1.1.0 in R (de Valpine et al. 2017). Each parameter's trace plot was visually inspected to ensure adequate mixing, and Gelman-Rubin statistics were confirmed to be less than 1.10. I considered a parameter to be significant if its 95% credible interval did not contain zero.

3.4 Results

A total of 3,928 observations of white-tailed deer were recorded across the 24 sites sampled. Malfunctioning equipment excluded four sites, which reduced the number of sites analyzed to 20. I only recorded a total of 28 observations of coyotes across six of the sites,

demonstrating non-human predators are rare in my study system. Approximately 81% of deer observations were not useable either because the photograph did not meet the inclusion criteria (e.g., head was not visible, animal was fleeing, etc.), or because audio data were not available for those observations (e.g., acoustic recorder batteries died). My final dataset consisted of 734 observations of white-tailed deer. Approximately 72% (n = 532) of observed deer were non-vigilant, while the remaining 28% (n = 202) were classified as vigilant. Deer were documented in groups ranging from 1 to 6 individuals (mean = 1.72, SD = 1.07). Ambient light values varied from 0.00 to 9,423.87 lux (mean = 669.20, SD = 1,380.54), while ambient noise varied from 60.54 to 85.99 decibels (mean = 71.56, SD = 5.48). Habitat openness ranged from 0.38 to 0.79 (mean = 0.62, SD = 0.09), and cumulative hourly raw visitors ranged from 0.00 to 25.50 (mean = 1.98, SD = 4.75). As a result, relative risk scores ranged between 0.00 and 13.98 (mean = 1.18, SD = 2.67). In addition to variation across sites, environmental conditions also varied across seasons and times of day, creating a dynamic set of conditions for deer to react to (Figure 3.1).

My analysis revealed a negative correlation between vigilance and ambient light (Figure 3.2; β = -0.35, 95% CI = -0.57 – -0.15), and a positive correlation between vigilance and ambient noise (Figure 3.2; β = 0.24, 95% CI = 0.08 – 0.40). Deer were 30% less likely to display vigilance behavior (odds ratio = 0.70, 95% CI = -0.57 – 0.86) in conditions where visible light increased by one standard deviation from the mean (SD = 1363.80 lux), and 27% more likely to display vigilance behavior (odds ratio = 1.27, 95% CI = 1.08 – 1.49) in conditions where noise increased by one standard deviation from the mean (SD = 5.55 dB). Herd size (β = -0.08, 95% CI = -0.25 – 0.08) and relative risk (β = -0.08, 95% CI = -0.28 – 0.11) both contained zero within their 95% credible intervals. The intercept was estimated to be -0.99 (95% CI = -1.15 – -0.83),

indicating that on average deer had a 0.27 probability of displaying vigilance behavior when all other variables are held at their mean.

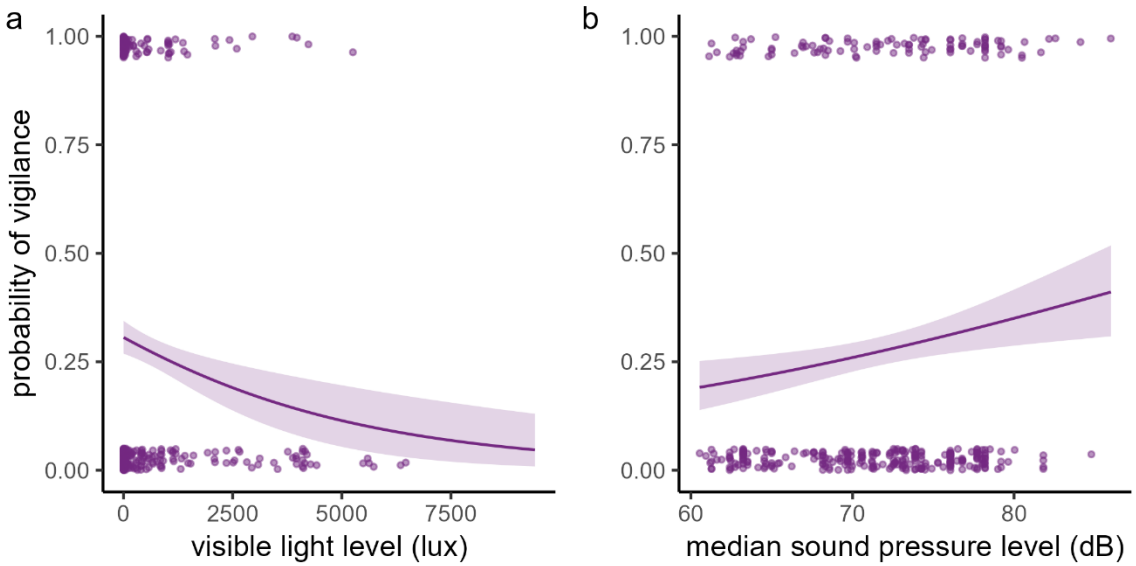


Figure 3.2 Effects of light levels (a) and median sound pressure (b) on the probability of deer vigilance. Mean predicted vigilance probability is depicted as a dark line, while 95% credible intervals are depicted as a shaded polygon. Points depict observed data.

Similar to vigilance behavior, my analysis found a positive correlation between ambient noise and foraging group size (Figure 3.3; $\beta = 0.09$, 95% CI = 0.04 – 0.15). However, ambient light ($\beta = 0.03$, 95% CI = -0.03 – 0.08) and relative risk ($\beta = -0.04$, 95% CI = -0.10 – 0.01) had no significant correlation with group size. The intercept was estimated to be 0.52 (95% CI = 0.46 – 0.57), indicating that the average foraging group size is 1.68 individuals when all other variables are held constant at their mean.

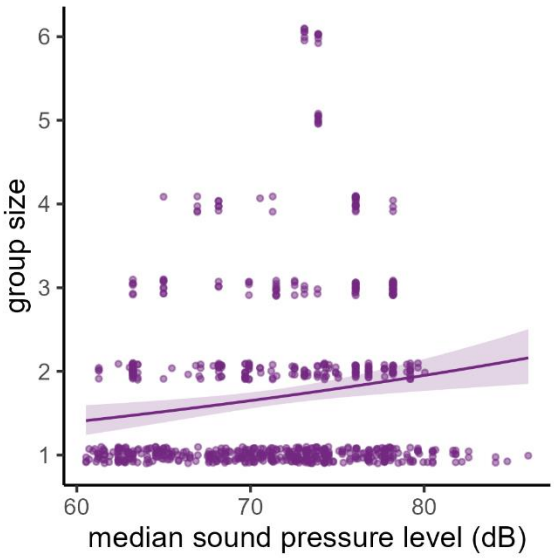


Figure 3.3 Effects of median sound pressure on foraging group size. Mean predicted group size is depicted as a dark line, while 95% credible intervals are depicted as a shaded polygon. Points depict observed data.

3.4 Discussion

Although vigilance behavior is well-studied in less developed areas, the direct threat of predation may conflate any insights into other mechanisms that drive anti-predator behavior, such as the prevalence of light to improve visual detection of predators, or the prevalence of noise to inhibit auditory detection of predators. This study overcame this limitation by studying white-tailed deer vigilance behavior in an urban setting where large non-human predators are generally absent and deer hunting is restricted. My findings suggest that urban white-tailed deer alter their vigilance behavior and foraging group size based on reduced visibility and increased ambient noise, even when there is little to no risk of predation on the landscape. Conversely, group size and relative risk of encountering humans – which I use as a proxy for disturbance or predation – do not have a measurable effect on vigilance behavior. The fact that deer continue to

exhibit anti-predator behavior despite reliably low rates of predation indicates that non-consumptive factors contribute to landscapes of fear (Palmer et al. 2023). These results suggest that deer moderate their anti-predator behavior based on their ability to perceive a change in predation risk as opposed to the actual severity of predation risk itself. Together, my results lend further support to the notion that landscapes of fear are manifestations of perception rather than predation (Gaynor et al. 2019; Palmer et al. 2023).

This analysis found a positive correlation between noise and both vigilance behavior and foraging group size, suggesting that noise inhibits prey from detecting an approaching predator and prompts proactive protective measures (Lynch et al. 2015). Prey species tend to be familiar with sounds associated with predation from a young age (e.g., Magrath et al., 2007). Such immediate recognition suggests that auditory cues are critical to prey survival, and explains why cue-masking noises would trigger antipredator responses. Additionally, anthropogenic noise pollution can add to ambient natural noise that would already hinder a prey's ability to hear predators (e.g., crickets chirping, water flowing, etc.). As a result, urban settings have the potential to be supersaturated with noise, perhaps explaining why noise was significantly correlated with both antipredator responses tested in this study.

Unlike noise, my analysis found that vigilance behavior decreased during the day when the intensity of light increased, but foraging group size was unaffected by light intensity. Low light conditions make it difficult for mammals to see individuals farther in the distance without the aid of bold and contrasting coloration, which predators generally lack (Penteriani and Delgado 2017). These results indicate that deer compensate for low visibility with vigilance, but reduce vigilance behavior when brighter conditions are restored. Alternatively, it is also possible

that deer have evolved a heightened sense of vigilance at night because most predators are nocturnal and nighttime has thus always been a particularly dangerous time irrespective of the light level (Gerkema et al. 2013; Gaynor et al. 2020).

Although noise and light both contribute to anti-predator behavior in deer, the threat of human contact – mediated by vegetative structure – had no significant correlation with vigilance behavior or foraging group size. Prey are known to adjust their anti-predator behavior in response to differing predator behaviors, with coursing predators (e.g., canids) prompting larger foraging groups and ambush predators (e.g., felids) eliciting vigilance behavior (Creel et al. 2014; Palomo-Munoz et al. 2024). Hunting literature suggests that humans act as coursing predators (Montgomery et al. 2022), but no studies have yet investigated whether recreating humans resemble coursing or ambush predators in their behavior patterns. Since deer did not respond to humans with either anti-predator behavior, it is possible that human behavior does not mimic either predation type. To better understand how humans contribute to animal behavior, future research should explore fine scale behavior and movement patterns of recreating humans and the responses these behaviors evoke in wildlife.

Historically, the landscape of fear has been disproportionality attributed to the effects of top-down regulation (Laundré et al. 2001; Dobson 2014). More recently, individual perception has been recognized as an important component of landscapes of fear since an individual cannot adjust their behavior to a threat they cannot perceive (Jordan and Ryan 2015; Gaynor et al. 2019). Because perception of top-down factors can be dependent on bottom-up factors, I propose that perceptual capacity is thus nested between top-down and bottom-up regulation. As such, I interpret perception as a ‘middle-out’ factor. While top-down regulation is of obvious

importance in the formation of a fear landscape, consideration of bottom-up (i.e., light level and noise) and middle-out (i.e., perception) factors can provide a more holistic understanding of landscapes of fear (Laundré et al. 2014). Although landscapes of fear are overwhelmingly associated with the presence of an apex predator, it may be the prey's ability to detect a predator – not the predator itself – that shifts behavior and enforces ecological balance.

3.5 Conclusion

Anti-predator behaviors are advantageous to prey but can only be effective if prey are able to detect predators (Jordan and Ryan 2015; Gaynor et al. 2019). Animals with the cognitive capacity to perceive predators may be dependent upon environmental conditions which either facilitate or hinder the detection of predators, such as ambient light and noise. My study found that deer showed heightened anti-predator behaviors under noisy and dark conditions despite reliably low predation pressure. These findings suggest that landscapes of fear require bottom-up and middle-out factors in addition to top-down pressures. As the world becomes brighter and louder (Bennie et al. 2015; Buxton et al. 2017), understanding the nonstructural aspects of predator-prey dynamics will become increasingly critical to the conservation and maintenance of ecosystems.

Chapter 4: Spatial and temporal overlap of domestic cats (*Felis catus*) and native urban wildlife

4.1 Introduction

Free-roaming domestic cats (*Felis catus*; hereafter, 'cats') impact native wildlife through predation and the transmission of disease, posing serious threats to native wildlife (Loss et al. 2013; Loyd et al. 2013; Thomas et al. 2016). Likewise, native wildlife can also pose risks to cats such as predation by native species like coyotes (Kays et al. 2015; Larson et al. 2020) and the transmission of rabies (Roseveare et al. 2009; Gehrt et al. 2013). These bidirectional risks are absent when cats are kept indoors, but manifest themselves when cats are allowed to roam freely outdoors.

The variation of risk across time and space is a fundamental concept in ecology (Brown et al. 1999; Mayor et al. 2009; Gaynor et al. 2019), and is applicable to free-roaming cat management since the bidirectional risks of cats are not uniform across the landscape. For instance, predation by cats is greatest near habitat edges (Kays and DeWan 2006; Herrera, M.V. Cove, et al. 2022; Pirie et al. 2022), and predation rates fluctuate based on the season and time of day (Thomas et al. 2012; Loyd et al. 2013). Likewise, cats face less predation risk where native predators are scarce (Gehrt et al. 2013; Kays et al. 2015), and predation risk is presumably greater for cats whose diel patterns match those of native predators. Similarly, the risk of cat-wildlife disease transmission increases with heightened interactions between species (Theimer et al. 2015). Thus, cats and native wildlife must be in proximity to each other for these risks to be realized, and the risk of negative interactions between species will be greatest where species overlap in space and time (Holmala and Kauhala 2009).

Location-based management policies that explicitly consider spatial variation in risk are helpful in managing wildlife populations (Stevens and Pfeiffer 2016; Davis et al. 2021). While permanent removal through adoption or euthanasia ensures elimination of cat-wildlife risks, trap-neuter-return (TNR) remains a common free-roaming cat management strategy that is spatially-explicit — cats are trapped, sterilized, and returned to the same location from which they were trapped (Longcore et al. 2009). However, this attention to location when releasing cats is primarily concerned with the individual cat's familiarity with its surroundings (E Robinson, *Personal Communication*), rather than to abate risks to or from cats. If the spatial variation in risk was an additional consideration in free-roaming cat management, cats might be spatially separated from areas in which high risk outcomes are likely. The degree to which cats and native wildlife overlap can thus be used to quantify the risk of negative outcomes between cats and native wildlife.

Here I assess the habitat use and diel patterns of cats and eight native mammal species in Washington, DC, I assessed landscape variables across multiple spatial scales to account for variations in species' spatial scale of response (Rettie et al. 2000; Gallo et al. 2018; Moll et al. 2020). I also predicted the probability of spatial overlap of cats and each native species to assess apparent risk of being preyed upon by cats or serving as a disease or predation risk to cats. I asked the following research questions: (1) what natural and anthropogenic features of the urban environment most influence the distribution of cats and native mammal species in urban areas?, (2) what is the probability of spatial overlap between cats and native mammal species?, and (3) to what degree do activity patterns overlap between cats and native mammal species?

I hypothesized that the presence of native mammal species would exhibit a positive correlation with natural features of the urban environment (e.g., tree cover, open water), but would have a negative correlation with most anthropogenic features (e.g., human population density and traffic). Due to the luxury effect commonly seen in urban ecosystems, I also hypothesized that native mammals would exhibit a positive association with average per capita income (Magle et al. 2021). Conversely, I hypothesized that the presence of cats would be negatively influenced by natural features and positively influenced by anthropogenic factors, but would display a negative relationship with average per capita income (Gehrt et al. 2013; Vanek et al. 2021; Cove et al. 2023). Because I hypothesize that the distribution of cats and native mammals would occupy different ends of an urban-natural continuum, I predicted that the degree of spatial overlap would be highest at the fringes of either species' habitat requirements and thus allow for spatially-explicit management policies. I further predicted that the known variation in cat diel activity would result in substantial activity overlap between cats and all native mammal species (Bennett et al. 2021). These findings identify areas with the greatest potential for bidirectional risk and can inform management policies that consider the wellbeing of cats and wildlife alike.

4.2 Methods

4.2.1 Study area

Washington, District of Columbia (hereafter 'DC') has a population of approximately 705,750 residents (~4,466 people per km^2; United States Census Bureau, 2020), and an estimated 7,296 free-roaming domestic cats (of which ~35% have undergone TNR; Cove et al., 2023). DC contains two major rivers and is situated at the ecotone of the coastal plains and Piedmont

regions (Ossi et al. 2015). The climate is temperate/tropical with an average of 110 cm of annual precipitation and average annual temperatures ranging from 21.6 °C to 6.9 °C (US National Oceanic and Atmospheric Administration 2024). An extensive park system is situated within the densely developed city, resulting in a heterogenous landscape of developed gray space, landscaped greenspace, and semi-natural greenspace (e.g., forested parks). DC resides in the ancestral homeland of the Nacochtank (also called Anacostan) people, and later the Piscataway people (Tayac 2014).

4.2.2 Dependent variables

Passive infrared-sensor camera traps (Reconyx HyperFire 2, Reconyx Inc., 3828 Creekside Ln, Ste 2, Holmen, WI 54636) were deployed across Washington, DC, between September-December 2018 (n = 192), April 2019-January 2020 (n = 867), and June 2020-October 2020 (n = 471). To select camera locations, a 64-ha grid was superimposed on the study area, and grid cells to be sampled were chosen based on the median household income and predominant landcover categories within each grid cell (Herrera et al. 2021). Cameras were placed at a location (sampling site) within each chosen grid cell based on accessibility and permitting. Although this sampling grid informed the original selection of sampling sites, these social-environmental variables were not used for this analysis.

Camera locations included public greenspaces (n = 796), private residences and institutions (n = 441), alleys (n = 265), and sidewalks (n = 28). Each camera deployment consisted of a single camera aimed at a probable corridor of animal movement (e.g. game trails, fence lines, etc.) from a height of <0.5 m, and was affixed to a vertical substrate using a nylon strap and cable lock. Each time a camera was triggered, five consecutive photographs were taken

with no delay period. At each sampling site, a camera was continuously active for 15 consecutive days and sites were not resampled (Herrera et al. 2021). Over the course of the study, 11 cameras were stolen, 8 deployments were tampered with such that they were no longer collecting data, and 3 cameras were damaged beyond repair after being struck by vehicles.

Photographs taken within one minute of each other were considered a single observation. All photographs were separately reviewed by two individuals, and all animals within each sequence were identified to species. If species-level identification was not possible, animals were identified to the lowest taxonomic level afforded by the photographs. Observations without animals visible were coded as 'blank.' All photographs were uploaded to the eMammal photo repository (McShea et al., 2016; see also: http://emammal.si.edu).

4.2.3 Spatial scales

Three grid arrays, each at different scales, were overlaid on the District of Columbia using ArcMap 10.8 (ESRI, 380 New York Street, Redlands, CA 92373). Each spatial scale was greater than the average domestic cat home range in urban areas (0.036 ± 0.056 km2; Kays et al., 2020) to achieve spatial independence, and included: 400x400 m (0.16 km2, hereafter 'small'), 800x800 m (0.64 km2, hereafter 'medium'), and 1x1 km2 (1 km2, hereafter, 'large') cell sizes (Figure 4.1). Grid cells were only included in the analysis if at least half of the cell's area was within DC's administrative boundary (Figure 4.1). At each spatial scale, observations from all cameras (sampling sites) located within a respective grid cell were combined and considered a single sampling unit (Figure 4.1). Respectively, 50%, 71%, and 77% of the total small, medium, and large grid cells were sampled.

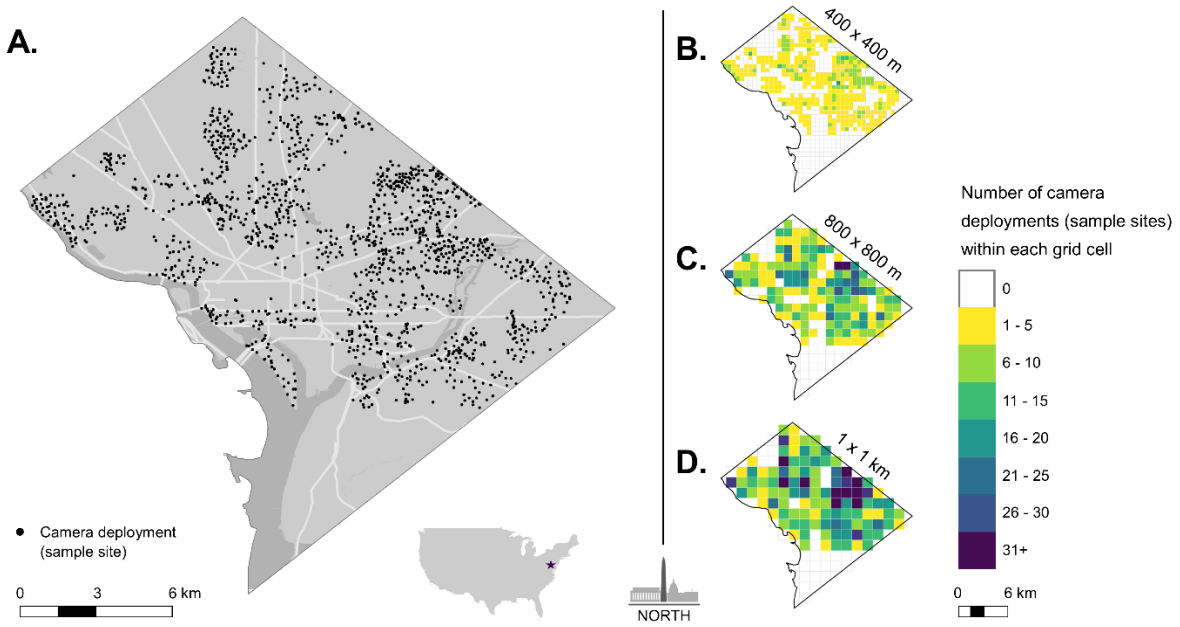


Figure 4.1 (A) All camera locations (sampling sites) in Washington, DC, **(B - D)** Sampling grids for each spatial scale. Data from all cameras within each sampling cell were pooled together. Sampling block colors indicate the number of cameras deployed within each sampling cell.

At each spatial scale, observation data from all cameras located within each grid cell were pooled to create daily detection histories (detected = 1, not detected = 0, not surveyed = NA) for the respective cell using the package 'CamtrapR' in R version 4.1.2 (Niedballa et al. 2016). Species included in this analysis were domestic cat due to its centrality to the research questions, and eastern chipmunk (*Tamias striatus*), eastern cottontail (*Sylvilagus floridanus*), eastern gray squirrel (*Sciurus carolinensis*), groundhog (*Marmota monax*), and white-footed mouse (*Peromyscus leucopus*) because they are native species known to be depredated by domestic cats (Loyd et al. 2013; Herrera, M.V. Cove, et al. 2022). Raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*) and Virginia opossum (*Didelphis virginiana*) were also included because they are disease vectors or are otherwise known to be a risk to cats through direct conflict or

interference competition (Carey and Mclean 1983; Jenkins et al. 1988; Sogliani and Mori 2019; Zecca et al. 2020; Hennessy and Hild 2021). Although the dynamics between coyotes (*Canis latrans*) and cats is a topic of growing ecological interest (e.g., Larson et al., 2020), coyote observations (n = 43) from the study area were too sparse to sufficiently analyze.

4.2.4 Independent variables

I broadly hypothesized that forested habitat (Bozek et al. 2007; Fidino et al. 2016; Lombardi et al. 2017), water sources (Fidino et al. 2016; Lombardi et al. 2017; Wait et al. 2020), human population density (Luck 2007; Lombardi et al. 2017), vehicular traffic (Goodwin and Shriver 2010 Nov; Chen and Koprowski 2016), and per capita income (Hope et al. 2003; Clarke et al. 2013) would influence the probability of presence for each species. I initially considered 23 variables that represented these broader categories and calculated them for each grid cell at each spatial scale (See Appendix E for a list of variables and methods for calculating each variable). I calculated the variance inflation factor for each mean-centered variable at each scale using the package 'USDM' in R (Naimi et al. 2014). Variables with a high degree of collinearity (variance inflation factor > 3) at any scale were removed from the overall analysis such that each spatial scale contained the same set of variables. A single variable was then selected for each category, with preference given to those that were considered more directly interpretable or deemed to have greater ecological significance. The final variables included in my models were percent canopy cover (forested habitat), percent open water, human population density, average daily traffic volume of roads within the sampling cell (vehicular traffic), and average per capita income (neighborhood income). All variables were scaled and centered to have a mean of 0 and standard deviation of 1.

To account for imperfect detection, I considered the number of cameras active in each grid cell, daily temperature, daily precipitation, the presence of fog, and moon phase on detection probability. The number of cameras active in each grid cell per day was calculated using *CamtrapR* (Niedballa et al. 2016). Daily precipitation (cm), presence of fog (yes = 1, no = 0), and daily maximum temperature (°C) data were obtained from local weather stations (National Oceanic and Atmospheric Administration 2021). Precipitation and temperature data were averaged if readings were available from multiple stations. The percent visible moon for the Eastern time zone was calculated for each sampling day using SKYCAL (National Aeronautics and Space Administration 2011) based on the time passed since the last new (0) or full (1) moon and did not consider nightly cloud cover. Environmental detection variables were unique to each sampling day rather than the sampling cell, while the number of active cameras was unique to each sampling cell. All variables were scaled and centered to have mean of 0 and standard deviation of 1.

4.2.5 Occupancy analysis

I fit single-season Bayesian occupancy models (MacKenzie Darryl, Nichols James, Royle J., Pollock Kenneth, Bailey Larissa 2017) using the 'ubms' package in R (Kellner et al. 2021), which uses 'rstan' for MCMC computation (Stan Development Team 2020). A single fully-parameterized model was fit for each species at each spatial scale. All parameters including intercepts were given vague Normal priors with mean of zero and standard deviation of one (Northrup and Gerber 2018). MCMC chains were constructed using the No-U-Turn Sampler, an extension of the Hamiltonian Monte Carlo algorithm (Hoffman & Gelman 2014). Four chains were constructed for each parameter, where each chain consisted of 100,000 iterations and a

burn-in of 50,000 iterations. Model convergence was assessed by visually inspecting each chain's trace plot, ensuring the Gelman-Rubin statistics were <1.1, and ensuring that all effective sample sizes were greater than 127,000. I considered any variable to have evidence of an effect if the 95% Bayesian credible intervals did not overlap zero.

