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CONSERVATION VALUE OF SUBURBAN WOODLANDS FOR A DECLINING SONGBIRD

Item Type	Dissertation (Open Access)
Authors	Klein, Melanie L
DOI	10.7275/35080682
Download date	2026-06-13 00:22:59
Link to Item	https://hdl.handle.net/20.500.14394/19198

**CONSERVATION VALUE OF SUBURBAN WOODLANDS FOR A DECLINING
SONGBIRD**

A Dissertation Presented

by

MELANIE L. KLEIN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2023

Department of Environmental Conservation
Wildlife, Fish, and Conservation Biology

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DEDICATION

In loving memory of:

My dad, Robert Klein, who shared my love of nature. He may not have understood the ins and outs of graduate school, but was always impressed by my endeavors nonetheless;

And Mush and Hazel, who's purrs, cuddles, trills, and chirps made life during graduate school so much more joyful.

May you rest in peace.

ACKNOWLEDGMENTS

This work would not be possible without my advisors, Dr. Paige Warren and Dr. Dave King. I am deeply grateful for your patience, encouragement, and feedback during this long and sometimes difficult journey. I could not have asked for co-advisors who better complimented each other. Whether working out last minute field protocol with Dave or meeting with Paige to discuss writer's block, I feel so thankful to have had support from both of you. I am greatly appreciative to my committee members, Dr. Todd Fuller and Dr. Robert Ryan, who provided invaluable expertise and feedback. This work would also not have been possible without funding from the National Science Foundation (NSF DGE-0907995), the U.S. Forest Service Northern Research Station, UMass Experiment Station project #MAS00020 (NIFA Macintyre-Stennis), USGS Science Support, and the Bradford G. Blodget Scholarship Fund for Ornithological Studies.

Fieldwork would not have been possible without the gracious permission of numerous landowners. This includes several private landowners, the Town of Amherst, the City of Springfield, the Massachusetts Department of Conservation & Recreation, the Massachusetts Division of Fisheries & Wildlife, and the University of Massachusetts Amherst. Field data collected by Kit Straley and her crew greatly improved my dataset, and chapter four would not be possible without Scott Schlossberg, who provided the 2011-12 fledgling dataset. I am fortunate to have had support from numerous hardworking field technicians: Jeff Ritterson, Andrew Gaspari, Lindsay Forrette, Sam Rock, Evan Ferrarone, and Erika Nevins. I am also grateful for the support of numerous volunteers in the field and the lab, especially Laurel Boser, Emma Nelson, Chris Kane, and Casey Wiener. Additional fieldwork support from James Smith, Evan Dalton, and

Calvin Ritter, as well as the fieldwork collaboration with my lab mate, Kit Straley and her field crew were invaluable.

I am very thankful for the Department of Environmental Conservation: everyone who worked in the front office and provided unrelenting logistical support, including Emily West and Linda Fortin, as well as all the other staff members who kept Holdsworth running; and all the faculty, postdocs, and fellow graduate students who have shared knowledge, support, and camaraderie over the years. Special thanks to members of the King lab, Warren lab, and Lerman lab. For valuable statistical help, I thank prior King lab members Dr. Mike Akresh and Dr. Jenny Smetzer.

I wish to acknowledge a few of the numerous mentors and advisors who guided me prior to graduate school: Eric Wiener, for helping me build my confidence as an ecologist, Emma Rainforth for pushing me to become a better scientific writer, and Eric Walters for graciously providing grant writing help.

I thank my family, especially my mom, Cami Klein, who taught me that not all red birds are robins, and who provided support and encouragement over the years. Numerous friends made my life during graduate school more positive. I cannot list them all, but I am particularly grateful for the support of Mayrolin Garcia, Amanda Lipsey, Lena Fletcher, Zalmay Moheb, Maritza Mallek, and Sam Rock and the Rock family. Last, but not least, I thank Douglas for providing purrs and laughs.

ABSTRACT

CONSERVATION VALUE OF SUBURBAN WOODLANDS FOR A DECLINING SONGBIRD

May 2023

MELANIE L. KLEIN, B.S., RAMAPO COLLEGE OF NEW JERSEY

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Urbanization and suburbanization (hereafter, used interchangeably) can create some of the most drastically altered habitats of all anthropogenic land uses. Despite this, many wildlife species, including roughly 20% of the world's birds, can be found in cities. Furthermore, research has shown that suburban forest patches can have important conservation value for birds. As urbanized areas rapidly grow, in terms of both geographical extent and human population, and as numerous bird species experience population declines, understanding how avian species fare in these areas has never been more vital. Not only is this knowledge timely for avian conservation, but for the human population, who, while increasingly disconnected from nature, can garner valuable health and wellbeing benefits from interacting with birds. In this dissertation, I compared avian success between suburban/urban forest patches (suburban sites) and larger swaths of contiguous forest (rural sites) in western Massachusetts. For the first part of my dissertation, I investigated the abundance of several bird species in suburban and rural sites. I then focused on nest survival and fledgling survival of a declining neotropical migrant, the Wood Thrush (*Hylocichla mustelina*), as well as the nest/fledgling predator community and the movement of post-fledgling Wood Thrushes. N-mixture models of 15

species indicated that neotropical migrants were more likely to have negative responses to urbanization compared to short distance migrants or resident species, but this pattern did not hold true for all species, including Wood Thrush. Survival analysis of 253 Wood Thrush nests indicated that survival was comparable between suburban and rural sites. Using predator surveys, I found that suburban sites had a higher abundance or density of potential nest/fledgling predators compared to rural sites. Video monitoring of Wood Thrush nests showed a suite of nest predators. These nest survival and predator survey results, taken together, are evidence of the “predation paradox” phenomenon- an apparent mismatch between predator abundance and actual predation in urbanized areas- for nesting Wood Thrush. Using survival analysis of 168 radio-tagged Wood Thrush fledglings, I found that survival was comparable between suburban and rural sites, indicating the existence of the predation paradox patterns for the understudied fledgling life stage. Rural fledglings moved farther, at any given age, than suburban fledglings, suggesting possible barriers to movement in suburban sites. Overall, the results of this dissertation work support the conservation value of suburban forest patches for Wood Thrush. More work is needed to better understand mechanisms of the predation paradox, as well as the impacts of potential barriers to movement for fledglings using suburban areas. Further work is also timely for assessing the conservation value of suburban forest patches for other sensitive species.

KEY WORDS: avian abundance, N-mixture models, point counts, urban trophic dynamics, predation paradox, nest survival, fledgling survival, Wood Thrush, survival analysis, suburban forest patches

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CHAPTER 1

INTRODUCTION

Conservation of wildlife often evokes images of protecting pristine ecosystems with vast stretches of seemingly untouched habitat. While protecting these spaces is very valuable, there are also few of these areas left on earth (Allan et al. 2017). For better or worse, humans have altered every ecosystem on the globe. Urbanization (and suburbanization, hereafter urbanization), while small in geographic area compared to other human-altered land cover (Houghton 1994, Foley et al. 2005, Schneider et al. 2010), is long lasting and has great impacts on species composition (Mckinney 2006) and biodiversity (Aronson et al. 2014). Urbanized areas are also growing rapidly in extent (Seto et al. 2011, IPCC 2014), and this expansion does not slow near protected areas (Seto et al. 2011). Urban and suburban areas still support a variety of wildlife species, however, including some that are endemic and/or endangered (Aronson et al. 2014). Even relatively small patches of habitat in urbanized landscapes can have great conservation value (Wintle et al. 2019). But not all greenspaces are equal when it comes to supporting biodiversity (Beninde et al. 2015). Understanding how well urban or suburban green spaces function as habitat for different taxa is key for contemporary wildlife conservation (Lepczyk et al. 2017).

Increasing the urgency and value of conservation research in urbanized areas is the fact that the majority of the world's human population lives in such places (IPCC 2014). That population continues to grow (Grimm et al. 2008, United Nations 2014). This likely contributes to a decline in the amount of interaction humans have with nature (Turner et al. 2004, Miller 2005, Soga and Gaston 2016). Not only is exposure to nature

vital to human health (Takano et al. 2002, Russell et al. 2013, Soga and Gaston 2016) and emotional wellbeing (Russell et al. 2013, Soga and Gaston 2016, Cox et al. 2017), but it affects people's interest in and support of conservation measures (Miller 2005, Ryan 2015, Soga and Gaston 2016). Conservation of wildlife in urban or suburban greenspaces is therefore not only important from a conservation point of view but is essential for the human inhabitants of these areas.

Conservation of birds in urbanized landscapes is vital and timely, for both birds and people. Populations of many bird species are declining, worldwide (Rosenberg et al. 2019). Roughly 20 percent of the world's bird species can be found in urbanized areas (Aronson et al. 2014), but urbanization favors some species over others (Chace and Walsh 2006, Croci, Butet, and Clergeau 2008). Birds also provide a myriad of ecosystem services (Whelan et al. 2015), and, with their widespread distributions, mobility, bright colors, and beautiful sounds, may have an especially important role in connecting people with nature. People commonly engage with birds, feeding or observing them (USDOJ et al. 2016), and many urban residents feel positive about birds that live in their neighborhoods (Belaire et al. 2015). Urban green spaces can be a key part of conservation for birds (Fischer and Lindenmayer 2002, Wintle et al. 2019), but research is needed on what factors affect the success of birds in urban or suburban greenspaces, how these factors differ by life stage, and how this affects regional bird populations (Marzluff and Ewing 2001, Lepczyk et al. 2017).

In this dissertation, my overall objective is to add to our understanding of avian ecology in urbanized landscapes by examining how birds fare in suburban and urban forest patches in western Massachusetts. I compare avian success between suburban or

urban forest patches (hereafter, suburban sites) and nearby forested preserves (hereafter, rural sites), in terms of abundance, nest survival, and fledgling survival as well as the nest (and fledgling) predator community. In the first research chapter (ch. 2), I use point counts to examine the distributions of several individual bird species found in both suburban and rural sites. I ask if and how migratory behavior, foraging guild, and regional population trend are associated with level of urbanization, as well as whether these trends can be generalized among multiple landscapes.

In the remaining two research chapters (ch. 3-4), I focus on one bird species that breeds in both our suburban and rural study sites. The Wood Thrush (*Hylocichla mustelina*), is a neotropical migratory passerine that has shown evidence of population decline (Sauer et al. 2013, 2017, Ahrestani et al. 2017) and has been identified as a species of conservation concern by local and national organizations [e.g., the North American Bird Conservation Initiative (NABCI 2016)]. In chapter three, I compare Wood Thrush nest survival between suburban and rural sites, and use point counts, trail camera surveys, and video nest-monitoring to compare the potential and actual nest predator community between these sites. I use Wood Thrush to investigate a phenomenon described in the urban ecology literature, termed the “predation paradox” (Fischer et al. 2012). This phenomenon describes an increase in potential predators for nesting birds and small mammals in urban areas, compared to rural areas, yet no concomitant increase in actual predation rates (Shochat 2004, Rodewald et al. 2011, Fischer et al. 2012). I ask whether the predation paradox can be observed in this study system and discuss possible mechanisms. In chapter four, I use radiotelemetry to compare Wood Thrush post-fledging survival and movement between suburban and rural sites. I extend questions

about the predation paradox to the fledgling life stage, asking whether patterns observed in nesting Wood Thrush hold true for this understudied (Ausprey and Rodewald 2011, Cox et al. 2014) and demographically important (Donovan and Thompson 2001, Cox et al. 2014) life stage. I also ask if and how post-fledging Wood Thrush movement and habitat use are associated with the level of urbanization.

Taken together, my dissertation forms a unique comparison of avian success in suburban and rural habitats. This research builds on an essential dataset investigating the species- and community-level changes that come with urbanization. It can help to inform management for avian conservation in landscapes with growing human populations and increasingly fragmented forests. Maximizing the potential of suburban forest patches, both for conservation value and human wellbeing, is timely and imperative.

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CHAPTER 2

DISTRIBUTION OF FOREST BREEDING PASSERINES ACROSS AND WITHIN SUBURBAN AND RURAL FORESTS

Abstract

The global growth in urbanization, declines in many avian populations, as well as important psychosocial benefits of birds to people, mean that understanding how to best conserve birds in urbanized landscapes is crucial and timely. We surveyed breeding passerines in two suburbanized landscapes in western Massachusetts, comparing abundances in remanent forest patches surrounded by suburban matrix to abundances in larger swaths of contiguous forest, and asked whether the effects of urbanization were associated with migratory behavior, regional population trend, and/or foraging guild, and whether these trends could be generalized across our two landscapes. We surveyed the forest-breeding bird community using 444 point count surveys between late May and early July in 2013 and in 2014. Results of N-mixture models of 15 species indicated that migratory species and, to some extent, insectivorous species were more likely to respond negatively to urbanization than resident or omnivorous species. We found no clear association between response to urbanization and regional population trend of a species. These patterns held true for both of our landscapes. However, some species also responded negatively to one of the two landscapes. Two species, the Wood Thrush (*Hylocichla mustelina*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), showed no clear response to urbanization and this warrants further study. This study highlights the value of suburban forest patches for many breeding passerines.

Introduction

Understanding how species respond to urbanization is of crucial conservation importance in the 21st century (Aronson et al. 2014). More generally, human land-use change is a major force affecting ecosystem functioning and biodiversity, worldwide (Foley et al. 2005). While urbanization does not cover as much area as agricultural land-use (Houghton 1994, Foley et al. 2005), local extinction rates and the loss of native species are often high in urban areas (McKinney 2002). Globally, urbanization is rapidly increasing in extent (McKinney 2002, Seto et al. 2011) and population (Grimm et al. 2008, United Nations 2014). Concurrently, the amount of wildland-urban interface on the landscape is growing (Radeloff et al. 2005), extending the impact of urbanization beyond its simple outline or footprint. Our knowledge of how natural communities are altered by these processes is increasingly important, not only for conservation, but for human wellbeing (Miller and Hobbs 2002, Russell et al. 2013).

Birds have unique value for human health and wellbeing, and therefore, conservation, in human-dominated areas. Many species are highly mobile, visually and aurally striking, and diurnal. Birds are also widespread, occurring in most habitats around the world (BirdLife International 2013). This means that frequent interactions occur between birds and people. Both feeding and observing birds are popular activities, and birds are the most frequently observed wildlife taxa by urban dwellers in the U.S. (USDOJ et al. 2016). This has important implications for the health and wellbeing of the growing urban population, who are increasingly disconnected from nature (Soga and Gaston 2016). Increased interactions with wildlife and natural areas can bring physical and psychological benefits to urban residents (Russell et al. 2013). Finally, human

interaction with birds and other wildlife has conservation value. People are more likely to attach importance and conservation value to the wild areas where they live if they understand or engage with them (Miller and Hobbs 2002, Ryan 2015). Birds can help draw interest, engagement, and learning about conservation and local wildlife. Conservation of birds where people live is essential, therefore, for both human well-being and for public participation and support for conservation.

Further increasing the urgency of avian conservation in urbanized areas are the results of a recent meta-analysis showing that many bird species in North America and around the globe are declining (Rosenberg et al. 2019). This meta-analysis reported a roughly 29% loss in abundance of North American bird populations since 1970, with about 57% of species in decline (Rosenberg et al. 2019). Given that about 20% of the world's bird species, spanning many families, have been found in cities, including some threatened species (Aronson et al. 2014), the effects of urbanization on bird populations cannot be overlooked. Urbanization alters species assemblages (Blair 1996, Crooks et al. 2004), favoring some groups, such as sedentary or resident species, over others, such as migrants (Chace and Walsh 2006, Croci, Butet, and Clergeau 2008). Although the avian species suffering declines span a large range of taxonomic groups and population sizes, migratory species tend to fare worse than resident species, in general (Rosenberg et al. 2019). Understanding how birds, particularly migrants, are impacted by urbanization can help us protect vulnerable species before it's too late.

In urbanized landscapes, pockets of remnant habitat can hold important value for avian conservation (Ferenc et al. 2014). These patches are often some of the only places in cities where a diversity of native plant species still exists, thus providing habitat for

birds as well as other vertebrates (Faeth et al. 2011). In some cases, remnant patches hold even higher conservation value, per area, than larger, contiguous habitat (Wintle et al. 2019). Even when not serving as core habitat, patches can facilitate connectivity in developed areas (Lindenmayer 2019), especially for mobile taxa, such as birds (Crocini, Butet, Georges, et al. 2008), and can provide essential ecosystem services for people (McKinney 2008, Kim 2016). Finally, they can help increase human connection to nature: small patches of remnant habitat may be the “wildest” places that many urban-dwellers experience on a regular basis. Not only is increased access to nature good for human health and wellbeing (Russell et al. 2013), but better understanding the ecology and conservation value of habitat patches can help engage citizens in conservation of their local habitats and perhaps even provide opportunities for citizen science (Miller and Hobbs 2002, Schuttler et al. 2018).

Over the past few decades, some broad generalizations about the diversity and abundance of birds in urban areas have been proposed. Many studies have found that bird species richness is lower in urbanized areas, compared to corresponding wildlands (Chace and Walsh 2006, Aronson et al. 2014, Evans et al. 2018). This diversity, however, may be higher in low-mid intensity urban lands than in either undeveloped or densely urbanized areas (Chace and Walsh 2006, Padilla and Sutherland 2022). Avian biomass or population density, on the other hand, may increase with increasing development (Chace and Walsh 2006, but see Padilla and Sutherland 2022). In addition, resident bird populations tend to respond more positively to urbanization than migrants (Chace and Walsh 2006, Kark et al. 2007). Non-native bird species tend to respond more positively than native species (Chace and Walsh 2006, but see Aronson et al. 2014). Finally,

granivorous and omnivorous (Crocì, Butet, and Clergeau 2008) birds tend to respond positively to urbanization, while insectivores tend to respond negatively (Chace and Walsh 2006, Kark et al. 2007, Hensley et al. 2019).

These generalizations are not without debate (see Saari et al. 2016, Evans et al. 2018), and several knowledge gaps remain. More fine-grained patterns must be detected to predict the responses of specific avian species to urbanization, in particular regions, and spanning the entire urban gradient. Patterns of species losses with urbanization are likely influenced by a combination of avian life history traits and level or form of urbanization (Evans et al. 2018). Guild responses to urbanization vary by both city and season (Pennington and Blair 2012, Zuckerberg et al. 2016, Hensley et al. 2019), and no single trait, alone, can predict whether a bird species will be able to tolerate (or thrive in) urban areas (Kark et al. 2007, Crocì, Butet, and Clergeau 2008). Within guild, some species may be more sensitive to urbanization than others (e.g. see Rodewald and Bakermans 2006). Which form of urbanization is studied, such as remnant habitat, urban matrix, or both, can also result in disparate results (Evans et al. 2018). For example, urban matrix often supports different species than remnant habitat (Crooks et al. 2004, Pennington and Blair 2012). For some species, the response to urbanization can be meaningfully generalized across the species' range, providing valuable conservation information (Callaghan et al. 2020). However, some species respond to urbanization differently throughout their range, meaning generalizations are not useful (Callaghan et al. 2020). Habitat or predation pressures (DeGregorio et al. 2016) may also vary across a species' range, potentially complicating generalizations. The Wood Thrush, for example, is impacted disparately by the Brown-headed Cowbird across the Wood Thrush's

breeding range (Hoover and Brittingham 1993). Given that Brown-headed Cowbird parasitism is affected by urbanization (Chace et al. 2003), estimating the Wood Thrush's response to urbanization across its range may be complex. For many bird species still found on the urban landscape, particularly those of conservation concern or with declining population trends, understanding variation in response to urbanization is timely and vital.

Many migratory passerines breed in the eastern United States, where both urban and exurban land use have increased dramatically since the middle of the last century (Brown et al. 2005) and where the amount of wildland-urban interface is greater than in most of the country (Radeloff et al. 2005). In addition to declines of North American avifauna more generally, Rosenberg et al. (2019) reported a roughly 17% loss in abundance with about 64% of species in decline for bird populations breeding in eastern North American forests. In this study, we examined bird population responses to urbanization across two "landscapes" in Western Massachusetts. In each landscape, we surveyed breeding passerines in patches of remnant habitat surrounded by suburban matrix and in larger, undeveloped forested areas.