Multiple techniques were used to assess model fit. Model residuals were compared against predicted values (both occupancy and detection) to assess the variation of deviance within each model, where the distribution of residuals was visually assessed for skew or clustering along the distribution of predicted values (Gelman et al. 2000; Broms et al. 2016; Wright et al. 2016). Posterior post-predictive values were obtained by using the model to simulate 100 datasets and comparing the proportion of zeros in these datasets against the proportion of zeros present in the observed dataset at each spatial scale, with matching proportions indicating good model fit (Broms et al. 2016; Wright et al. 2016). Additionally, the Pareto k diagnostic values were calculated for each model, where values less than 0.5 indicated good model fit (Vehtari et al. 2017). Finally, the MacKenzie-Bailey chi-squared statistic and resulting Bayesian p-value were also calculated for each model, where the Bayesian p-value is interpreted similarly to a frequentist p-value (MacKenzie and Bailey, 2004; *but see also* Wright et al., 2016). Diagnostic tests were conducted using the 'ubms' package (Kellner et al. 2021), and indicated good model fit for all models.

To assess the spatial overlap of each native wildlife species with cats, I calculated the percent canopy cover, percent open water, human population density, average daily traffic volume, and average per capita income for all grid cells across the study area, and used my occupancy models to predict the probability of occupancy for each species in each grid cell

(including unsampled cells) at each spatial scale. The probability of spatial overlap between cats and each native wildlife species was calculated for each grid cell by multiplying the posterior distribution of predicted occupancy probabilities for cats by the posterior distributions of predicted occupancy probabilities for each wildlife species. I derived this parameter for all grid cells at all three spatial scales. When predicting occupancy probabilities across the landscape, each detection variable was held constant at its respective mean value.

4.2.6 Temporal analysis

I considered each species' 95% kernel activity isopleth, the smallest duration of time in which 95% of observations occur, to be each species' active period (Oliveira-Santos et al. 2013). Prior to calculation, observation timestamps were converted from a linear timescale to a circular timescale by equating each timestamp to its respective value between 0 and 1 (e.g., noon = 0.5, etc.), then multiplying each value by 2π to arrive at radians (Ridout and Linkie 2009). The '*circular*' package was then used to calculate a 95% kernel isopleth with a smoothing parameter of 5 (Oliveira-Santos et al. 2013; Agostinelli and Lund 2022). The smoothing parameter accounts for inordinate peaks in activity which might arise from different criteria to bin multiple observations into a single observation (Oliveira-Santos et al. 2013). Mean observation times were also calculated, then back-transformed to a linear timescale for ease of interpretation.

Activity overlap was calculated using circular time via the 'overlap' package in R. A smoothing parameter of 3 was used per Ridout & Linkie (2009). The estimate of overlap between cats and each species ($\hat{\Delta}_4$) consists of the proportion of the larger activity curve that is shared by the smaller activity curve. The overlap estimate is reported as a value between 0 and 1, where 0 indicates no overlap and 1 indicates identical activity patterns (Lashley et al. 2018).

Cumulative species-level activity estimates were assumed to be representative of individual activity patterns (Rowcliffe et al. 2014).

4.3 Results

4.3.1 Domestic cat occupancy

At the largest scale (1km x 1km), the 95% credible interval for each variable overlapped zero, indicating no strong effect of the variables at that scale (Figure 4.2). At the medium scale (800m x 800m), open water had the greatest negative influence on cat occupancy (β_M = -1.68, 95% BCI = -2.66 – -0.76) followed by canopy cover (β_M = -0.78, 95% BCI= -1.25 – -0.33). Cats were 46.4% less likely to occur (odds ratio (OR) = 0.55, 95% BCI = 0.26 – 0.83) at sites with a 1 standard deviation (SD) increase from the mean percent open water, and 18.9% less likely to occur (OR = 0.81, 95% BCI = 0.67 – 0.92) with a one SD increase from the mean canopy cover. No variables had a positive effect on cat occupancy at the medium scale.

Open water also had the greatest negative effect on cat occupancy at the smallest scale (400m x 400m; β_S = -1.30, 95% BCI =-1.86 – -0.80), followed by canopy cover (β_S = -0.68, 95% BCI = -0.94 – -0.44), and per capita income (β_S = -0.40, 95% BCI = -0.68 – -0.14). An increase of 1 SD from the mean in canopy cover decreased cat occupancy by 24.4% (OR = 0.76, 95% BCI = 0.66 – 0.85). Cat occupancy would also decrease 46.9% (OR = 0.53, 95% BCI = 0.34 – 0.73) with a one SD increase from the mean of open water and 14.1% (OR = 0.86%, 95% BCI = 0.76 – 0.95) with a one SD increase from the mean per capita income. Human population density had the greatest positive effect on cat occupancy at the smallest scale (β_S = 0.83, 95% BCI = 0.48 – 1.23). Cats were 23% more likely to occur (OR = 1.23, 95% BCI = 1.14 – 1.35) at sites with an increase of one SD from the mean human population density. The mean probability of domestic

cat occupancy across the entire study area was 0.66 (0.28 SD) at the small spatial scale, 0.75 (0.26 SD) at the medium spatial scale, and 0.81 (0.21 SD) at the large spatial scale (Table 4.3; Appendix G & H).

4.3.2 Vector species occupancy

At the largest scale, percent canopy cover had a positive effect on red fox (β_L = 1.0, 95% BCI = 0.22 – 2.05) and raccoon (β_L = 0.96, 95% BCI = 0.12 – 1.91) occupancy, and per capita income had a negative effect on Virginia opossum occupancy (β_L = -0.76, 95% BCI = -1.32 – -0.24]). All other variables' 95% credible intervals overlapped zero (Figure 4.2; Appendix G & H).

Canopy cover also had a positive effect on raccoon occupancy at the medium scale (β_M = 1.10, 95% BCI = 0.38 – 1.96) and per capita income had a negative effect on Virginia opossum occupancy at this scale (β_M = -0.95, 95% BCI = -1.44 – -0.50; Figure 4.2). Red fox occupancy at the medium scale was positively correlated with canopy cover (β_M = 1.82, 95% BCI = 1.07 – 2.63), open water (β_M = 1.63, 95% BCI = 0.32 – 3.03), and daily traffic volume (β_M = 1.12, 95% BCI = 0.10 – 2.17), but negatively correlated with human population density (β_M = -0.95, 95% BCI = -1.88 – -0.02; Figure 4.2; Appendix G & H).

At the smallest scale, canopy cover had a positive effect on red fox (β_S = 1.75, 95% BCI = 1.33 – 2.21), raccoon (β_S = 1.42, 95% BCI = 1.05 – 1.83), and Virginia opossum (β_S = 0.41, 95% BCI = 0.19 – 0.63) occupancy, and open water had a positive effect on fox (β_S = 0.74, 95% BCI = 0.20 – 1.31) and raccoon (β_S = 0.55, 95% BCI = 0.08 – 1.07) occupancy (Figure 4.2). Human population density had a negative effect on the presence of red fox (β_S = -0.70, 95% BCI = -1.16 – -0.34) and raccoon (β_S = -0.38, 95% BCI = -0.69 – -0.09), and per capita income had a

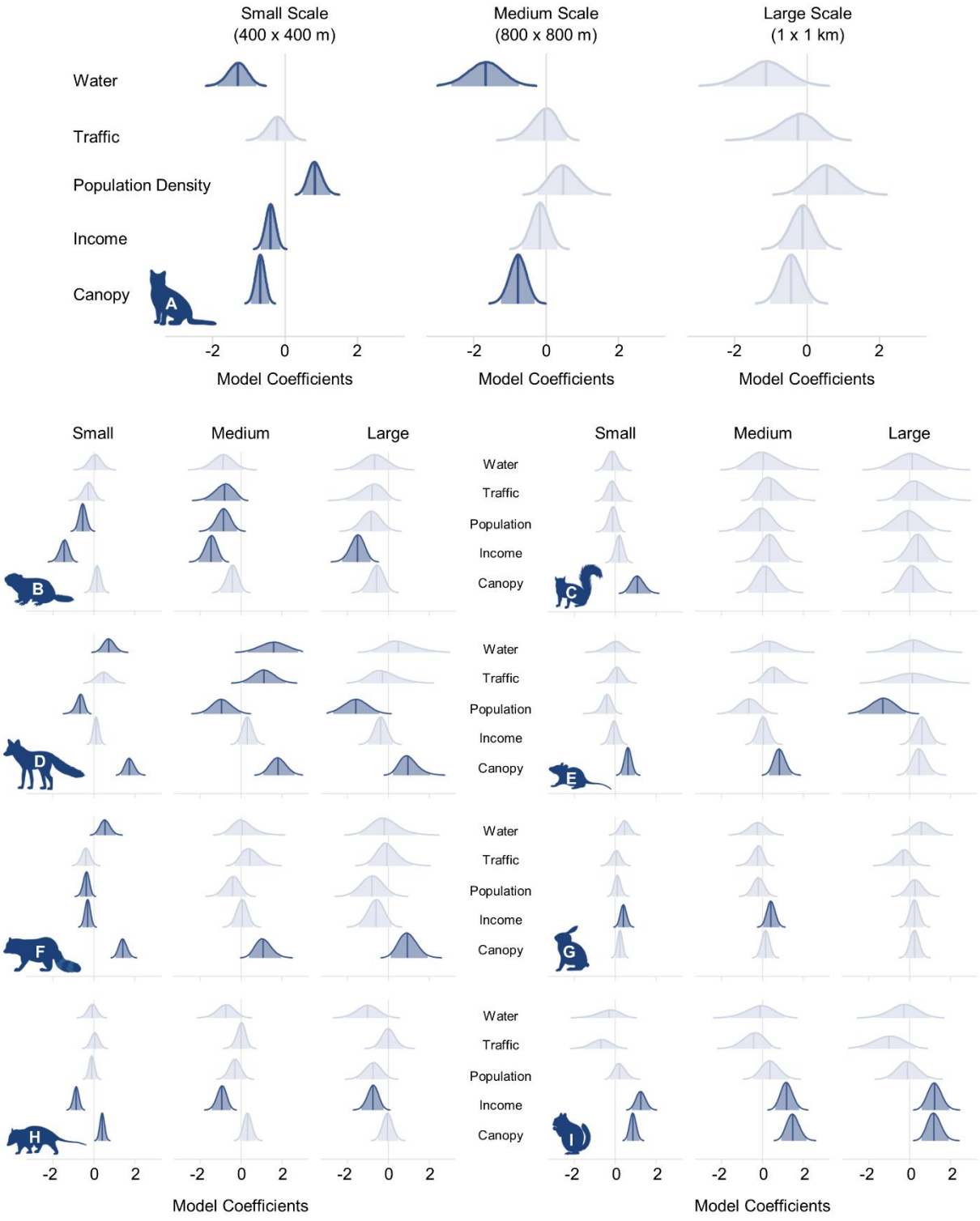

Small Scale
(400 x 400 m)
Medium Scale
(800 x 800 m)
Large Scale
(1 x 1 km)
Water
Traffic
Population Density
Income
Canopy
A
-2
0
2
Model Coefficients
Small
Medium
Large
B
C
D
E
F
G
H
I
Population
Model Coefficients

Figure 4.2 Posterior distributions of model coefficients for (A) domestic cat, (B) groundhog, (C) eastern gray squirrel, (D) red fox, (E) white-footed mouse, (F) raccoon, (G) eastern cottontail, (H), Virginia opossum, and (I) eastern chipmunk. Solid blue lines indicate the full posterior distribution and shaded regions represent the 95% Bayesian credible interval. Vertical blue lines denote the median posterior value. Distributions colored in light blue indicate that the 95% credible interval overlapped zero.

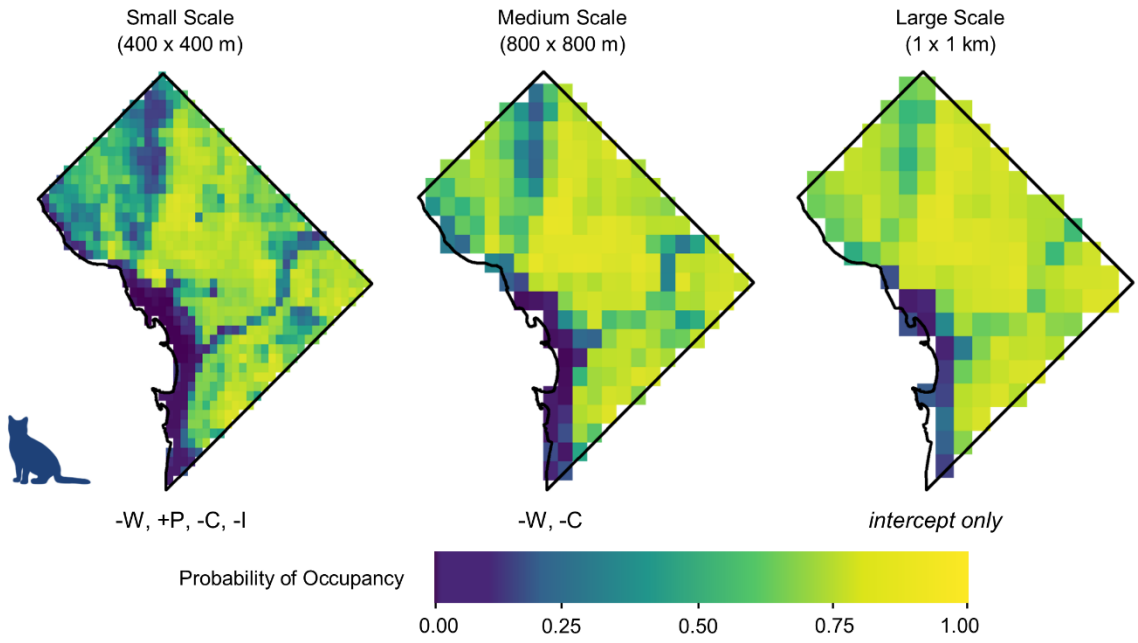


Figure 4.3 Occupancy probabilities for domestic cats across Washington, DC, at three spatial scales using the mean posterior value for each parameter. Cooler colors signify lower occupancy probability, while warmer colors signify higher occupancy probability. Initials below each map denote the variables whose 95% credible interval did not overlap zero, in their order of magnitude (W = water, C = canopy cover, P = human population density, I = per capita income, T = traffic). A positive sign preceding each initial signifies a positive relationship, while a negative sign signifies a negative relationship. Maps show predicted occupancy using the median value for each parameter.

negative effect on raccoon (β_S = -0.31, 95% BCI = -0.58 – -0.05) and Virginia opossum (β_S = -0.87, 95% BCI = -1.14 – -0.62) occupancy (Table 4.1; Figure 4.2; Appendix G & H).

4.3.3 Prey species occupancy

At the large spatial scale, canopy cover had a positive effect on eastern chipmunk occupancy (β_L = 1.20, 95% BCI = 0.59 – 1.89), per capita income had a negative effect on groundhog occupancy (β_L = -1.53, 95% BCI = -2.26 – -0.88), and human population density had a negative effect on white-footed mouse occupancy (β_L = -1.33, 95% BCI = -2.56 – -0.19). Each variable's 95% credible interval overlapped zero at the large scale for both eastern cottontails and eastern gray squirrels (Figure 4.2; Appendix F, G & H).

At the medium scale, per capita income had a positive effect on eastern cottontail (β_M = 0.42, 95% BCI = 0.03 – 0.83) and eastern chipmunk (β_M = 1.19, 95% BCI = 0.62 – 1.80) occupancy (Figure 4.2), but had a negative effect on groundhog occupancy (β_M = -1.48, 95% BCI = -2.09 – -094]). Human population density (β_M = -0.87, 95% BCI = -1.57 – -0.21) and traffic volume (β_M = -0.84, 95% BCI = -1.80 – -0.04) also had negative effects on groundhog occupancy (Figure 4.2). Canopy cover had a positive effect on both eastern chipmunk (β_M = 1.50, 95% BCI = 0.92 – 2.14) and white-footed mouse (β_M = 0.84, 95% BCI = 0.32 – 1.43) occupancy (Figure 2.1). Similar to the larger scale results, each variable's 95% credible interval overlapped zero for eastern gray squirrels (Figure 4.2; Appendix F, G & H).

At the smallest scale, canopy cover had a positive effect on occupancy for eastern chipmunk (β_S = 0.87, 95% BCI = 0.57 – 1.18), white-footed mouse (β_S = 0.62, 95% BCI =0.29 – 0.97), and eastern gray squirrel (β_S = 1.10, 95% BCI = 0.51 – 1.75). Per capita income had a positive effect on occupancy for eastern cottontail (β_S = 0.40, 95% BCI = 0.11 – 0.71) and eastern chipmunk (β_S = 1.25, 95% BCI = 0.81 – 1.73), but had a negative effect on groundhog

occupancy (β_S = -1.46, 95% BCI = -1.92 – -1.06; Figure 4.2). Human population density also had a negative effect on groundhog occupancy (β_S = -0.55, 95% BCI = -0.89 – -0.20; Figure 4.1).

4.3.4 Probability of spatial overlap

Predicted overlap of cats and wildlife species varied by species and scale. Vector species displayed greater predicted overlap with cats than did prey species (Table 4.1). Across species, predicted overlap was greatest at the largest spatial scale (Figure 4.4; Table 4.1). The species with the highest probability of overlap with cats was raccoon, with a mean probability of overlap of 0.72 at the largest spatial scale (Table 4.1). Eastern chipmunk has the lowest probability of overlap with cats, with a mean probability of overlap of 0.06 at the smallest spatial scale (Table 4.1).

4.3.5 Activity pattern and temporal overlap

Cats exhibited a cathemeral activity pattern, with a 95% activity isopleth – the smallest duration of time that contains 95% of observations (hereafter, 'isopleth') – of 22.45 hours with a mean activity time of approximately midnight. Red fox, raccoon, and Virginia opossum adhered to nocturnal activity patterns, with an isopleths of 17.77, 13.56, and 13.19 hours and mean activity times of approximately 00:15, 01:30, and 00:45, respectively. Eastern cottontail and white-footed mouse were the only prey species to also exhibit a nocturnal activity pattern, displaying isopleths of 18.32 and 15.60 hours with a mean activity time of 01:20 and 00:00, respectively. Groundhog, chipmunk, and eastern gray squirrel all adhered to diurnal activity patterns, and displayed isopleths of 15.17, 13.86, 14.20 hours and mean activity times of 13:30, 12:00, and 13:15, respectively.

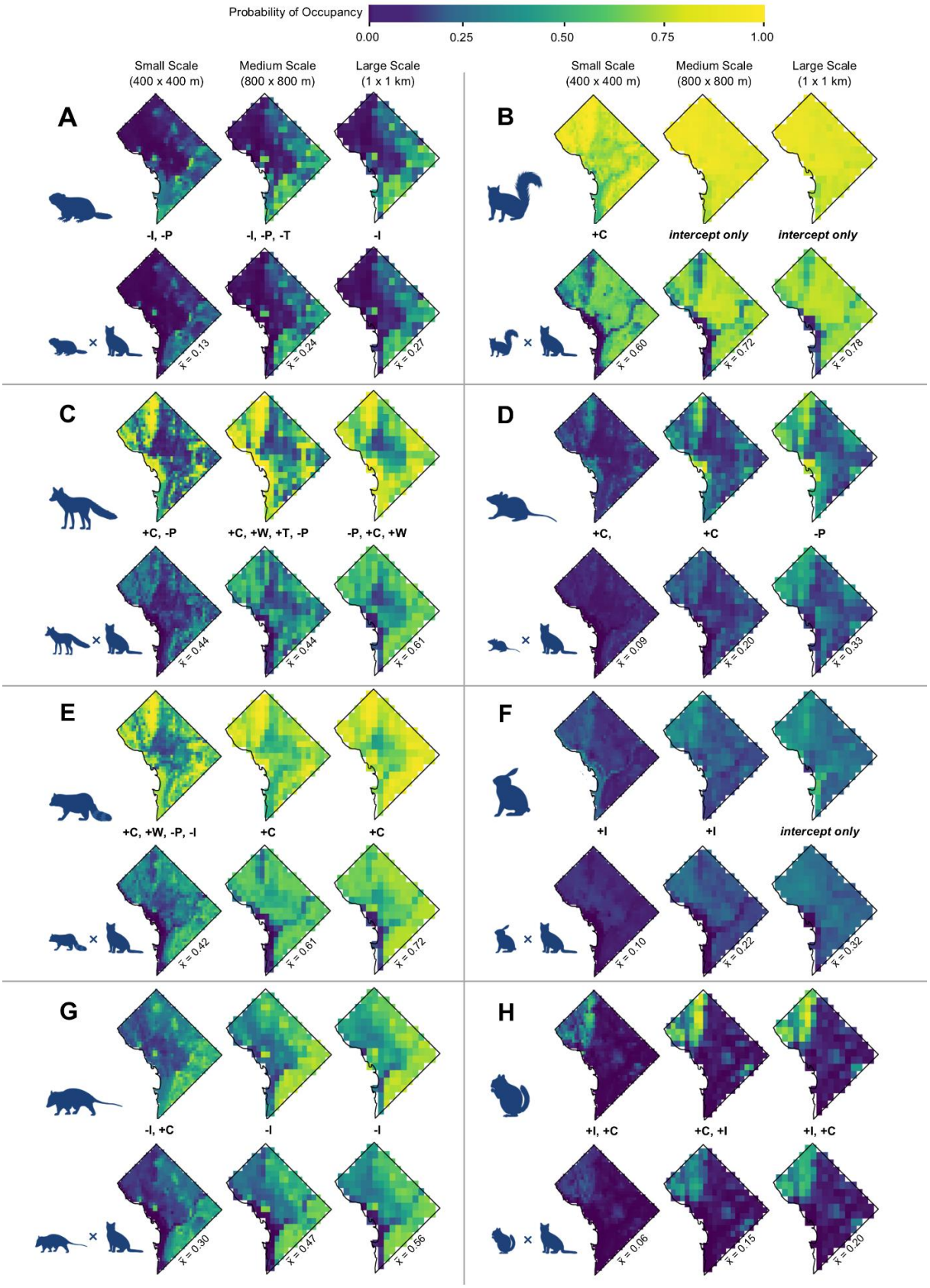

Probability of Occupancy
0.00
0.25
0.50
0.75
1.00
Small Scale (400 x 400 m)
Medium Scale (800 x 800 m)
Large Scale (1 x 1 km)
A
-I, -P
-I, -P, -T
-I
x̄ = 0.13
x̄ = 0.24
x̄ = 0.27
B
+C
intercept only
intercept only
x̄ = 0.60
x̄ = 0.72
x̄ = 0.78
C
+C, -P
+C, +W, +T, -P
-P, +C, +W
x̄ = 0.44
x̄ = 0.44
x̄ = 0.61
D
+C,
+C
-P
x̄ = 0.09
x̄ = 0.20
x̄ = 0.33
E
+C, +W, -P, -I
+C
+C
x̄ = 0.42
x̄ = 0.61
x̄ = 0.72
F
+I
+I
intercept only
x̄ = 0.10
x̄ = 0.22
x̄ = 0.32
G
-I, +C
-I
-I
x̄ = 0.30
x̄ = 0.47
x̄ = 0.56
H
+I, +C
+C, +I
+I, +C
x̄ = 0.06
x̄ = 0.15
x̄ = 0.20

Figure 4.4 Predicted occupancy probabilities and probability of spatial overlap with cats for (A) groundhogs, (B) eastern gray squirrels, (C) red fox, (D) white-footed mice, (E) raccoon, (F) eastern cottontail, (G), Virginia opossum, and (H) eastern chipmunk across Washington, DC. Occupancy color gradient is identical to Figure 4.3. For each species, the top row depicts the median occupancy probability across the study area. The second row for each species depicts the median probability of spatial overlap.

Table 4.1 Mean predicted occupancy across Washington, DC, for each species, and mean predicted overlap between cats and native mammal species. The standard deviation for each mean value is included within parentheses.

Species	Mean occupancy probability (400m x 400m)	Mean occupancy probability (800m x 800m)	Mean occupancy probability (1km x 1km)	Mean probability of overlap with cats (400m x 400m)	Mean probability of overlap with cats (800m x 800m)	Mean probability of overlap with cats (1km x 1km)
Domestic cat	0.66 (0.28)	0.75 (0.26)	0.81 (0.21)	NA	NA	NA
Raccoon	0.68 (0.22)	0.82 (0.11)	0.88 (0.10)	0.42 (0.20)	0.61 (0.22)	0.72 (0.20)
Red fox	0.49 (0.30)	0.66 (0.27)	0.77 (0.20)	0.44 (0.21)	0.44 (0.21)	0.61 (0.22)
Virginia opossum	0.44 (0.19)	0.60 (0.21)	0.67 (0.18)	0.30 (0.20)	0.47 (0.25)	0.56 (0.23)
Eastern gray squirrel	0.9 (0.08)	0.96 (0.02)	0.95 (0.03)	0.60 (0.26)	0.72 (0.27)	0.78 (0.23)
White-footed mouse	0.18 (0.11)	0.33 (0.20)	0.46 (0.23)	0.09 (0.04)	0.20 (0.11)	0.33 (0.18)
Eastern cottontail	0.19 (0.09)	0.31 (0.11)	0.42 (0.10)	0.10 (0.05)	0.22 (0.10)	0.32 (0.10)
Groundhog	0.20 (0.19)	0.31 (0.26)	0.33 (0.27)	0.13 (0.15)	0.24 (0.24)	0.27 (0.25)
Eastern chipmunk	0.12 (0.17)	0.22 (0.27)	0.25 (0.28)	0.06 (0.07)	0.15 (0.17)	0.20 (0.23)

The coefficient of overlap ($\hat{\Delta}_4$) between cats and wildlife was greatest in nocturnal species. Red fox had the highest degree of overlap of the vector species ($\hat{\Delta}_4$ = 0.73), while overlap between cats and raccoons ($\hat{\Delta}_4$ = 0.56) and Virginia opossums ($\hat{\Delta}_4$ = 0.54) was lower. Eastern cottontail displayed the greatest temporal overlap with cats of the prey species ($\hat{\Delta}_4$ = 0.78), followed by white-footed mouse ($\hat{\Delta}_4$ = 0.69). Diurnal prey species — i.e., eastern gray squirrel ($\hat{\Delta}_4$ = 0.45), groundhog ($\hat{\Delta}_4$ = 0.52) and eastern chipmunk ($\hat{\Delta}_4$ = 0.45) — displayed less activity overlap with cats than did nocturnal prey species but still exhibited temporal overlap near or greater than 50% (Figure 4.5).

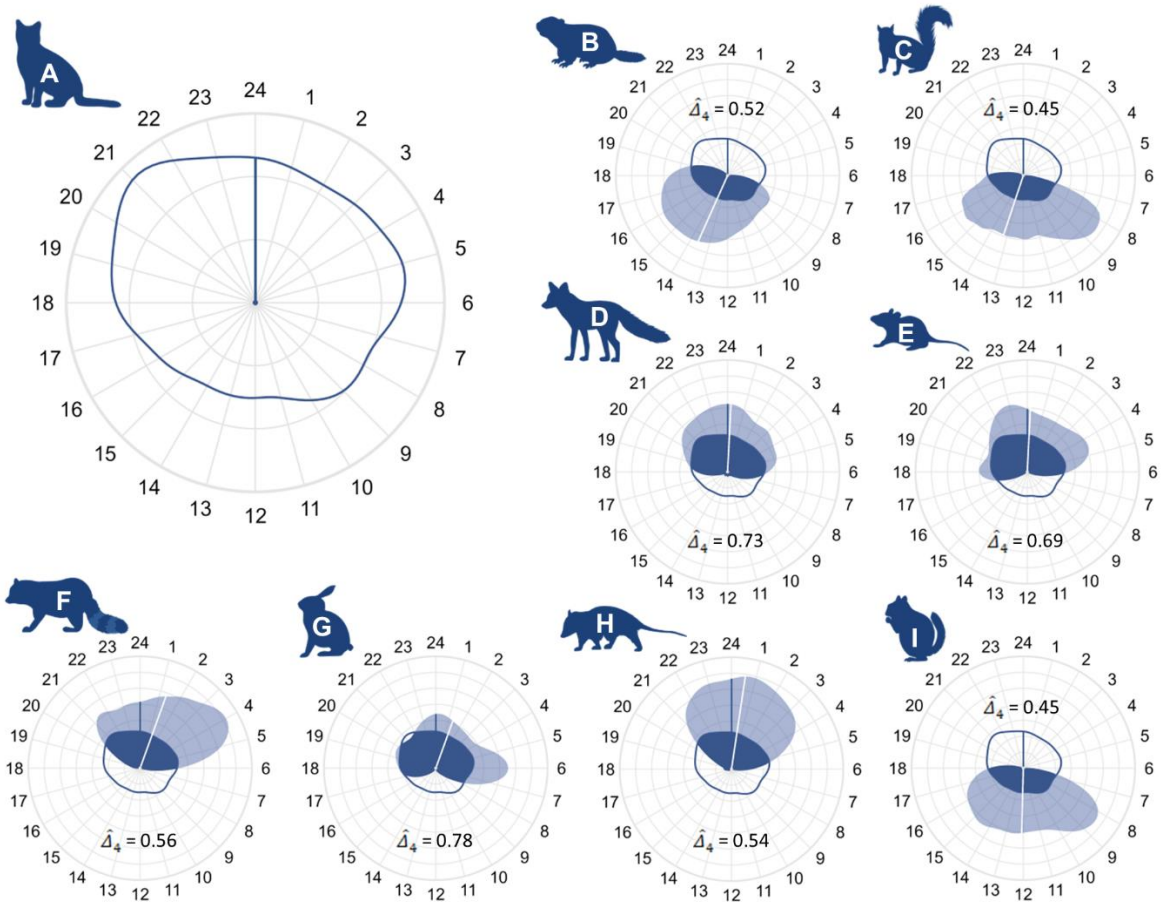


Figure 4.5 Activity patterns and temporal overlap plotted on a 24-hour clock for (A) cats, (B) groundhogs, (C) eastern gray squirrels, (D) red fox, (E) white-footed mice, (F) raccoon, (G) eastern cottontail, (H), Virginia opossum, and (I) eastern chipmunk. Plots depict cat activity density and mean activity time using a dark blue line, while the light blue polygon and white line are used for the species of interest. Activity overlap (area beneath both curves) is colored in dark blue. Note that plot A utilizes a different scale than plots B-I.

4.4 Discussion

This analysis suggests that cats and native mammal species overlap both spatially and temporally across Washington, DC, Since temporal overlap was high (> 0.50) between cats and all native species except eastern grey squirrel and eastern chipmunk, my analyses suggest that species are likely to share active hours wherever they overlap spatially. Because cat-wildlife activity overlap is plausible across the diel period, the risk of negative outcomes such as predation and rabies transmission is more greatly mediated by spatial rather than temporal overlap. I used single-season occupancy models at three spatial scales to identify species-habitat relationships of free-roaming domestic cats and eight native mammal species common in urban areas. I then used my model results to estimate the probability of spatial overlap between native mammals and domestic cats based on the most influential landscape characteristics for each species (Figure 4.4).

These findings largely supported my first and second hypotheses that native mammal occupancy is correlated with natural variables, while cat occupancy is correlated with anthropogenic variables. I also used kernel density functions to estimate diel patterns and activity overlap between cats and each species (Figure 4.5). The results from this analysis supported my third hypothesis that temporal overlap is substantial between cats and native mammals. These findings suggest that species interactions are not likely to be mediated by conflicting diel

patterns, but rather that temporal overlap is possible wherever there is spatial overlap. Given the inherent risks presented by interactions among cats and native mammals, excluding cats from areas with high probabilities of spatial overlap with native species would preserve the safety and welfare of both cats and native wildlife.

This analysis revealed considerable temporal overlap between cats and most mammal species. High temporal overlap at the species level is likely due to the cathemeral activity pattern displayed by cats allowing for temporal overlap with other species across the entire diel period regardless of those individual species' diel patterns. Individual cats are not continuously active, but the collective cathemeral pattern is achieved by staggered active periods among individuals (Oliveira-Santos et al. 2013; Bennett et al. 2021; Vanek et al. 2021). Although this study examined the collective activity pattern of cats, management efforts may benefit from future research which examines how these activity patterns differ across the urban landscape and correlate with landscape characteristics (Gallo et al. 2022). Because the species-level opportunity for temporal overlap is relatively indiscriminate, opposing diel periods between cats and other mammal species cannot be relied upon to predict interactions between cats and wildlife. Rather, spatial overlap may prove more insightful since cats (as a species) can be considered as constantly active wherever they occur across the urban landscape.

The spatial distribution of cats was not associated with any variables at the large spatial scale, indicating that the distribution of cats is primarily influenced by smaller-scale landscape features. At the medium and small spatial scales, cats demonstrated negative associations with open water and canopy cover (natural features) but had positive associations with high human population density and low-income areas (anthropogenic features). These findings are consistent

with previous research on outdoor cats that have found free-roaming cats tend to stay within approximately 100 m of their home and spend most of their time (>90%) in built environments (Gehrt et al. 2013; Doherty et al. 2015; Cove et al. 2018; Kays et al. 2020; Cove et al. 2023). These results further support the notion that humans influence where cats are found in urban areas rather than habitat availability alone (Doherty et al. 2015).

Since humans heavily influence the spatial distribution of cats, humans also determine the risks faced by cats and the risks that cats impose on native wildlife – signifying that actions can be taken to mitigate these bidirectional risks. Prohibiting the release (e.g., TNR) or subsidization (e.g., feeding) of cats in areas where spatial overlap with vector species is high may reduce the risk of disease transmission (Gerhold and Jessup 2013; Theimer et al. 2015). Likewise, limiting cats from areas of high spatial overlap with native prey species would likely reduce mortality from cats (Seymour et al. 2020). Environmental characteristics which correlate with species-specific habitat use can offer insight regarding potential spatial overlap, and thus inform management practices which reduce cat-wildlife interactions.

I found that in most cases, native mammal species exhibited the opposite habitat requirements compared to cats. While cats had a negative association with canopy cover and water at the small and medium scales, all native species except groundhog and white-footed mouse exhibited positive responses to canopy cover, and red fox and racoon had a positive response to water at the same scales. Conversely, cats had a higher probability of occupancy in areas of high human population density at the smallest spatial scale, yet groundhog, red fox, and raccoon had a negative response to human population density at that same scale. These divergent habitat relationships suggest that cats and native mammals can be spatially separated in the urban

environment if cat population management is considerate of these differences and prohibits cats near favorable wildlife habitat.

The risk of disease transmission between cats and wildlife is still possible regardless of spatial (e.g., *transmission of toxoplasmosis to other ecosystems via runoff*; Conrad et al., 2005) or temporal (e.g., *transmission of toxoplasmosis via fecal oocytes*; Davis et al., 2018) overlap, but is most apparent when both spatial and temporal overlap are achieved (Holmala and Kauhala 2009). Unlike toxoplasmosis, rabies requires physical interaction in order to be transmitted (Beran and Frith 1988). Of the three vector species included in this analysis, raccoon and red fox are the most likely to transmit rabies to cats (Carey and Mclean 1983; Jenkins et al. 1988; Blanton et al. 2010; Ma et al. 2021). The mean probabilities of spatial overlap between domestic cats and either raccoon or red fox were substantial (Figure 4.4). The notable degree of spatial overlap between cats and these species may facilitate routes of transmission between the species, and subsequently to humans (Roseveare et al. 2009; Keesing and Ostfeld 2021), bearing troubling implications for both public health and animal welfare.

Vaccination of animals significantly reduces the risk of disease transmission throughout a community (Roebling et al. 2014; Pieracci et al. 2019), but is not a reliable means of stopping transmission among free-roaming cats. Cat population control efforts, such as TNR, often vaccinate cats prior to their release (e.g., Kreisler et al., 2019). However, cats enrolled in TNR programs are rarely trapped more than once, allowing some vaccines to expire within their lifetime (Roebling et al. 2014). Furthermore, herd immunity cannot be achieved if the transmission rate exceeds the vaccination rate, which is often the case for TNR programs (Roebling et al. 2014). Since vaccination of free-roaming cats does not reliably inhibit disease

transmission, mitigation strategies must rely on the disruption of transmission via restricting contact between cats and common vectors (Beran and Frith 1988; Roebling et al. 2014). Management practices that restrict free-roaming cats from areas where such contact is probable (areas of spatial overlap) can achieve such disruption (Roebling et al. 2014).

The risk of zoonotic disease transmission is further amplified by biodiversity loss (Jones et al. 2008; Johnson et al. 2020; Keesing and Ostfeld 2021), such as that attributed to free-roaming cats (Loss et al. 2013; Loyd et al. 2013; Doherty et al. 2016; Loss and Marra 2017). Thus, native biodiversity would benefit from management that simultaneously seeks to preserve habitat and remove non-native predators such as free-roaming cats from habitat patches. Yet, these efforts could be thwarted by cats living outside of, but still able to access, those habitat patches. My study found that spatial overlap between cats and prey was relatively limited due to divergent habitat associations. However, cats are known to have higher rates of predation at forest edges (Kays and DeWan 2006; Herrera, M.V. Cove, et al. 2022; Pirie et al. 2022). Location-specific cat management policies that minimize free-roaming cats based on the probability of species overlap might address this concern by limiting cat populations in habitat-adjacent areas where the probability of overlap is still relatively high.

This study identifies landscape variables that contribute to the occupancy of several native mammal species in urban areas. The results vary by species and scale, but broadly indicate that wildlife species are primarily driven by habitat availability (canopy cover and access to water), while free-roaming domestic cats display inverse associations with habitat availability and respond positively to anthropogenic variables (high human population density and low socioeconomics). Furthermore, this study suggests that cats are active, at the population level,

across the entire diel period. Thus, if a wildlife species overlaps with cats spatially, it also overlaps with cats temporally to some degree. Free-roaming cat management programs and public health programs alike would benefit from the explicit consideration of potential species overlap across the landscape. Since temporal overlap is ubiquitous, management strategies should focus on spatially separating cats from wildlife, and thereby reduce risks to both populations. While such risks can be avoided altogether by keeping cats indoors — until that goal is realized — removing or excluding cats from areas with high probabilities of spatial overlap with various wildlife species would provide an intermediate solution that simultaneously protects biodiversity and the well-being of domestic cats.

Chapter 5: Prey selection and predation behavior of free-roaming domestic cats (*Felis catus*) in an urban ecosystem: implications for urban cat management

5.1 Introduction

Free-roaming domestic cats (*Felis catus;* hereafter 'cats') are both common and found at high densities in urban areas worldwide (Gehrt et al. 2013; Legge et al. 2017; Hansen et al. 2018). Cats with outdoor access are subjected to numerous risks, including possible vehicle collisions (Rochlitz 2003), heightened exposure to zoonotic disease (Roseveare et al. 2009; Gehrt et al. 2013), exposure to toxins (Berny et al. 2010; Tan et al. 2020), increased potential for abuse (Gomes et al. 2021), and possible predation by native predator species (Kays et al. 2015; Larson et al. 2020; Tan et al. 2020). Similarly, cats pose a risk to wildlife through the transfer of zoonotic disease (Lehrer et al. 2010) and direct predation (Loss et al. 2013; Loyd et al. 2013; Cove et al. 2018). Despite these risks, the management of free-roaming cat populations is often controversial (Crawford et al. 2019; Wolf et al. 2019; Calver et al. 2020; Read et al. 2020).

Numerous stakeholders share an interest in free-roaming cats, resulting in a diverse and nuanced spectrum of proposed management solutions ranging from complete tolerance of outdoor cats to population control to euthanasia. Although sentiments vary internationally (Hall et al. 2016; Foreman-Worsley et al. 2021), organizations in the United States that advocate for the welfare of domestic animals largely prefer management options such as Trap-Neuter-Return (hereafter, 'TNR') where cats are allowed to remain outdoors, but are surgically sterilized and unable to reproduce (Boone et al. 2019). Veterinary professionals also tend to favor TNR, but not overwhelmingly (Jessup 2004; Sherwood et al. 2019). Some cat owners view cats' outdoor

access as integral to the cat's welfare (Crowley et al. 2019), and similarly prefer management options like TNR that provide sterilized cats some degree of caretaking from humans while still living outdoors (Loyd and Hernandez 2012; Parsons et al. 2018; Crowley et al. 2019). Conservationists and advocates for native animal welfare, on the other hand, argue that the ecological impact of predation by cats is too great to justify their outdoor access (Calver et al. 2011; Loss et al. 2013; Crawford et al. 2019) and often recommend the complete banning of outdoor cats or fines for unrestrained cats (Calver et al. 2011; Loss and Marra 2017). Given disagreements between stakeholders, comprehensive management decisions are often delayed or unrealized (Wald et al. 2013), and this may be, in part, because stakeholders tend to focus on all-or-nothing decisions rather than shared goals such as improved animal welfare and/or pest management (Wald et al. 2013). A multi-angled and collaborative approach to free-roaming cat management may circumvent these entrenchments and will likely be integral to reducing the impact of cats on native wildlife. Here I assess environmental factors that influence predation behavior of cats and recommend data-driven and achievable approaches to free-roaming cat management in an urban area.

As obligate carnivores, cats prove efficient hunters of small-bodied vertebrates (Bradshaw 2006) and are often used as a biological control for pest management, especially against non-native rodents (Crowley et al. 2019; Foreman-Worsley et al. 2021). While cats may be known for their predation of non-native rats, most studies conclude that such predation is relatively rare and is unlikely to suppress rat populations (Glass et al. 2009; Parsons et al. 2018). Instead, cats prefer smaller (<250g) prey items such as non-native house mice (*Mus musculus*) and other small-bodied species like native rodents, songbirds, butterflies, and reptiles (Childs 1986; Loss et al. 2013; Loyd et al. 2013; Parsons et al. 2018; Fleming et al. 2020). In a

comprehensive review, however, Loss et al. (2013) found that the predation of non-native mice and rats by domestic cats increased with urbanization. Since a cat's diet is proportional to local prey availability (van Heezik et al. 2010; Kutt 2012; Krauze-Gryz et al. 2017), it follows that cats within less biodiverse urban areas may prey more frequently on non-native species, and potentially provide a service by preying on non-native rodents to some extent (van Heezik et al. 2010). If true, management approaches may benefit from focusing their efforts on reducing cat populations in more ecologically sensitive areas where the predation of native fauna is more prevalent (Loss and Marra 2017). Such an approach would take into consideration a cat's potential to control non-native species, while reducing the probability of predation on native species.

The implementation of cat exclusion zones around areas of ecological concern has been one approach to location-specific cat management and has been implemented to reduce the risk of biodiversity loss (e.g., Lilith et al., 2008). This approach allows free-roaming cat programs (e.g., TNR programs and sanctioned cat care) to operate in areas with a low probability of impact on native species (Lilith et al. 2008; Metsers et al. 2010). Cat exclusion buffer zones have traditionally been drawn around nature reserves using only the average home range size for cats as a buffer distance (Lilith et al. 2008; Metsers et al. 2010). This approach assumes that native wildlife are constrained to the reserve boundaries, and that variation in cat roaming behavior is minimal. However, in urban areas, many native species are found beyond the borders of green spaces (Herrera, Michael V. Cove, et al. 2022), and variation in cat roaming behavior can be substantial (Metsers et al. 2010; Kays et al. 2020). Designating buffer zones based on biological aspects of cat predation rather than administrative boundaries may facilitate more impactful cat management policies.

The goal of this study was to investigate the spatial drivers of predation by free-roaming cats in Washington, DC, USA, and propose location-specific management options based on my findings. My specific research questions were (1) do habitat characteristics and supplemental feeding correlate with predation events by cats?, (2) do cats within a TNR program have lower predation rates?, and (3) what variables influence prey selection (native vs. non-native prey species)? Since cats are known to hunt regardless of whether or not they are sterilized (e.g., Castillo and Clarke, 2003), and cat populations tend to congregate where there is access to supplemental food (e.g., Cove et al., 2018; Kays and DeWan, 2006), I hypothesized that overall predation would not be impacted by a cat's inclusion in a TNR program, but that overall predation rates would be highest where supplemental food was most abundant. I also hypothesized that the composition of prey species would reflect their availability across the landscape (Krauze-Gryz et al. 2017), with predation of native species being greatest near forested areas and predation of non-native species being greatest in more developed areas. I used these results to develop cat-exclusionary buffer zones that are based on the behavior of cats. The findings provide biologically relevant information about cat predation that can inform free-roaming cat management in urban areas.

5.2 Methods

5.2.1 Study area

I conducted this study in Washington, DC, which is the sixth largest metropolitan area in the US, with a population of approximately 705,750 residents (~4,466 people per km^2; United States Census Bureau, 2020). The city boundary resides at the confluence of the Potomac and Anacostia Rivers (Ossi et al. 2015) in the ancestral homeland of the Nacochtank (also called

Anacostan) people, and later the Piscataway people (Tayac 2014). The climate is temperate/tropical with an average of 110 cm of annual precipitation and an average summer and winter temperature of 21.6 °C and 6.9 °C, respectively (US National Oceanic and Atmospheric Administration 2024). Despite intense development, approximately 22% of the city is public park. Approximately half of the parkland is forested and contains an assemblage of oaks (*Quercus spp.*), maples (*Acer spp.*), and American beech (*Fagus grandifolia*), consistent with Northeastern upland forests (Ossi et al. 2015).

5.2.2 Data collection

Reconyx HyperFire 2 remotely-triggered trail cameras (Reconyx Inc., 3828 Creekside Ln, Ste 2, Holmen, WI 54636) were deployed at 1,530 sampling sites across Washington, DC, as part of the DC Cat Count project (Herrera et al. 2021). Sampling site locations were distributed across the city and were roughly proportionate to the city's socioeconomic stratification (low, medium, and high median household income) and landcover classifications (forested, moderate development, high development). Sampling sites included private residences and institutions (n = 441), public greenspaces (n = 796), alleys (n = 265), and sidewalks (n = 28) within each income-landcover stratification (high income-forested = 11%, medium income-forested = 9%, low income-forested = 2%, high income-moderate development = 8%, medium income-moderate development = 30%, low income-moderate development = 12%, high income-high development = 1%, medium income-high development = 21%, low income-high development = 6%).

Camera deployments occurred between September-December 2018 (n = 192), April 2019-January 2020 (n = 867), and June-October 2020 (n = 471). At each sampling site one camera was continuously active for 15 consecutive days, after which the site was not sampled

again (one sampling period per site). Cameras were affixed to a solid substrate at a height of <0.5-m using a nylon strap and lock and aimed at a probable corridor of animal movement (e.g. game trails, fence lines, alley). Cameras were set to take five consecutive photographs with no delay period between each camera trigger. See Herrera, et al. (2021) for additional study design details.

5.2.3 Data processing

Photos collected from each camera underwent a multi-stage review process to identify each animal to species and were uploaded to the eMammal photo repository (McShea et al., 2016; *see also*: http://emammal.si.edu). Photos taken in rapid succession (<1 minute apart) were considered a single observation. During photo review, animals were also inspected for prey items. If an animal was determined to be carrying a prey item, it was assumed to be a predation event and both the predator and prey species were recorded. I then classified each prey species into native or non-native categories. Brown rat (*Rattus norvegicus*), house mouse (*Mus musculus*), and European starling (*Sturnus vulgaris*) were classified as non-native species. All other identifiable prey items were classified as native species. Prey that were not identifiable to species were recorded as 'unknown animal', 'unknown bird', or 'unknown rodent' and were included in analyses investigating overall predation rates, but excluded from analyses that considered whether a species was native or non-native. These methods likely yield a conservative estimate of predation frequency since predators often consume their prey on-site rather than transport it (Parsons et al. 2018; Windell et al. 2019). Additionally, predation events from photographs may be biased towards larger species as smaller species are harder to see in the photos. It is also possible that prey were scavenged rather than predated, and the correlation

between predation rates and carrying rates may vary across individuals, times, and locations. However, this approach offers a non-invasive sampling method for predation events and has become increasingly common in recent years (e.g., Bowler et al., 2020; Fernandes Lima Luciano et al., 2020; Herrera and Cove, 2020; Keiter et al., 2020; Meek and Wishart, 2017; Windell et al., 2019).

Domestic cats were identified as having participated in a TNR program by the presence of a notched or flattened left ear-tip (here after an "ear-tip"). If the ear was not clearly visible, TNR status was recorded as 'unknown' unless the individual cat was otherwise identifiable and known to have been sterilized (e.g., previous photos of the same individual). Although an ear-tip is indicative that a cat has been sterilized, the lack of an ear-tip does not imply that sterilization has not taken place, as this is not standard practice for owned pet cats. I was not able to identify the sex or age of individuals, as sterilization often impacts physical development and sex-driven characteristics such that they often cannot be identified in photographs.

5.2.4 Independent variables

Feeding location density was calculated based on responses to a city-wide household survey pertaining to owned cats, which was administered electronically as part of the DC Cat Count (Gramza & Flockhart *In Review*). Any cat was considered to be owned if it was fed by someone at least once per week, regardless of indoor or outdoor status. Respondents were asked 'what type of outdoor access does your cat have?' To meet the survey's definition of being an owner of a free-roaming domestic cat, the respondent must feed at least one cat outdoors at least once per week. The number of respondents that answered 'outdoors always' were retained and considered to be a cat feeding location. These responses are not specific to managed colonies of

free-roaming cats nor individual pets, but rather reflect any situation in which food is supplied for consumption by cats outside the home. To maintain survey participant anonymity, responses were aggregated to 400x400-m grid cells across the entire city. Cat feeding location density (feeding locations/km^2) was calculated by summing the cell values for each grid cell that fell within a 171-m fixed-radius site buffer based on the upper estimate of the average home range size of an urban cat (area = 0.092 km^2; Kays, et al. 2020) and dividing that sum by the total area of the corresponding cells. Twelve predation events occurred at three sites within grid cells that did not contain survey responses, so were instead assigned the mean feeding location density from the most adjacent grid cells.

Forest boundaries were created using a 1-m resolution landcover dataset (Chesapeake Bay Program 2023) by isolating raster cells that were classified as 'tree canopy'. Continuous adjacent cells were considered a 'patch' and patches with continuous cover greater than 0.004 km^2 and a width of at least 37-m were considered a 'forest' per the US Forest Service definition (Robertson and Mason 2016). Distance between the camera location and the nearest forest edge was calculated using the *near* tool in ArcMap 10.8 (*ESRI*, 380 New York Street, Redlands, CA 92373). Distance values were considered negative if a camera was within a forest patch.