We asked two overarching questions, with associated predictions. First: how do the abundances of individual breeding passerine species differ between suburban and rural forests? Specifically, to what extent are the effects of urbanization associated with migratory behavior, regional population trend, or foraging guild? And second: can these trends be generalized across multiple suburban landscapes within the region?

For the first question, we predicted that neotropical migrants, particularly those with declining population trends, would have negative responses to urbanization, while

residents and short distance migrants would have positive or neutral responses. However, in contrast with studies that focus on the urban matrix, we predicted that negative effects of urbanization would be less dramatic or even absent for some migratory species. If this is the case, it would suggest there is potential for conservation value of suburban forest patches. Given that responses of birds of different dietary guilds can vary based on level or form of urbanization (White et al. 2005), we predicted that foraging guild would be a weaker predictor of response to urbanization in the forest patches than migratory behavior and in contrast to studies that focus on the urban matrix. For the second question, we predicted that within species and guild, the effect of urbanization would be similar across the two study “landscapes”, meaning that generalizations are possible throughout the study area. To the extent that generalizations are not possible, exploration of the differences between these two landscapes can yield greater understanding of the mechanisms behind avian responses to urbanization.

Understanding the responses of individual bird species to remnant habitat in urban or suburban areas may be key for their conservation. For some species, such as many of the migrants in our study, population declines could mean that time is limited. Knowledge about which generalizations can safely be made regarding bird responses to urbanization can help support avian conservation, as well as help direct conservation resources where they are most needed. Harnessing the conservation and social power of remnant habitat in urbanized areas can bring positive change in our rapidly urbanizing world.

Study Area

This study focused on two urbanizing landscapes in Western Massachusetts: a northern landscape associated with the towns of Amherst and Hadley and nearby contiguous forested areas, and a southern landscape associated with the city of Springfield and nearby contiguous forested areas. In each landscape, data collection centered on two study areas, with varying degrees of suburban development. This yielded a total of four study areas grouped into two landscapes (Fig. 2.1), each with a collection of forested sampling locations: 1) forest patches surrounded by low- to mid-intensity suburban development and some agricultural lands, in the towns of Amherst ($42^{\circ}23'N$, $72^{\circ}31'W$) and Hadley, Hampshire County (hereafter, Amherst study area); 2) forested land near the Quabbin Reservoir ($42^{\circ}25'22.33''N$, $72^{\circ}20'48.08''W$) in Franklin County, approximately 15 km east of Amherst (hereafter, Quabbin study area); 3) forest patches surrounded by mid- to high-intensity urban/suburban development in the city of Springfield ($42^{\circ}06'05''N$, $72^{\circ}35'25''W$), Hamden County, approximately 30 km south of the Amherst area (hereafter, Springfield study area); and 4) forested land in the Facing Rock Wildlife Management Area ($42^{\circ}13'7.92''N$, $72^{\circ}27'27.91''W$) in the town of Ludlow, Hamden County, approximately 25 km south of the Amherst and Quabbin study areas and 20 km northeast of the Springfield study area (hereafter, Facing Rock study area).

For the suburban (Amherst and Springfield) study areas, we used forest patches that were identified as part of a concurrent study on nesting Wood Thrush (*Hylocichla mustelina*). Thus, these were patches of forest that contained potential Wood Thrush habitat in the towns of Amherst and Hadley, and in the city of Springfield. Patches were randomly selected from the pool of potentially suitable sites, spanning the available size

gradient. In 2013, we used ten patches in the Amherst study area and five patches in the Springfield study area, adding five patches to each study area in 2014. Many of the Amherst patches are owned by the town as conservation land. Patch size ranged from <5 ha to ~36 ha, but, in the suburban areas, there is some level of connectivity between many of the forest patches. Average elevation of the Amherst study sites is 67m, ranging from 45m to 115m. Average elevation of the Springfield study sites is 61m, ranging from 34m to 79m. These study areas, and Western Massachusetts in general, contain a high proportion of wildland-urban interface (Radeloff et al. 2005), similar to many low-moderately urbanized areas of eastern north America.

The Quabbin study area forest is part of the 10,000-ha Quabbin Reservation, which surrounds the Quabbin Reservoir, and is owned by the Massachusetts Department of Conservation and Recreation. On the reservation, limited timber harvesting occurs and has led to an increase in the amount of forest openings and edge. Facing Rock Wildlife Management Area is an approximately 500-ha property owned by the Massachusetts Department of Fish and Game. It contains foot trails, and two transmission lines run through the property. The average elevation at the Quabbin study site is 273m, ranging from 168m to 335m. The average elevation of the Facing Rock study site is 150m, ranging from 116m to 167m.

All sites are within USDA ecoregion 221a (Eastern Broad-leaf Forest), either the Connecticut River Valley region (221Af) or the Central Uplands region (221Ah). Dominant tree species in the region included red maple (*Acer rubrum*), red oaks (*Quercus rubra* & *Quercus vetutina*), and white pine (*Pinus strobus*). Other common tree species included black birch (*Betula lenta*), eastern hemlock (*Tsuga canadensis*), Ash (*Fraxinus*)

spp., white oak (*Quercus alba*), and sugar maple (*Acer saccharum*). Common mid-understory plants included a number of invasive shrub species [multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera*) spp., Japanese barberry (*Berberis thunbergii*)], as well as native shrubs including *Rubus* spp., highbush blueberry (*Vaccinium corymbosum*), and witch hazel (*Hamamelis virginiana*), and seedlings and saplings of tree species.

Methods

Field methods

Characterizing land use among landscapes

To quantify the landscape context around the sampling locations, we used GIS data to categorize percentage land use within 500m intersecting buffers surrounding the study sites. We condensed land use categories from MassGIS (2005) into three categories, omitting water: non-forested developed (NFDE), non-forested open (NFOP), and forested (FORE) (Appendix 1). We calculated the percent area of each of the three land use categories within the buffers. The NFDE and FORE categories were strongly, negatively correlated, and the NFOP and FORE categories were correlated, to a lesser degree. We therefore removed FORE and retained two land use measures (NFDE and NFOP) to quantify landscape context.

Point counts

We surveyed the forest-breeding bird community, using point count surveys, in 2013 and 2014, between late May and early July (when the spring migration was complete and before the fall migration had begun). Point count stations were at least 250

m apart and at least 50 m from patch edges, and most were located on trails or dirt logging roads (in the Quabbin study area), with little to no canopy gap. In suburban study areas, two stations were located within each forest patch. To minimize the difference in edge effect between our urban and rural sites, at least half of the Quabbin point count stations were placed adjacent to logging cuts (between 50 and 100 m away from the edge of the cut), throughout the study area. Sixty survey locations (i.e., point count stations) were used in 2013: 20 stations in the Amherst study area, 10 stations in the Springfield study area, 20 stations in the Quabbin study area, and 10 stations in the Facing Rock study area. All point count stations were used again in 2014, and an additional 28 stations were added: 8 in the Amherst study area, 10 in the Quabbin study area, and 10 in the Springfield area- for a total of 88 point count stations. At each station, a survey was conducted three times per season (total surveys: 180 in 2013, 264 in 2014). During each survey, a trained observer conducted a 10-minute, 50-m radius count of all birds seen or heard. Surveys were conducted between sunrise and five hours post-sunrise, and we systematically varied the timing of surveys by randomizing the starting location on each day. Surveys were not conducted in windy or rainy conditions. Survey methods were adapted from Ralph et al. (1993) and Manley et al. (2006).

Vegetation surveys

To account for habitat variation within our forested sites, we conducted a vegetation survey in either 2013 or 2014 at each of the point count locations. At each point count location, we centered a five-meter radial plot, counted all live, woody stems reaching knee-height (0.5 m), in two size classes (≤ 2.5 cm = “small”, 2.5 – 8 cm =

“large”). We identified to species and measured the diameter at breast height of all trees in the radial plot.

Statistical analyses

Land use

We used one-way ANOVAs and Tukey multiple comparisons of means to compare the percent NFDE and percent NFOP land use within the buffers among the four groups of sites used in each year.

N-mixture models

We modeled the distribution of forest-breeding bird species using N-mixture models with log-links (Royle 2004). These hierarchical models use marginalization to account for detection in multi-site repeated counts of unmarked animals (Fiske and Chandler 2011). We modeled the two years of data separately to meet the model assumption of population closure (Fiske and Chandler 2011) and because additional sites were used in 2014. Following Smetzer et al. (2014) and Roberts and King (2017), we restricted the analysis to males, and we only modeled the distribution of bird species present in at least 10% of plots; also, all species modeled had at least 30 male observations per year (see Appendix 2 for full species list). We used the package unmarked (Fiske and Chandler 2011) in R version 4.0.3 (R Core Team 2022) to model the distribution of the 15 species (23 species by year combinations) that fit these criteria. We initially included detection variables “OTime”, the start time of the survey, “QTime”, the quadratic start time, ODate, the Ordinal day of the survey, “QDate”, the quadratic Ordinal date, and “Obs”, the observer. Date and Time variables were standardized. Initial environmental variables were “Landscape”, a categorical variable encoding the

northern vs southern landscapes, “Type”, a categorical variable encoding urban vs rural study areas, and “PC1” and “PC2”, two principal components derived from my vegetation surveys. The “Obs” variable was highly correlated with the “Landscape” variable, due to logistical constraints in sampling, so we removed the observer variable. The second principal component was also later removed, as it was not supported in any model for any species.

Principal components analysis (PCA)

We calculated six vegetation variables from the vegetation data we collected: basal area of trees (>10 cm DBH), basal area of small trees (10-22 cm DBH for softwoods, 10-30 cm for hardwoods), basal area of large trees (>22 cm DBH for softwoods, >30 cm for hardwoods) [following Degraaf and Chadwick (1987) to categorize large vs small trees], percent basal area of conifers, density of small stems (≤ 2.5 cm in diameter at knee height), and density of large stems (> 2.5 and ≤ 8 cm in diameter at knee height). Basal area of large trees was strongly correlated with basal area of trees, so we excluded it and conducted a PCA with the remaining five variables. We included the first two principal components as environmental variables for the N-mixture models. The first principal component (eigenvalue = 1.37) loaded negatively for % basal area of conifers and slightly negatively for total basal area (Appendix 3). The second principal component (eigenvalue = 1.15) loaded negatively for large stems and slightly positively for basal area and basal area of small trees (Appendix 3). PC1 can be interpreted to be related to forest composition or forest structure, while PC2 is associated with more forested areas, as opposed to earlier successional areas.

Model selection and ranking

For each dataset, we used a best-subsets approach for model selection, modeling all combinations of variables. We first selected the detection model with the lowest AIC, corrected for small sample sizes. We then used this detection model to select the best environmental models, modeling all combinations of environmental variables with the best detection model. We considered environmental variables supported if they were in any models within two delta AICc of the top model and considered them highly supported if a 95% confidence interval did not contain zero (Burnham & Anderson 2002).

Finally, we summarized model results by bird species. For each species, we included migratory status and foraging guild, obtained from Billerman et al. (2020), and regional population trend, obtained from (Sauer et al. 2013).

Results

Land use comparisons

One-way ANOVAs showed significant differences in both percent of developed land (NFDE) and percent of open land (NFOP) among the four groups of study areas, in both sampling years (all p-values < 0.001; Fig. 2.2). Tukey tests for NFDE showed that both the Amherst and Springfield study areas had significantly higher percentages of NFDE land use than either the Quabbin or Facing Rock study areas ($p < 0.001$). For the 2014 sites, Springfield sites also had a significantly higher percentages of NFDE land use than the Amherst sites ($p < 0.001$). Tukey tests for NFOP showed that the Amherst sites had a significantly higher percentages of NFOP land use than any of the other three groups of study sites ($p < 0.001$).

N-mixture model results

We report results of environmental models selected using the best detection variable by species. For detailed results for each dataset (23 species-year combinations), and for detection variables used, see Appendix 4.

Urbanization was strongly supported in a top model for 13 of the 15 species (Table 2.1). Landscape was strongly supported in a top model for 10 species. The interaction term (Landscape * Type) and the vegetation principal component variable were each strongly supported in a top model for one species. Nine species had two or more variables strongly supported in a top model.

Of the 15 species, five responded positively to urbanization. Three of these five species are residents in the study area while one, the Gray Catbird (*Dumetella carolinensis*), is partially residential and a short distance migrant, and the fifth, Eastern Wood-pewee (*Contopus virens*), is a long-distance migrant. All but the Eastern Wood-pewee are omnivorous. Four of the five species show an increasing or stable population trend in the study area, although the Black-capped Chickadee (*Poecile atricapillus*) also shows a more recent slight decline (Sauer et al. 2013). The fifth species, Eastern Wood-pewee, shows a declining population trend in the study area (Sauer et al. 2013). Gray Catbird and Black-capped Chickadee also responded negatively to the Springfield landscape.

Eight of the 15 species responded negatively to urbanization. All are neotropical or long-distance migrants, except Common Yellowthroat (*Geothlypis trichas*), which has a mixed migration strategy. Three of these eight species show declining population trends in the study area, another three [American Redstart (*Setophaga ruticilla*), Black-throated

Green Warbler (*Setophaga virens*), Scarlet Tanager (*Piranga olivacea*)] show somewhat stable population trends with possible, especially more recent, declines, and the remaining two species show increasing or stable population trends (Sauer et al. 2013). Seven of these species also responded negatively to the Springfield landscape. For one species, the American Redstart, the vegetation variable, PC1, was strongly supported, and for the Red-eyed Vireo (*Vireo olivaceus*), the interaction variable for Landscape * Type was strongly supported.

Two species did not have urbanization in a top model [Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Wood Thrush]. Both species are long distance or neotropical migrants and are omnivorous. Both species show a declining population trend in the study area (the Wood Thrush being of conservation concern) (Sauer et al. 2013). Rose-breasted Grosbeak also showed a negative response to the Springfield landscape.

Discussion

Responses to urbanization

We found that the effect of urbanization on birds differed by migratory behavior. As predicted, resident species tended to show a positive or neutral response to urbanization, while neotropical and long-distance migratory species tended to show negative responses. This supports previous literature on this topic (Chace and Walsh 2006, Croci, Butet, and Clergeau 2008, but see Evans et al. 2018). Our results were also consistent with previous literature for many of the particular species that we modeled (Friesen et al. 1995, Kluza et al. 2000, Rodewald and Bakermans 2006, Loss et al. 2009, but see Loss et al. 2009, which includes urban matrix, for Northern Cardinal) . However, minimal data seem to exist for some species, particularly American Redstart, Black-

throated Green Warbler, and Chestnut-sided warbler (*Setophaga pensylvanica*), and this study adds new information about responses to urbanization for those species.

Responses to urbanization based on diet in this study support the trend that birds with insectivorous diets are more negatively affected by urbanization than those with omnivorous diets (Crocini, Butet, and Clergeau 2008, Hensley et al. 2019). We predicted that support for these patterns would be weak, given the nature of the study sites (forested patches as opposed to urban matrix). For insectivorous species, however, there was fairly strong support. Only Eastern Wood-pewee, the sole aerial insectivore in the study, responded positively to urbanization. Responses of omnivorous species were mixed.

Contrary to our predictions, we found no discernible pattern in response to urbanization based on range-wide population trends (increasing, decreasing, stable). It is noteworthy that range-wide population trends, particularly for individual species, can be subject to interpretation, and that rates of change may not be consistent for larger intervals of time (see Sauer et al. 2013). Furthermore, all the declining species in this study were long-distance migrants, although they varied in diet. The two declining, (non-aerial) insectivorous species responded negatively to urbanization, while the two declining, omnivorous species did not respond to urbanization, and the declining, aerial insectivore responded positively to urbanization. Range-wide population trends, on their own, may not be the best predictor of responses to urbanization.

Three species in this study responded to urbanization differently than predicted based on migratory or diet status, suggesting that generalizations about the response of avian groups to urbanization must be used cautiously and may not apply to every species. The Eastern Wood-pewee was the only declining species, only long-distance migrant,

and only insectivore in the study that responded positively to urbanization (but, notably, this species was the only aerial insectivore in the study). The wood-pewee has been reported with mixed responses to urbanization, responding positively to (low-level) development in some studies (Kluza et al. 2000) and negatively in other studies, albeit to different degrees (Friesen et al. 1995, Rodewald and Bakermans 2006). The two species that did not respond to urbanization in this study, the Rose-breasted Grosbeak and the Wood Thrush, are declining, omnivorous, long-distance migrants. Given the declining regional population trends of these species, this finding, suggesting a neutral response to at least some forms of urbanization for these species, warrants further investigation. Seemingly few studies have measured the response of Rose-breasted Grosbeak to urbanization, although Rodewald and Bakermans (2006) reported a neutral or slightly positive response of this species to urbanization surrounding riparian forest patches.

For Wood Thrush, it was surprising that urbanization was not strongly supported because this species is sometimes seen as an example of a sensitive, forest-interior bird species. Wood Thrush have been found to show a negative response to urbanization (Friesen et al. 1995, Kluza et al. 2000, Rodewald and Bakermans 2006), although the strength of this response has varied from study to study. Our results are not consistent with many of these studies. While variation in our dataset for this species may complicate our findings, our results are consistent with our research on breeding success and nest predation of Wood Thrush in the Amherst and Quabbin study areas, which suggests that Wood Thrush are breeding successfully in these urban forest patches (see chapter three). Factors such as Brown-headed Cowbird (*Molothrus ater*) nest parasitism (minimal in our study areas), regional variation in the nest predator community, and regional habitat

variation are possibilities accounting for differences between our study and those in the western part of the Wood Thrush's breeding range (e.g. Rodewald and Bakermans 2006).

Between landscape comparison

The interaction parameter (Landscape * Type) was only strongly supported for one species, suggesting that most species in this study responded to urbanization consistently between landscapes. This supports our prediction that responses to urbanization can be meaningfully generalized across multiple suburban or urban landscapes within a region for at least some species. The interaction effect was strongly supported for Red-eyed Vireo. Visualizing the data for this species (Fig. 2.3) suggests that, while abundance is lower in both suburban study areas, the effect is weaker for the northern landscape (Amherst and Quabbin) than it is for the southern landscape (Springfield and Facing Rock).

Ten species responded negatively to the southern landscape. One explanation for this finding is the landscape context around the study areas beyond the categorical Type designation ("suburban" and "rural"). While both urban study areas had a higher percentage of developed land than the rural study areas, our analysis of GIS data confirmed a higher percentage of developed land in the Springfield study area, compared to the Amherst study area, for the 2014 study sites. Further, the Amherst area study area had more open land than any of the other study areas. It is feasible that species responding negatively to both the Landscape and Type variable were responding to the increased development in the Springfield study area compared to the Amherst area. The two species which responded positively to urbanization and negatively to the southern landscape (Black-capped Chickadee and Gray Catbird) may have been affected by the

increased open area in the Amherst study area. Gray Catbirds do use habitat associated with agriculture (Smith et al. 2020), so it is possible that this influenced their response to the landscapes. This also supports the idea that avian diversity and the abundances of some avian species are higher in moderate levels of urbanization because of increased landscape heterogeneity (Chace and Walsh 2006, Padilla and Sutherland 2022). The Rose-breasted Grosbeak was the only species that did not respond to the level of urbanization (Type variable) but responded negatively to the southern landscape. Visualizing the data (Fig. 2.4) shows that this species was rarely detected in the southern region at all, while it was detected with similar frequency in the two northern groups of study sites. This result suggests that some species, such as the Rose-breasted Grosbeak, may be responding to variation on a coarser scale than we measured.

The differences between the Amherst and Springfield study areas can also be viewed through a lens of filtering species from a regional species pool (Aronson et al. 2014, Hensley et al. 2019). Hensley et al. (2019) compared bird assemblages between three cities in the U.S. Southwest and found that birds were “filtered” differently among the cities, based on migratory status, dietary guild, and habitat preferences. While our Amherst and Springfield sites are closer together than the cities in that study (<50 km vs >200 km), we can conceptualize the Springfield study area as filtering out more species than the Amherst study area. Some cities can provide habitat for a relatively high subset of the regional avian species pool (Aronson et al. 2014), and understanding the filters for particular cities, such as habitat variables within and near the urban area (Hensley et al. 2019), including residential yards (Lerman and Warren 2011), and bird species

characteristics such as diet guild (Hensley et al. 2019), can be important for conservation in human-dominated areas (Aronson et al. 2014).