Percent impervious surface was calculated by isolating cells from the above-mentioned 1-m resolution dataset (Chesapeake Bay Program 2023) classified as 'structures,' 'impervious surfaces,' 'impervious roads,' 'tree canopy over structures,' 'tree canopy over impervious surfaces,' and 'tree canopy over impervious roads.' These cells were then reclassified as a single 'impervious surface' category. I calculated the proportion of impervious surface within the 171-m fixed-radius home range buffer around camera locations that contained predation events.

5.2.4 Analysis

Prior to analysis, I standardized all numeric covariates by mean-centering each covariate and dividing by the standard deviation. Covariates were tested for collinearity using the Pearson correlation coefficient and found no evidence of collinearity ($r < 0.7$).

To assess whether predictor variables affected the overall predation rate of free-roaming cats, I used a negative-binomial model to assess the number of predation events as a function of each predictor variable. To account for differences in cat activity across the study area, I included the number of cat observations at each predation site as an offset term in my model. A global model with all covariates was fit and found to be over-dispersed ($\hat{c} = 1.72$); thus, justifying the negative-binomial distribution to account for overdispersion of the data. Competing models were built using all additive combinations of the four predictor variables, and a null model (n = 15 models). Models were ranked using Akaike information criterion corrected for small sample size (AIC_c) and models within 2 ΔAIC_c were considered my top models. Models were fit using the MASS package (Venables and Ripley 2002) and AIC_c values were calculated using the AICcmodavg package (Mazerolle 2023) in R version 4.0.0.

I estimated the probability of a prey item being a native species using a binomial model (native species = 1; non-native species = 0). Due to a small sample size, the competing model set was limited to univariate models of each predictor variable, and a null model (n = 5 models). I also estimated the probability of a prey item being a brown rat using a binomial model (rat = 1; non-rat = 0). All possible additive combinations of the predictor variables, and a null model, were used as the model set (n = 15 models). Models were again ranked using AIC_c and models within 2 ΔAIC_C were considered my top models.

5.2.5 Formation of buffer zones

I overlaid a 30x30-m grid on the study area, and each predictor variable was calculated for each grid cell. The top model for the probability of a prey species being native was run to estimate a probability for each grid cell and used as a measure of relative risk across the study area. Four probability thresholds were selected to represent varying levels of risk: 0%, 10%, 25%, and 50% probability that a prey item would be a native species. At each threshold, cells with probabilities at or above the threshold level were considered part of the exclusionary buffer. A secondary 170-m buffer was added to the risk buffer to account for roaming distance of cats based on the average cat home range (Kays et al. 2020). The proportion of the city encompassed by each risk threshold's buffer was calculated by dividing the terrestrial area of the buffer by the total terrestrial area of the city.

5.3 Results

I captured 33,134 observations of cats (22% of all animal observations) over 22,268 trap nights. I documented 73 instances of cats carrying a prey item ($n_{ear\ tip}$= 29, $n_{no\ ear\ tip}$ = 44) at 38 sites. Two additional predation events were documented in which it was not possible to determine if the cat had been ear-tipped; these records were not included in these analyses. Predation events from non-cat predators are described in Appendix I.

5.3.1 Total predation

The total number of cat predation events at a site was best predicted by a cat's prior participation in a TNR program (*ear-tipped* β = -0.80, 95% CI: -1.41 – -0.19) and local feeding location density (β = 0.46, 95% CI: 0.17 – 0.75; Table 5.1). While I did find a decrease in overall predation – on average – by a cat's prior participation in a TNR program, when predicted across

covariate gradients I found that the confidence intervals of ear-tipped (TNR) and non-ear-tipped cats largely overlapped each other (Figure 5.1). Feeding location density alone was the second-best model (ΔAIC_c = 1.72, β = 0.60, 95% CI: 0.29 – 0.91; Table 5.1) and the third ranked model (ΔAIC_c = 1.74; Table 5.1) consisted of TNR (*ear-tipped* β = -0.71, 95% CI: -0.96 –- -0.46), feeding location density (β = 0.45, 95% CI: 0.18 – 0.72), and distance to nearest forest (β = -0.14, 95% CI: -0.39 – 0.11; Figure 5.1).

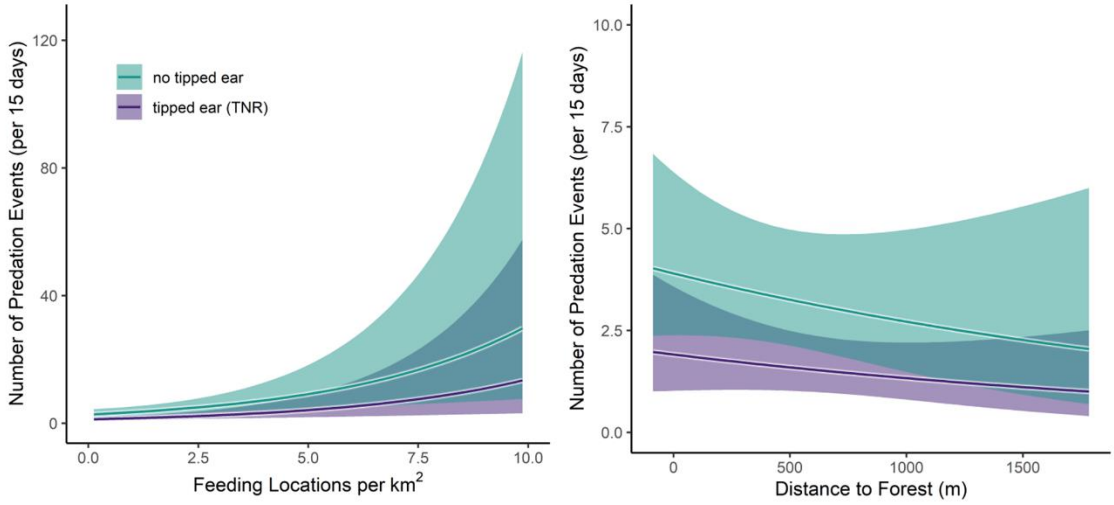


Figure 5.1 Predicted number of total predation events (solid lines) and 95% confidence interval (shaded polygons) as a function of feeding location density predicted from the top model (left) and distance to forest edge predicted from the third top model (right). When predicting across distance to forest edge, density of feeding locations was held constant at the mean density. A tipped ear indicates participation in a TNR program.

Table 5.1 Model selection results for (A) overall predation rates, (B) probability of prey being a native species, and (C) probability of prey being a brown rat. Models that received less support than the null model are not listed. Covariates are abbreviated as *food* (density of feeding locations within home range), *forest* (distance to forest edge), *TNR* (ear-tip visible), and *impervious* (percent impervious surface within home range).

Model	*k*	Log Liklihood	AIC_c	ΔAIC_c	AIC_c Weight
(A) Overall Predation					
TNR + food	4	-75.06	159.23	0.00	0.33
Food	3	-77.15	160.95	1.72	0.14
TNR + food + forest	5	-74.62	160.96	1.74	0.14
forest + food	4	-76.27	161.65	2.42	0.10
TNR + impervious + food	5	-75.01	161.74	2.51	0.09
impervious + food	4	-77.12	163.34	4.12	0.04
TNR + impervious + food + forest	6	-74.56	163.59	4.36	0.04
TNR	3	-78.51	163.67	4.44	0.04
impervious + food + forest	5	-76.16	164.04	4.81	0.03
TNR + forest	4	-77.92	164.95	5.72	0.02
TNR + impervious	4	-78.36	165.83	6.60	0.01
TNR + impervious + forest	5	-77.69	167.09	7.87	0.01
null	2	-81.63	167.57	8.35	0.01
(B) Predation of Native Species					
forest	2	-15.41	35.06	0.00	0.98
impervious	2	-19.82	43.88	8.81	0.01
food	2	-20.95	46.15	11.08	0.00
null	1	-22.32	46.73	11.67	0.00
(C) Predation of Brown Rats					
forest + food + impervious	4	-37.22	83.03	0.00	0.22
forest + impervious	3	-38.36	83.06	0.04	0.22
forest	2	-39.47	83.11	0.08	0.21
forest + food	3	-38.71	83.77	0.75	0.15
forest + impervious + TNR	4	-38.33	85.24	2.21	0.07
forest + TNR	3	-39.47	85.28	2.26	0.07
forest + food + TNR	4	-38.65	85.90	2.87	0.05
food + impervious	3	-47.17	100.69	17.66	0.00
impervious	2	-48.37	100.90	17.87	0.00
TNR + impervious	3	-48.19	102.73	19.70	0.00
food + impervious + TNR	4	-47.12	102.84	19.81	0.00
null	1	-50.43	102.91	19.89	0.00

5.3.2 Probability of preying on native species

Cats were detected transporting 8 identifiable species. Of the 73 domestic cat predation events, 11% (n = 8) of prey items were native species, 60% (n = 44) were non-native, and the remaining 29% (n = 22) could not be identified to species (Table 5.2). An additional predation event of a 9th identifiable species by a cat whose TNR status could not be determined was not included in the models, but is listed in Table 5.2. Distance to forest edge received the greatest model support for predicting whether a prey species was native or non-native (β = -2.27, 95% CI: -3.81 – -0.73; Table 5.1; Figure 5.2).

Table 5.2 Tabulated documented predation events by domestic cats regardless of TNR status in Washington, DC (2018-2020). Predation data for non-feline predators are available in Appendix F.

Prey Species		Class	Number of Predation Events
Brown Rat	*Rattus norvegicus*	Mammal	34
House Mouse	*Mus musculus*	Mammal	9
Unknown Rodent Species	NA	Mammal	6
White-footed Mouse	*Peromyscus leucopus*	Mammal	3
Eastern Gray Squirrel	*Sciurus carolinensis*	Mammal	1
Southern Flying Squirrel	*Glaucomys volans*	Mammal	1
Unknown Bird Species	NA	Bird	4
European Starling	*Sturnus vulgaris*	Bird	1
Northern Cardinal	*Cardinalis cardinalis*	Bird	1
Mourning Dove	*Zenaida macroura*	Bird	1
Yellow-throated Warbler	*Setophaga dominica*	Bird	1
Unknown Snake Species	NA	Reptile	1
Unknown Species	NA	Unknown	12

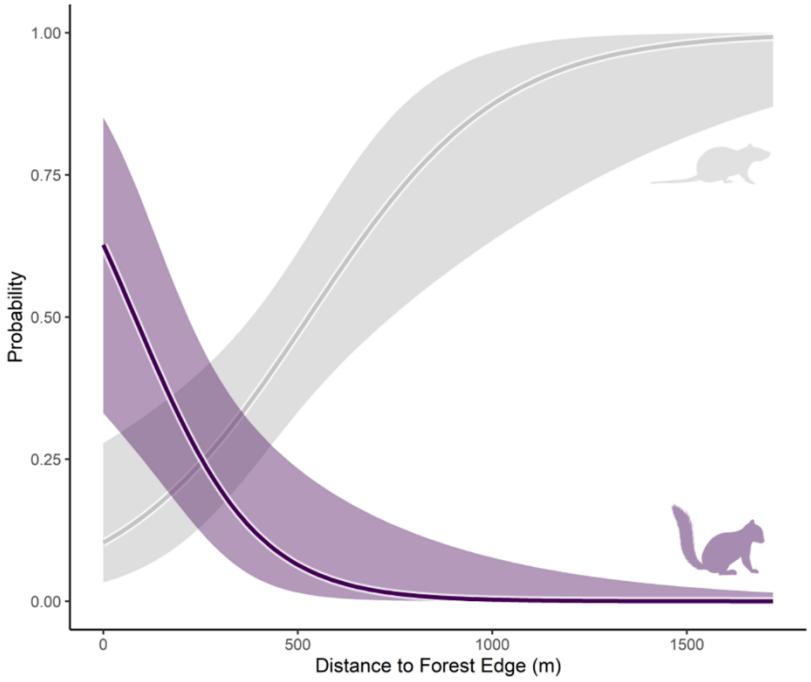


Figure 5.2 Probability (solid line) and 95% confidence interval (shaded polygon) of a prey species being native (purple) or a non-native brown rat (gray) predicted as a function of distance to forest edge. Where applicable, other covariates within the model were held constant at their mean value.

5.3.3 Predation of non-native brown rats

Thirty four of the 44 (77%) predated non-native species were brown rats (Table 5.2). Predation of rats was best explained by distance to forest ($\beta = 1.52$, 95% CI: 0.66 – 2.38; Figure 5.2), percent impervious surface ($\beta = 0.58$, 95% CI: -0.11 – 1.27) and feeding location density ($\beta = -0.46$, 95% CI: -1.08 – 0.16; Table 5.1). Models containing distance to forest edge ($\beta = 1.44$, 95% CI: 0.64 – 2.24) and impervious surface ($\Delta AIC_c = 0.04$; $\beta = 0.49$, 95% CI: -0.19 – 1.17); distance to forest edge alone ($\Delta AIC_c = 0.08$; $\beta = 1.55$, 95% CI: 0.72 – 2.38); and distance to forest edge ($\beta = 1.65$, 95% CI: 0.75 – 2.53) and feeding location density ($\Delta AIC_c = 0.75$; $\beta =$ -

0.37, 95% CI: -0.97 – 0.23) were all within 2 ΔAIC_c (Table 5.1). For all four top models, distance to forest edge was the only variable with 95% confidence intervals that did not overlap zero.

5.3.4 Buffer zones to reduce the probability that a prey species is native

I used the results of my top model explaining the predation risk for native species (distance to forest edge) to designate cat exclusion buffer zones based on 4 probability levels: 0% (808-m), 10% (416-m), 25% (254-m), and 50% (81-m), plus an additional 171-m to account for the average cat home range. The near-zero probability that a cat preys upon a native species (<1% probability threshold + home range buffer; 979-m buffer) would require excluding cats from 91.7% of the study area (Figure 5.3). A 10% (587-m), 25% (425-m), and 50% (251-m) buffer would consist of 81.0%, 73.8%, and 62.1% of the total land area, respectively (Figure 5.3).

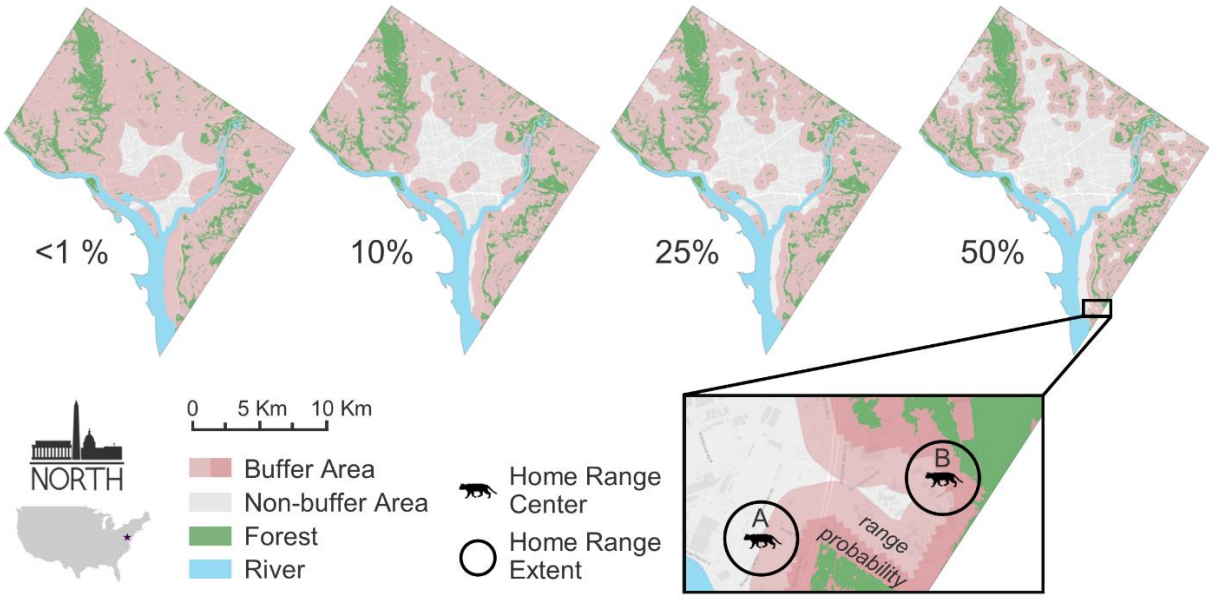


Figure 5.3 Buffer zones in Washington, DC, based on the probability of predation of native species and average cat home range. Within the inset, home range A illustrates how the additional range buffer positions the end of a cat's range at the probability threshold. Conversely, home range B does not utilize a home range buffer and the cat's range extends into the forest despite being centered at the cusp of the probability threshold.

5.4 Discussion

Biodiversity loss via predation by free-roaming domestic cats is well-documented (Doherty et al. 2016). Such loss can include the extirpation of ecosystem services and keystone species that are integral to the health of the ecosystem (Doherty et al. 2016; Cove et al. 2018; Trouwborst et al. 2020), especially in areas already subject to external stressors such as urban environments (Francis and Chadwick 2015; Trouwborst et al. 2020). While predation by cats may be the motivation for many population management decisions (e.g, Calver et al., 2011), predatory behavior is often not an explicit consideration in the formation of such decisions (Longcore et al. 2009), possibly due to a scarcity of data pertaining to predatory behavior across urban landscapes. By implementing location-specific management decisions based on predation behavior, the impact of cats on native biodiversity could be notably reduced. This study found that feeding location density and TNR status were the strongest predictors of local predation rates by cats. Furthermore, I found that the probability of a prey species being native increased closer to forest edges, and the probability of a prey species being a brown rat increased as distance to forest edge increased. These findings can inform free-roaming cat management that protects native wildlife without relying on policies that are unlikely to be implemented at a large scale such as total bans on cats.

Supplemental feeding of cats is often conducted to satiate a cat's drive to hunt (Robertson 2008; Cecchetti et al. 2021). However, most studies conclude that cats receiving subsidized food

continue to prey upon native wildlife (Castillo and Clarke 2003; Kays and DeWan 2006; Loyd et al. 2013; Cove et al. 2018). Furthermore, supplemental food reduces the territoriality of individual cats, allowing cat populations to persist at greater densities (Warner 1985; Kays and DeWan 2006; Tennent and Downs 2008), and presumably attracts rodents and other scavenging prey species (Hawkins et al. 1999). These unintended consequences of supplemental food potentially amplify population-level predation rates (Kays et al. 2020). This analysis found that cat feeding location density had a positive relationship with the number of predation events (Table 5.1). Although TNR status was also included in two of the three top models, the 95% confidence intervals of ear-tipped and non-ear-tipped cats largely overlapped (Figure 5.1), indicating a non-significant difference between the predation rates of these two sub-populations. Considered together, these findings support claims that subsidized populations of cats continue to have an adverse effect on local wildlife regardless of whether they are sterilized or cared for (e.g., Castillo and Clarke, 2003; Cove et al., 2018; Kays and DeWan, 2006; Longcore et al., 2009).

Cat management decisions to preserve biodiversity would benefit from considering the spatial location of outdoor feeding sites. Currently, other municipalities may find it difficult to enact these management recommendations since feeding locations are often run by individuals and their locations are not readily known (Finkler et al. 2011). I recommend that stakeholders work together to document and share data on free-roaming cat feeding locations, while ensuring the privacy of individuals who feed cats. Such an initiative would provide practitioners with the data necessary to better manage cat populations and minimize their predation on native wildlife.

Despite their reputation for suppressing rat populations, cats often select smaller and easier-to-catch prey in lieu of rats when possible (Childs 1986; Glass et al. 2009). However, cats are opportunistic generalists, and their prey composition is generally proportionate to local prey availability (Kutt 2012; Krauze-Gryz et al. 2017). My study found that the probability of rat predation increases with distance to the forest edge (Figure 5.2), presumably as a function of greater rat availability in the more urbanized matrix (Loss et al. 2013; Feng and Himsworth 2014). Conversely, the probability of a prey species being native had an inverse relationship with distance to forest edge (Figure 5.2). Since prey selection was greatly influenced by the degree of urbanization (i.e., impervious cover) and the distance to an urban forest, the predation of native species may be reduced by limiting free-roaming cats to developed areas where native species are less common (*but see also:* van Heezik et al., 2010).

My recommendations are based on the nature of predation rather than solely on administrative park boundaries, or the average roaming distance of cats, as previously reported (Lilith et al. 2008; Metsers et al. 2010). However, roaming distances are important to consider. For example, if the center of a cat's home range is located at the boundary of a risk threshold buffer, the cat's home range can extend roughly 170-m past this threshold and into areas that have a greater probability of native predation (Figure 5.3). Therefore, I recommend adding the average home range of an urban cat to the risk threshold buffers (home range + buffer distance). This analysis indicates that a buffer zone of 979-m (171-m home range + 808-m exclusion buffer) from forested areas would likely achieve near-zero probability (<1%) of predation of native species. Alternative buffer widths based on the probability of native predation and cat home range include 587-m (10% probability of preying on native species), 425-m (25% probability of preying on native species), and 251-m (50% probability of preying on native

species) from forest edges (Figure 5.3). I believe that a 25% probability risk threshold would be an attractive recommendation for multiple parties. This value is well below chance for prey being a native species and the threshold occurs at the approximate distance from the forest edge in which the probability of a cat preying upon a non-native brown rat becomes greater than the probability of a cat preying upon native wildlife (Figure 5.2).

Once local stakeholders agree on an acceptable buffer size, I recommend communities use these buffers as the basis for location-specific management policies that will ultimately remove the local population. Examples of such policies include, but are not limited to, implementing any of the following within the buffer area: issuing fines to pet owners who allow their cats to roam (Selby et al. 1979), prohibiting the feeding of outdoor cats (Hawkins et al. 1999), establishing a cat curfew (Lilith et al. 2010; Metsers et al. 2010), targeted removal of free-roaming cats (Boone et al. 2019), or banning cats altogether (Metsers et al. 2010). Because of differences in stakeholder perceptions, local geography and ecology, access to funding, and means of enforcement, a universal solution is not possible. As such, stakeholders should work together to determine the policies best suited for their community. Additionally, I advocate that all stakeholders involved in the formation of these policies work to jointly communicate and implement policies to avoid polarization.

Biodiversity loss from non-native predators is a pressing environmental issue compounded by habitat loss and fragmentation (Doherty et al. 2016). The ecological loss inflicted by cats is well-documented (Loss et al. 2013). While some non-native species are relatively self-sufficient and are largely beyond human control, cats pose a unique situation in which their continued persistence on the landscape can be largely attributed to human actions

(Finkler et al. 2011; Doherty et al. 2015). Professionals across relevant fields largely agree that cats face and impose risks when outdoors, however proposed management actions differ (Wald et al. 2013; Leong et al. 2018; Sherwood et al. 2019; Foreman-Worsley et al. 2021). Here I present data-driven management recommendations with the goal of protecting areas of ecological concern rather than uniformly attempting to preserve the entire urban landscape. I believe that such a paradigm shift continues to satisfy the goals of most relevant stakeholders and offers a collaborative approach to free-roaming cat management.

5.5 Conclusions

My analysis suggests that predation by free-roaming domestic cats is highest when supplemental food is abundant, and that the probability of a cat preying upon native species increases closer to forest edges. I contend that buffer zones based on a combination of probability of native species predation and cat home range will serve as a reasonable approach to urban free-roaming cat management. Since the probability of native predation increases with proximity to forest edges, and greater access to supplemental food increases local predation by populations of free-roaming cats, I recommend (1) that acceptable probabilities of native predation be agreed upon by local stakeholders and (2) management that ultimately removes the local free-roaming cat population within a distance from forests that meet those probability thresholds. While these measures may reduce the risk of predation of native species, the risk to native species will only be eliminated by keeping cats indoors.

Chapter 6: Nature viewed through a kaleidoscope: An updated framework of ecosystem regulation

6.1 Introduction

The ecosystem concept is intentionally inclusive. The idea considers all actors – biotic and abiotic alike – and their interactions. Despite this wholistic idea, ecologists often divide ecosystems based on their perceived regulatory factors. In reality, ecosystems are not exclusively governed by either top-down or bottom-up forces, but are instead influenced by a balance of the two (Hunter and Price 1992). Take, for instance, the bison-prairie system (*Bison bison*). While the bison needs the prairie for sustenance, the act of grazing alters the composition of the very plants it relies on (Ratajczak et al. 2022). The bison requires the grassland to persist, but the grassland requires the bison to thrive. Under the traditional top-down/bottom-up framework, such a system would be attributed to either the bison or the grasses rather than recognizing their mutual contributions. In this way, reliance on the top-down/bottom-up paradigm to understand ecosystem regulation is misleading. Ecosystems are managed based on an understanding of the actors present and their relations. As a result, management decisions can be greatly influenced by whether the system is thought to be governed by top-down or bottom-up forces (Kay 1998; Turkington 2009). Management that is solely based on top-down regulation often seeks to restore or support dominant predators on the landscape (e.g., reintroduction of wolves to Yellowstone National Park; Laundré et al. 2001), whereas management based on bottom-up regulation often seek to restore or support native habitats (e.g., dune construction at Prime Hook National Wildlife Refuge; Stevens and Trembanis 2012). Like this bison and the prairie, conducting either top-down or bottom-up management contributes to an asymmetrical ecosystem that, in reality, requires both forms of regulation to flourish. Supporting one form of regulation over the other

will prompt change in the system, ultimately producing an outcome that is different than what it would have been without human intervention.

The role that humans play in regulating ecosystems is often overlooked or ignored in traditional top-down/bottom-up studies. Human intervention has long been recognized as a feature of ecosystem regulation. From indigenous land management practices spanning thousands of years (McCann 1999), to pervasive global climate change (Weiskopf et al. 2020), humans have long exercised their influence over ecosystems with stunning efficiency (Albuquerque et al. 2018). Today, the role of humans has become so widely recognized that scholars have argued that we have entered a new geologic period in which humans are the primary driver of geologic change (Lewis and Maslin 2015; *but see also* Witze 2024). Despite a long history of environmental manipulation by humans (Hunter 1996; Periman 2006) and an established recognition of the importance of considering this manipulation in ecological thought (Pickett and McDonnell 1993), our most fundamental understanding of ecosystem regulation ignores our own omnipresent role. Throughout this dissertation, I show that humans provide an additional regulating force that transcends the traditional top-down/bottom-up mechanisms by influencing bottom-up forces in some cases, but influencing top-down forces in others.

Perhaps one reason humans are scarcely included in theoretical conceptions of ecosystem regulation is that we, like any other animal species, can be logically considered a top-down pressure without need for specific mention. This approach appears justifiable given the ample evidence for humans as global super-predators (Roopnarine 2014; Darimont et al. 2015; Lennox et al. 2022) and constructors of landscapes of fear (Smith et al. 2017; Suraci et al. 2019). Humans are, however, ecosystem engineers and our simultaneous impact on bottom-up processes is equally influential (Albuquerque et al. 2018). Humans exercise substantial control of

nutrient availability through the application of synthetic fertilizers (Malagó and Bouraoui 2021); control the hydrologic cycle through irrigation, channeling, wetland draining, and altered precipitation dynamics via global climate change (Vörösmarty and Sahagian 2000; Wu et al. 2013); create specific vegetative communities through agriculture and landscaping (Carnus et al. 2006; Leong et al. 2018); and determine the distribution of habitats through urban planning and land use policies (Langpap and Wu 2008; Fahey et al. 2012). While humans undeniably apply top-down pressure on ecosystems, we are equally responsible for much of the bottom-up regulation present across ecosystems globally.

While the colloquial top-down/bottom-up paradigm seemingly does not allow for a system to experience both forces of regulation simultaneously, this idea has in fact persisted in the ecosystem regulation literature for quite some time (Turkington 2009). Shortly after Hairston, et al. (1960) introduced the framework, it was critiqued for an over-simplification of regulatory dynamics (Murdoch 1966). The concept was eventually amended to acknowledge that regulating forces are bidirectional and thus ecosystems experience top-down and bottom-up regulation simultaneously (Hunter and Price 1992; Hunter 2001). Although theory has allowed for both forms of regulation to act in tandem, individual actors were historically assumed to exert either top-down or bottom-up regulation, but not both top-down *and* bottom-up regulation. However, recent insight into organism-mediated nutrient recycling has sparked debate as to whether herbivores, which exert top-down regulation through plant consumption, also contribute to bottom-up regulation by altering nutrient availability across the landscape via urination, decomposition, etc. (Leroux and Loreau 2015). While consensus has not yet been reached, it is at least clear that the ecological role of some actors impacts both top-down and bottom-up functions even if the actor is not directly responsible for both forces.

The traditional framework to understand ecological regulation is profound, but is not without its shortcomings. In the original framework, unidirectional regulation precipitated from bottom-up forces throughout the ecosystem to create a directional framework (Hairston et al. 1960). Upon recognition of simultaneous bottom-up and top-down forces, the framework shifted to one of centrifugal forces with ecosystem function nestled between both regulators. Here, I propose an even more expansive framework that allows both forces to directly impact each other, and which deliberately considers the unique role of both humans and time (Figure 6.1). Although generalizations are bound to oversimplify, it is my hope that this updated framework can offer a more holistic understanding of ecosystem regulation in the context of the familiar bottom-up/top-down framework.

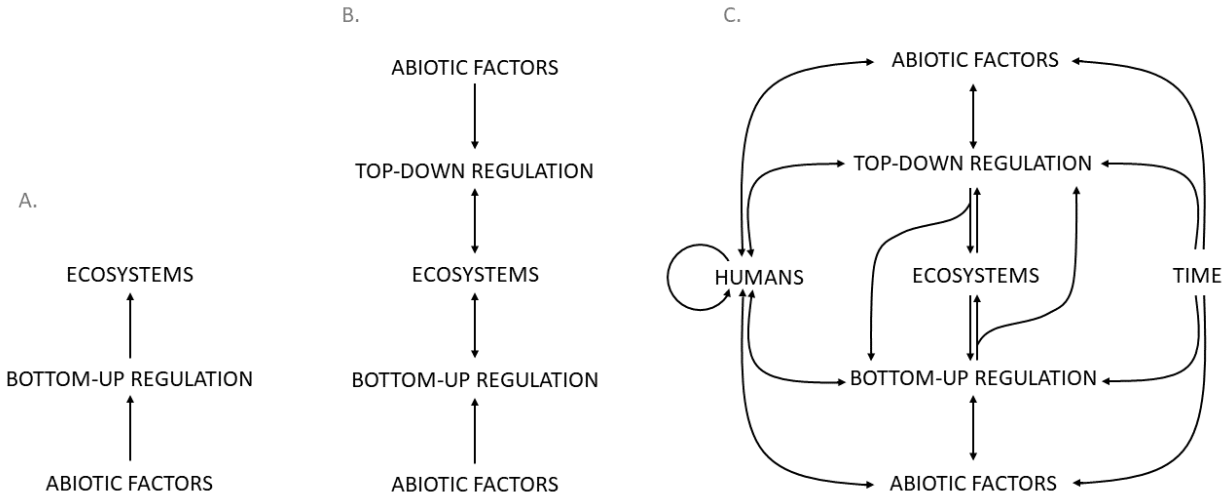


Figure 6.1 Conceptual diagrams of ecosystem regulation frameworks, including (A) an adaptation of the initial bottom-up framework presented in Hairston (1960) and visualized in Hunter and Price (1992), (B) an adaptation of the revised bottom-up/top-down framework presented and visualized in Hunter and Price (1992), and (C) a visualization of the proposed kaleidoscope framework.

6.2 Framework components

6.2.1 Abiotic conditions

In this framework, I separate abiotic forces from vegetation to allow for a more nuanced discussion of ecosystem regulation. The regulation of plants, not the ecosystem as a whole, was the focus of early iterations of the top-down/bottom-up framework (Hairston et al. 1960). As a result, plants were not included as regulating factors. Interpretations have since shifted to collectively consider both abiotic factors and plants as bottom-up forces, creating a category with inclusion criteria that is too broad to derive meaningful inference. Even under narrower inclusion criteria, the breadth of abiotic factors alone are substantial. While geomorphic properties such as nutrient cycling, hydrology, and soil chemistry undoubtably exercise substantial control over the vegetative communities that I work in (Wang et al. 2022), I did not measure these abiotic factors. Instead, I focused on abiotic factors with direct ties to animal persistence and behavior.

Abiotic factors often vary in predictable ways and form the foundation of wildlife behavior. For instance, regular daily fluctuation of light and temperature are the basis of circadian rhythms and thus underly variation in animal activity that permits niche partitioning and fosters biodiversity. In Chapter Three, I found that variation in ambient light also contributes to the expression of vigilance behavior in white-tailed deer. Ambient noise also contributes to vigilance, as well as prompts deer to form larger foraging groups. While these features are non-structural, structural features also contribute to wildlife behavior and distribution. In Chapter Four I illustrate the effect of water availability on species distributions, as well as the effect of temperature and rain on the detectability of those species. While plants and animals exploit relations to achieve greater fitness, abiotic variables have no such goals. Still, the existence of

such factors exhibits substantial pressure on organisms with cascading effects on species behavior and community composition.

6.2.2 Bottom-up regulation

Vegetation offers nutrition directly to herbivorous species, and indirectly to carnivorous species, thereby aligning it with the nutrient-minded interpretation of bottom-up resources presented in early iterations of the framework (e.g., Hairston et al. 1960). In the context of wildlife, however, I redefine bottom-up regulation as vegetative resources broadly (e.g., food, habitat, etc.). Without such resources, wildlife species have no stage on which their functions and relations can play out (Stiling and Rossi 1997; Elmhagen and Rushton 2007). As a result, wildlife fundamentally relies on bottom-up forces. This was most apparent in Chapter Two, which found that greenspace area played an outsized role on the number of bird species present. Likewise, canopy cover was a significant driver of species occupancy for seven of the nine species examined in Chapter Four. In line with the foundational literature on bottom-up/top-down regulation, my own research highlights the critical role bottom-up resources have on ecosystem form and function (Hairston et al. 1960; Stiling and Rossi 1997).

While bottom-up resources are credited for their role in establishing ecosystems, their contribution to top-down regulation is often overlooked. Predators require habitat to the same extent that herbivores do. Furthermore, prey availability is directly dependent upon vegetative resources. Because predators rely on bottom-up resources for shelter and as an indirect source of nutrition, top-down regulation is inherently dependent upon bottom-up regulation (Stiling and Rossi 1997). In Chapter Four, I found that canopy cover was a major factor governing the probability of predators and prey overlapping. Since forested habitat is largely responsible for the local species assemblage, it also influences local predation dynamics by controlling the available

prey species as seen in Chapter Five. Taken together, these results indicate that predation pressure is largely dependent on vegetation. Thus, bottom-up forces regulate ecosystems directly by providing food and shelter for herbivores, and indirectly by similarly providing shelter and fostering a prey community for predators.

6.2.3 Top-down regulation

Although top-down regulation is colloquially considered predation pressure, the traditional definition includes any resource limitation caused by an actor from a higher trophic level. As a result, herbivory constitutes top-down regulation on plants to the same extent that predation constitutes top-down regulation on animals (Hairston et al. 1960; Turkington 2009). Both forms of top-down regulation were present in Chapter Three, which investigated the degree to which the threat of predation curbed foraging behavior in white-tailed deer. Chapters Four and Five also examined predation pressure, and found that predation risk varies across the urban landscape. While urbanization has been found to reduce predation rates (Fischer et al. 2012), my results broadly show that the presence of predators still contributes to altered prey composition, distribution, and behavior in urban areas.

While I did not study the effect of top-down regulation on bottom-up resources in my dissertation research, the ties are well documented in ecological literature. Chronic herbivory has been found to have far-reaching effects by altering the age stratification and plant diversity of habitat patches (Jenkins and Howard 2021). Selective grazing and seed dispersal can similarly impact the vegetative community by opening niche space and furthering the distribution of progeny (Forbes et al. 2019). Regardless of the mechanism by which herbivory impacts bottom-up resources, such actions from herbivorous species can be moderated via population control by predators (Laundré et al. 2001; Ripple and Beschta 2012). While such control directly impacts

vegetation by reducing herbivory and seed dispersal, the abandonment of prey carcasses indirectly contributes to vegetation by returning a burst of nutrients back into the soil via decomposition (Cederholm et al. 1999). Although these well-documented mechanisms are not considered in my own work, they elucidate how top-down regulation impacts bottom-up regulation both directly and indirectly.

6.2.4 Humans

Humans exert unique pressures on ecosystems that remain absent from ecosystem regulation frameworks despite abundant research into the impact of humans on ecosystems (Pickett and McDonnell 1993; Pickett et al. 2017). Landscapes have been altered by humans for thousands of years, which has in turn influenced the species present in ecosystems (Kay 1998; McCann 1999; Swetnam et al. 1999; Lunt and Spooner 2005; Lunt and Spooner 2005; Erb et al. 2012; Fahey et al. 2012; Francis and Chadwick 2015; Lewis et al. 2015; Schmid et al. 2018; Weiskopf et al. 2020). The resulting communities adopt new dynamics to survive within their novel context, further altering ecosystems even when such systems appear undisturbed by humans (Kay 1998; Doherty et al. 2016; Miller et al. 2017; Smith et al. 2017; Parsons et al. 2019; Bonnet-Lebrun et al. 2020; Start et al. 2020). While the findings of Chapter Two are consistent with the species-area relationship, they are novel in that they highlight the importance of human planning processes in the creation habitat for wildlife. Beyond determining the local species pool, human-planned greenspaces (i.e., urban canopy cover) was found to change the distribution of species in Chapters Four and Five. Furthermore, Chapter Three connects anthropogenic noise pollution to changes in animal behavior. Together, these anthropogenic influences clearly alter bottom-up regulation in urban systems. At the same time, humans contribute to top-down regulation as well. Urban development discourages apex predators, which

created the predator-free landscape required by Chapter Three's analysis. Human factors were also found to contribute to species distributions in Chapter Four, and human actions were directly responsible for altered predation dynamics in Chapter Five.

In addition to contributing to both bottom-up and top-down ecosystem regulation, humans are themselves influenced by both forms of regulation and create an intraspecies feedback loop that further alters these dynamics. Like any other species, humans rely on bottom-up resources for food and shelter, and are influenced by climatic conditions (Guo et al. 2010; Wu et al. 2013). On the other hand, an argument can be made that humans experience frequent top-down regulation via sickness and disease (Holt and Pickering 1985; Haydon et al. 2003). Thus, humas not only contribute to ecosystem dynamics, but are themselves affected by such dynamics (Holling 2001). The impact of these human-ecosystem relations are not evenly distributed, however. Vulnerability can vary based on sociodemographic factors, creating feedback loops that privilege some and put others at an extreme disadvantage (Holifield 2001; Landrigan et al. 2010; Almassi 2021; Roberts et al. 2022). Both historical and perpetuated injustices have created landscapes that deliver environmental benefits to affluent communities (e.g., air purification and shade), while presenting disadvantaged communities with chronically adverse conditions and simultaneously limiting their capacity to respond to such conditions through systematic oppression (e.g., urban heat islands and pollution; Gaffin et al. 2008; Miranda et al. 2011; Verbeek 2019; Schell et al. 2020). Because social dynamics carry such tremendous power over how individuals affect and are affected by both bottom-up and top-down processes, humans are uniquely depicted with a self-seeking arrow in this framework (Figure 6.1). Although feedback loops are present in all components of this framework, I specifically call attention to them here because of their grave consequences and our moral obligation to address them. Using our social

power to address these inequalities will not only improve our understanding of ecological processes, but can also contribute to a more equitable world.

6.2.5 Time

While time has long been understood to impact ecological processes, it was excluded from the traditional model of ecosystem regulation (Stiling and Rossi 1997). Time inherently underlies all ecological processes. Some phenomena occur on relatively small time-scales, such as the day-long presence of dayflowers (*Commelinaceae*). Other phenomena require slightly longer timescales, such as the years-long transition from juvenile to adult in some species, or the centuries-long transition from nascent to old-growth forest. Some processes, like glaciation and continental drift, require even longer periods of time. The steady march of time has given rise to well-studied phenomenon such as phenology, ecosystem succession, extinction debt, and species accumulation (Calabrese and Fagan 2004; Ramalho and Hobbs 2012; Chang and Turner 2019; Montaña et al. 2022). In my own research, time was a significant predictor of avian community metrics in Chapter Two, was the underlying cause of the light-dark cycle measured in Chapter Three, and was inherent in the measures of sampling effort included in Chapters Four and Five. Despite the importance of considering time, it is absent from our traditional frameworks (Ramalho and Hobbs 2012). I include time in this framework in hopes that explicit consideration of time will further improve our understanding of ecosystem regulation.

6.3 Looking through the kaleidoscope

While the traditional top-down/bottom-up framework has aided our collective understanding of ecosystem regulation, it is not without its short comings. Here, I expand on the existing framework by allowing bottom-up and top-down regulation to not only influence the

ecosystem simultaneously, but also to influence each other. Furthermore, I add humans and time as additional determinants of ecosystem regulation, and allow social dynamics to mediate the relationships between humans and the environment. Throughout this chapter, I use my own dissertation research to justify these adjustments to the conventional framework.

Considered together, these adjustments act as a figurative kaleidoscope. Colorful beads, which here represent top-down regulation, tumble and cascade to create a unique pattern. Despite their power to produce striking scenes, they are held in place and consistently forced to reorganize by the tube itself, representative of bottom-up regulation. All the while, the patterns aren't visible without holding the kaleidoscope to the light — a nod to the abiotic factors further informing the ecosystem's form and function. Finally, the kaleidoscope's pattern is completed by the subtle internal mirror that casts the beads into the circular pattern of a rose window. Although the angle of the kaleidoscope's mirror keeps the viewer from seeing themself, the symbolism of self-reflection remains. Humans play an integral role in the organization of ecosystems, but our traditional ecological frameworks act as if we are absent. To truly understand ecosystems we must indeed look to nature, but we must also take a long look in the mirror.

Appendices

Appendix A. Data sources for historical greenspace analysis (Chapter 2)

Appendix A-1. Information pertaining to the maps depicting the park systems of Washington, DC, Minneapolis, MN, and Pittsburgh PA. Year ranges with an asterisk (*) denote that multiple data sources were compiled. Year ranges with an exclamation point (!) indicate that the digital shapefile contained data accurate to the year range at the time of download, but periodic upkeep may render the file irrelevant to said date range today.

Years represented	Publication year	Name	Publisher	Medium	Physical location	Available online
Washington, DC						
1905-1909	1905	Map of the city of Washington	Norris Peters Co.	Physical map	Library of Congress Geography and Map Division	Yes[1]
1910-1914	1910	Map of Washington, D.C.	Walker Lith. & Pub. Co.	Physical map	Library of Congress Geography and Map Division	Yes[2]
1915-1919	1918	Map of Washington, D.C.	Turner, Edgar D.	Physical map	Library of Congress Geography and Map Division	Yes[3]
1920-1924	1921	Map of the permanent system of highways, District of Columbia	DC Office of the Engineer Commissioner	Physical map	Library of Congress Geography and Map Division	Yes[4]
1925-1929	1926	Reservations under the jurisdiction of the office of public buildings and public parks of the National Capital: Location	DC Office of Public Buildings and Public Parks	Physical map	Library of Congress Geography and Map Division	No

		map (Revisions as of Oct. 1, 1926)				
1930-1934	1931	Reservations under the jurisdiction of the office of public buildings and public parks of the National Capital: Location map (Revisions as of Jun. 1, 1931)	DC Office of Public Buildings and Public Parks	Physical map	Library of Congress Geography and Map Division	No
1935-1939	1935	Map of the permanent system of highways, District of Columbia	DC Office of the Engineer Commissioner	Physical map	Washington D.C. Public Library System	Yes[5]
1945-1949	1945	Map of the public parks [of the] District of Columbia	United States National Park Service	Physical map	Library of Congress Geography and Map Division	No
1950-1954	1953	Washington and vicinity	United States Army Map Service & Regional Highway Planning Committee for Metropolitan Washington	Physical map	Library of Congress Geography and Map Division	Yes[6]
1955-1959	1959	District of Columbia	National Capital Planning Commission	Physical map	Library of Congress Geography and Map Division	Yes[7]
1965-1969	1965	Map of the permanent	DC Office of the Surveyor	Physical map	Library of Congress	No

		system of highways, District of Columbia			Geography and Map Division	
1975-1979	1978	Comprehensive plan for the National Capital, general land use objectives, 1970-1985	National Capital Planning Commission	Physical map	Library of Congress Geography and Map Division	Yes[8]
1980-1984	1980	Washington, D.C. transportation map	DC Department of Transportation	Physical map	Library of Congress Geography and Map Division	No
1985-1989	1989	Park system of the nation's capital and environs	United States National Park Service	Physical map	Library of Congress Geography and Map Division	Yes[9]
1990-1994	1992	Washington, D.C. transportation map	DC Department of Public Works	Physical map	Library of Congress Geography and Map Division	No
1995-1999	1998	Washington, D.C. street and visitor's guide	AAA	Physical map	Library of Congress Geography and Map Division	No
2000-2004!	2004	Existing land use	DC Office of the Chief Technology Officer	Shapefile	NA	Yes[10]
2005-2009	2005	2006 Comprehensive Plan: Existing land use maps	DC Office of Planning	PDF	NA	Yes[11]
2010-2014	2010	DC Street Map	DC Office of Planning	PDF	NA	Yes[12]
2015-2019*!	2019 2019	Parks and recreation areas	DC Office of the Chief Technology Officer	Shapefile	NA NA	Yes[13] Yes[14]

	2019	NPS land resources division boundary and tract data service Parcel lots	United States National Park Service DC Office of the Chief Technology Officer	Shapefile Shapefile	NA	Yes[15]
Minneapolis, MN						
1910-1915	1913	City of Minneapolis, 1913	F.W. Yarwood	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	Yes[16]
1920-1924	1920	City of Minneapolis	McGill-Warner Company	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	Yes[17]
1925-1929	1929	City of Minneapolis election map	Minneapolis City Clerk (Chas. C. Swanson)	Physical map	Hennepin County Library, James K Hosmer Special Collections	Yes[18]
1930-1934	1931	City of Minneapolis election map	Minneapolis City Clerk (Chas. C. Swanson)	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	No
1935-1939	1937	City of Minneapolis	McGill-Warner Co.	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	No
1940-1944	1941	Map of Greater Minneapolis compliments	Gile Letter Service	Physical map	University of Minnesota Libraries, John R.	No

		of Hotel Vendome			Borchert Map Library	
1945-1949	1947	City of Minneapolis election Map	Minneapolis City Clerk (Chas. C. Swanson)	Physical map	Hennepin County Library, James K Hosmer Special Collections	Yes[19]
1950-1954	1954	The premier street map of Minneapolis and vicinity	Geographia Map Company, Inc.	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	No
1960-1964	1960	Existing public facilities	City of Minneapolis Planning Commission	Physical map	Hennepin County Library, James K Hosmer Special Collections	Yes[20]
1965-1969	1968	1968 Twin Cities land use map	Twin Cities Metropolitan Planning Commission, (digitized in 2014 by David M. Levison and Wei Chen)	Shapefile	NA	Yes[21]
1970-1974	1971	Minneapolis St. Paul street map	Rand McNally and Company	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	No
1975-1979	1978	1978 Twin Cities land use map	Twin Cities Metropolitan Planning Commission, (digitized in 2014 by David M. Levison and Wei Chen)	Shapefile	NA	Yes[22]

1980-1984	1984	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
1985-1989	1987	Hudson's indexed map of Minneapolis and suburbs	Hudson Map Company	Physical map	University of Minnesota Libraries, John R. Borchert Map Library	No
1990-1994	1990	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
1995-1999	1997	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
2000-2004	2000	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
2005-2009	2005	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
2010-2014	2010	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
2015-2019	2016	Generalized land use - historical	Metropolitan Council	Shapefile	NA	Yes[23]
Pittsburgh, PA						
1925-1929	1926	Pincott & McNeil's Map of Greater Pittsburgh	H.C. Lippincolt	Physical map	Heinz History Center, Detre Library and Archives	No
1930-1934	1931	Automobile Club of Pittsburgh's detailed street map of Pittsburgh and environs	George F. Cram Company	Physical map	Heinz History Center, Detre Library and Archives	No
1935-1939	1938	Pittsburgh with detail maps of North Park	Gulf Refining Company	Physical map	Heinz History Center, Detre	No

		and South Park			Library and Archives	
1940-1944	1940	Street map, City of Pittsburgh	City of Pittsburgh Department of City Planning	Physical map	Heinz History Center, Detre Library and Archives	No
1945-1949	1946	Sight-seeing tour of Pittsburgh	Gulf Refining Company	Physical map	Heinz History Center, Detre Library and Archives	No
1950-1954	1952	Ideal atlas of Pittsburgh and vicinity, including map of 55 miles about Pittsburgh complete street index	Geographia map company, inc.	Physical map	Heinz History Center, Detre Library and Archives	No
1955-1959	1958	Map of the City of Pittsburgh, bicentennial edition	City of Pittsburgh Department of City Planning	Physical map	Heinz History Center, Detre Library and Archives	No
1960-1964	1962	The “Z” atlas and map of Pittsburgh, PA and Mount Oliver, PA	G. & L. Zatkovich, t/a “Z” Map Company	Physical map	Heinz History Center, Detre Library and Archives	No
1975-1979	1978	Atlas of greater Pittsburgh, including Allegheny County, parts of Washington County, Westmoreland County,	Geographia map company, inc.	Physical map	Heinz History Center, Detre Library and Archives	No

		Beaver County				
1980-1984	1981	Pittsburgh and vicinity	American Automobile Association (AAA)	Physical map	Heinz History Center, Detre Library and Archives	No
1985-1989	1988	Pittsburgh and vicinity	American Automobile Association (AAA)	Physical map	Heinz History Center, Detre Library and Archives	No
1990-1994	1993	The complete atlas of southwestern Pennsylvania Metropolitan Pittsburgh	Marshall Penn-York Company.	Physical map	Heinz History Center, Detre Library and Archives	No
2005-2009	2008	Parks and trails map	City of Pittsburgh Department of City Planning	PDF	NA (received via personal communication with City of Pittsburgh Department of City Planning)	No
2010-2014	2013	Existing open space system	City of Pittsburgh Department of City Planning	PDF	NA	Yes[24]
2015-2020	2019* !	PGHWebParks Allegheny County - Parcels	City of Pittsburgh Allegheny County/Pennsylvania Spatial Data Access	Shapefile Shapefile	NA NA	Yes[25] Yes[26]

Appendix A-2 Historical census data. Information pertaining to the population estimates of Washington, DC, Minneapolis, MN, and Pittsburgh PA, organized by census year.