Vegetation structure

Only one species, the American Redstart, responded to the vegetation structure variable (modeled as PC1). PC1 was associated with lower percent basal area of conifers, and weakly associated with lower basal area and higher basal area of small trees (Appendix 3). Redstarts had a positive estimate for PC1, which fits with habitat preferences of American Redstarts, preferring deciduous to coniferous vegetation in their breeding range (Sherry et al. 2020). The lack of response to the vegetation variable by all other species in my analysis differs from other work that demonstrated the importance of plant structure and composition in forest patches for occupancy and abundance of certain bird species (Kennedy et al. 2011, Duren et al. 2017). Our results may differ from this literature, in part, because the vegetation structure and composition were measured at a relatively small scale (radial plots around point count locations) within the study sites and because the vegetation structure did not differ drastically among sites.

Study limitations

The inferences of this study may be limited by uneven sampling between the northern and southern landscapes. Additionally, observer identity was removed from the N-mixture models because of correlation with the study landscape. While most of the species in this study were highly detectable, we cannot rule out an effect of observer identity on the results. Two other habitat factors (elevation and soil moisture) were not looked at but were likely correlated with the level of urbanization, and we cannot rule out effects of these factors.

Conservation implications and conclusions

This study supports general findings in the literature that neotropical migrants are more likely to be negatively affected by urbanization than residents or short distance migrants and that insectivorous species are more likely to be negatively affected by urbanization than at least some omnivorous species. Unfortunately, many insectivorous, migratory bird species may respond negatively to urbanization, even within forest patches in a relatively low-density urban landscape with some connectivity between patches, such as those in this study. However, there are exceptions to this trend. Furthermore, the differences between the northern and southern urban study sites suggest that these relationships may be moderated by landscape factors.

We suggest that conservation targeted at overall bird communities might reasonably use these generalizations about avian responses to urbanization, keeping in mind that not all species will follow the patterns. If, on the other hand, the conservation goals focus more on the management of individual species, particularly those that are declining, it is ideal to base decision-making on multiple studies of the target species and not to assume a species will respond identically in different cities or in different regions. Our study also reinforces the conservation value of suburban or urban conservation lands and remnant habitat discussed by others (Wintle et al. 2019). Such habitat should not be overlooked and may support even some of the most sensitive species, such as the Wood Thrush in our region. Research on the responses of individual declining or vulnerable species to urbanization is timely. The conservation value of remnant habitat for some species, such as the Rose-breasted Grosbeak in this study, for example, is unclear. If remnant habitat has little value for a declining species such as this, it may be a higher

priority to focus on protecting more intact habitat, but if remnant habitat does have conservation value, then protecting or improving such habitat where this species breeds or improving connectivity may be an important supplement to other conservation work.

This work has implications, not only for avian conservation, but for the wellbeing of an increasingly urban human population. That remnant habitat can support at least some declining species is hopeful, especially given that the world is becoming increasingly urbanized, and more people are living in urban areas than ever before (United Nations 2014). Capitalizing on forest patches, such as those in this study, for conservation, has the potential to provide opportunities for increasing access to and interaction with nature. This is particularly important given the inequitable access to natural resources that exists in many urban areas, with people of color and those of a lower economic status being less likely to enjoy a diverse bird community where they live (Leong et al. 2018, Warren et al. 2019). Educating and involving the public in the ecology of relatively small forest patches near where they live also has the potential to help increase citizen attachment to the natural world, sense of place (Toomey et al. 2020), and, hopefully, even interest in environmental stewardship (Romolini et al. 2019).

Tables

Table 2.1: Results of N-mixture models by species. Species in bold are declining, based on (Sauer et al. 2013). Diet (O= omnivore, I = insectivore) and migratory guild were obtained from Billerman et al. (2020). Variables are marked (with + or -, indicating direction, for Type and Landscape, and with x for Interaction effect and PC1) if they were strongly supported in at least one year for the given species.

*Varied by error distribution for 2013; see Appendix D for more details

**Mostly migratory, some residential, but migratory in study area; short – long distance migrant

Species	Type: Urban	Landscape: Springfield	Int (T * L)	PC1	Diet	Migration
Black-capped Chickadee (BCCH) <i>(Poecile atricapillus)</i>	+	-			O	Resident
Eastern Wood-pewee (EAWP) <i>(Contopus virens)</i>	+				I	Long-distance migrant
Gray Catbird (GRCA) <i>(Dumetella carolinensis)</i>	+	-			O	Mixed / short distance
Northern Cardinal (NOCA) <i>(Cardinalis cardinalis)</i>	+				O	Resident
Tufted Titmouse (TUTI) <i>(Baeolophus bicolor)</i>	+				O	Resident
American Redstart (AMRE) <i>(Setophaga ruticilla)</i>	-	-		x	I	Neotropical migrant
Black-throated Green Warbler (BTNW; <i>Setophaga virens</i>)	-	-			I	Neotropical migrant
Chestnut-sided Warbler (CSWA; <i>Setophaga pensylvanica</i>)	-	-			I	Neotropical migrant
Common Yellowthroat (COYE) <i>(Geothlypis trichas)</i>	-	-			I	Migrant**

Species	Type: Urban	Landscape: Springfield	Int (T * L)	PC1	Diet	Migration
Ovenbird (OVEN) (<i>Seiurus aurocapilla</i>)	-	-			I	Neotropical migrant
Red-eyed Vireo (REVI) (<i>Vireo olivaceus</i>)	-	-	x		O	Neotropical migrant
Scarlet Tanager (SCTA) (<i>Piranga olivacea</i>)	-				O	Long-distance migrant
Veery (VEER) (<i>Catharus fuscescens</i>)	-	-			O	Neotropical migrant
Rose-breasted Grosbeak (RBGR; <i>Pheucticus ludovicianus</i>)		-			O	Long-distance migrant
Wood Thrush (WOTH) (<i>Hylocichla mustelina</i>)					O	Neotropical migrant

Figures

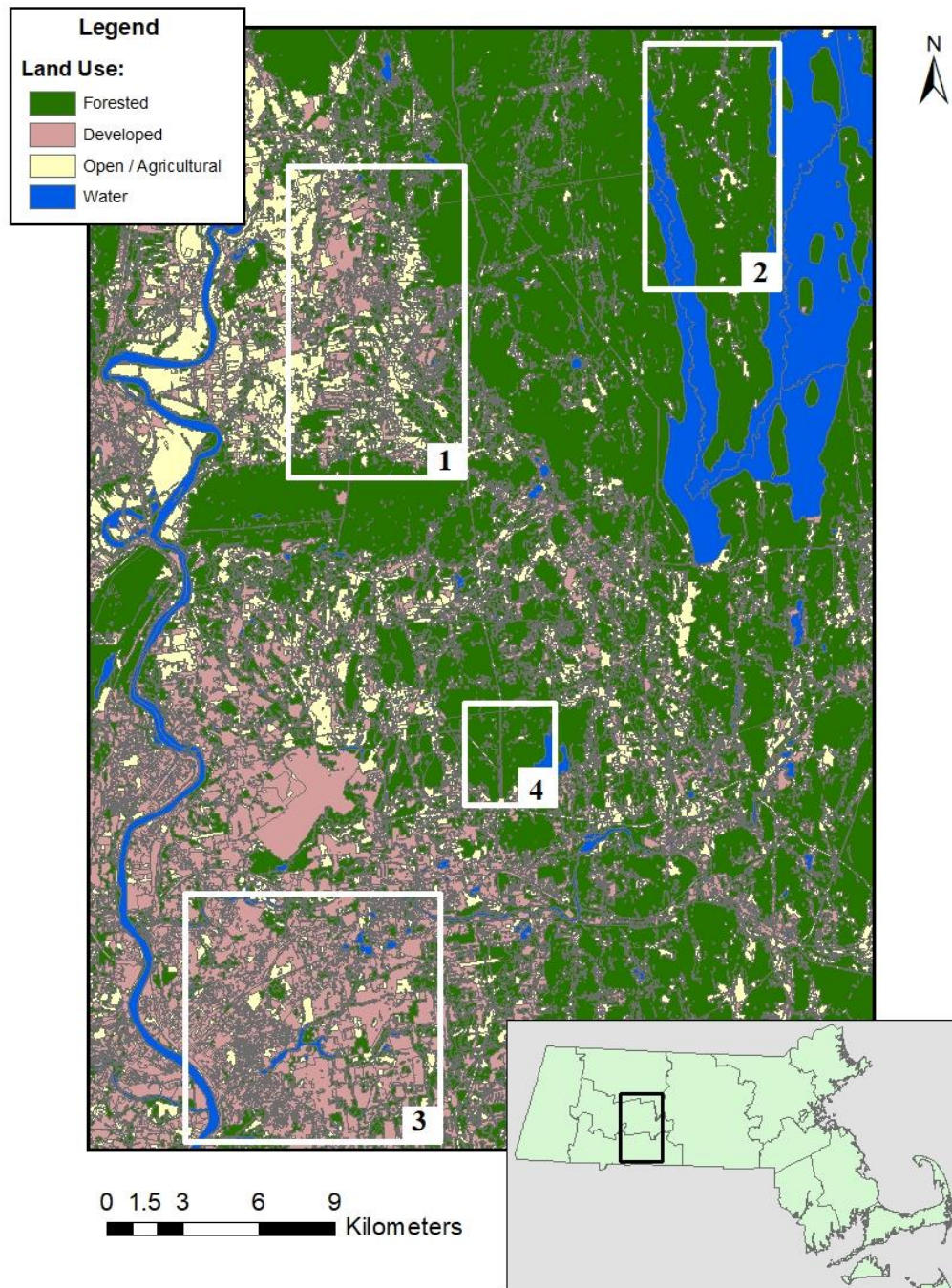


Figure 2.1: Map of the four study areas: 1) Amherst study area, 2) Quabbin study area, 3) Springfield study area, and 4) Facing Rock study area. Land use categories are shown. The inset map of Massachusetts shows county boundaries. Land Use layer from MassGIS (2005).

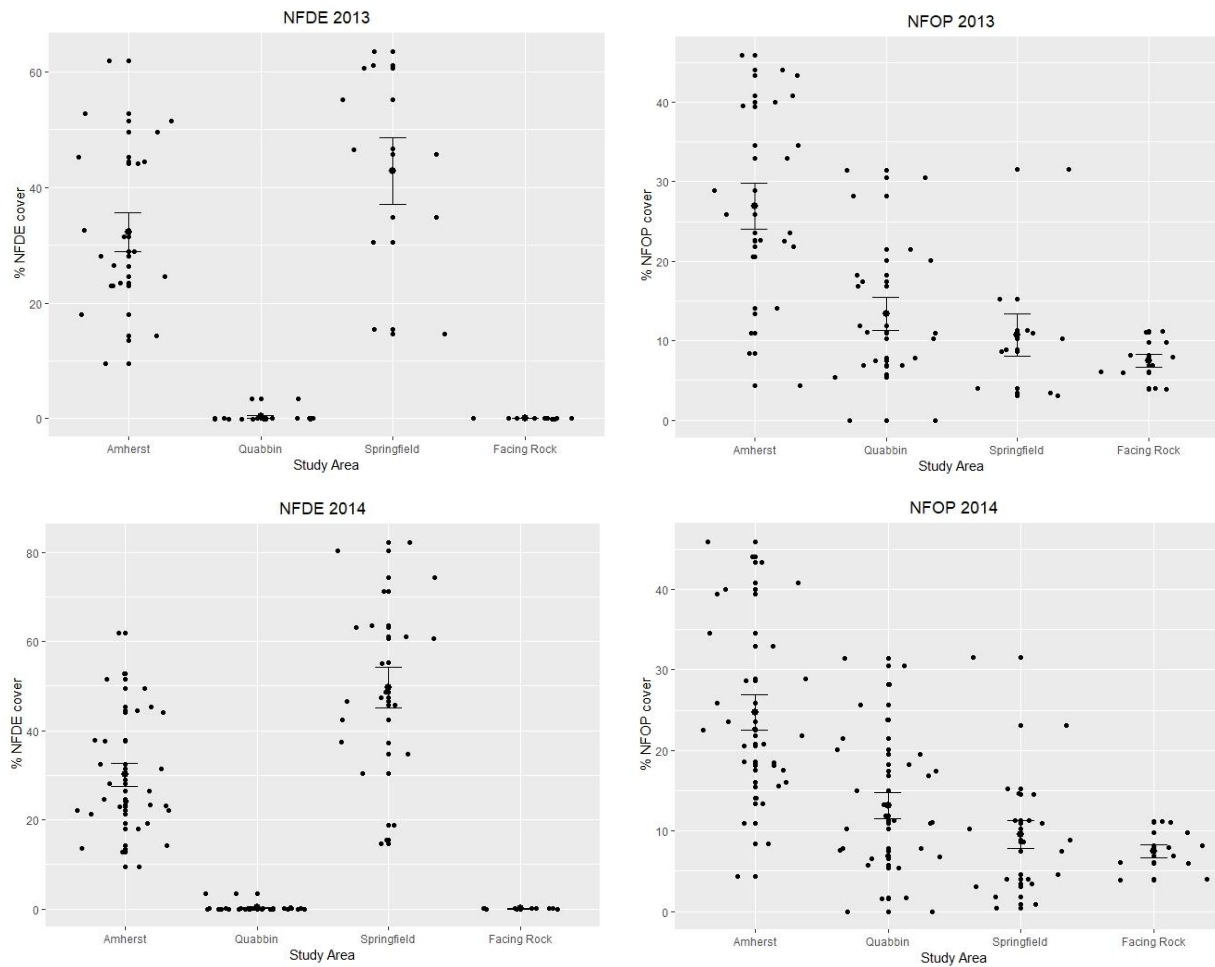


Figure 2.2: Scatterplots (with jitter applied) of percent non-forested Open (NFOP) and non-forested developed (NFDE) land use within 500m buffers around sites in each of four study areas, with mean and standard error bars. Jitter applies a random displacement distance to each point of an otherwise categorical variable to prevent overlapping points. Mean and SEs plotted.

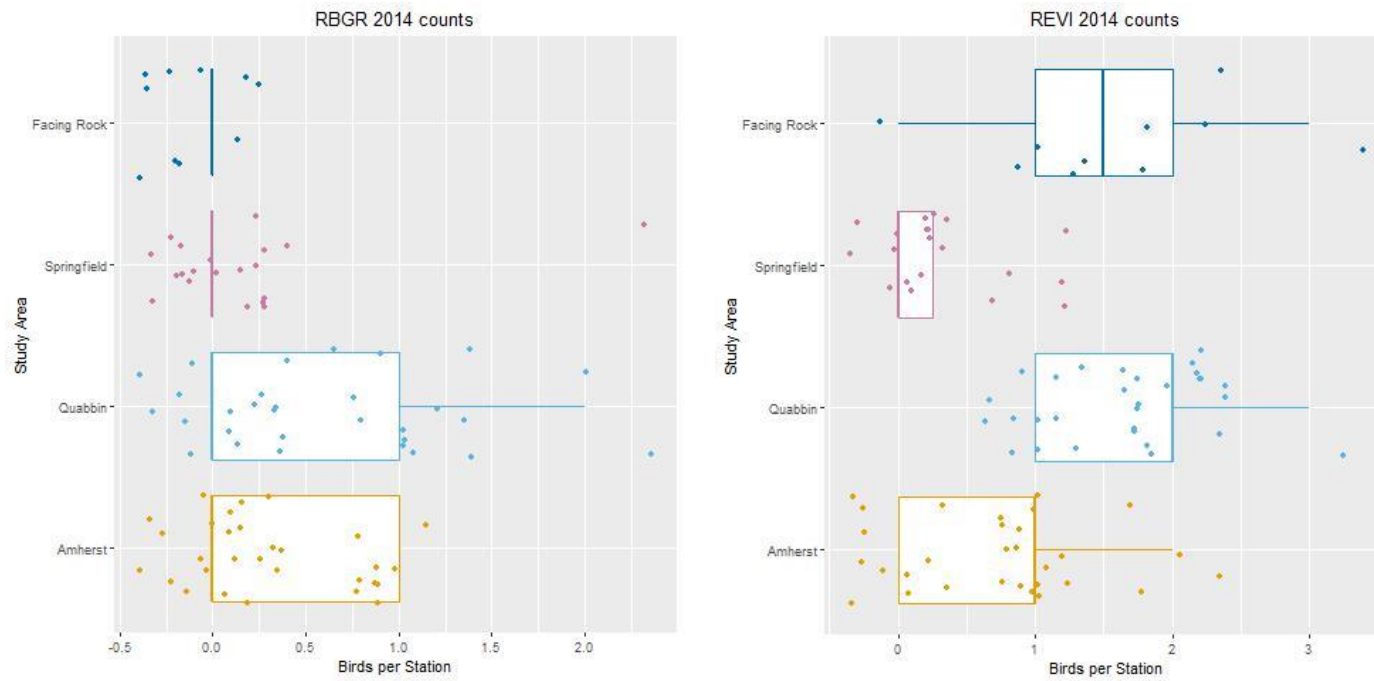


Figure 2.3: Boxplots (with jitter applied) of raw count data for Red-eyed vireo. Jitter applies a random displacement distance to each point of an otherwise categorical variable to prevent overlapping points.

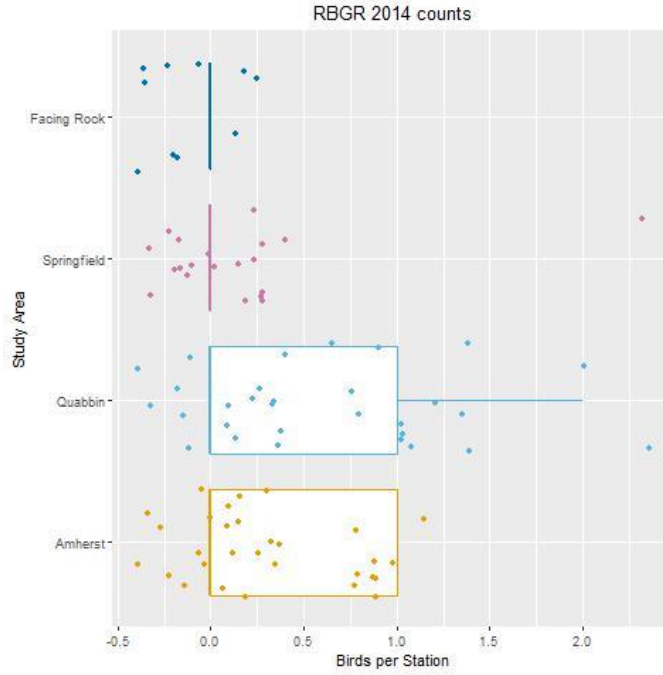


Figure 2.4: Boxplots (with jitter) of raw count data for Rose-breasted Grosbeak. Jitter applies a random displacement distance to each point of an otherwise categorical variable to prevent overlapping points.

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CHAPTER 3

REVISITING THE PREDATION PARADOX IN WESTERN MASSACHUSETTS

Abstract

Despite a high observed abundance of potential nest predators in urban and suburban areas, predation pressure on passerine bird nests has often been reported to be similar or lower in these areas than on undeveloped or rural lands. Understanding this seemingly counterintuitive set of patterns has important conservation value, especially for passerine species experiencing population declines. We surveyed the nest predator community and modeled nest survival of a declining neotropical migrant, the Wood Thrush (*Hylocichla mustelina*), in suburban forest patches and on rural forested land in western Massachusetts. Generalized linear models showed higher counts of potential predators, based on 444 point counts, and more potential predators per trap night, based on 100 trail-camera surveys, in suburban forest patches, compared to undeveloped forested land. We used RMark to model the survival of 253 Wood Thrush nests found over five field seasons. Our results indicated that nest survival of Wood Thrush in our study sites was not significantly different between suburban and rural nests. Our results are consistent with previous findings of counterintuitive or paradoxical patterns of nest predation in urbanized landscapes. We also used video-monitoring to observe a suite of nest predators at Wood Thrush nests, including sciurids and diurnal raptors. We discuss some of the hypotheses that have been proposed for mechanisms to account for the predation paradox, including compositional changes in the predator community and the consumption of subsidies by potential nest predators.