Years represented*	Publication year	Publication Name	Publication Section	Table	Available online

1900 1910 1920 1930 1940 1950 1960 1970 1980	1981	1980 Census of population	Number of inhabitants, United States summary	Table 27: Rank and population of cities of 100,000 or more in 1980: 1790-1980	Yes[27]
1990 2000	2000	City and Town Postcensal Tables: 1990-2000	District of Columbia	NA	Yes[28]
			Minnesota	NA	
			Pennsylvania	NA	
2010 2020	2021	City and Town Population Totals: 2010-2020	District of Columbia	NA	Yes[29]
			Minnesota	NA	
			Pennsylvania	NA	

**Human population values were imputed for survey periods which fell in between two censuses. See methods section for more detail.*

Appendix A-3 Access to online to historical data. Hyperlinks to data available online (permalinks where possible):

1. https://lccn.loc.gov/87691449
2. https://lccn.loc.gov/87691461
3. https://lccn.loc.gov/87691479
4. https://lccn.loc.gov/80693350
5. http://hdl.handle.net/1961/dcplislandora:51
6. https://lccn.loc.gov/87693114
7. https://lccn.loc.gov/87693319
8. https://lccn.loc.gov/79694203
9. https://lccn.loc.gov/89693069
10. https://opendata.dc.gov/datasets/DCGIS::existing-land-use/about
11. https://planning.dc.gov/page/existing-land-use-maps
12. https://planning.dc.gov/node/594592
13. https://opendata.dc.gov/datasets/parks-and-recreation-areas
14. https://www.arcgis.com/home/item.html?id=c8d60ffcbf5c4030a17762fe10e81c6a
15. https://opendata.dc.gov/datasets/DCGIS::parcel-lots/about
16. http://purl.umn.edu/187162
17. http://purl.umn.edu/187164
18. https://collection.mndigital.org/catalog/mpls:1484#/image/0
19. https://collection.mndigital.org/catalog/mpls:1485#/image/0
20. https://collection.mndigital.org/catalog/mpls:1454#/image/0

21. https://hdl.handle.net/11299/162666
22. https://hdl.handle.net/11299/162667
23. https://metrocouncil.org/Data-and-Maps/Research-and-Data/Metadata/Landuse-Hist-Research.aspx
24. https://apps.pittsburghpa.gov/dcp/OpenSpacePGH%20lo%20res.pdf
25. https://pghgishub-pittsburghpa.opendata.arcgis.com/datasets/pittsburghpa::pghwebparks/about
26. https://www.pasda.psu.edu/uci/SearchResults.aspx?Keyword=parcels
27. https://www2.census.gov/prod2/decennial/documents/1980/1980censusofpopu8011uns_bw.pdf
28. https://www.census.gov/data/tables/time-series/demo/popest/2000-subcounties-eval-estimates.html
29. https://www.census.gov/programs-surveys/popest/technical-documentation/research/evaluation-estimates/2020-evaluation-estimates/2010s-cities-and-towns-total.html

Appendix B. Potential avian traits (Chapter 2)

Appendix B-1. Potential trait variables considered for analysis of urban birds. Traits were ultimately selected for parsimony and ease of interpretation.

Variable	Justification	Metric	Data type	Data source	Used in final analysis?
Diet	Specific diet items contribute to ecological niche and have cascading implications on ecosystem	Consumption of invertebrates	Proportion of diet in increments of 10 (integer)	Diet.Inv (Elton)	used to calculated diet breadth
		Consumption of endotherms	Proportion of diet in increments of 10 (integer)	Diet.Vend (Elton)	used to calculated diet breadth
		Consumption of ectotherms	Proportion of diet in increments of 10 (integer)	Diet.Vect (Elton)	used to calculated diet breadth
		Consumption of fish	Proportion of diet in increments of 10 (integer)	Diet.Vfish (Elton)	used to calculated diet breadth
		Consumption of unknown material	Proportion of diet in increments of 10 (integer)	Diet.Vunk (Elton)	used to calculated diet breadth
		Consumption of scavenged material	Proportion of diet in increments of 10 (integer)	Diet.Scav (Elton)	used to calculated diet breadth
		Consumption of fruit	Proportion of diet in increments of 10 (integer)	Diet.Fruit (Elton)	used to calculated diet breadth
		Consumption of nectar	Proportion of diet in increments	Diet.Nect (Elton)	used to calculated diet breadth

			of 10 (integer)		
		Consumption of seeds	Proportion of diet in increments of 10 (integer)	Diet.Seed (Elton)	used to calculated diet breadth
		Consumption of other plant material	Proportion of diet in increments of 10 (integer)	Diet.PlantO (Elton)	used to calculated diet breadth
		Diet breadth	Number of diet categories in Elton Traits greater than 0 (integer)	Number of diet categories in Elton Traits greater than 0 (integer)	yes
Behavior	Foraging behavior elicits specific species-environment interactions that contribute to the species' ecological role, and might be also limited by habitat loss in urban areas	Foraging behavior: below water	Proportion of foraging strategy in increments of 10 (integer)	ForSrat.watbelowsurf (Elton)	used to calculated foraging breadth
		Foraging behavior: water surface	Proportion of foraging strategy in increments of 10 (integer)	ForStrat.watarroundsurf (Elton)	used to calculated foraging breadth
		Foraging behavior: ground	Proportion of foraging strategy in increments of 10 (integer)	ForStrat.ground (Elton)	used to calculated foraging breadth
		Foraging behavior: understory	Proportion of foraging strategy in increments of 10 (integer)	ForStrat.understory (Elton)	used to calculated foraging breadth

		Foraging behavior: mid-canopy	Proportion of foraging strategy in increments of 10 (integer)	ForStrat.midhigh (Elton)	used to calculated foraging breadth
		Foraging behavior: canopy	Proportion of foraging strategy in increments of 10 (integer)	ForStrat.canopy (Elton)	used to calculated foraging breadth
		Foraging behavior: aerial	Proportion of foraging strategy in increments of 10 (integer)	ForStrat.aerial (Elton)	used to calculated foraging breadth
		Foraging breadth	Number of foraging categories in Elton Traits greater than 0 (integer)	Number of diet categories in Elton Traits greater than 0 (integer)	yes
	Migratory species will have different resource needs which may be altered by habitat availability in urban areas	Migration	Categorical, consisting of: migratory, partially migratory, sedentary	Migration (bird behavior)	no
	Territoriality might not be as prevalent in urban areas where habitat is limited and resources concentrated	Territoriality	Categorical, consisting of: none, strong, weak	Territoriality (bird behavior)	no
	Nesting areas in cities greatly differ from those	Nest Placement	Categorical, consisting of: cavity,	Nest Placement (bird behavior)	no

	in non-urban areas		exposed elevated, exposed ground		
	Nocturnal species can avoid humans, reducing anthropogenic pressure	Nocturnal species can avoid humans, reducing anthropogenic pressure	Binary (1 = yes, 0 = no)	Nocturnal (Elton)	no
Mobility	Urban areas have smaller habitats, so species with larger ranges might not be able to persist. Alternatively, large-ranged birds might out perform since they can obtain resources from habitat patches across the city	Range Size	Continuous	Log Range Size (bird behavior)	yes
	Leg dimensions influence mobility	Tarsus length	Continuous	Tarsus.length (Avonet)	No
	Wing dimensions influence mobility	Wing length	Continuous	Wing.length (Avonet)	no
Morphology	General indicator of body size, small species might fare better given anthropogenic pressures	Body Mass	Continuous	BodyMass.Value (Elton)	yes
	General indicator of body size	Tail length	Continuous	Tail.length (Avonet)	no
Fecundity	r-selected species are hypothesized to	Clutch size	Continuous (log-	LogClutchSize (bird behavior)	yes

	do better in dynamic/disturbed environments such as cities		transofmred)		

Appendix C. Stratification of sampling sites (Chapter 3)

Appendix C-1. Stratification categories used to select sampling sites for anti-predator behavioral analysis. Sites were drawn from a larger, long-term array of camera traps.

Classification	Percent Impervious Surface	Distance to roadway (m)	Number of sites selected
Low impervious & far from roadway	<= 18%	>= 1400	4
Low impervious & moderate distance from roadway	<= 18%	701 - 1399	4
Low impervious & close to roadway	<= 18%	<= 700 m	4
Moderate impervious & far from roadway	18.01 – 35.99%	>= 1400	3
Moderate impervious & moderate distance from roadway	18.01 – 35.99%	701 - 1399	4
Moderate impervious & close to roadway	18.01 – 35.99%	<= 700 m	5
High impervious & moderate distance from roadway	>= 36%	701 - 1399	2
High impervious & close to roadway	>= 36%	<= 700 m	4

Appendix D. Stratification of sampling sites (Chapter 3)

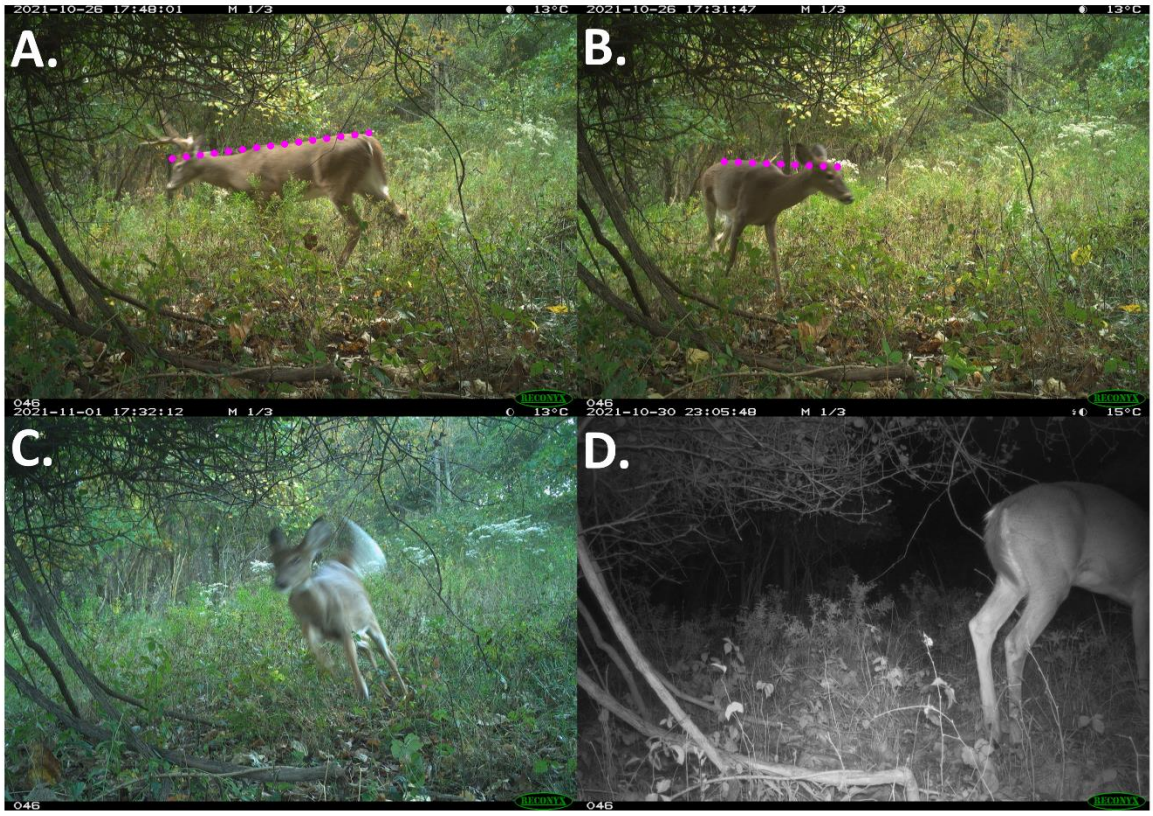
Appendix D-1. Example of a photograph of a vigilant deer. Note that the deer's head is clearly held above the body, visualized here as a dotted pink line.



Appendix D-2. Example of a photograph of a non-vigilant deer. Note that the deer's head is clearly held below the body, visualized here as a dotted pink line.



Appendix D-3. Examples of photographs of deer that were excluded from analysis. Reasons for exclusion include (A&B) postures that hold the head in line with the body (visualized here as a dotted pink line), representing neither vigilant nor non-vigilant behavior, (C) fleeing, and (D) photographs in which the head is not visible.



Appendix E. Data sources for anti-predator analysis (Chapter 3)

Appendix E-1. Data sources used to analyze anti-predator behavior in deer. Stable hyperlinks are used when possible.

Variable	Locale	Year(s) of Data Collection	Resolution/ Unit	Data Collector	Name Data Source	Data Location
NDVI	Study Area	2020 - 2021	30x30 m	Earth Resources Observation and Science Center	USGS EROS Archive - Landsat Archives - Landsat 8-9 OLI/TIRS Collection 2 Level-2 Science Products	1
Points of interest	Study Area	2020 - 2021	Feature (point)	SafeGraph	Points of Interest (POI) dataset	2
Rumple	Fairfax County, VA	2018	Point cloud (submeter)	United States Geological Survey	VA_Fairfax_County_2018	3
	Montgomery & Prince George's Counties, MD, & Washington, DC	2014	Point cloud (submeter)	United States Geological Survey	MD_VA_Sandy_NCR_2014	4

1. https://www.usgs.gov/centers/eros/science/usgs-eros-archive-landsat-archives-landsat-8-9-olitirs-collection-2-level-2
2. https://www.safegraph.com/products/places
3. https://rockyweb.usgs.gov/vdelivery/Datasets/Staged/Elevation/LPC/Projects/USGS_LPC_VA_Fairfax_County_2018
4. https://rockyweb.usgs.gov/vdelivery/Datasets/Staged/Elevation/LPC/Projects/Sandy_Supplemental_NCR_VA_MD_DC_QL2_LiDAR/MD_VA_Sandy_NCR_2014

Appendix F. Potential occupancy variables (Chapter 4)

Appendix F-1. Potential occupancy variables across five variable categories found to impact species occupancy in previous research. Variables followed by an asterisk (*) were used in this analysis. Details on how each variable was calculated are listed after the table.

Variable Category	Potential Variable	Unit or Metric
Habitat availability	Hypothesis: A positive relationship exists between habitat availability and species occupancy.	
	Canopy cover *	%
	Non-landscaped green space	%
	Ground-based (non-canopy) green space	%
	Park area	m^2
	Park interior-edge ratio	unitless
Water availability	Hypothesis: A positive relationship exists between water availability and species occupancy.	
	Open water *	%
	Open water	m^2
Human Disturbance	Hypothesis: A negative relationship exists between human disturbance and species occupancy.	
	Human population density *	n / km^2
	Human population	n
	Impervious surface	%
	Cumulative building footprint	%
	Average distance between buildings	m
Vehicular Disturbance	Hypothesis: A negative relationship exists between vehicular disturbance and species occupancy.	
	Average daily traffic volume *	n / day
	Road area	%
	Road area	m^2
	Alley area	%
	Alley area	m^2
	Roadway (road and alley) area	%
	Roadway (road and alley) area	m^2
Socioeconomic	Hypothesis: The relationship between socioeconomic factors and species occupancy varies across species.	
	Average per capita income *	USD / person
	Total income	USD

Total population experiencing poverty	n
Total population experiencing poverty	%

Method of Calculation

Variables were measured at the sampling cell level using ArcMap 10.8. Each variable's shapefile was associated with each sampling cell using the Intersect tool. After the shapefile was divided by sampling cell, the relevant spatial geometry was calculated by adding a new column and using the Calculate Geometry tool. Data for each cell were either summed and divided by the area of the cell to achieve percent extent (e.g., percent canopy cover), or were averaged across the cell to achieve a mean value (e.g., daily traffic).

Most landscape variables utilized a 1-meter resolution landcover database. However this dataset was created using arial imagery and was not entirely sufficient for creating a water layer due to riparian forests. The municipal water layer was overlaid, and features that were unique (e.g., Rock Creek) were retained. The resulting layer was used in analysis.

Population density and per capita income was calculated using the 2018 CDC Vulnerability Dataset. The proportion of each census tract occurring in each sampling cell was calculated and multiplied by the number of people residing in each tract. This value was multiplied by the average per capita income of the census tract. The total income for each sampling cell was calculated by adding this value for all census tracts contained within a sampling cell. The average per capita income was calculated by dividing the total income for each cell by the total number of residents for each cell. The census tract that contains the National Mall did not contain any income data, and was assigned the mean per capita income of all the adjacent tracts.

Datasets

The following datasets were used to calculate variables. Variables that were included in this analysis are noted by an asterisk(*).

2018 Traffic Volume. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2020. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/2018-traffic-volume?geometry=-77.476%2C38.801%2C-76.550%2C38.988

- Daily traffic volume* (n)

Alleys and Parking. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2020. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/DCGIS::alleys-and-parking/about

- Alley area (m2)
- Percent alley (%)
- Roadway area (alleys and roads; m2)
- Percent roadway area (alleys and roads; %)

Building Footprints. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2015 [Updated 2020 February 19]. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/building-footprints-2017?geometry=-77.475%2C38.809%2C-76.549%2C38.997

- Average distance between buildings (m)
- Percent built area (%)

CDC Social Vulnerability Index 2018 - USA. Atlanta, GA (USA): Center for Disease Control and Prevention. 2018. Accessed 2020 December 16. Available at: https://www.arcgis.com/home/item.html?id=cbd68d9887574a10bc89ea4efe2b8087

- Total human population (n)
- Human population density* (n/km2)
- Total income (USD)
- Average per capita income* (USD/person)
- Total population experiencing poverty (n)
- Percent of population experiencing poverty (%)

Chesapeake Bay High-resolution Land Cover Project. Annapolis, MD (USA): Chesapeake Conservancy Conservation Innovation Center. 2014 [updated 2020 June 1]. Accessed 2020 December 16. Available at: https://www.chesapeakeconservancy.org/conservation-innovation-center/high- resolution-data/land-cover-data-project/

- Open water area (m2)
- Percent open water* (%)
- Percent canopy cover* (%)
- Percent Semi-natural habitat (%)
- Percent Impervious surface (%)
- Percent Ground-based greenspace (%)

National Parks by Name. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2014. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/national-parks-by-name?geometry=-77.484%2C38.806%2C-76.558%2C38.993

- Park area (m2)
- Park interior-edge ratio (unitless)

Parks and Recreation Area. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2021. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/DCGIS::parks-and-recreation-areas/about

- Park area (m2)
- Park interior-edge ratio (unitless)

Roads 2013. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2020. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/DCGIS::roads-2013/about

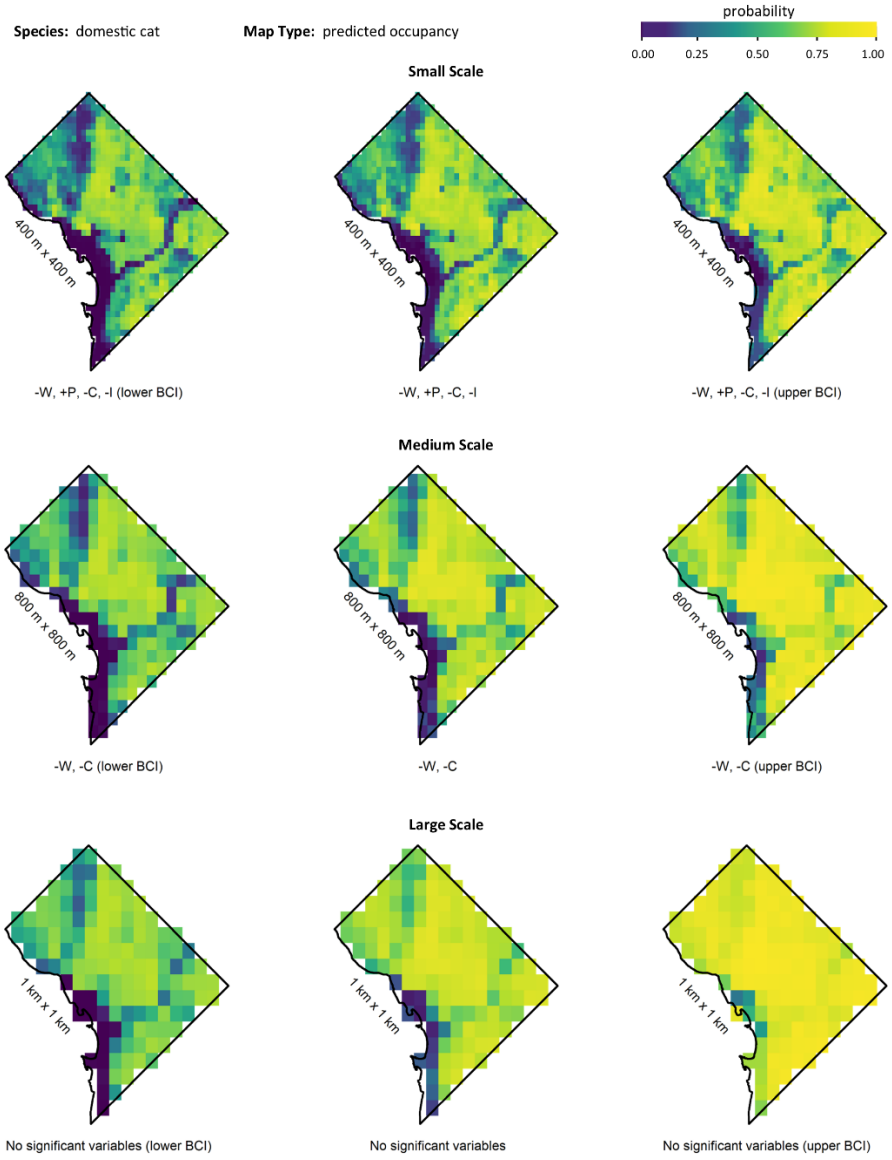
- Road area (m2)
- Percent road (%)
- Roadway area (alleys and roads; m2)
- Percent roadway area (alleys and roads; %)

Waterbodies. Washington, D.C. (USA): D.C. Office of the Chief Technology Officer. 2019-[updated 2020 February 10]. Accessed 2020 December 16. Available at: https://opendata.dc.gov/datasets/waterbodies?geometry=-77.258%2C38.913%2C-76.795%2C39.006

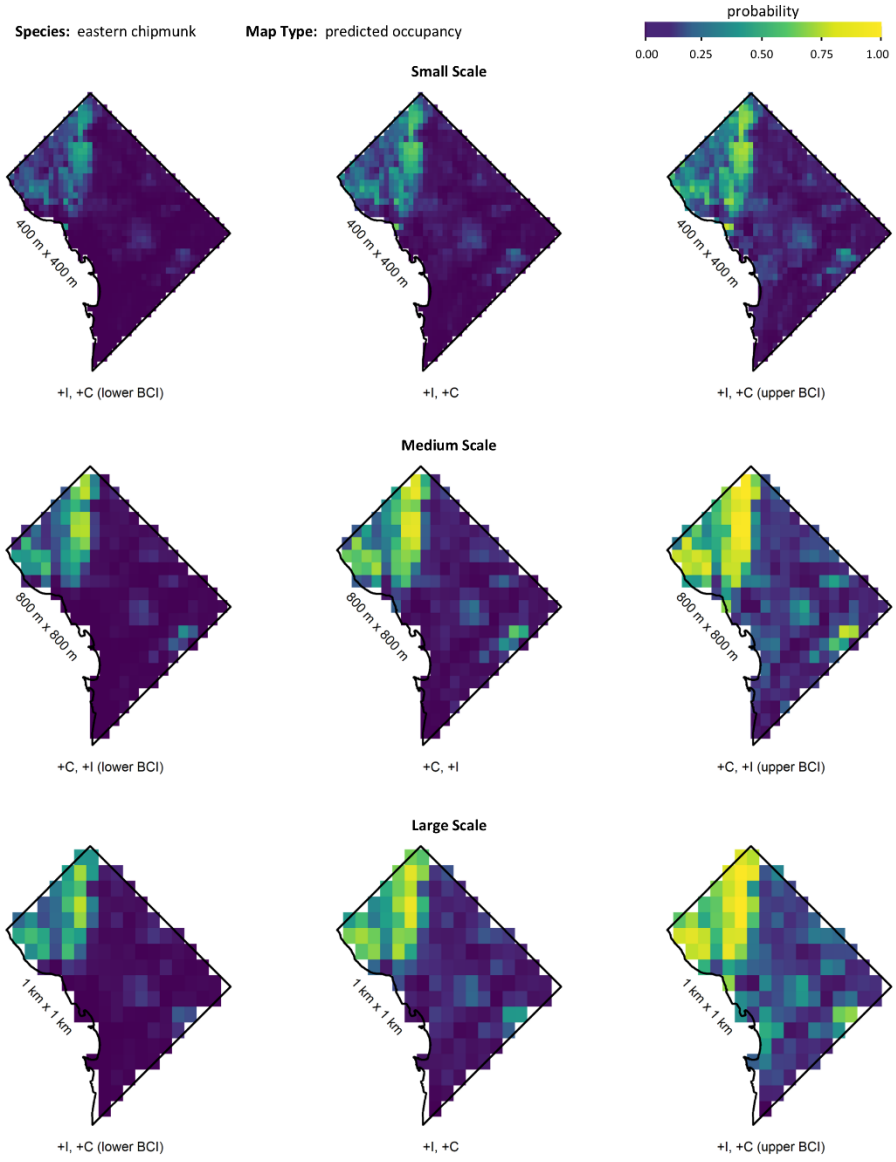
- Open water area (m2)
- Percent water* (%)

Appendix G. Occupancy maps using lower/upper credible intervals (Chapter 4)

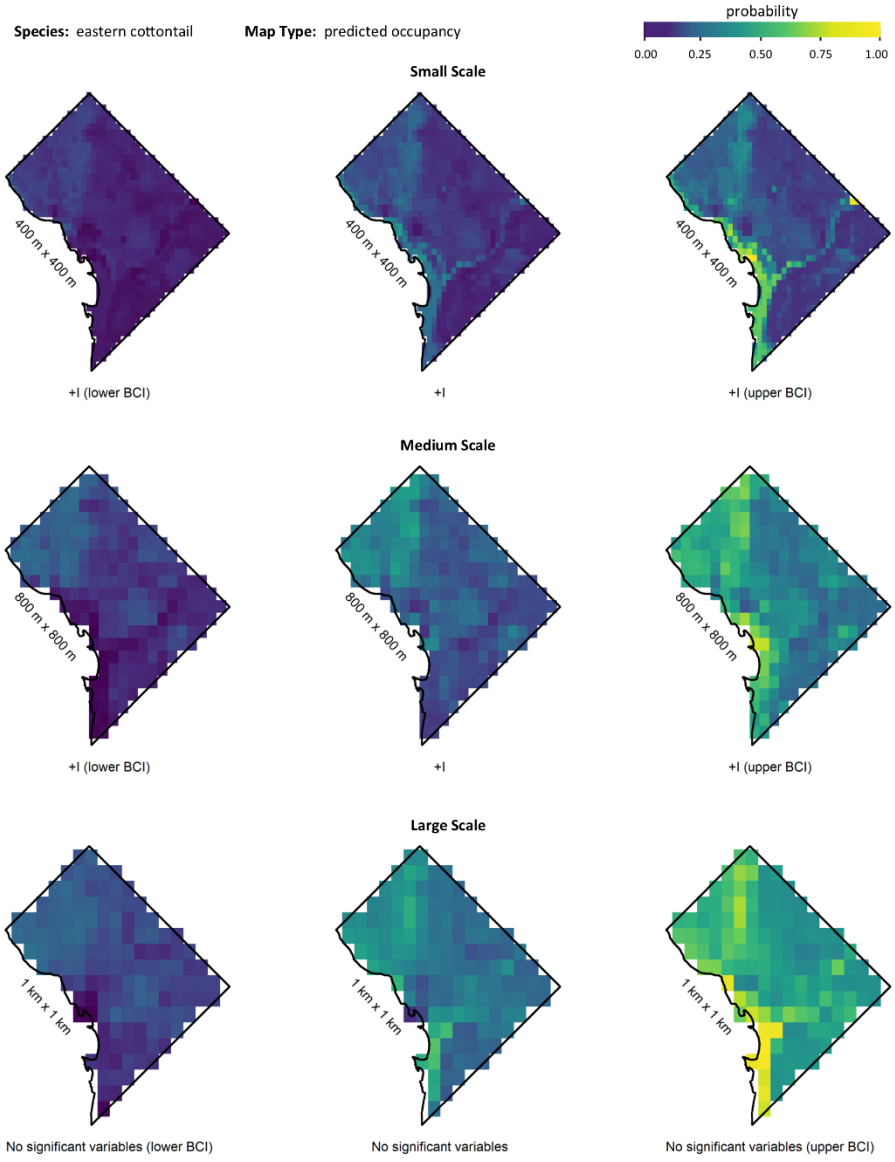
Appendix G-1. Predictive occupancy maps for domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



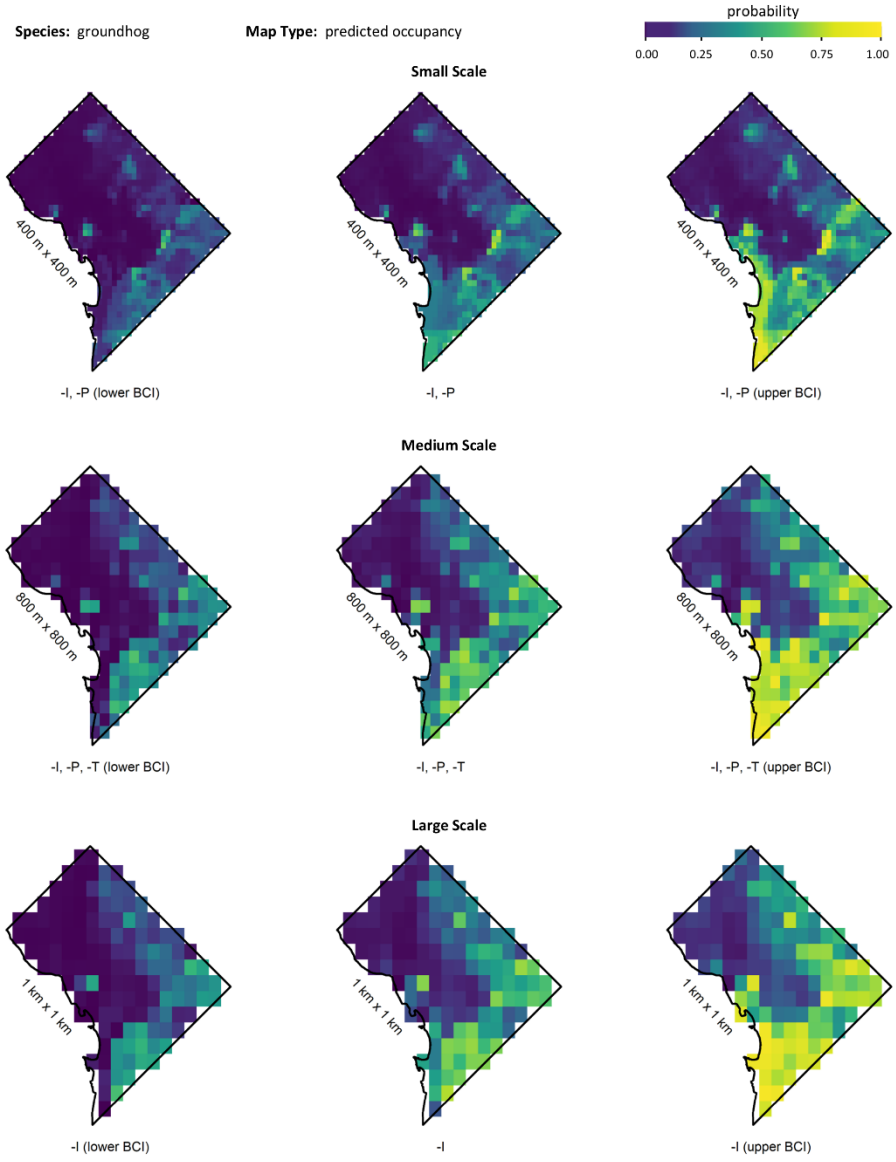
Appendix G-2. Predictive occupancy maps for eastern chipmunk (*Tamias striatus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



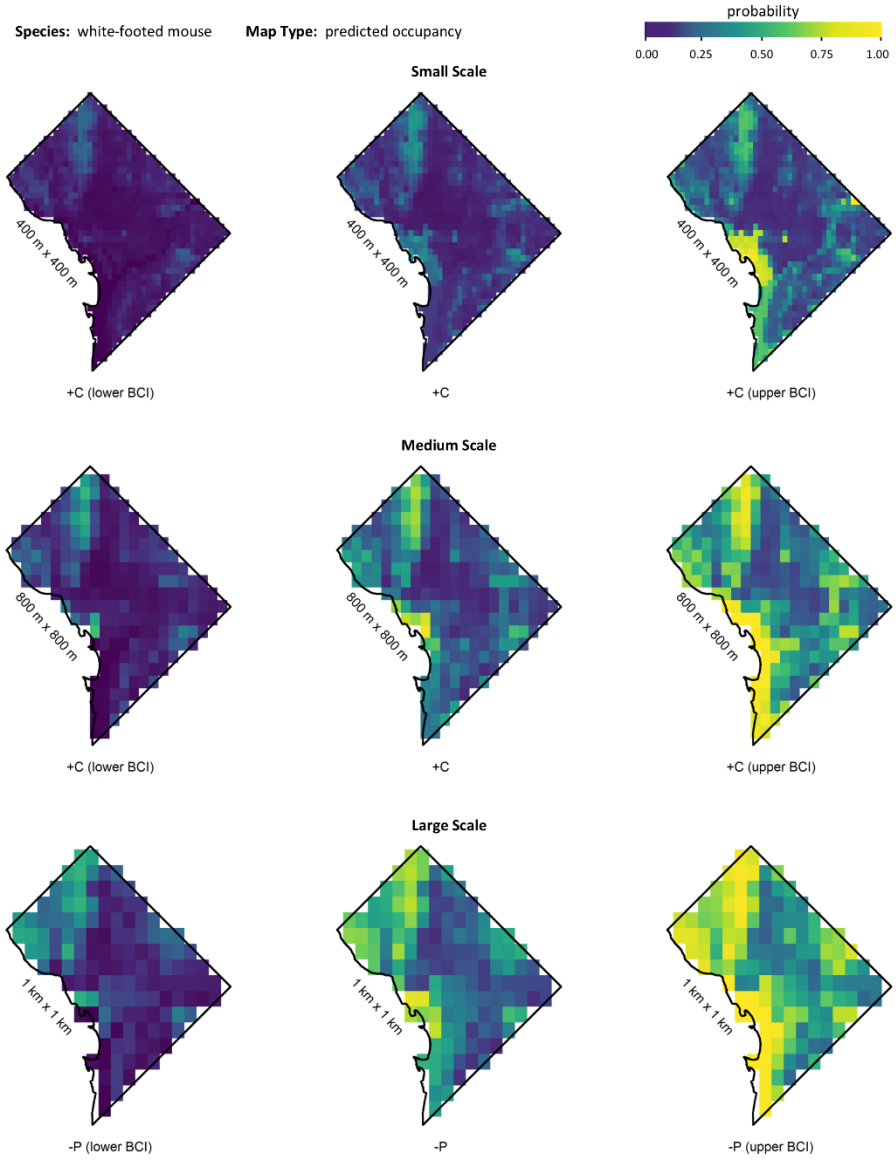
Appendix G-3. Predictive occupancy maps for eastern cottontail (*Sylvilagus floridanus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



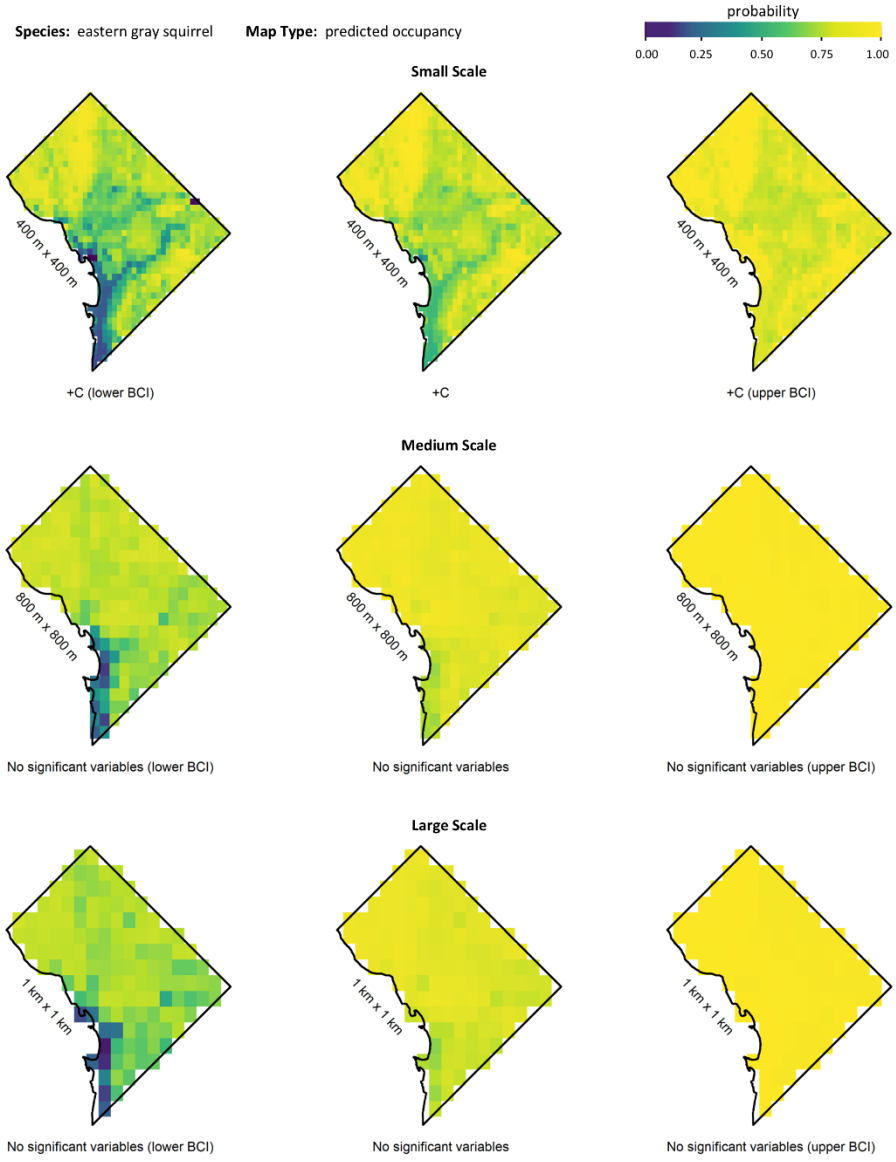
Appendix G-4. Predictive occupancy maps for groundhog (*Marmota monax*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



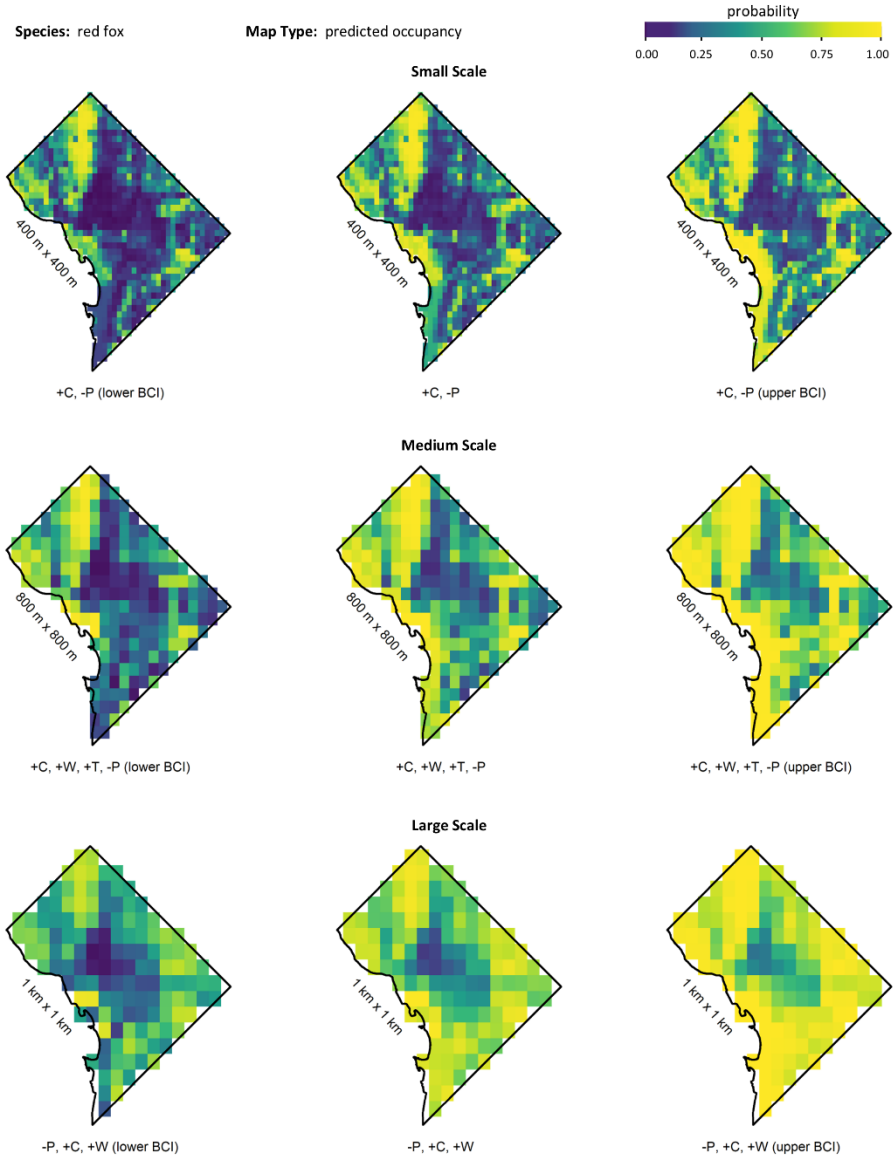
Appendix G-5. Predictive occupancy maps for white-footed mouse (*Peromyscus leucopus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



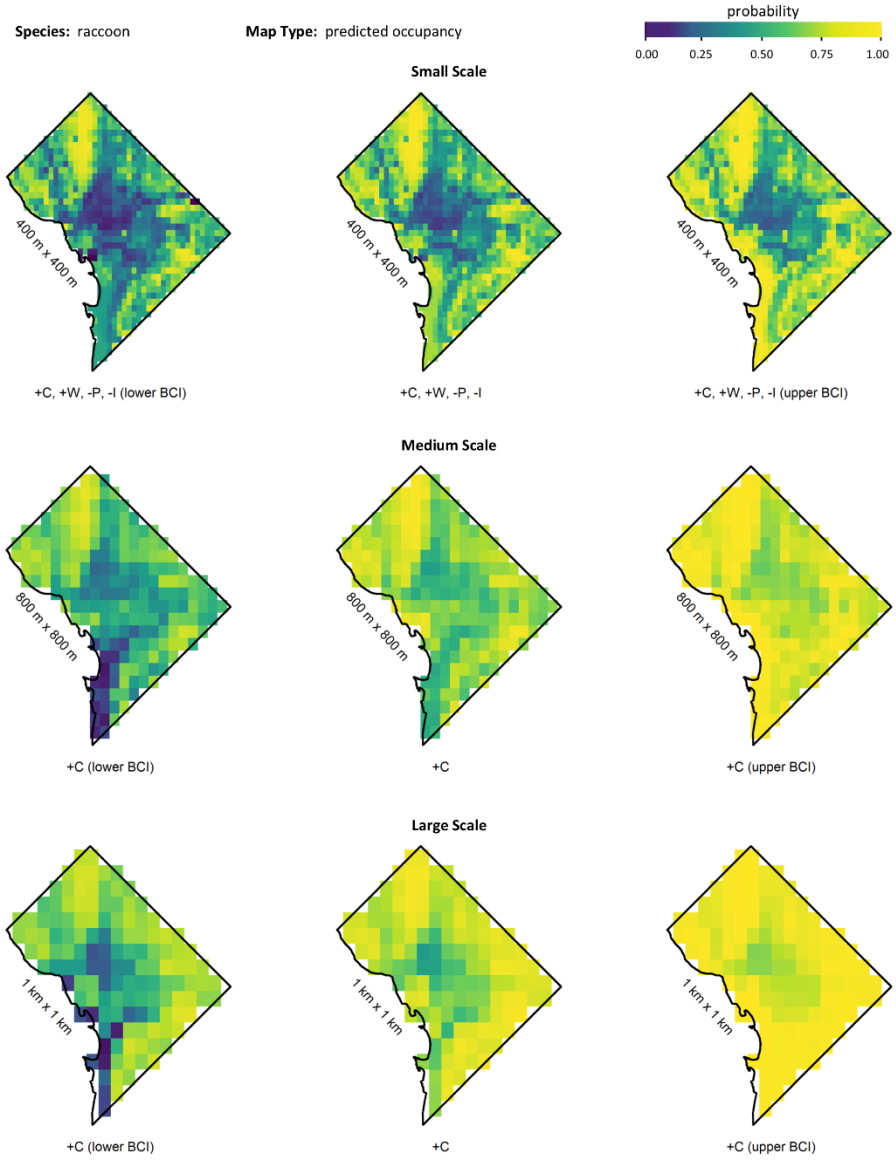
Appendix G-6. Predictive occupancy maps for eastern gray squirrel (*Sciurus carolinensis*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



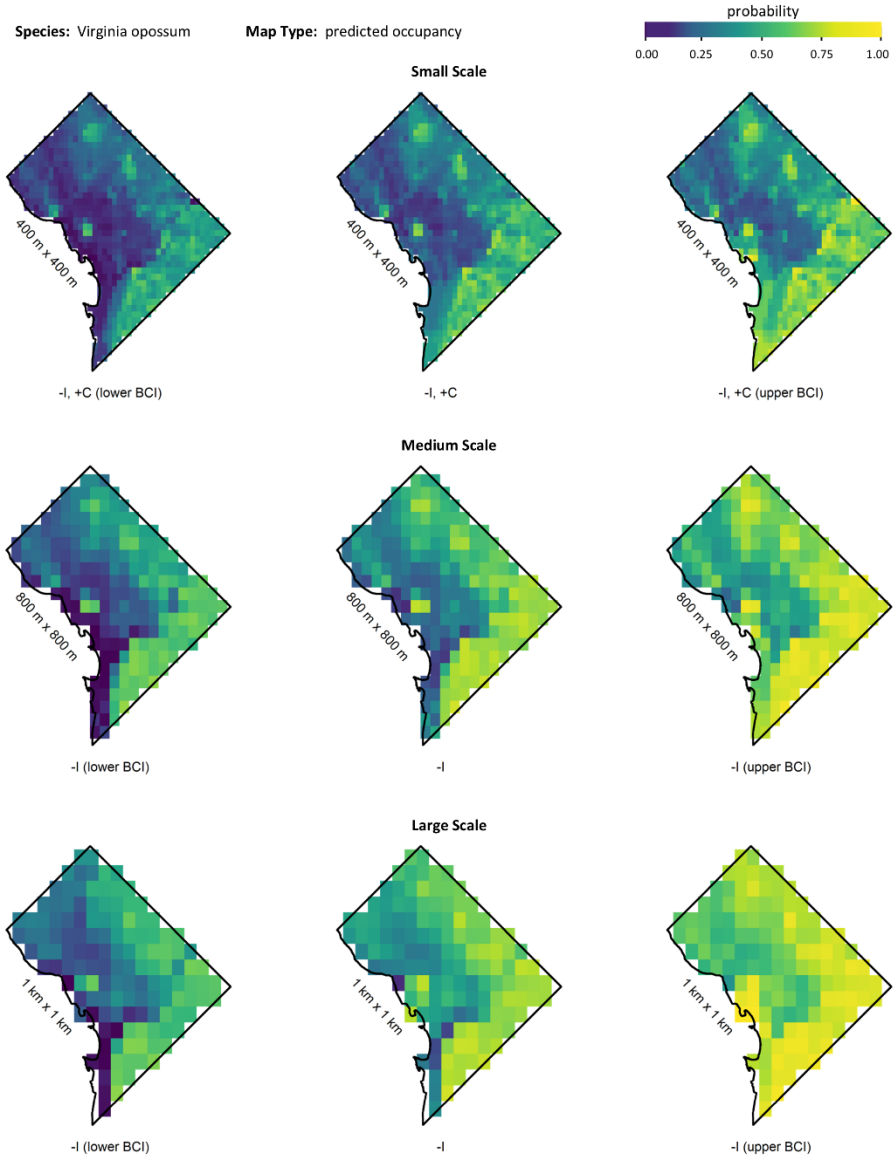
Appendix G-7. Predictive occupancy maps for red fox (*Vulpes vulpes*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



Appendix G-8. Predictive occupancy maps for raccoon (*Procyon lotor*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.

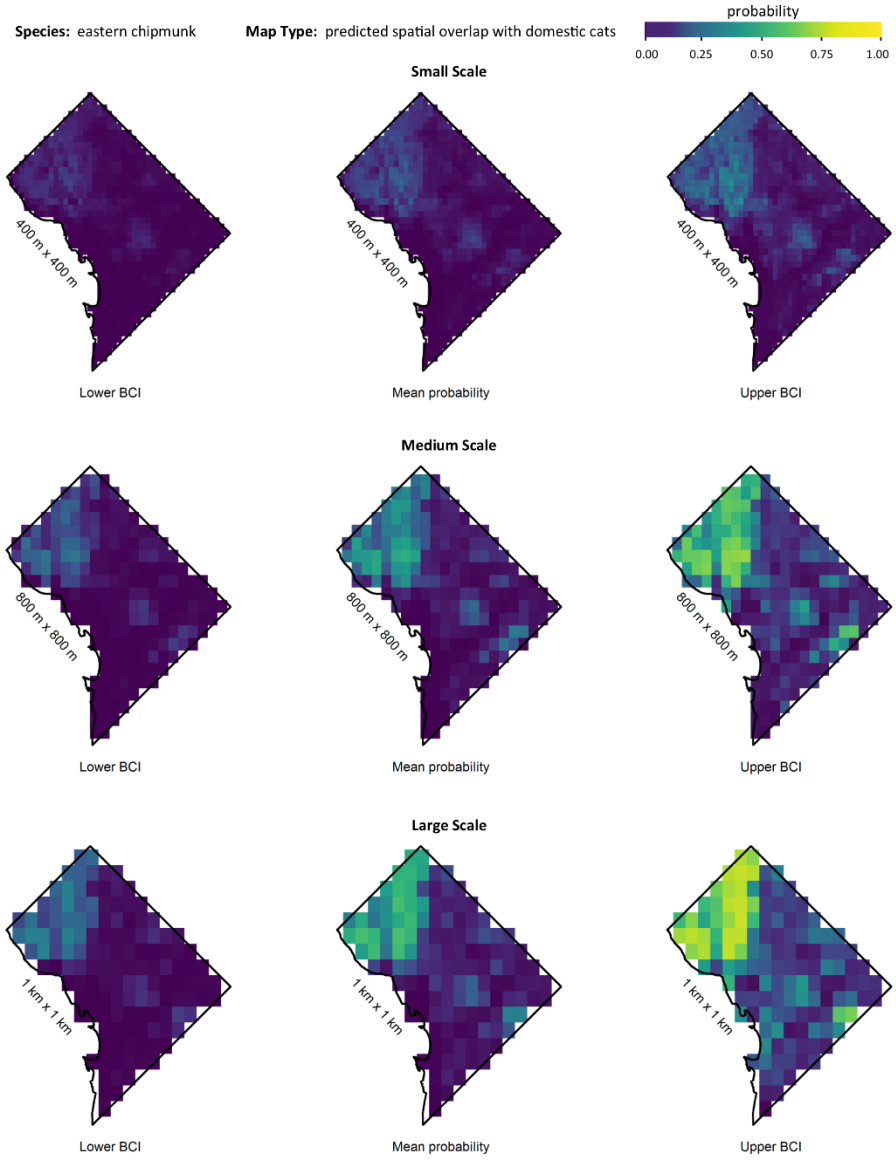


Appendix G-9. Predictive occupancy maps for Virginia opossum (*Didelphis virginiana*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each estimated parameter.