Introduction

Urban and suburban areas are characterized by many ecological changes, including habitat loss and fragmentation (McKinney 2002), altered air temperatures, hydrology, and soil moisture, and increased stream erosion (Pickett et al. 2011). There is less of a consensus, however, about the ecological changes in these areas involving species interactions, such as those related to trophic dynamics. Top-down (i.e. predators) and bottom-up (i.e. food supply) trophic processes are essential parts of the functioning of virtually all ecological communities (Faeth et al. 2005), and both are altered in urban areas, but questions regarding whether or not this translates into generalizable patterns have produced conflicting and variable results (Shochat 2004, Faeth et al. 2005, Shochat et al. 2006, Rodewald and Shustack 2008a, Rodewald et al. 2011, Fischer et al. 2012).

Large and carnivorous predators tend to be rare in urban areas, while mid-level, mammalian, vertebrate predators (mesopredators), which are generally omnivorous, are often present (Iossa et al. 2010) and even survive at higher densities than in non-urban areas (Crooks and Soulé 1999, Sorace 2002, Prange and Gehrt 2004, Chace and Walsh 2006, Rodewald et al. 2011). The increase of mesopredator populations associated with the loss of apex predators, or mesopredator release, has been observed in many ecosystems, including those altered by urbanization (Soulé et al. 1988, Crooks and Soulé 1999, Prugh et al. 2009, Brashares et al. 2010). In urban or suburban areas, this pattern could be a result of direct interaction (or lack thereof) between mesopredators and apex predators, since humans tend to remove or exclude large and apex predators from these areas; or it could simply be a response of both groups to habitat or landscape changes (Litvaitis and Villafuerte 1996, Vance-Chalcraft et al. 2007), since mesopredators tend to

have wide diet breadths and smaller ranges (Iossa et al. 2010). Either way, there is a trend of higher mesopredator densities in urban areas (Fischer et al. 2012). Cascading effects from mesopredator release, in which prey animals are negatively affected by the increase in mesopredators, are also widespread (Faeth et al. 2005, Ritchie and Johnson 2009, Brashares et al. 2010). In addition to native, mammalian mesopredators, introduced mesopredators such as domestic cats (*Felis catus*) are common in residential areas (Sims et al. 2008), and corvids, including crows and jays, tend to thrive in urban areas (Fischer et al. 2012). All of this adds up to a theoretically high predator environment for smaller prey animals, including songbirds (i.e., predator proliferation; Fischer et al. 2012) in urban and suburban areas.

Because predation is the main cause of nest failure in passerine birds (Martin 1993), investigating how urban trophic changes affect nest predation is key to understanding how birds are affected by the urban environment. A wide variety of animals depredate bird nests, including wild mammalian mesopredators (Pietz and Granfors 2000, Renfrew and Ribic 2003, Stake and Cimprich 2003, Peterson et al. 2004, Rodewald and Kearns 2011, Stracey 2011), domestic cats (Renfrew and Ribic 2003, Rodewald and Kearns 2011, Stracey 2011), raptors (Farnsworth and Simons 2000, Pietz and Granfors 2000, Renfrew and Ribic 2003, Stake and Cimprich 2003, Rodewald and Kearns 2011, Stracey 2011, Reidy and Thompson 2012), corvids (Farnsworth and Simons 2000, King et al. 2001, Stake and Cimprich 2003, Peterson et al. 2004, Rodewald and Kearns 2011, Stracey 2011, Reidy and Thompson 2012), Brown-headed Cowbirds (*Molothrus ater*; Pietz and Granfors 2000, Renfrew and Ribic 2003, Stake and Cimprich 2003, Rodewald and Kearns 2011, Reidy and Thompson 2012), other songbirds

(Rodewald and Kearns 2011), rodents (Pietz and Granfors 2000, King et al. 2001, Stake and Cimprich 2003, Rodewald and Kearns 2011, Stracey 2011, Reidy and Thompson 2012), snakes (Farnsworth and Simons 2000, Renfrew and Ribic 2003, Stake and Cimprich 2003, Peterson et al. 2004, Rodewald and Kearns 2011, Stracey 2011, Reidy and Thompson 2012), some large mammals [deer (*Odocoileus virginianus*; Pietz and Granfors 2000), black bear (*Ursus americanus*; Farnsworth and Simons 2000)], and even insects (Stake and Cimprich 2003, Peterson et al. 2004, Reidy and Thompson 2012; and reviewed by Richardson et al. 2009, Degregorio et al. 2016). This suite of nest predators varies considerably among different regions and habitats, as well as among bird species (DeGregorio et al. 2016), and many of these taxa thrive in urban areas. However, despite the high potential predator environment, the survival of both adult and nestling songbirds tends to be similar or greater in urban areas than in non-urban areas, suggesting that the actual predation pressure may not be elevated in urban areas for birds (Rodewald and Shustack 2008a, b, Chamberlain et al. 2009, Rodewald et al. 2011, Fischer et al. 2012, Vincze et al. 2017). Some evidence suggests that the survival of other prey animals, such as rodents, is similarly high in urban areas (Fischer et al. 2012). These incongruous observations- potential vs actual predation have been collectively identified as “the predation paradox” (Shochat 2004, Rodewald et al. 2011, Fischer et al. 2012). Others have also noted that urban trophic dynamics do not follow the “rules” that are typically thought to govern trophic dynamics in non-urban systems (Faeth et al. 2005, Shochat et al. 2006).

More research is needed to determine how widespread the aforementioned phenomenon is; no clear framework exists yet to predict where the predation paradox

occurs or how and where various factors contribute. Studies are needed in a wide array of urban systems, as there may be a great deal of variation from region to region and system to system; many authors have warned against generalizing about urban trophic dynamics (Ritchie and Johnson 2009, Brashares et al. 2010, Vincze et al. 2017) noting that generalizations can sometimes lead to conservation actions having negative effects. For example, habitat heterogeneity and geographic region can affect interactions between apex and mesopredators (Ritchie and Johnson 2009), meaning that the degree to which removing apex predators affects mesopredators may vary among habitats and regions. Productivity and species diversity can also dampen both mesopredator release and the strength of trophic cascades (Brashares et al. 2010). In highly species-diverse systems, the links between apex and mesopredators may not be as strong, in part because of wide diet niches (Brashares et al. 2010). Furthermore, the effectiveness of the specific apex and mesopredator species at capturing prey plays a role in the strength of cascading relationships (Vance-Chalcraft et al. 2007). If only ineffective or opportunistic mesopredators succeed in urban areas, then even with high densities, they may not suppress prey populations (Stracey 2011, Fischer et al. 2012). Lastly, anthropogenic resource subsidies, including water, household trash, bird seed, and fruits from exotic plants, are common in urban areas, but vary in availability, type, and quality (Borgmann and Rodewald 2005, Faeth et al. 2005, Chace and Walsh 2006, Shochat et al. 2006, Robb et al. 2008, Rodewald and Shustack 2008a). Potential nest predator taxa also vary in their diet breadths (Iossa et al. 2010) and ability to utilize anthropogenic foods, and some species may reduce their consumption of vertebrate prey as a result of these supplements

(Rodewald et al. 2011, Fischer et al. 2012). A wide variety of studies are needed in order to form a more complete picture of the predation paradox.

In this study, we aim to contribute to deriving generalizations about the predation paradox by testing the phenomenon in a region where limited such studies have been conducted and where there is a high proportion of wildland-urban interface (Radeloff et al. 2005). We also aim to contribute to the dataset of confirmed predation events at songbird nests, of which little data exists from the study area: we know of only one study that video-recorded predation events at passerine nests in the northeastern United States (King and DeGraaf 2006, DeGregorio et al. 2016). We use a declining bird species, the Wood Thrush (*Hylocichla mustelina*), which is generally associated with mature forest but also breeds in urban forest patches, as a model species.

The Wood Thrush is a forest-nesting passerine that has shown a declining population trend in recent decades (Sauer et al. 2013, 2017, Ahrestani et al. 2017). It has been identified as a species of conservation concern by organizations both locally and nationally, including the U.S. Fish and Wildlife Service (USFWS 2008) and the North American Bird Conservation Initiative (NABCI 2016). While the cause of Wood Thrush population decline is not clear, loss of habitat in its breeding range has been implicated as a potential limiting factor (Rushing et al. 2016). In some, more urban, parts of this species' breeding range, limiting factors are less clear (Rushing et al. 2016). While some studies have found that Wood Thrush respond negatively to development (Friesen et al. 1995), other studies have found that this response varies by region (Phillips et al. 2005) or have not found a clear response (Mancke and Gavin 2000, Newell and Kostalos 2007).

In western Massachusetts, the Wood Thrush breeds in large, remaining tracts of forest, as well as smaller, more isolated forest patches surrounded by urban and suburban development where abundances do not seem to differ from larger forests (Chapter 2). These forest patches provide a natural experiment, allowing the comparison of “suburban” and “rural” Wood Thrushes and their predators. Here, we test whether the predation paradox can be detected in suburban and rural forests in Western Massachusetts. We use the Wood Thrush as our focal species, replicating a similar approach to that which has been used in other landscapes (Rodewald et al. 2011, Stracey 2011). We note that existing work on similar questions for Wood Thrush (Rodewald et al. 2011, Friesen et al. 2013) has been conducted in the western part of the Wood Thrush’s range, where parasitism by Brown-headed Cowbirds is greater than in New England (Hoover and Brittingham 1993), and where the proportion of wildland-urban interface tends to be lower (Radeloff et al. 2005).

Our objectives were to 1) compare counts of potential nest predators, including nocturnal and secretive taxa, between suburban and rural forests, 2) compare nest survival of Wood Thrush in suburban and rural sites, looking at the level of urbanization as well as nest-level factors, and 3) identify nest predators depredating Wood Thrush nests in suburban and rural sites, using nest-level video monitoring. These results will allow us to test for the existence of the predation paradox in western Massachusetts, identify predators of Wood Thrush eggs and chicks, and contribute to a broader dataset on urban trophic dynamics.

Study Area

We collected data in two urbanizing landscapes in Western Massachusetts: a northern landscape associated with the towns of Amherst and Hadley and nearby contiguous forested areas, and a southern landscape associated with the city of Springfield and nearby contiguous forested areas. In each landscape, data collection centered on two study areas, with varying degrees of suburban development. This yielded a total of four study areas grouped into two landscapes (see Fig. 2.1), each with a collection of forested sampling locations: 1) forest patches surrounded by low- to mid-intensity suburban development and some agricultural lands, in the towns of Amherst (42°23'N 72°31'W) and Hadley, Hampshire County (hereafter, Amherst study area); 2) forested land near the Quabbin Reservoir (42°25'22.33"N 72°20'48.08"W) in Franklin County, approximately 15 km east of Amherst (hereafter, Quabbin study area); 3) forest patches surrounded by mid- to high-intensity urban/suburban development in the city of Springfield (42°06'05"N 72°35'25"W), Hamden County, approximately 30 km south of the Amherst area (hereafter, Springfield study area); and 4) forested land in the Facing Rock Wildlife Management Area (42°13'7.92"N 72°27'27.91"W) in the town of Ludlow, Hamden County, approximately 25 km south of the Amherst and Quabbin study areas and 20 km northeast of the Springfield study area (hereafter, Facing Rock study area).

We used the northern sites (Amherst and Quabbin) as a comparison with each other and collected data on both Wood Thrush nest survival and potential predator activity in those sites. We used the southern sites (Springfield and Facing Rock) as a second comparison but only collected potential predator data in those sites.

For the suburban sites, we identified forest patches containing potential Wood Thrush habitat in the towns of Amherst and Hadley and in the city of Springfield. Patches were randomly selected from the pool of potentially suitable sites, spanning the available size gradient. In 2013, we used ten patches in the Amherst area and ten patches in the Springfield area, adding five patches to the Amherst area in 2014. Many of the Amherst patches are owned by the town as conservation land. The area used for nest searching and monitoring in each patch ranged from <5 ha to ~36 ha. Average elevation of the Amherst study sites is 67 m, ranging from 45 m to 115 m. Average elevation of the Springfield study sites is 61 m, ranging from 34 m to 79 m.

The Quabbin study area forest is part of the 10,000-ha Quabbin Reservation, which surrounds the Quabbin Reservoir, and is owned by the Massachusetts Department of Conservation and Recreation. On the reservation, limited timber harvesting occurs and has led to an increase in the amount of forest openings and edge. Facing Rock Wildlife Management Area is an approximately 500-ha property owned by the Massachusetts Department of Fish and Game. It contains foot trails, and two transmission lines run through the property. The average elevation at the Quabbin study site is 273, ranging from 168 m to 335 m. The average elevation of the Facing Rock study site is 150m, ranging from 116 m to 167 m.

All sites are within USDA ecoregion 221a (Eastern Broad-leaf Forest), either the Connecticut River Valley region (221Af) or the Central Uplands region (221Ah). Dominant tree species in the region included red maple (*Acer rubrum*), red oaks (*Quercus rubra* & *Quercus vetutina*), and white pine (*Pinus strobus*). Other common tree species included black birch (*Betula lenta*), eastern hemlock (*Tsuga canadensis*), Ash (*Fraxinus*)

spp., white oak (*Quercus alba*), and sugar maple (*Acer saccharum*). Common mid-understory plants included a number of invasive shrub species [multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera*) spp., Japanese barberry (*Berberis thunbergii*)], as well as native shrubs including *Rubus* spp., highbush blueberry (*Vaccinium corymbosum*), and witch hazel (*Hamamelis virginiana*), and seedlings and saplings of tree species.

Methods

Field methods

Predator point counts

In 2013 and 2014, between late May and early July, we surveyed potential nest predators, using diurnal point count surveys, in all four study areas. Point count stations were located at least 250 m apart and at least 50 m from forest edges, and most were located on trails or dirt logging roads with little to no noticeable canopy gap. In suburban sites, two stations were located in each forest patch. To minimize the difference in edge effect between our suburban and rural sites, at least half of the Quabbin point count stations were placed adjacent to logging cuts (between 50 and 100 m away from edge of the cut), throughout the study area. Sixty survey locations (i.e., point count stations) were used in 2013: 20 stations in the Amherst study area, 10 stations in the Springfield study area, 20 stations in the Quabbin study area, and 10 stations in the Facing Rock study area. All point count stations were used again in 2014, and an additional 28 stations were added: 8 in the Amherst study area, 10 in the Quabbin study area, and 10 in the Springfield area- for a total of 88 point count stations. At each station, a survey was conducted three times per season (total surveys: 180 in 2013, 264 in 2014). During each

survey, a trained observer conducted a 10-minute, 50-m radius count of all potential predators seen or heard. Surveys were conducted between sunrise and five hours post-sunrise, and we systematically varied the timing of surveys by randomizing the starting location on each day. Surveys were not conducted in windy or rainy conditions. Survey methods were adapted from Ralph et al. (1993) and Manley et al. (2006).

Trail camera surveys

In 2013 and 2014, between May and July, we surveyed potential predators, using motion-sensing trail cameras, in the Amherst and Quabbin study areas. We used trail camera surveys to supplement our point count surveys and to account for nocturnal and secretive potential predator species that are more likely to be missed on diurnal point counts (Ancorenaz et al. 2012). In the Amherst study area, one station was located in each forest patch. Twenty survey locations (trail camera stations) were established in 2013: 10 in the Amherst study area and 10 in the Quabbin study area. These stations were used again in 2014, and an additional 10 stations were added: 5 in the Amherst study area and 5 in the Quabbin study area (30 stations total). Trail camera stations were roughly centered in the Amherst forest patches, generally halfway (125 m) between two point count stations, and always in forested habitat. In the Quabbin forest, survey locations were generally approximately 125 m from a point count station, always in forested habitat. We displaced trail camera stations away from logging roads by a randomly selected distance between 10 and 20 m. At each trail camera station, a digital, motion-sensor trail camera (Bushnell Trophy Cam) was deployed for two ten-day periods during each breeding season. The trail camera was attached to a tree, approximately one meter from the ground; it was positioned facing bait, which was attached to a second tree, three

to five meters from the camera. In order to attract both carnivorous and omnivorous mammals, we used bait consisting of a raw chicken leg and ~1/3 dried ear of corn, placed inside a chicken wire cone (adapted from Manley et al. 2006). Trail camera stations were checked and rebaited approximately five days into each 10-day survey period. We set trail cameras to capture up to two images every five minutes.

Nest monitoring

From 2013 to 2017, we searched for Wood Thrush nests during the breeding season in the Amherst and Quabbin study areas. We visited sites starting in early-mid May and located territories based on Wood Thrush song and activity. Nests were located using behavioral and habitat cues, and sites were visited through mid-late July, when Wood Thrush activity declined. We monitored each nest every 3-4 days until it was no longer active. We limited disturbance by not checking nests, or only checking nests with binoculars, when potential predators (e.g. raptors) were seen in the vicinity and by avoiding the creation of dead-end trails to nests (Martin and Geupel 1993, Ralph et al. 1993). When nests were in the building stage or late nestling stage, we checked nests with binoculars, if possible, to minimize abandonment or force-fledging, respectively (Ralph et al. 1993). Nests were considered fledged or failed when there was substantial evidence that a) at least one chick had fledged (e.g. chicks were almost fully feathered at the last active nest check or b) that the nest was depredated (e.g. eggs or chicks too young to fledge disappeared without clear evidence of other environmental causes), following Manolis et al. (2000), or based on video confirmation of fledging or failure for those nests that were video-recorded.

In all years, we monitored a subset of nests using video cameras. Cameras were placed at nests that had a full clutch of eggs, as camera placement during building or laying may increase the change of nest abandonment (Stake and Cimprich 2003), or that had chicks younger than ~9 days old, after which they were at least partially feathered and likely to force-fledge. Because altering nest concealment can affect predation rates (Richardson et al. 2009), we avoided significantly altering the vegetation around the nests: we only clipped minimal small branches or twigs when they directly obscured the camera's view, provided they were not within ~0.5 m from the nest. We note that there is some evidence that video-monitoring can have a small, likely positive, effect on nest survival (Richardson et al. 2009). However, our cameras were small and relatively inconspicuous, we avoided major changes in nest-concealment, and we kept nest visitation virtually identical between video-recorded and non-recorded nests, following recommendations made by Richardson et al. (2009). Furthermore, we did not use video monitoring alone to determine nest survival.

Video systems were partially user built, modeled after (Cox et al. 2012). At each video-monitored nest, a weatherproof, bullet-type security camera (Marshall Electronics V-1214-IR) was installed by a trained observer, no closer than ~1 m from the nest; when possible, the camera was placed 1-1.5 m from the nest, but was sometimes placed as far as 4-7 m from the nest. The camera was secured to a nearby branch, or, occasionally, a wooden stake, using chicken wire. It was then connected to a small, handheld digital video recorder (DVR; Ultra Mini Portable CCTV Security Video Recorder MPEG4), using an SD card to store data. Both the camera and the DVR were powered by a 12-volt sealed lead-acid battery. All equipment, aside from the camera, was concealed in a

Tupperware container ~5-15 m from the nest and covered with a brown or green tarp (for camouflage and additional rain protection). This system allowed continuous video monitoring of nests. Batteries and memory cards were replaced every three days, during standard nest check visits when possible. In 2014, we attached camouflage cloth to the security cameras and the first ~0.25 m of the cables (following King et al. 2001). At nests above approximately three meters, ladders were used to place cameras. Video-recorded nests were monitored on the same schedule as non-recorded nests, with the exception of slightly more conservative nest checks during the older nestling phase (i.e., when nests looked empty with binoculars and there was no adult activity, at non-recorded nests, we had no way of knowing, with certainty, if a nest was empty without looking inside. At video-recorded nests, we were able to err on the side of caution by not approaching nests that looked empty but that possibly contained older nestlings, which were likely to force-fledge upon close approach).

Vegetation sampling

Because nest site selection and nest concealment may be important factors influencing nest predation (Martin and Roper 1988, Borgmann and Rodewald 2004), and because vegetation characteristics may differ between urban and rural areas (Pickett et al. 2011), we collected vegetation data at Wood Thrush nests in 2013 and 2014. Surveys were conducted after nests were no longer active, in August and September. First, we recorded the height and plant species substrate of each nest. Then, five-meter radial plots were centered around Wood Thrush nests. To characterize vegetation structure in each radial plot, we counted all live, woody stems reaching knee-height (0.5 m), in two size classes (≤ 2.5 cm = “small”, 2.5 – 8 cm = “large”).