Appendix H. Overlap maps using lower/upper credible intervals (Chapter 5)

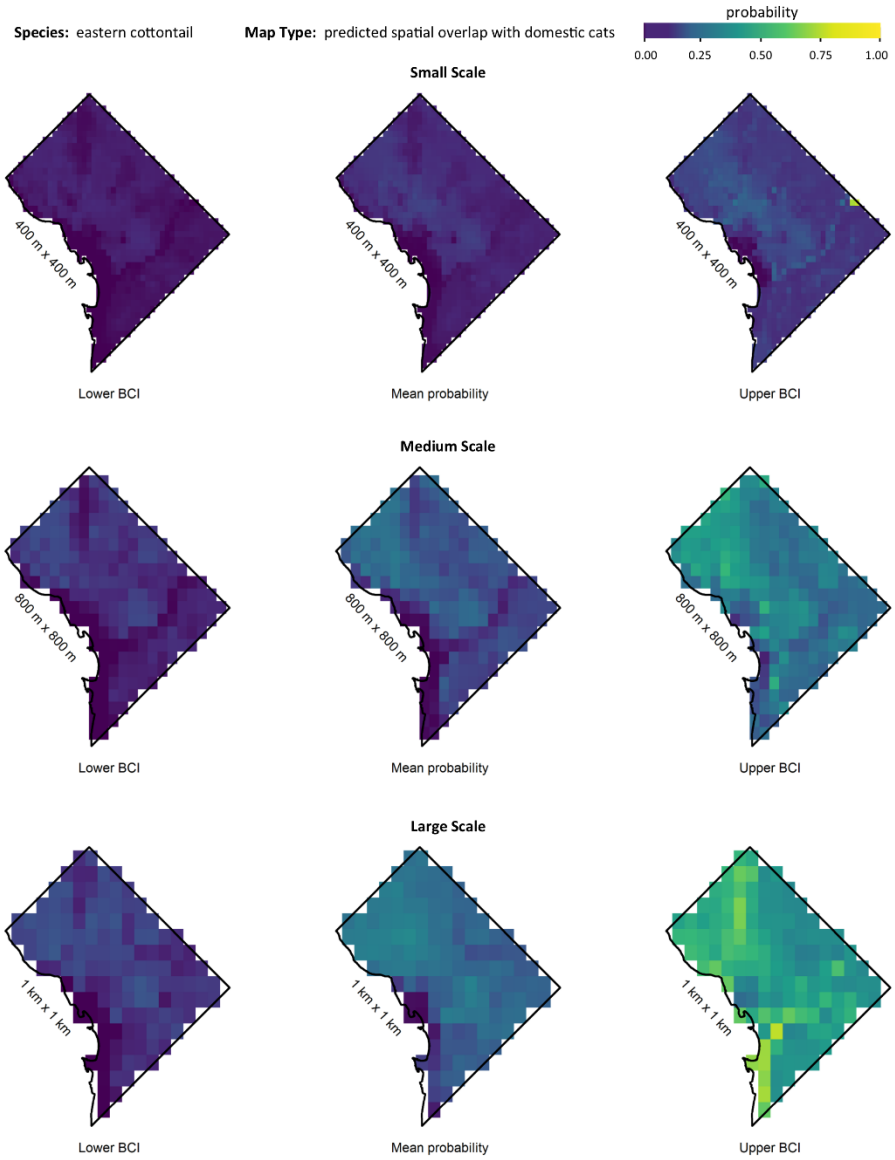
Appendix H-1. Predictive overlap maps between eastern chipmunk (*Tamias striatus*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



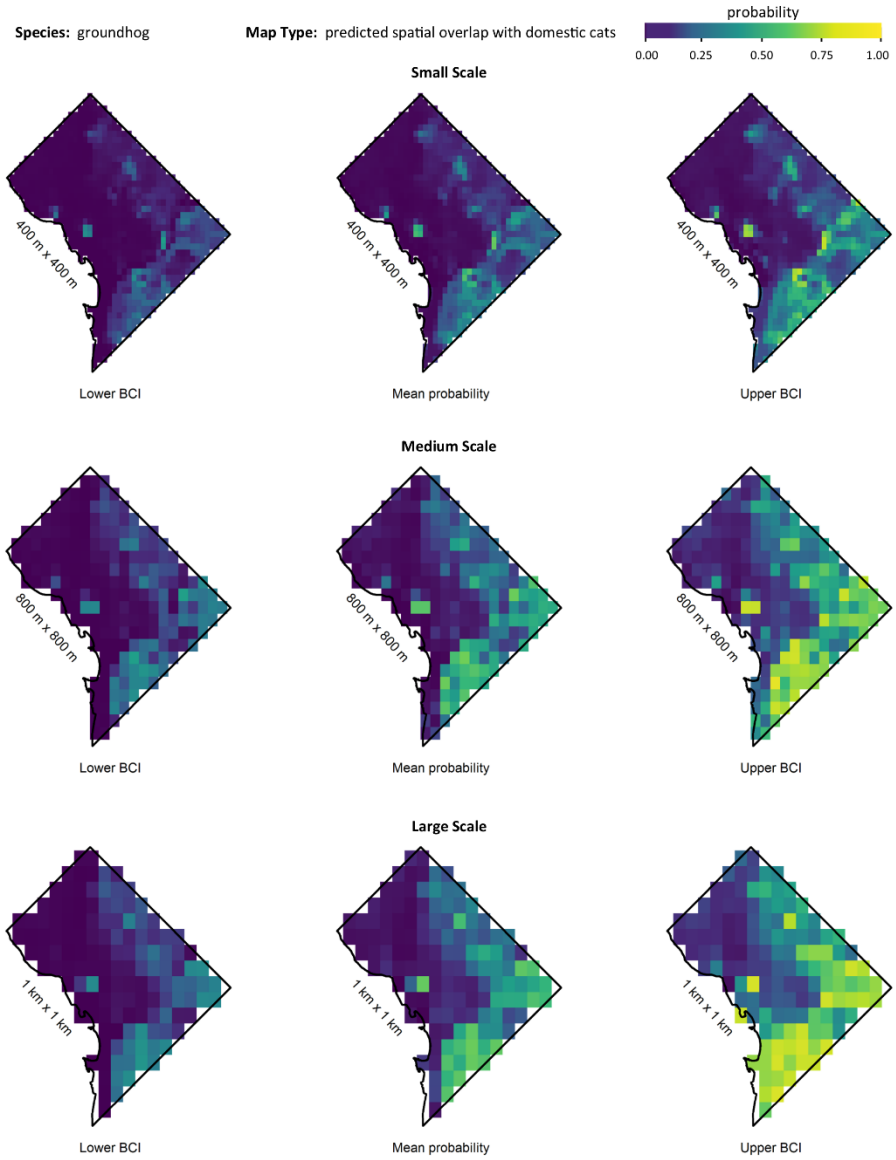
Appendix H-2. Predictive overlap maps between eastern chipmunk (*Tamias striatus*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



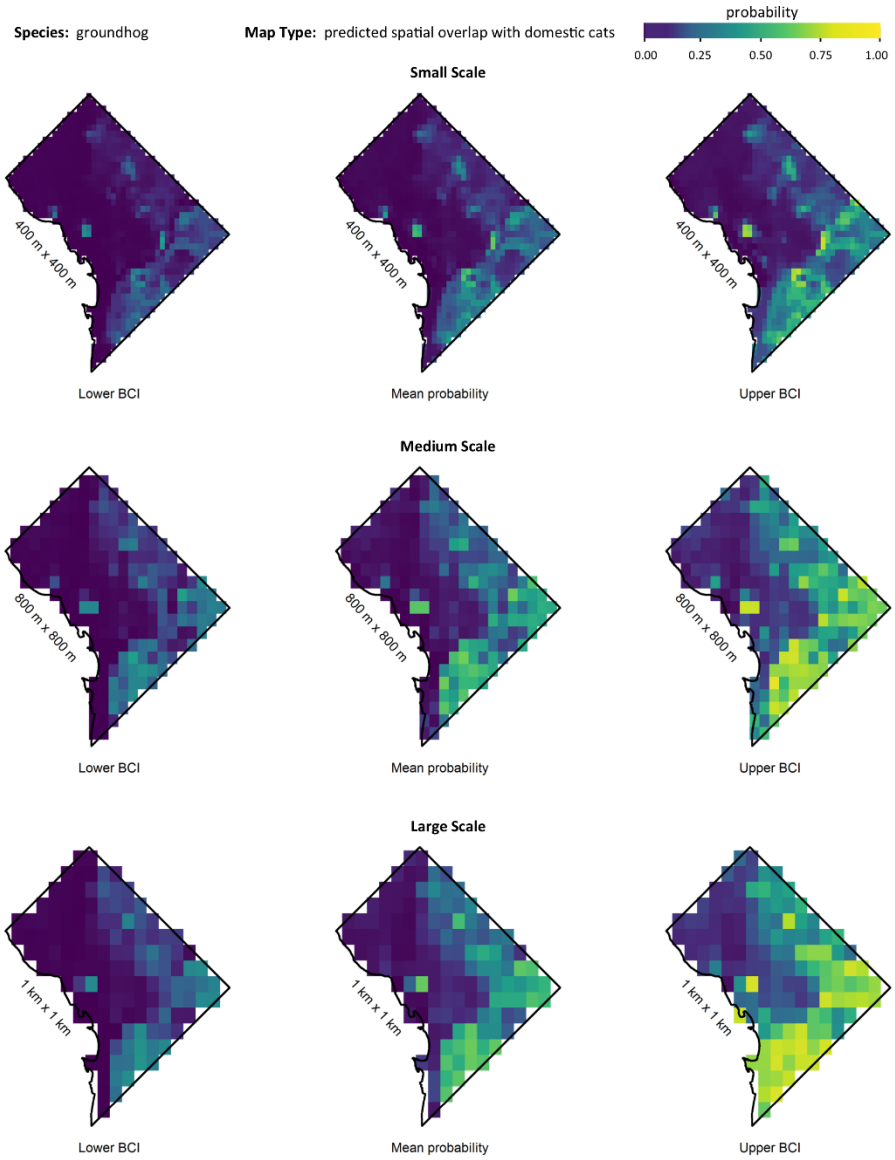
Appendix H-3. Predictive overlap maps between eastern cottontail (*Sylvilagus floridanus*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



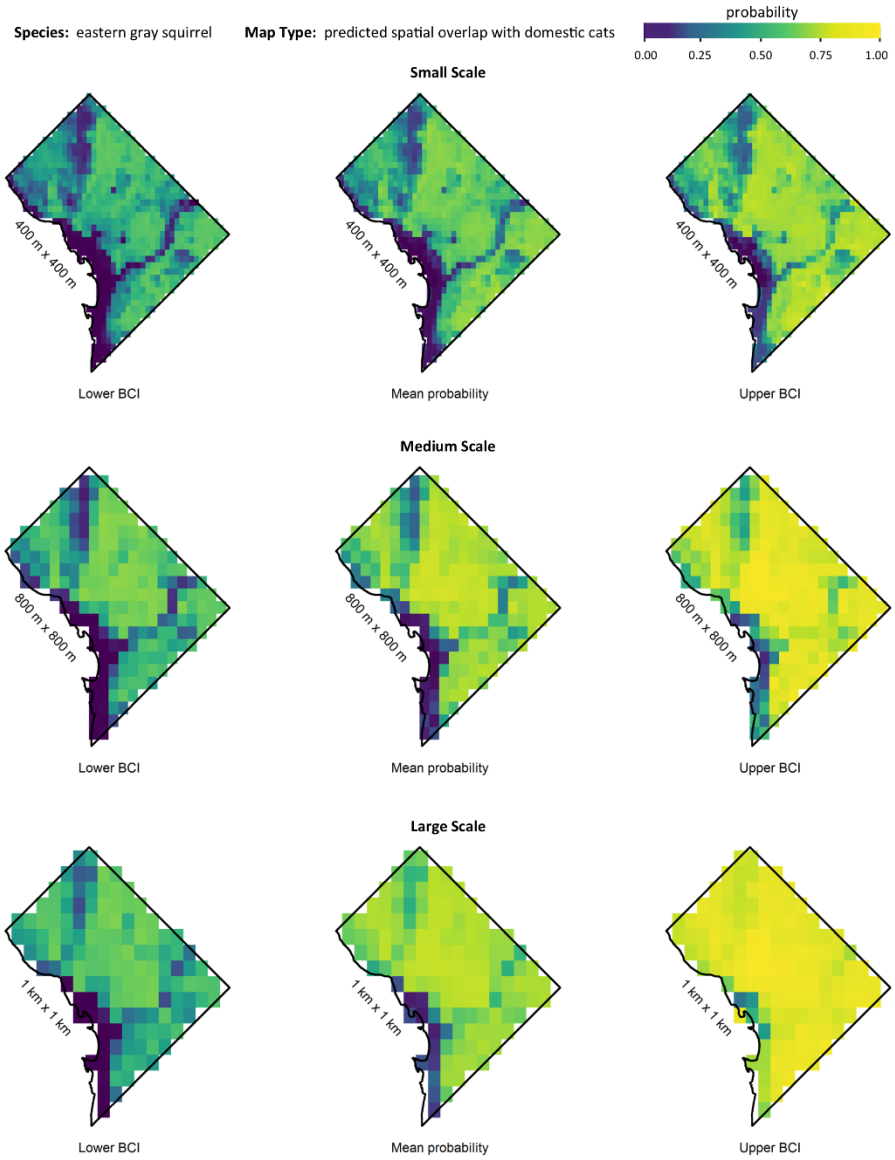
Appendix H-4. Predictive overlap maps between groundhogs (*Marmota monax*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



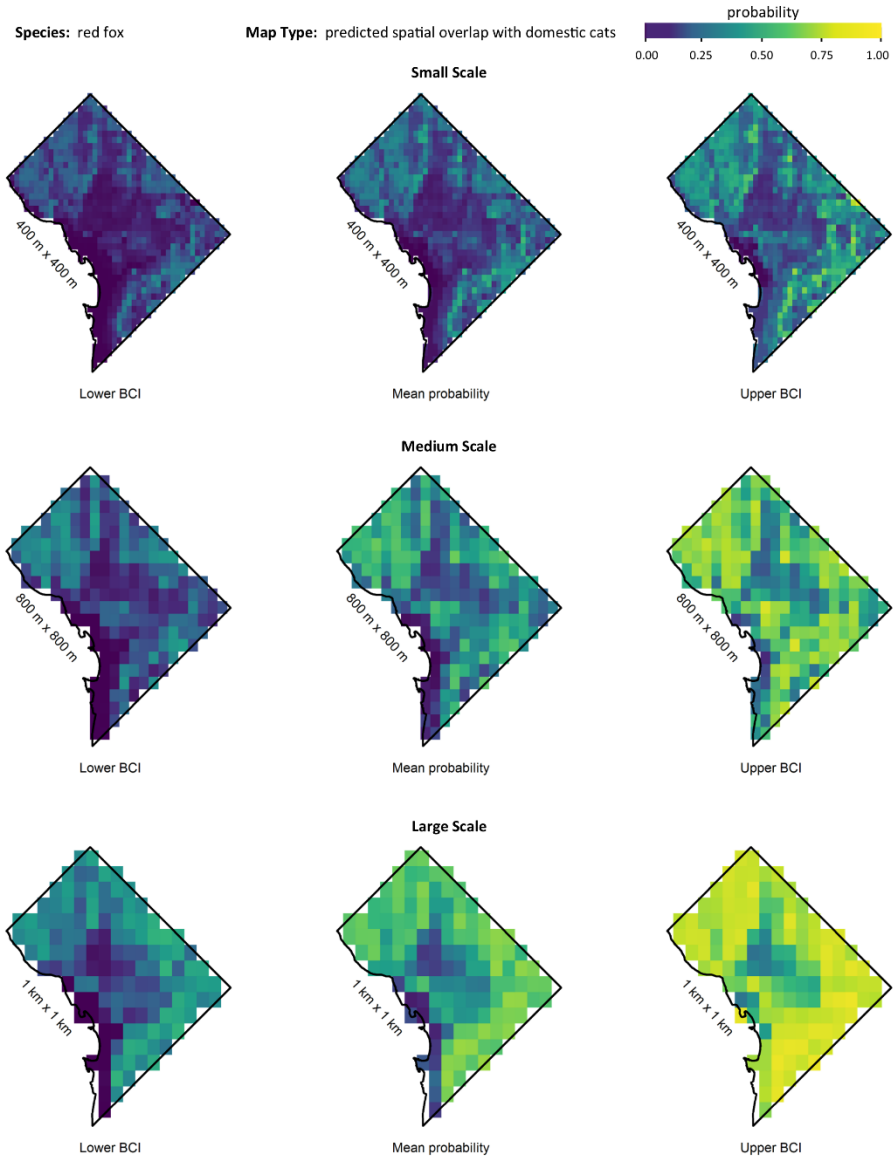
Appendix H-5. Predictive overlap maps between white-footed mice (*Peromyscus leucopus*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



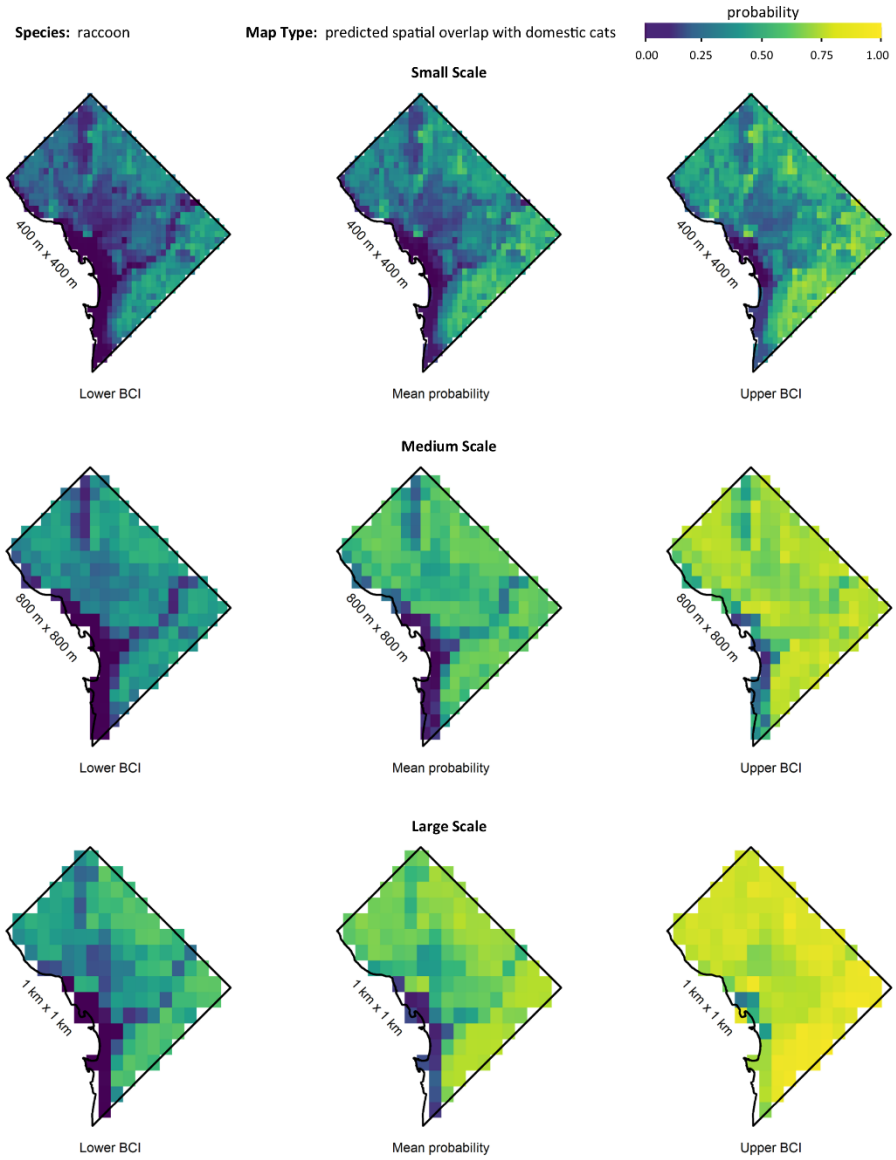
Appendix H-6. Predictive overlap maps between eastern gray squirrel (*Sciurus carolinensis*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



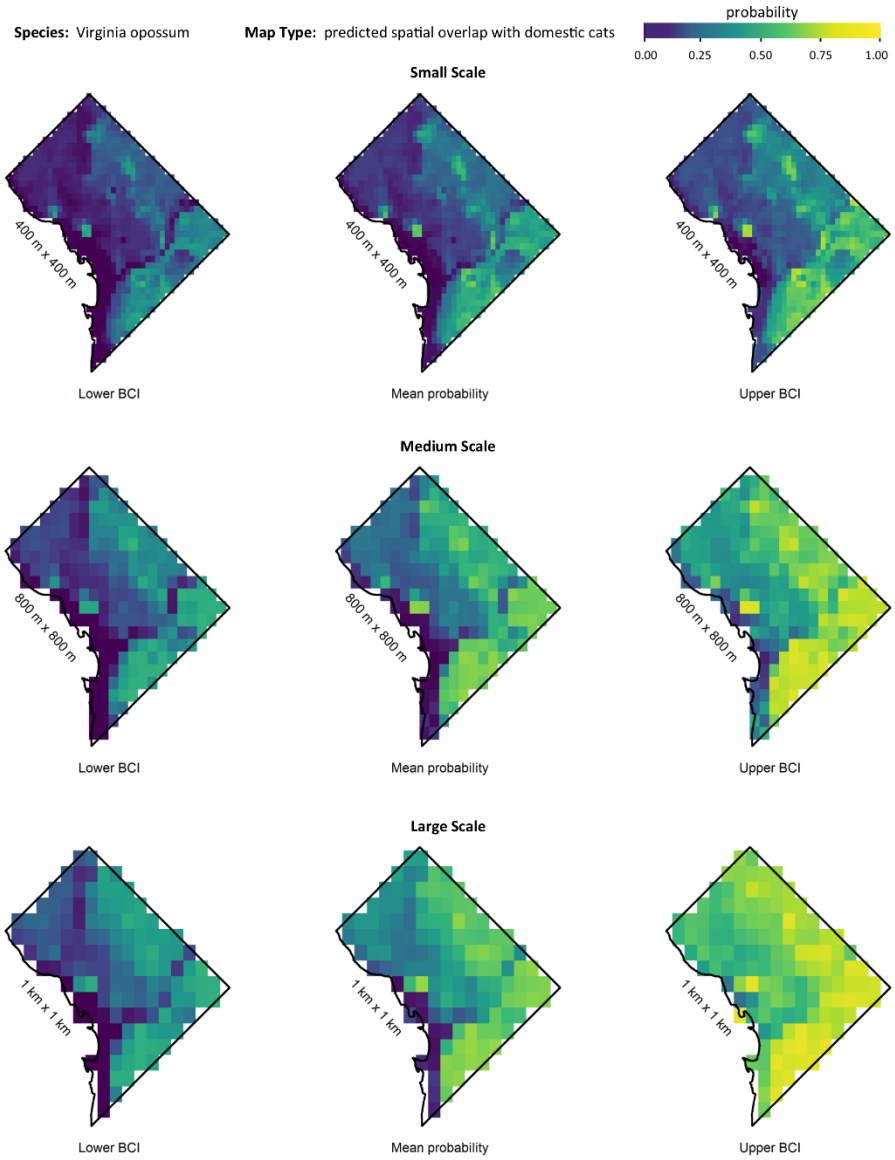
Appendix H-7. Predictive overlap maps between eastern red fox (*Vulpes vulpes*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



Appendix H-8. Predictive overlap maps between raccoon (*Procyon lotor*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



Appendix H-9. Predictive overlap maps between Virginia opossum (*Didelphis virginiana*) and domestic cats (*Felis catus*) across the District of Columbia at three spatial scales (top to bottom) using the lower (left), median, and upper (right) 95% credible interval values for each species' estimated parameters.



Appendix I. Predation data from non-feline predators (Chapter 5)

Appendix I-1. Documented predation events by all non-feline predators in Washington, D.C. (2018-2020).

Predator species	Prey Species	Number of predation events
Red Fox *Vulpes vulpes*	Unknown species	13
	Virginia opossum *Didelphis virginiana*	3
	Easter gray squirrel *Sciurus carolinensis*	2
	Eastern cottontail *Sylvilagus floridanus*	1
	White-tailed deer *Odocoileus virginianus*	1
	Black-crowned night heron *Nycticorax nycticorax*	1
Red-tailed hawk *Buteo jamaicensis*	Brown rat *Rattus norvegicus*	1
	European starling *Sturnus vulgaris*	1
	Rock dove *Columba livia*	1
	Eastern worm snake *Carphophis amoenus*	1
Virginia opossum *Didelphis virginiana*	Eastern gray squirrel *Sciurus carolinensis*	2
Gray fox *Urocyon cinereoargenteus*	Unknown species	1

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