Statistical analysis

We used generalized linear models (GLMs) with a negative binomial distribution to compare counts of potential predators, based on point count surveys, between years (2013 & 2014) and between suburban and rural sites. For each point count station, for each year, we determined the number of confirmed individuals of each predator species (i.e., the maximum number of individuals observed at any one of the three repeated surveys). We then pooled all species of potential predators for each station. A zero-inflated negative binomial model did not show significance for the zero portion, so we used the negative binomial distribution, which is recommended for over-dispersed count data such as ours (Bolker 2008). We removed one outlier model because it reflected a flock of Common Grackles. We also ran GLMs with a poisson distribution of three subsets of predators: all bird species, corvids only, and all squirrel species.

To compare counts of potential predators detected on trail camera surveys, between years and between suburban and rural sites, we used GLMs with a lognormal distribution, as the data was continuous and skewed but not overdispersed. We acknowledge that using trail camera surveys to estimate relative abundance is contentious (Jenks et al. 2011, Sollmann et al. 2013), and we primarily present these results as a supplement to our point count survey data. For each trail camera station, for each year, we estimated the number of individuals of each species as the maximum number of individuals observed during either one of the two survey periods. We considered photos of individuals of the same species to be the same individual if they were within the same 30-minute window (Yasuda 2004), unless they were uniquely identifiable.

We used program MARK, run through the R package “RMark”, to model daily survival rate (DSR). Program MARK derives maximum likelihood estimates of DSR and variances, numerically. It allows for the inclusion of multiple environmental covariates, including time-varying covariates (Dinsmore and Dinsmore 2007). Categorical, group covariates included were “Site Type”, categorizing nests from suburban or rural sites, and “Year”. Individual covariates included were “Time”, a continuous variable for the day of the year, “Nest Height”, the height of the nest, “NestSub”, the plant substrate where the nest was built, binned into five coarse groups, and “Nest Age”, a continuous variable for nest age, beginning with the first egg laid. Nest Age was estimated from lay dates, hatch date, and / or chick development. We ran a single covariate model with each variable. We also ran two interaction models: Nest Height * Site Type and Nest Age * Site Type. We did not include stem density in our model because we primarily collected vegetation data in 2013 and 2014. However, a 2013-2014 subset model showed no evidence that stem density affected nest survival. We then used Akaike Information Criterion (AIC), corrected for small sample sizes, to rank the models. We considered models within two delta AICc from the top model to be supported, provided that their confidence intervals did not overlap zero.

For each video-recorded nest, we watched video footage from the time period when activity at the nest ceased. While we attempted to confirm the fate of each chick, we counted nests as fledged or failed based on confirmation of at least one chick’s fate in each nest. We tabulated footage type, (failed, fledged, camera failure, etc.) by site type (suburban or rural), year, and predator species detected.

We compared stem density surrounding the nest, nest height, and nest substrate between suburban and rural sites using Mann-Whitney U and Fisher tests.

Results

Potential predator surveys

The “Year” term was not significant in any of the potential predator GLMs, so we present pooled data for 2013 and 2014. The GLMs for Amherst (suburban) vs. Quabbin (rural) point count surveys showed more potential nest predators on Amherst counts than on Quabbin counts ($p = 0.003$; Table 3.1a). The GLMs for Springfield (urban) vs Facing Rock (rural) point count surveys showed more potential nest predators on Springfield counts than on Facing Rock counts ($p < 0.001$; Table 3.1b). Two of the three subsets of point count predators, all bird species and corvids, had significant results (greater in suburban sites), while the third, all squirrel species, did not, perhaps reflecting contrasting patterns of different squirrel species. The GLMs for Amherst and Quabbin trail cameras showed more potential predators detected per trap night on Amherst cameras than on Quabbin cameras ($p = 0.02$; Table 3.2).

We recorded a greater number of gray squirrels (*Sciurus carolinensis*; 21 vs 4) and Blue Jays (*Cyanocitta cristata*; 32 vs 14), and a lesser count of American red squirrels (*Tamiasciurus hudsonicus*; 5 vs 11) in the Amherst study area compared to the Quabbin study area, on our point count surveys. Counts for Blue Jays, gray squirrels, and American red squirrels reflected the same patterns in the Springfield vs Facing Rock study areas. We observed the same trend on our trail cameras for gray squirrels (2.88 vs 0.38 per trap night). Additionally, we recorded raccoons (*Procyon lotor*; 1.47 vs 0.34 per trap night) and Virginia Opossums (*Didelphis virginiana* ;1.36 vs 0.50 per trap night) at a

higher rate and black bears (0.45 vs 1.07 per trap night) at a lower rate in the Amherst study area compared to the Quabbin study area on our trail cameras.

The number of predator species detected with point count surveys (2013 and 2014 combined) was 6 on Quabbin surveys (n = 150), 12 on Amherst surveys (n = 144), 6 on Facing Rock surveys (n = 60), and 7 on Springfield surveys (n = 90). The number of predator species detected with trail camera surveys was 10 on Quabbin surveys and 15 on Amherst surveys. See Appendix B for species observed on point count surveys, Appendix E for species observed on trail cameras, and Appendix F for species accumulation curves of point count surveys.

Nest survival

We located and monitored 335 Wood Thrush nests during five field seasons. Eight nests were likely abandoned, one nest failed due to possible disease, and 14 only had one nest check before fledging; these nests were not included in our analysis. Of the remaining 312 nests, 49 could not be aged and 13 nests did not have nest height and/or nest substrate recorded (three of these overlapped with nests without age). These were not included in the reported analysis. We ran the analysis without the nest age variable, including 299 nests, and found that “Year” was the best model. However, confidence intervals overlapped zero for all years except 2016.

Of the 253 nests included in our analysis from 2013-2017, 185 were coded as fledged (including nests with unknown fates that were censored); 59 of these were Quabbin nests, while 126 were Amherst nests. The other 68 nests were coded as failed; 20 of these were Quabbin nests, while 48 of these were Amherst nests. The confidence intervals of all models, aside from the null model and the “Nest Age” model, overlapped

zero. This included the “Site Type” model, comparing survival between the Quabbin and Amherst study areas for all years combined (Real parameter estimates: Quabbin: 0.985, $se = 0.003$; Amherst: 0.984, $se = 0.002$). “NestAge” was ranked the top model using AIC, and no other model was within 2 delta AICc of this model (Table 3.3). Daily nest survival declined with nest age (Fig. 3.1).

Video-recorded predation

We placed cameras at 197 nests during the 2013-2016 field seasons. Of these, 157 were at Wood Thrush nests, 34 were at Gray Catbird (*Dumetella carolinensis*) nests, and the remaining six included Northern Cardinal (*Cardinalis cardinalis*), Ovenbird (*Seiurus aurocapilla*), Red-Eyed Vireo (x2; *Vireo olivaceus*), Chestnut-sided warbler (*Setophaga pensylvanica*), and Eastern Towhee (*Pipilo erythrophthalmus*) nests. 19% of Quabbin video-recorded nests and 15.7% of Amherst video-recorded nests were confirmed depredated (Table 3.4a). 41.3% percent of Quabbin video-recorded nests and 45.5% of Amherst vide-recorded nests were confirmed fledging at least one chick on video (Table 3.4a).

We identified 11 predator taxa depredating nests on video, 9 of which were recorded at Wood thrush nests (Table 3.4b). The highest proportion of predations at rural nests were by black bears, followed by raptors and then flying squirrels (*Glaucomys sabrinus*; Table 3.4b). However, all bear predations were in 2015 and were confirmed to be the same radio tagged individual with her cubs; this bear had been baited, trapped, and collared on the peninsula as part of another project. The highest proportion of predations at suburban nests were by raptors, followed by squirrels (primarily gray squirrels) and unknown small mammals (Table 3.4b)

Vegetation

A Mann-Whittney U test showed no significant difference in stem density in our radial plots between suburban and rural site types ($p = 0.16$). A Mann-Whittney U test for nest height showed a significant difference ($p = 0.02$); nests in the Quabbin were higher than Amherst nests. A Fisher test showed that the distribution of nest substrates, grouped into five classes, was significantly different ($p > 0.001$) between Quabbin and Amherst nests. However, this mirrored the distribution of available substrate types as measured at point count locations (see supplementary materials).

Discussion

Our findings support the predation paradox phenomenon that has been observed in other studies (Shochat 2004, Fischer et al. 2012, Vincze et al. 2017). We detected significantly more potential predators, using point count surveys, in both suburban study areas compared to their respective rural study areas. We also found more predator detections on trail camera surveys in the Amherst study area compared to the Quabbin study area. These findings align with the first of the two components of the predation paradox: predator proliferation, or an increase in potential predators in urban areas compared to rural or undeveloped areas (Fischer et al. 2012). The second component of the predation paradox is predation relaxation, which refers to reduced predation pressure in urban areas. We found that Wood Thrush nest survival did not differ significantly between the Amherst and Quabbin study areas. While this finding does not explicitly support predation relaxation, our study does demonstrate a decoupling of predator abundance and predation risk, consistent with the predation paradox. In addition, these findings align with many other nest survival studies of songbirds in forest patches, which

have frequently shown no difference in survival between urban and rural areas (Chamberlain et al. 2009, Fischer et al. 2012). Thus, our study fits within the range of apparently paradoxical observations that have been made elsewhere.

Several hypotheses for mechanisms to account for the predation paradox have been suggested elsewhere (Faeth et al. 2005, Shochat et al. 2006, Fischer et al. 2012), variously invoking changes in prey community, predator community, and resource subsidies. It is important to note that a) none of these hypotheses are mutually exclusive (Fischer et al. 2012), and b) the support, or lack thereof, for each of these hypotheses may be region or system specific. Our data provides greater support for some of these hypotheses than others, though none can be outright rejected by our data.

The first of the hypotheses that we address is the “predator composition” hypothesis (Fischer et al. 2012), which states that some of the more effective predator species existing in undeveloped areas are “replaced” by predators that consume proportionally less vertebrate prey in urban areas (Stracey 2011, Fischer et al. 2012). Our predator community data- point count surveys, trail camera surveys, and predator taxa data from the subset of nests that were depredated on video- support the idea that the composition of potential predators of bird nests differs between urban and rural landscapes (Stracey 2011) and offers limited or equivocal support for the predator composition hypothesis. Three potentially important nest predators were either less commonly observed or not observed in our suburban sites: black bears (on trail cameras), American red squirrels (on point counts), and flying squirrels (on trail cameras). Both black bears and flying squirrels were detected depredating a higher proportion of rural nests than suburban nests. While we did not confirm American Red Squirrels depredating

nests, they are known nest predators (King and DeGraaf 2006, DeGregorio et al. 2016). By contrast, the species more commonly observed in suburban areas than in rural areas included gray squirrels (on point counts and trail cameras), Blue Jays (on point counts), raccoons (on trail cameras), and Virginia opossums (on trail cameras). Gray squirrels were confirmed nest predators in both our suburban and rural sites and depredated a higher proportion of suburban nests than rural nests. However, we did not detect any predation by Blue Jays, raccoons, or opossums on video in our study, although these species are also known nest predators (DeGregorio et al. 2016, Malpass et al. 2018) and another species of Corvid, the American Crow, was detected on video depredating a higher proportion of urban nests than rural nests. Our surveys suggest that gray squirrels, alone, could numerically compensate for the reduced numbers of key rural predators, such as black bear, American red squirrel, and flying squirrel. Since suburban Wood Thrush nest survival was no higher than rural nest survival in our study, it is possible that the more abundant suburban nest predators- corvids, gray squirrels, raccoons, and opossums- constitute a weaker predator community than that of their rural counterparts.

The second hypothesis that we address is the “predator subsidy consumption” hypothesis (Fischer et al. 2012); it states that, given the high resource availability, urban predators shift their diets to consume proportionally more non-prey food, meaning that an increase in predators doesn’t coincide with a higher rate of nest predation (Faeth et al. 2005, Chace and Walsh 2006, Shochat et al. 2006, Rodewald et al. 2011, Fischer et al. 2012). This hypothesis relies on the assumption that urban areas contain more non-animal food, in the form of anthropogenic resource subsidies, than rural areas. While we did not quantify anthropogenic resource subsidies in our sites, other studies have suggested that

urban areas contain more anthropogenic food than rural areas (Borgmann and Rodewald 2005, Faeth et al. 2005, Shochat et al. 2006, Rodewald and Shustack 2008a). We cannot support or refute this hypothesis, as we did not collect data on the diet of actual or potential predators in our study system. However, one of the most abundant (potential *and* actual) nest predators in our study was the gray squirrel, which is known to take advantage of urban resource subsidies such as bird food (Bowers and Brawn 1996, Parker and Nilon 2008, Bonnington et al. 2014). It is possible that this species would be depredating even more nests if it weren't for its consumption of supplemental food. It is also possible that raccoons and Virginia opossums, which were commonly recorded potential predators in our suburban sites, but which we did not document depredating any nests, are relying, instead, on supplemental food. We note that nocturnal predators, particularly small-bodied ones, were likely underrepresented in our sample. While our video cameras recorded at night with infrared light, distance to the nest and vegetation made night views extremely variable from nest to nest.

Three other hypotheses for the predation paradox have been suggested in the literature; we do not have evidence relating to these, but we discuss them briefly here. The “prey hyperabundance” hypothesis states that certain prey species become hyperabundant in urban areas because they consume anthropogenic resource subsidies; as a result, urban predators cannot effectively limit the population of these species (Marzluff 2001, Fischer et al. 2012). This is unlikely to apply directly to the Wood Thrush, although our observations suggest, anecdotally, that suburban Wood Thrush may have smaller and denser territories. Next, the “prey specialization” hypothesis describes predators switching their diets to focus on the aforementioned hyperabundant species,

consequently reducing predation pressure on other species (Fischer et al. 2012). The diet switching of raptors has been observed elsewhere (Estes and Mannan 2003, Roth and Lima 2003, Stracey 2011); it is theoretically possible that raptors predation in our study system is affected by raptor consumption of hyperabundant prey in forest fragments, such as small mammal species (Sorace 2002) and / or hyperabundant prey species in the urban matrix surrounding forest fragments, such as the non-native House Sparrows (*Passer domesticus*). Finally, the “prey composition” hypothesis states that prey species that are more sensitive to predation “drop out” of the community in urban areas, leaving a higher proportion of less sensitive or urban adapted species, which are depredated at lower rates (Shochat 2004, Fischer et al. 2012). This hypothesis is better addressed at a larger scale with multiple bird species so we will not address this here.

Again, none of the aforementioned hypotheses are mutually exclusive. It is possible, for example, that some of the predator species that we saw increase in our urban sites are less effective predators than those more abundant in our rural sites, and that, additionally, that they consume more anthropogenic food in urban areas. Based on our results of potential predator assemblage and video-depredations, we suggest that the most likely mechanisms for the predation paradox patterns in our study area, for Wood Thrush, are some combination of predator composition changes, predator subsidy consumption, and prey specialization. Additional studies, especially those on the diet of various predator species and raptor abundance, are needed to disentangle these mechanisms.

It is essential to place our study in context, given that conflicting results between studies may be due, in part, to variation in both study system and species assemblage. One key difference among predation paradox studies is whether the study was conducted

in the urban matrix (e.g. in residential yards) or in patches of native habitat. Since the Wood Thrush is a forest dependent species, we suggest that our study be compared primarily with other studies conducted in native habitat patches. Another factor that may affect results is the portion of the urban-rural gradient that was studied. Our Amherst sites, where our suburban nest survival data was collected, consist of forest patches surrounded by a variety of land use types, including low, medium, and some high intensity urban development as well as pasture, open land, and some agricultural land. Our Springfield sites consist of forest patches surrounded by higher intensity development- mostly medium and high intensity urban development. Future studies of Wood Thrush and other mature forest-nesting birds could include more detailed data collection in forest patches surrounded by higher density urban matrix similar to our Springfield sites. Our study is likely relevant to many declining passerine species, which, like the Wood Thrush, may not be able to breed in patches within more densely developed matrix or in the urban matrix itself. Finally, we observed very low Brown-headed Cowbird parasitism (less than 10 Wood Thrush nests were parasitized throughout all the years of our study) and we did not observe snake predation at any Wood Thrush nests. These findings may be region-specific, as cowbird parasitism of Wood Thrush has been observed at higher rates in other parts of the Wood Thrush's range (Hoover and Brittingham 1993, Trine 1998, Rodewald and Kearns 2011, Friesen et al. 2013) and snake predation has been observed at Wood Thrush nests in other parts of the Wood Thrush's range (Farnsworth and Simons 2000, Williams and Wood 2002).

Management implications and data needs

We cautiously suggest that relatively small, suburban forest fragments may have positive demographic effects for Wood Thrush. In our study, this species had relatively high nest survival, in both suburban forest fragments and a larger, more contiguous forest. However, as discussed above, the matrix surrounding our forest patches contains relatively low-density development, and patterns observed in our study area may not hold true in areas where the matrix is more densely developed. Furthermore, in our study, many of the forest patches are fairly mesic and have some level of connectivity with other suburban forest, as they are managed by the local conservation commission (among other things, the Amherst Conservation Commission strives to protect wetlands, trail connectivity, and wildlife corridors). We do not know whether these factors played a role in Wood Thrush success in our forest patches.

Data on the diets of predators, improved nocturnal video-recording of nests, surveys of potentially hyperabundant prey species in and around forest patches, and surveys of raptors would help to more fully explore the mechanisms driving the predation paradox in future studies similar to ours. Given that the Wood Thrush is declining throughout its range, research on causes of decline other than nest survival should also be investigated. This includes, but is not limited to, chick provisioning, chick condition, post-fledgling survival, and adult condition and survival during wintering and breeding stages (Brown and Roth 2002, Sillett and Holmes 2002, Faaborg et al. 2010, Vitz and Rodewald 2011). Finally, further video-monitoring of passerine nests in the northeast United States is warranted, especially given the high level of urban development in that region (Radeloff et al. 2005).

Tables

Table 3.1: Negative binomial general linearized model results for predator point counts (2013-14).

a) Amherst vs Quabbin sites

Coefficients:				
	Estimate	Std. Error	Z value	Pr (> z)
(Intercept)	0.3989	0.1506	2.648	0.00810**
Site Type: Suburban	0.4446	0.1501	2.962	0.00305**
Year: 2014	0.1354	0.1531	0.884	0.37647
Null deviance: 118.26 on 98 degrees of freedom				
Residual deviance: 108.46 on 96 degrees of freedom				

b) Springfield vs Facing Rock sites

Coefficients:				
	Estimate	Std. Error	Z value	Pr (> z)
(Intercept)	0.40649	0.21917	1.855	0.0636 .
Site Type: Suburban	1.00447	0.22430	4.478	7.53e-06 ***
Year: 2014	0.06033	0.19725	0.306	0.7597
Null deviance: 78.927 on 49 degrees of freedom				
Residual deviance: 55.479 on 47 degrees of freedom				

Table 3.2: Generalized linear model results for trail cameras surveys in Amherst vs Quabbin sites.

Coefficients:				
	Estimate	Std. Error	Z value	Pr (> z)
(Intercept)	0.30929	0.07166	4.316	8.12e-05 ***
Site Type: Suburban	0.18612	0.07661	2.429	0.019 *
Year: 2014	0.04205	0.07819	0.538	0.593
Null deviance: 3.9022 on 49 degrees of freedom				
Residual deviance: 3.4480 on 47 degrees of freedom				

Table 3.3: Wood Thrush nest survival models (2013-2017) AIC output from RMark. n = 253.

Model	# par	AICc	Delta AICc	weight	Deviance
S(~NestAge)	2	539.5277	0.000000	0.581802395	535.5249
S(~Year)	5	542.6585	3.130785	0.121600161	532.6445
S(~NestAge * SiteType)	4	542.6585	3.471427	0.102556834	534.9898
S(~1)	1	542.6585	3.914899	0.082161056	541.4417
S(~NestHeight)	2	542.6585	5.302690	0.041049796	540.8276
S(~SiteType)	2	542.6585	5.896780	0.030500432	541.4217
S(~Time)	2	542.6585	5.916330	0.030203743	541.4412
S(~NestHeight * SiteType)	4	548.6644	9.136657	0.006036366	540.6551
S(~SubstrateGrouped)	5	549.4433	9.915555	0.004089216	539.4293

Table 3.4: Results from video-monitored nests: a) Footage type, b) Predator taxa observed at Wood Thrush nests, c) Predator taxa observed at nests of other bird species.

a) Footage type for all nests with video cameras (2013-2016). Note that for one of the “Not Recorded” videos and one of the “Other” videos, a predator was identified and included in the predator groups in table b. n = 157 Wood Thrush nests, 40 other nests.

Footage Type	Rural	Suburban	Total
Abandoned	4 (6.3%)	3 (2.2%)	7 (3.6%)
Force fledged (by observer)	2 (3.2%)	13 (9.7%)	15 (7.6%)
Force fledged (by predator)	2 (3.2%)	5 (3.7%)	7 (3.6%)
Fledged	26 (41.3%)	61 (45.5%)	87 (44.2%)
Not Recorded	7 (11.1%)	11 (8.2%)	18 (9.1%)
Other	3 (4.8%)	8 (6.0%)	11 (5.6%)
Predation	12 (19.0%)	21 (15.7%)	33 (16.8%)
Unknown	7 (11.1%)	12 (9.0%)	19 (9.6%)
Total	63 (100.0%)	134 (100.0%)	197 (100.0%)

b) Taxa of predators observed on video (2013-2016) at Wood Thrush nests. Includes partial predation and force-fledging due to predators. Only videos with a confirmed predation event are reported here. Raptor spp. includes: *Accipiter spp.*, *Buteo spp.*, Barred Owl (*Strix varia*), unknown small owl [Eastern Screech-Owl (*Megascops asio*) or Northern Saw-Whet Owl (*Aegolius acadicus*)], and unknown raptor. Squirrel spp. includes: Gray squirrel (*Sciurus carolinensis*) and unknown squirrel species.

Predator Group	Rural	Suburban	Total
Black bear (<i>Ursus americanus</i>)	4 (33.3%)	0 (0.0%)	4 (11.8%)
Crow (<i>Corvus brachyrhynchos</i>)	0 (0.0%)	3 (13.6%)	3 (8.8%)
Flying squirrel (<i>Glaucomys sabrinus</i>)	2 (16.7%)	1 (4.5%)	3 (8.8%)
Passerine spp.	0 (0.0%)	1 (4.5%)	1 (2.9%)
Raptor spp.	3 (25.0%)	8 (36.4%)	11 (32.4%)
Unknown small mammal	2 (16.7%)	4 (18.2%)	6 (17.6%)
Squirrel spp.	1 (8.3%)	5 (22.7%)	6 (17.6%)
Total	12 (100.0%)	22 (100.0%)	34 (100.0%)

c) Taxa of predators observed on video at non- Wood Thrush nests. n = 6 at Gray Catbird (*Dumetella carolinensis*) nests and n = 1 at a Chestnut-sided Warbler (*Setophaga pensylvanica*) nest. Snake spp. was either a black racer (*Coluber constrictor*) or black rat snake (*Pantherophis alleghaniensis*).

Species	Rural	Suburban
Accipiter spp	0	1
Buteo spp	1	0
Domestic cat (<i>Felis catus</i>)	0	1
Unknown meso mammal	0	1
Snake spp.	1	0
Squirrel spp.	0	2
Total	2	5

Figures

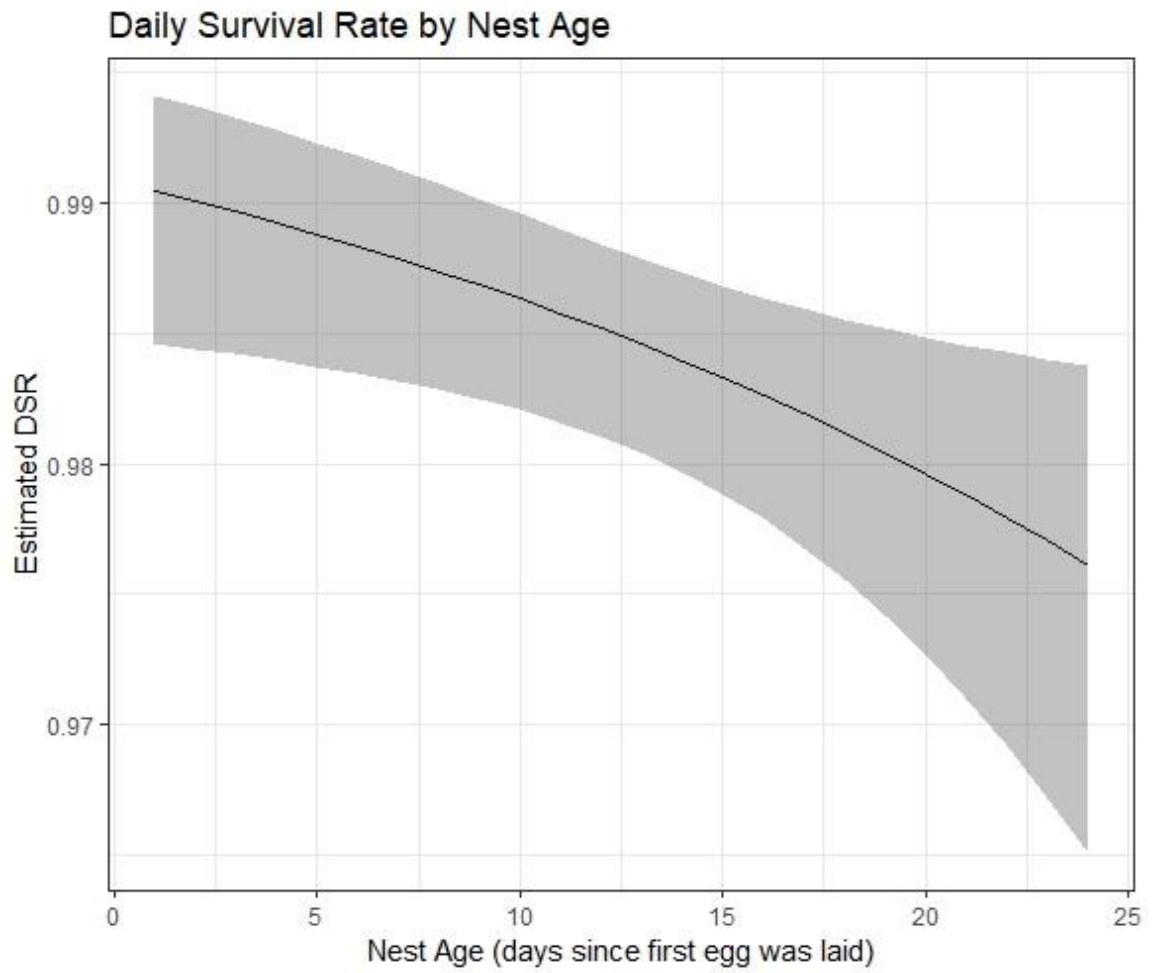


Figure 3.1: Daily survival rate (DSR) of Wood Thrush nests by nest age.

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CHAPTER 4

POST-FLEDGING SURVIVAL, MOVEMENT, AND HABITAT USE OF WOOD

THRUSHES IN A SUBURBANIZED LANDSCAPE

Abstract

Research has shown that suburban forest patches can have important conservation value for birds. This is a hopeful sign, because the extent of urbanization is increasing, many avian populations are declining, and urban areas are where most people interact with wildlife. There is evidence that, despite an increased density of potential predators, breeding success of birds in urban or suburban forest patches is comparable to that in rural areas. However, extremely limited data exists on the fledgling life stage of birds in urban or suburban areas. We used radio telemetry to look at the survival, movement, and habitat use of fledging Wood Thrushes (*Hylocichla mustelina*) originating from nests in suburban forest patches and in larger swaths of rural, undeveloped forest in western Massachusetts. We tracked 168 fledglings over four field seasons and found that survival was similar for rural and suburban fledglings. Fledglings had lower mortality as they aged. Force-fledging and being left outside the nest after radio-tagging had a negative effect on survival, and we developed techniques to minimize its occurrence. We also found that rural fledglings moved farther from their natal nests, at any given age, than suburban fledglings. Fledglings in both types of study site used denser stems than would be expected from availability, and fledglings used a higher proportion of open land cover as they aged.

Introduction

As many bird species experience population decline (Rosenberg et al. 2019), viable habitat within urban and suburban areas, including forest patches, can be key for conservation (Wintle et al. 2019). Despite numerous ecological changes occurring with urbanization, including changes in species assemblages (Iossa et al. 2010, Pickett et al. 2011), many bird species have been found to occupy (Croci, Butet, Georges, et al. 2008; Duren et al. 2017) and breed in (Powell et al. 2003, Brown and Roth 2004, Rodewald and Shustack 2008*b*, Rodewald et al. 2013, Adalsteinsson et al. 2018) urban or suburban forest patches. However, there is a lack of research on the success of birds in these habitats, especially during the post-fledging life stage (Ausprey and Rodewald 2011), when young birds have left the nest but have not yet left on their first migration. This understanding is essential for avian conservation in urbanized landscapes.

Conservation of birds in urban and suburban forest patches is also valuable for people. More people now live in urbanized areas than elsewhere, and the human population in these areas continues to grow (Grimm et al. 2008, United Nations 2014). Many urban dwellers lack the access or opportunity to engage with nature (Turner et al. 2004, Miller 2005), with dire consequences for human health – both physical (Takano et al. 2002, Russell et al. 2013, Soga and Gaston 2016) and psychological (Russell et al. 2013, Soga and Gaston 2016, Cox et al. 2017). Birds may have a particular ability to facilitate human connection with nature, as they are widespread, often diurnal, and many are visually and aurally prominent. Many urban residents find birds appealing (Belaire et al. 2015, Cox and Gaston 2015) and worth conserving (Sharma and Kreye 2022). Birds are also commonly fed and observed by suburban and urban inhabitants (USDOI 2016).

Improving avian conservation in urbanized landscapes, then, has the potential to deepen residents' connection with nature, which, in addition to directly benefiting people, can increase human interest and engagement in nature and conservation (Miller 2005, Ryan 2015, Soga and Gaston 2016).

Numerous changes that occur with urbanization can alter the ecological and species interactions within and around urban and suburban forest patches (Iossa et al. 2010, Shochat et al. 2010, Pickett et al. 2011). Habitat loss and fragmentation (McKinney 2002); altered air temperatures, hydrology, and soil moisture; and increased stream erosion (Pickett et al. 2011) are all characteristic of urbanized landscapes. Species interactions, including competition (Shochat et al. 2010) and trophic dynamics (Faeth et al. 2005), are also altered. For example, large and carnivorous predators often decrease in abundance, while mid-level vertebrate predators, which are generally omnivorous, often increase in abundance in urbanized areas (Crooks and Soulé 1999, Prange and Gehrt 2004, Chace and Walsh 2006, Rodewald et al. 2011). What this means for lower trophic levels, and in particular, predation of nesting birds, has been the subject of numerous studies and discussion (Patten and Bolger 2003, Rodewald et al. 2011, Fischer et al. 2012).

A phenomenon deemed “the predation paradox” has been described in the urban ecology literature (Fischer et al. 2012). The paradoxical findings say that, often, in urbanized areas, there are more *potential* predators for nesting birds and small mammals, as compared to rural areas, yet there is no increase in predation rates (Rodewald and Shustack 2008*a, b*, Chamberlain et al. 2009, Rodewald et al. 2011, Fischer et al. 2012, Vincze et al. 2017). For birds, this work has primarily been conducted during the nesting

life stage, and research on the consequences of altered urban trophic dynamics for birds in the post-fledging life stage (hereafter, “fledglings”) has been minimal.

While fledging is considered “success” in most studies of avian nest survival, a bird must also survive the weeks or months after it leaves the nest before it can become a (potentially) breeding adult. This life stage plays an important demographic role, possibly even more than that of nest survival (Donovan and Thompson 2001, Cox et al. 2014). The rate of mortality soon after fledging can also be higher than mortality during the nestling stage (Naef-Daenzer and Grübler 2016). Despite its demographic importance, the post-fledging life stage, during which time the young birds of many passerine species become increasingly mobile and independent, is understudied compared to other life stages (Cox et al. 2014), particularly in urbanized areas (Ausprey and Rodewald 2011). This is partly because observing the movement or survival of young birds in the weeks or months post-fledging is difficult, as they are both secretive and mobile. In the past few decades, radio telemetry technology has increasingly allowed researchers to observe and track small, mobile animals, including fledgling songbirds. Radio-telemetry during the post-fledging period can now provide valuable data on the movement and survival of young birds, as well as the relative importance of factors affecting post-fledging survival (Cox et al. 2014). However, little information exists about the survival, movement, or habitat use of fledging birds in urbanized areas (Cox et al. 2014, Adalsteinsson et al. 2018).

Key differences between the nesting and post-fledging life stages warrant investigation of predation during the post-fledging life stage. When nestling birds leave the nest and become fledglings, they are much more mobile and, theoretically, may not

stay within forest patches. Therefore, changes in mortality risk or changes in predation may occur, and new sources of mortality, such as from car and window strikes, may occur (Adalsteinsson et al. 2018). Predation and survival can be markedly different between the nesting and post-fledging life stages (Schmidt et al. 2008, Shipley et al. 2013, Jenkins et al. 2016). Thus, relationships between predation and survival in the fledgling stage cannot necessarily be predicted from that of the nesting phase.

Our previous work (Klein et al, in prep) investigated the predation paradox in Wood Thrush (*Hylocichla mustelina*), a declining, forest-nesting, neotropical migrant. We found support for this phenomenon when comparing nest survival and predation between suburban forest patches and a larger, contiguous forested site in western Massachusetts. However, whether these patterns hold true for the post-fledging life stage is unknown.

While a number of studies have looked at survival of post-fledging Wood Thrushes, most have been in intact or managed forest habitat (Anders et al. 1997, Vega Rivera et al. 1998, Lang et al. 2002, Schmidt et al. 2008, Schlossberg et al. 2018), and one in an agricultural landscape (Fink 2003). A few studies have investigated post-fledging survival of Wood Thrush in suburban or urban areas (Powell et al. 2003, Brown and Roth 2004, Adalsteinsson et al. 2018), but no study that we know of has compared suburban and rural fledgling survival of this species. This knowledge is key to understanding the value of suburban forest patches for and the impacts of urbanization on Wood Thrushes and can provide valuable information on suburban predator-prey dynamics, in general.

The first objective of our study was to compare survival of fledgling Wood Thrushes between suburban and rural sites to determine whether there was evidence of the predation paradox (similar survival in suburban and rural sites) for the post-fledging life stage. To do this, we used radio telemetry to track fledgling Wood Thrushes in both suburban forest fragments and larger swaths of rural, undeveloped forest. Our previous work showed that there were more potential nest and fledgling predators in suburban sites than in rural sites (Klein et al. in prep). If the survival of suburban and rural fledglings is not significantly different, this would suggest that the predation paradox, for which we found evidence in nesting Wood Thrushes, also holds true for fledglings. If, on the other hand, survival is different between suburban and rural birds, this would suggest that differences in mobility, behavior, and/or habitat use of fledglings alters their vulnerability to predation or alters the suite of predators compared to that of nestlings.

Fledgling movement and habitat use

In the period between fledging and first migration, Wood Thrushes are not constrained to their natal territory. Young birds may disperse several kilometers from their natal territory just a few weeks after fledging (Anders et al. 1998, Vega Rivera et al. 1998). In suburban forest patches such as our suburban study sites, leaving the natal territory may also mean leaving the natal forest patch- and therefore facing drastic habitat changes (Ausprey and Rodewald 2013). Fledglings may also face barriers to movement that come with the fragmented nature of the landscape (Fink 2003). Furthermore, some aspects of the suburban environment may attract fledglings, such as residential properties containing bird feeders or water (Whittaker and Marzluff 2009) or fruiting plants (Vega Rivera et al. 1998). While movement and habitat use during this life stage is

understudied, especially post-independence (Powell et al. 2003; Streby, Peterson, et al. 2015), there is evidence that fledgling bird movement is influenced by habitat variables such as habitat edge, invasive plants (Ausprey and Rodewald 2013), vegetation structure (King et al. 2006), and fruit availability (Vega Rivera et al. 1998). Fledglings of mature forest-nesting birds, including the Wood Thrush, have also been shown to use, perhaps preferentially, early successional habitat such as regenerating clear-cuts, as well as other denser-than-average vegetation (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006, 2011, Chandler et al. 2012). Effects of using these early successional habitats on survival have been equivocal (Schlossberg et al. 2018, Vernasco et al. 2018). For Wood Thrush, distance traveled from the natal nest as fledglings age can vary from under a kilometer to at least six kilometers (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Powell et al. 2003). What movement and habitat use looks like for post-fledging Wood Thrushes in a suburban landscape, and how that may affect their survival, is an important knowledge gap.

Our second objective in this study was to investigate and compare fledgling Wood Thrush movement and habitat use in the suburban and rural environment. Specifically, we examined how distance traveled from the nest; relative use of forested, developed, and open land; and microhabitat structure and composition are associated with the suburban environment. If the suburban landscape creates movement or dispersal barriers for fledgling birds, then we would expect rural birds to move significantly farther than suburban birds. Conversely, if suburban birds need to cover more land to find suitable habitat, then we would expect them to move farther than rural birds. These scenarios are not mutually exclusive, which could make patterns difficult to detect. Since all nests

monitored in this study were in forested habitat, we expected all very young fledglings to be found, primarily, in forested land. However, given the evidence of fledglings using denser than average vegetation and early successional habitat (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006, 2011, Chandler et al. 2012), we predicted that, as they age and become more mobile, some fledglings would shift to a higher proportion of non-forested habitat. For younger fledglings remaining within forested land, we predicted that they would use denser than average vegetation at the microhabitat scale. Conceivably, some developed land, such as lawns and habitat edges, could be used by fledglings similarly to other early successional habitat. Developed land could also be avoided if it is not seen as viable habitat or, alternatively, preferred if birds are attracted to elements of yards or fruit trees.

Investigating the survival, movement, and habitat use of fledgling Wood Thrushes in suburban forest patches and rural forests can help us better understand the conservation value of suburban forest patches for this declining species. Furthermore, in this study, we investigate two areas of research with scant data: how fledgling birds are affected by urban trophic dynamics, and how movement and habitat use of fledgling birds is altered in the suburban landscape. Understanding can lead to better conservation measures, which benefit both birds and people.

Study Area

Study sites were categorized as “suburban” or “rural”. For the suburban study sites (Fig. 4.1), we identified forest patches containing potential Wood Thrush habitat in western Massachusetts. Patches were randomly selected from the pool of potentially suitable sites, spanning the available size gradient. Five forest patches were used in 2011-

12, and 10 patches were added in 2016-17, for a total of 15 patches. Forest patches were surrounded by low- to mid-intensity suburban development and some agricultural lands, in the towns of Amherst (42°23'N, 72°31'W) and Hadley, Hampshire County. An analysis of a subset of our study sites found that development occupied a mean of 34% of the land area within 2 km of the study sites. Sites generally consisted of mature forest with dense understory, largely consisting of invasive shrub species. Many of the suburban forest patches were owned by municipalities as conservation land. The area used for nest searching and monitoring in each patch ranged from <5 ha to ~36 ha. Average elevation of the suburban study sites was 67 m above sea level.

Five rural study sites (Fig. 4.1) were used for our data collection. These sites consisted of primarily undeveloped lands approximately 10-30 km north and east of Amherst. These sites were in heavily forested, undeveloped landscapes (mean developed area within 2 km = 0.5%). Two of the rural study sites consisted of unmanaged forests, with little recent logging. The other three rural sites were in heavily managed forests with a mean of 21% of area in an early-successional stage. Prior work has revealed that reproductive success and post-fledging survival of Wood Thrushes did not differ between managed and unmanaged rural sites (Schlossberg et al. 2018), so we grouped them for comparison with suburban sites in this study. Average elevation of the rural sites averaged 282 m above sea level.

Dominant tree species in the region included red maple (*Acer rubrum*), red oaks (*Quercus rubra* and *Quercus vetutina*), and white pine (*Pinus strobus*). Other common tree species included black birch (*Betula lenta*), eastern hemlock (*Tsuga canadensis*), Ash (*Fraxinus* spp.), white oak (*Quercus alba*), and sugar maple (*Acer*

saccharum). Common mid-understory plants included a number of invasive shrub species [multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera* spp.), Japanese barberry (*Berberis thunbergii*)], as well as native shrubs such as *Rubus* spp., highbush blueberry (*Vaccinium corymbosum*), and witch hazel (*Hamamelis virginiana*), and seedlings and saplings of tree species.

Methods

My data was collected by two research teams. Data from 2011 and 2012 were collected by my collaborators, from both rural and suburban study sites. Data from 2016 and 2017 were collected by my field crew and myself, from suburban study sites.

Field methods

Nest searching and monitoring

We searched for Wood Thrush nests each year, from early to mid-May, as nesting activity was just being initiated, through mid-late July, when Wood Thrush nesting activity declined. Nests were located using behavioral cues and searching suitable habitat. We monitored each nest every 2-4 days and took precautions, such as avoiding dead end trails and checking nests with extendible mirrors or binoculars, to avoid disturbance and abandonment (Martin and Geupel 1993, Ralph et al. 1993). A subset of nests was monitored with weatherproof video cameras as part of a related study. We monitored nests containing older chicks more frequently (sometimes daily), from a distance, with binoculars.

Radio-tagging and tracking fledglings

Chicks were briefly removed from the nest, banded, measured, and radio tagged at 8 to 10 days post-hatch in 2011-12 and at 10 to 12 days post-hatch in 2016-17. Up to three chicks (median = 2) were banded from each nest. Radio transmitters (*Blackburn Transmitters*, Nacogdoches, TX) were attached using leg-loop harnesses, following Streby, McAllister, et al. (2015). Transmitters and harnesses, combined, weighed ~1.5g. If chicks force-fledged while approaching the nest, we attempted to capture them. In 2011-12, some birds were captured incidentally, after force-fledging from high nests. Because the researchers could not access those high nests, the birds were left on the ground or on a branch below the nest after radio-tagging and banding. In 2011-12, birds that failed to remain in the nest after being replaced (i.e., “force-fledged”) were returned to the nest once after jumping out, and if they jumped out again, they were left on the ground or on a branch below the nest. Due to concerns about the negative effects of force-fledging on survival (Schlossberg et al. 2018), in 2016-17 we took the following precautions when returning birds to the nest: we packed up all equipment and moved away from the nest, while one or two observers approached the nest to return chicks; chicks were positioned carefully inside the nest, with heads facing out. The observer then gently placed an open hand over the chicks for a few seconds, holding the hand there longer if the birds were active upon returning. Observers then left, staying out of view of the chicks, if possible (i.e., the observer’s hand, covering the nest, was higher than the observer’s head). Most chicks stayed in the nest when returned; if a chick force-fledged upon return to the nest, we attempted to return it again and followed the same procedure. If a bird repeatedly force-fledged, we left it under the nest on the ground, but this was an extremely rare occurrence (1 of 38 fledglings).

After nestlings were radio-tagged, an observer returned to the nest 1-2 days later. If birds were no longer in the nest, the fledged birds were located using a handheld receiver (*Communication Specialists, Inc.*, Orange, CA or *Telonics, Inc.*, Mesa, AZ) and Yagi antennae. An observer returned to locate each fledgling approximately every 2-3 days. When fledglings were located, GPS location, bird status (alive/dead) and any other family members present were recorded. Fledglings were tracked until there was evidence of mortality (e.g., transmitter recovered with fledgling body parts), until their tags had been recovered, or until their tags had been active for 6-8 weeks (when the radio transmitter batteries were reaching the end of their lives) and the observer could no longer obtain a clear signal.

Vegetation surveys

To investigate differences between available and used habitat by fledglings, we collected vegetation data for each radio-tagged fledgling, when possible. Vegetation data was collected at each of the first three locations where a fledgling was resighted (not including the nest site, and not including visits when the location of the bird could not be clearly pinpointed). For each of the three locations, we also collected vegetation data at a paired point, 50 m away in a randomly selected direction. At each fledgling and random location, in a five-meter radial plot centered around the point, we collected two kinds of vegetation data: 1) We counted all live, woody stems reaching knee-height (0.5 m) in two size classes (≤ 2.5 cm, or “small” and 2.5 – 8 cm, or “large”), and 2) We conducted a pole contact sub-survey at 12 locations within each radial plot, at one, three, and five-meters from the center of the plot, along the cardinal axes. At each sub-survey, the highest

vegetation contacting the pole, in two categories (≤ 0.5 m, 0.5-3 m) was identified to genus or species.

Statistical analyses

We used program Mark (White and Burnham 1999), run through the R (R Core 2022) package “RMark” (Laake 2013), to conduct mark recapture analysis of post-fledging survival. Program Mark numerically derives maximum likelihood estimates of daily survival rates (DSR) and variances and allows for inclusion of environmental covariates (Dinsmore and Dinsmore 2007). We used “Nest Survival” models in RMark, as these models are appropriate for “ragged” telemetry data such as ours. Group covariates included were “SiteType” (suburban or rural), “Year”, and “Ground”. The Ground variable coded for whether the bird was left on the ground (i.e., force fledged/not successfully returned) or remained inside the nest cup when the observers left the nest. Individual covariates included were “Time” (a continuous variable for the day of the season, starting from the first day a fledgling was tracked) and “FAge” (age of fledgling on each day of the season, starting from the day it left the nest). The FAge covariate was included because post-fledging survival tends to improve with the age of the bird and most mortality occurs within the first few days or weeks of fledging (King et al. 2006, Naef-Daenzer and Gruebler 2016). Because the Year and SiteType variables were correlated ($r = 0.49$), we included a Year*SiteType interaction model. Because the Ground and SiteType variables were slightly correlated ($r = -0.29$) (leaving bird on the ground after tagging was more frequent in the rural sites, in part due to the difference in field protocol), we included a Ground*SiteType interaction model. We also ran the analysis with and without the individuals left on the ground. We removed observations

from any bird that was found dead but was never confirmed alive outside the nest, as these could have been instances of nest predation as opposed to fledgling predation. For birds with uncertain fates, we censored their observations at the last observation where the bird's status (alive or dead) was known. We treated all tagged birds as independent, based on evidence that sibling Wood Thrush fledging fates are not correlated (Adalsteinsson et al. 2018).

We used ArcMap (version 10.8.2) to identify the land use cover type for each resighting location for each fledgling. Land use cover categories, obtained from MassGIS (2005), were binned into three categories: forested, non-forested developed, and non-forested open (see Appendix 1 for categories). To compare land use, standardized by bird, we calculated the percentage of all resights for each bird in each land use category. We then used a Kruskal-Wallis test for each of the three land use bins to test for a difference between suburban and rural sites. To look at land use over time, we calculated the total resights, over all birds, in each of the three land use groups. We then split the resights into the first 3 weeks post fledging, or “early” [roughly the age when fledglings start becoming independent from adults (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003)], and 3+ weeks after fledging, or “late” and compared with a chi-squared test of all birds, as well as a chi-squared test for suburban only and rural only birds. For significant Chi-square test results ($p < 0.05$), we conducted a post-hoc test on the residuals.

For each resight location of each bird, we used ArcMap to calculate the distance (in meters) from the nest (or, occasionally, from the first tracking location due to missing nest data). We then conducted a generalized mixed model (GLMM) with a log gamma link to compare distance from nest between urban and rural birds. Fixed effects were site

type (suburban vs rural) and days since fledge, while random effects were tag number (i.e., individual bird ID) and nest ID. We compared the full model and nested models with AIC. We used a gamma link, as it works well for continuous, positive data w/overdispersion and right skew. However, because a gamma distribution cannot contain zeros, we replaced the zeros (indicating fledglings that remained at or returned to the nest site or very near to it) with 0.25 m (a distance within the margin of error of our GPS units). One fledgling made one much greater movement (over twice the distance of the next largest movement) than any other fledgling. This was a rural bird that apparently crossed the Quabbin Reservoir in 2012. This movement was over 15 standard deviations (sd) from the mean, while other outliers in this dataset were between three and six sd from the mean. We ran the GLMM with and without this outlier to see what effect this datapoint had on our results.

We used paired Wilcoxon tests to compare small and large stem density between fledgling resight (i.e., used) and random (i.e., available) points. We used unpaired Wilcoxon tests to compare small and large stems between suburban and rural sites (for used and available points separately).

To examine vegetation composition, we calculated the percentage of upper pole contacts (0.5-3 m) of each plant species or plant category across all birds in four categories (used – suburban, used – rural, available – suburban, available – rural). We combined unidentified or inconsistently identified plant species, as well as species with < 5 contacts per category into “other”. This resulted in eight categories of plants (Appendix 2). We then ran chi-squared tests to compare used and available vegetation for suburban birds, used and available vegetation for rural birds, and used suburban vs. used rural

vegetation. Finally, we used Chi-square post-hoc tests to determine which plant groups accounted for differences between groups.

Results

We radio-tagged 177 fledglings over four field seasons. Nine birds were removed from the dataset for the mark-recapture analysis because they were never confirmed alive post fledging. This left 168 fledglings: 99 rural birds from 43 nests and 69 urban birds from 37 nests (fledglings per year: 40 in 2011, 90 in 2012, 36 in 2016, and 2 in 2017). During the course of the study, 30 birds were left on the ground after tagging: 29 of 130 (~22%) fledglings in 2011-12, and 1 of 38 (<3%) fledglings in 2016-17. Of the 168 birds in the survival analysis, 18 rural birds and 13 suburban birds were found dead during our study. All deceased birds had evidence of predation (i.e., several feathers, feet, and/or other body parts).

In the survival analysis, fledgling age (FAge) and being left on the ground after radio tagging (Ground) were the only parameters that affected fledgling survival. Fledgling age positively affected daily survival rates (DSRs), while being left on the ground after radio tagging negatively affected DSRs (Fig. 4.2). CIs did not overlap zero for the intercept only model, fledgling age model, ground model, nor the (Ground + FAge). Interaction effects of both interaction models (Ground*FAge, Ground*SiteType) had CIs that overlapped zero. The confidence intervals for the Time (ordinal day), Year, and SiteType models overlapped zero. AICc ranked the Ground*FAge interaction model as the top model, followed by the additive Ground+FAge model (within 2 delta AICc; Table 4.1). We did not include the Year*SiteType interaction model in our final model set because the CIs of both single variable models overlapped zero.

For the survival dataset with force-fledged birds removed, there were 138 fledglings: 72 rural birds from 30 nests and 66 urban birds from 36 nests. All models for this dataset, aside from the null model and the fledgling age model, had confidence intervals overlapping zero. AICc ranked fledgling age as the top model and no other models within two AICc.

The dataset for the land use tests contained 149 fledglings: 92 rural birds from 41 nests and 57 suburban birds from 34 nests. As expected, based on the level of development near the study sites, fledglings from rural sites used a higher proportion of forested land compared to fledglings from suburban sites (Kruskal-Wallis test; $H = 10.28$, $p = 0.001$; Fig. 4.3), while fledglings from suburban sites used a higher proportion of developed land compared to fledglings from rural sites (Kruskal-Wallis test; $H = 36.78$, $p < 0.001$; Fig. 4.3). There was no difference in proportion of open land used between fledglings from suburban and rural sites (Kruskal-Wallis test; $H = 1.31$, $p = 0.25$; Fig. 4.3). Land use by fledglings changed over time for all birds (Chi-square test; $\chi^2 = 25.45$, $p < 0.001$) and for rural birds only (Chi-square test; $\chi^2 = 15.92$, $p < 0.001$). The proportion of open land used was less in the first three weeks post-fledging compared to later weeks for all birds combined (Chi-square post hoc test; $p < 0.001$) and for rural birds only (Chi-square post hoc test; $p < 0.001$; Fig. 4.4). Conversely, proportion of forested land used was greater in the first three weeks post-fledging compared to later weeks for all birds combined (Chi-square post hoc test; $p < 0.001$) and for rural birds only (Chi-square post hoc test, $p < 0.001$; Fig. 4.4). A similar trend of increasing proportion of open land used and decreasing proportion of forested land used over time was also observed for urban

birds only, but these trends were only marginally significant (Chi-square test; $\chi^2 = 5.22$; $p = 0.07$; Fig. 4.4).

The dataset for distance from nest GLMM contained 149 birds: 92 rural birds from 41 nests, 57 suburban birds from 34 nests. AIC ranked the full model (Fixed effects: site type, days since fledge; random effects: tag number, nest ID) as the top model (Table 4.2). Distance from nest increased with time since fledging ($\beta = 0.07$, $p < 0.001$; Fig. 4.5), and rural birds traveled significantly farther than suburban birds ($\beta = -0.41$, $p < 0.001$; Fig. 4.5). We subsequently included year as a random effect, given the relationship (see statistical methods) of site type and year, but this did not have any effect on the results so we do not report those values. Neither the direction nor significance of any GLMM coefficient was affected by the removal of the largest outlier (Fig. 4.5), so the outlier was retained.

We analyzed vegetation structure at resight (“used”) and random (“available”) points for 105 birds: 82 rural birds from 37 nests and 23 suburban birds from 19 nests. Vegetation stem density was greater at used points than at available points for both suburban and rural fledglings (paired Wilcoxon tests; suburban small stems: $V = 1287.5$; $p = 0.01$; suburban large stems: $V = 1111$, $p < 0.001$; rural small stems: $V = 16614$; $p = 0.004$; rural large stems: $V = 15754$, $p < 0.001$; Fig. 4.6a,b). The density of small stems was significantly greater at used suburban points compared to used rural points (Wilcoxon test; $W = 4880.5$; $p < 0.001$) and was also significantly greater at available suburban points compared to available rural points (Wilcoxon test; $W = 5501.5$; $p = 0.005$). The density of large stems was marginally greater at used rural points than at used suburban points (Wilcoxon test; $W = 8169$; $p = 0.09$; Fig. 4.6c,d) and was significantly

greater at available rural points than at available suburban points (Wilcoxon test; $W = 8861.5$, $p = 0.004$).

The dataset used for vegetation composition contained 118 birds: 95 rural birds and 23 suburban birds. Composition surveys were from 683 vegetation surveys: 561 in rural sites and 122 in suburban sites. Suburban birds used vegetation groups proportionally to availability (Chi square test; $\chi^2 = 9.16$; $p = 0.1$; Fig. 4.7), while rural birds used eastern hemlock more and ferns less than would be expected from availability (Chi square test; $\chi^2 = 66.86$, $p < 0.001$; Fig. 4.7). The composition of available plants was different for rural sites than for suburban sites (Chi square test; $\chi^2 = 466.9$, $p < 0.001$; Fig. 4.7). White pine and native deciduous broadleaf plants each made up a greater proportion of available vegetation at rural points compared to suburban points, while nonnative broadleaf plants made up a greater proportion of vegetation at suburban points compared to rural points (see appendix three for post hoc test p values). Accordingly, rural birds used a higher proportion of white pine and a lower proportion of non-native broadleaf plants than did suburban birds. Rural birds also used a higher proportion of eastern hemlock than did suburban birds (Chi square test; $\chi^2 = 445.17$, $p < 0.001$; Fig. 4.7).

Discussion

The survival of fledgling Wood Thrushes in this study did not differ between suburban sites and rural sites. This is a hopeful indication of the ability of suburban forest patches to support viable populations of this declining species, particularly in light of the critical importance of the fledging life stage for driving population trends. Examining the movement and habitat use of fledgling Wood Thrushes in our study system gave more

support for the viability of suburban forest patches, as most suburban fledglings spent the majority of their first few weeks post fledging within their natal forest patch, and the differences between suburban and rural habitat use were not drastic. However, our results did highlight some clear differences in movement or mobility of suburban and rural birds, as well as some differences plant species used.

Fledglings and the predation paradox

Our results on fledgling survival align with previous findings on nest survival and the predation paradox, in the literature (Rodewald and Shustack 2008a,b, Chamberlain et al. 2009, Rodewald et al. 2011, Fischer et al. 2012, Vincze et al. 2017) and in our previous work (Klein et al. in prep.) Despite evidence from our previous work, in an overlapping set of study sites, that there are significantly more potential predators for young Wood Thrushes in suburban areas than in rural areas (Klein et al. in prep), fledgling survival did not differ significantly between suburban and rural sites. To the best of our knowledge, this is one of the first studies comparing fledging survival between urban and rural habitats (and see Ausprey and Rodewald 2011), providing evidence of the predation paradox beyond the nesting life stage for birds.

Several hypotheses for mechanisms accounting for the predation paradox have been proposed (Fischer et al. 2012). We did not directly test these in this study, but we suggest that our findings may support two of these hypotheses. First, the predator composition hypothesis posits that the suite of predator species is altered in urban or suburban sites, compared to that in rural sites, and that the urban predators are weaker or more omnivorous predators (Fischer et al. 2012). Data from our previous work (Klein et al in prep.) suggests that the composition of suburban and rural predators are different

from each other in our study landscape. Furthermore, some of the most common confirmed predators on egg or nestling Wood Thrushes in that study, such as species in the sciurid family, are small-bodied and may not be able to depredate fledglings easily. The second hypothesis is the predator subsidy consumption hypothesis, which posits that the diet of predators in suburban or urban areas shifts to contain fewer depredated animals and more anthropogenic food resources (Rodewald et al. 2011, Fischer et al. 2012). Again, sciurids are common potential predators in our suburban study landscape, and they are an omnivorous and opportunistic species that are known to take advantage of human-provided food resources. Other common potential predators in our study system, including raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and birds in the corvid family, are also omnivorous and may use suburban resource subsidies (Rodewald et al. 2011, Fischer et al. 2012). These two hypotheses are not mutually exclusive. Further research is needed to identify mechanisms for the predation paradox patterns for both nesting and fledgling birds.

While predation has been documented as the primary source of mortality for fledgling birds, even in urbanized landscapes (Ausprey and Rodewald 2011, Shipley et al. 2013, Naef-Daenzer and Gruebler 2016, Adalsteinsson et al. 2018), some studies have recorded anthropogenic causes of mortality as well. Adalsteinsson et al. (2018) documented both car and building strikes as a cause of death for some post-dispersal Gray Catbird and Wood Thrush fledglings, and Jackson et al. (2011) observed mortality due to window strikes in Eastern Bluebird (*Sialia sialis*) fledglings. We did not record any sources of direct anthropogenic mortality in this study.

Fledgling habitat use, movement, and urbanization

We found that rural fledglings moved significantly farther from the nest than did suburban birds. Because fledgling Wood Thrushes stay with one or more adults in the first few weeks after fledging (Anders et al. 1998, Vega Rivera et al. 1998, Rivera et al. 2000, Fink 2003), this could be a function of adult habitat selection, at least during the first few weeks post fledging. Research has shown that adult Wood Thrushes and similar species can be either relatively sedentary or relatively mobile while tending to fledgling birds (Anders et al. 1998, White and Faaborg 2008), in part based on whether or not they are raising another brood (Rivera et al. 2000). However, given that rural fledglings moved farther than suburban fledglings at all ages (Fig. 4.5), it is likely that fledgling habitat selection itself also played a role in this trend. This could suggest that, similar to Wood Thrushes in other fragmented habitats (Fink 2003), suburban birds face more barriers to dispersal than rural birds. Another possibility is that suburban fledglings were able to take advantage of resources, such as fruit, available in forest patches, thereby reducing their need to travel. Vega Rivera et al. (1998) suggested that foraging is a key factor motivating fledgling movement.

As in other studies (Zhou et al. 2022), fledglings in our study moved farther from the nest as they got older (Fig. 4.4). Regardless of age, however, most suburban birds were found in forested land cover (Fig. 4.3), supporting the idea that developed land cover may have created barriers to movement for fledglings. Maps of fledging movement (Fig 4.8) suggest that some suburban fledglings that moved outside of forest patches followed forested, and possibly open-land, corridors.

While fledglings of all ages were found primarily in forested land cover (Fig. 4.3), rural fledglings used a lower proportion of forested habitat, and a higher proportion of open habitat, as they aged. Visualizing the data over time suggests similar patterns for suburban birds, albeit not statistically significant (Fig. 4.4). This supports our prediction that older, more mobile fledglings would use a greater proportion of early successional habitat than younger fledglings. It also supports literature suggesting that fledglings of mature forest nesting bird species may prefer early successional habitat (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006, Chandler et al. 2012). Suburban fledglings used developed land at a similar rate to open land, at least initially. We observed a small number of older (post-dispersal age) fledglings using suburban yard vegetation and we observed fledglings of varying ages using edge habitat in a quarry. However, most fledglings did not use developed landcover (Fig. 4.3), and, overall, our findings suggest that developed areas in our study area were generally avoided by suburban fledglings. Developed land was virtually unavailable for rural fledglings.

Both suburban and rural fledglings used areas with denser stems than would be expected based on availability. This supports our prediction and aligns with other studies that have found that fledgling Wood Thrushes (Anders et al. 1998, Vega Rivera et al. 1998) and fledglings of other mature forest nesting bird species (Vitz and Rodewald 2011) use denser than average vegetation. Furthermore, despite differences in stem density between our rural and suburban sites (rural sites had a greater density of large stems and a lower density of small stems than suburban sites), fledgling survival did not differ, suggesting that fledglings were able to find protective cover in both types of sites. This finding is in line with other work, which has found that the use of dense, understory

vegetation may help protect fledglings from predation in both fragmented and unfragmented habitat (Fink 2003, Cox et al. 2014), and that dense tangles of invasive shrubs have no negative affect on fledgling bird survival (Ausprey and Rodewald 2011). The differences in stem density between suburban and rural sites is likely a reflection of species composition, as we found a higher proportion of white pine (which tends to form stands of “large” stem size saplings) in rural sites and a higher proportion of nonnative woody shrubs (often forming thickets with many “small” stems) in suburban sites. Our finding of only relatively minor differences in the composition of used vegetation between suburban and rural fledglings (Fig. 4.7) also supports the idea that fledgling can find the vegetative habitat they require in both types of sites.

Force-fledging reduced fledgling survival

Force-fledging, when a nestling leaves the nest before the expected age and level of development, is usually a response to a potential predator. The effects of force-fledging by research observers on the health or later survival of birds has not been studied extensively (Streby et al. 2013). The little work that exists found no negative effects of observer force-fledging on fledgling survival (Streby et al. 2013). Our findings, and previous work published by our collaborators on a subset of the same birds (Schlossberg et al. 2018) demonstrates that observer force-fledging can have detrimental effects on the survival of fledging Wood Thrushes, at least when radio-tagged birds are not successfully returned to the nest after handling (Fig. 4.2). This has important implications for studies of nesting passerines, particularly for vulnerable or declining species. We developed techniques that successfully encouraged nestlings to stay in the nest: ~22% of fledglings were left outside the nest in 2011-12, before the adoption of these techniques, while <3%

of fledglings were left outside the nest in 2016-17, after the adoption of these techniques. These techniques included packing up all belongings before placing nestlings back in the nest and holding a hand over nestlings in the nest to help them settle back down. We suggest that similar methods be used, and that more caution exercised when handling nestling Wood Thrushes and other vulnerable species.

Study limitations and future directions

While our rural and suburban data were collected by different observers and in different years, we have no reason to believe this impacted our results. Radio-tracking methods were consistent across years, except where discussed above. Neither Year nor SiteType were top models in our survival analysis, and the interaction of these terms was not significant. Including a random effect of year in our GLMM did not alter the results. One other limitation comes from the technology we used. Battery life likely limited the amount of data we could collect on older fledglings. It is also possible that tracking birds that dispersed was more difficult in suburban sites than in rural sites, given the barriers and interference that can be caused by buildings and infrastructure. Finally, our sample size of suburban birds was smaller than that of rural birds. This, combined with the high survival of fledglings in our study, reduced the power of subsets of survival data, and therefore we could not include land use or distance from nest in the survival models.

Given the differences in distance moved from the nest between suburban and rural fledglings in our study, future work including distance moved from the nest in suburban and rural sites in survival analysis would be valuable. The one study that we know of that looked at distance traveled by suburban Wood Thrush fledglings found that moving farther actually increased survival (Adalsteinsson et al. 2018). Furthermore, asking the

same questions that we asked here in an urbanized landscape with less connected forest patches or with forest patches surrounded by denser urban matrix will give further insight into the generalizability of our findings.

Conservation implications and conclusions

This study, along with our previous work (Klein et al. in prep), suggests that suburban forest patches can support viable populations of Wood Thrushes. While some important differences in movement and land use exist between suburban and rural fledglings and warrant further study, we suggest that suburban forest patches, especially those with high connectivity, not be overlooked as important habitat for vulnerable, forest-nesting birds such as the Wood Thrush. Known for its spectacular song, the Wood Thrush is an ideal species to draw neighboring humans into the urban wilds. It is encouraging, for both avian conservation and human connection with nature, that a species typically labeled as sensitive to urbanization can succeed in a suburban landscape such as ours

Tables

Table 4.1: Results from RMark “nest survival” model for fledgling Wood Thrush survival in suburban and rural sites

Model	Npar	AICc	DeltaAICc	Weight	Deviance
S(~Ground * FAge)	4	265.2953	0	6.70E-01	257.2847
S(~Ground + FAge)	3	267.0554	1.760056	2.78E-01	261.049
S(~FAge)	2	270.3881	5.09282	5.25E-02	266.385
S(~Ground)	2	283.1154	17.8201	9.04E-05	279.1122
S(~Ground * SiteType)	4	284.9885	19.69321	3.54E-05	276.9779
S(~1)	1	287.8413	22.545979	8.51E-06	285.8402
S(~Time)	2	289.2439	23.94856	4.22E-06	285.2407
S(~SiteType)	2	289.8271	24.53175	3.15E-06	285.8239
S(~Year)	4	293.0384	27.74309	6.33E-07	285.027

Table 4.2: Generalized linear mixed model results for fledgling distance from nest. Full model contains fixed effects: site type (suburban vs rural), days since fledging; random effects: individual bird/tag ID, nest ID. Nests and Birds models contain all but the other random effect. DaysOnly and SiteOnly contain both random effects.

Model	Degrees of freedom	AIC
Full	6	14930.03
Nests	5	14949.21
Birds	5	14944.38
Fixed Only	4	15109.68
DaysOnly	3	15163.86
SiteOnly	3	15868.86

Figures

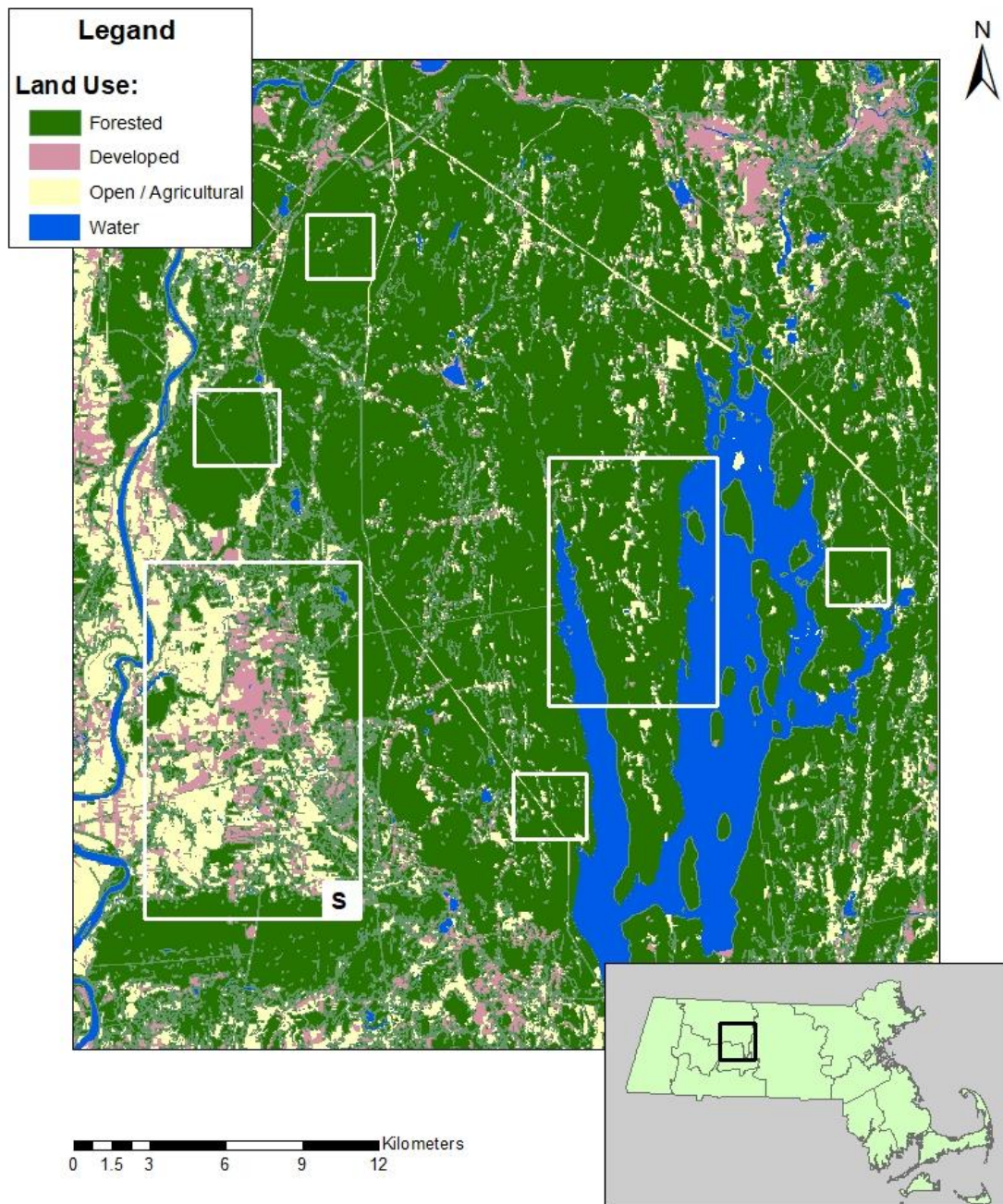


Figure 4.1: Map of the study areas where fledglings were tagged: Box marked with “S” demarcate the suburban study area, while the other 5 boxes demarcate rural study areas. Land use categories are shown. The inset map of Massachusetts shows county boundaries. Land Use layer from MassGIS (2005).

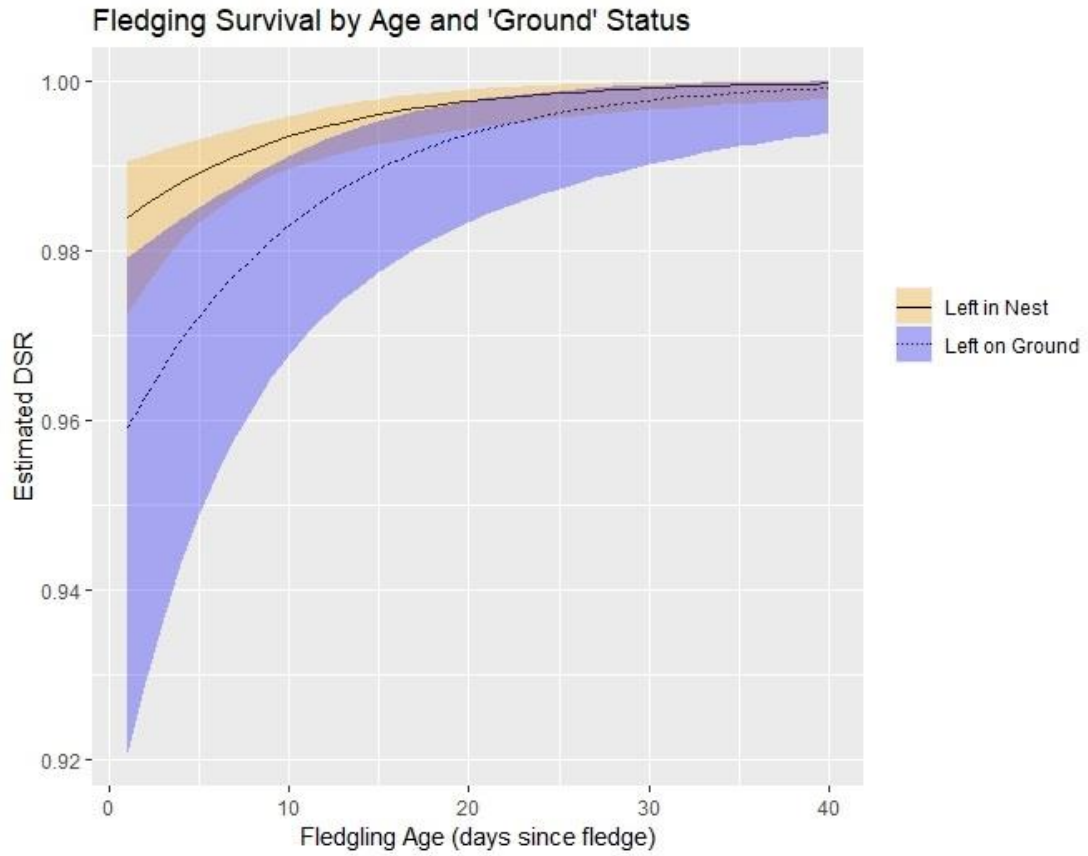


Figure 4.2: Daily survival rate (DSR) of Wood Thrush fledglings, based on additive (Ground + FAge) survival model.

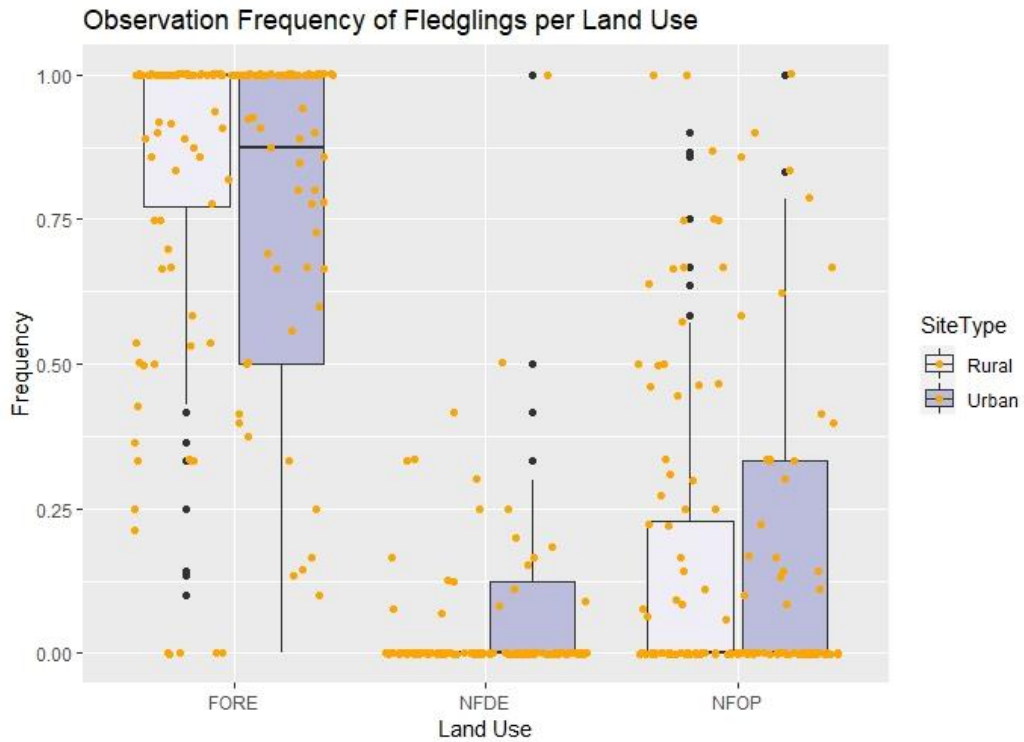


Figure 4.3: Frequency of observations in each land use category [forested (FORE), non-forested developed (NFDE), and non-forested open (NFOP)] for each fledgling over the entire sampling period. Individual data points (individual birds) are in yellow (jitter applied), outliers for boxplots are in black.

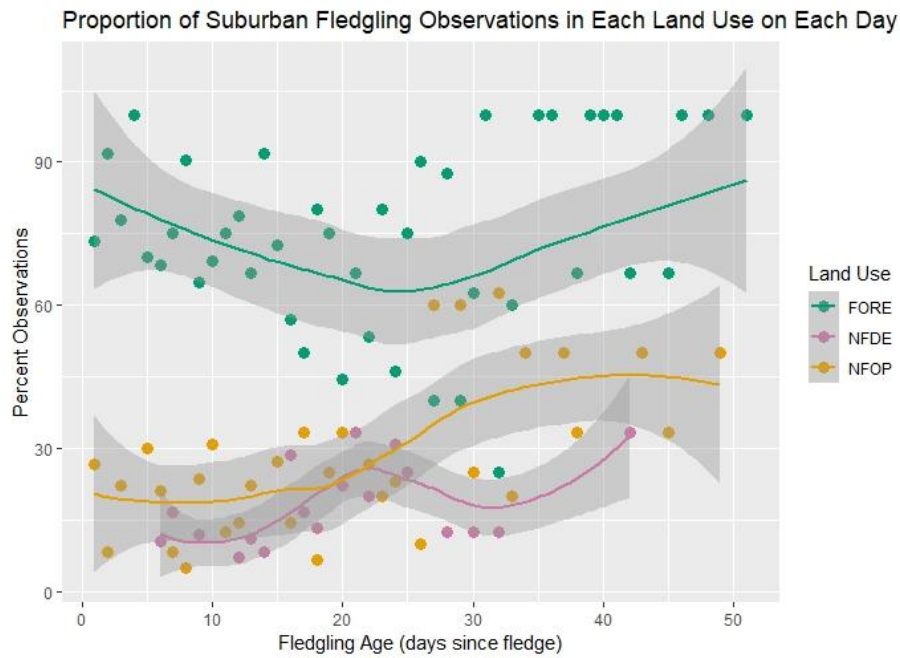
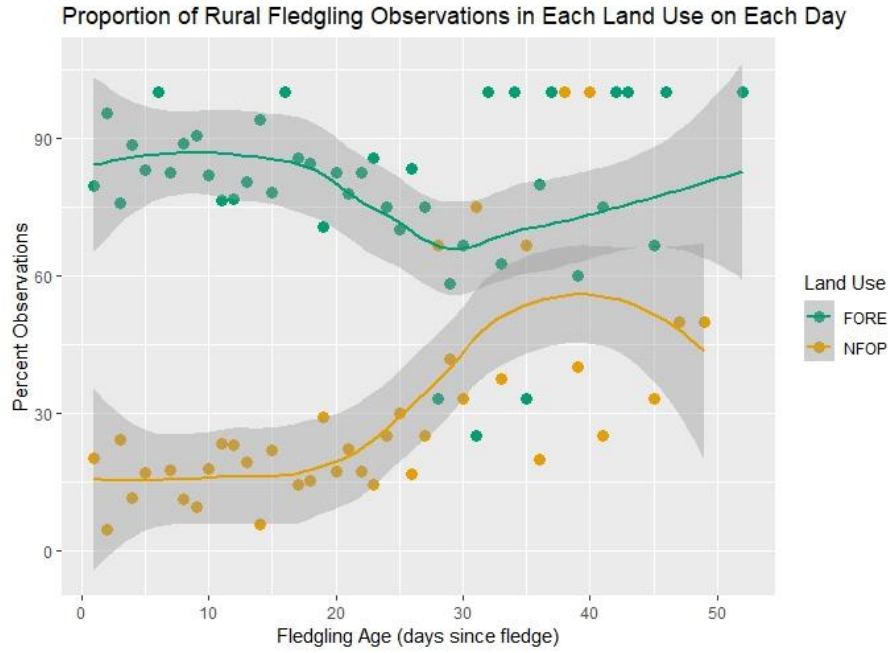


Figure 4.4: Proportion of fledglings using each land use category [Forest (FORE), Non-forested developed (NFDE), and Non-forested open (NFOP)] on each day (top: rural, bottom: suburban). LOESS curves plotted.

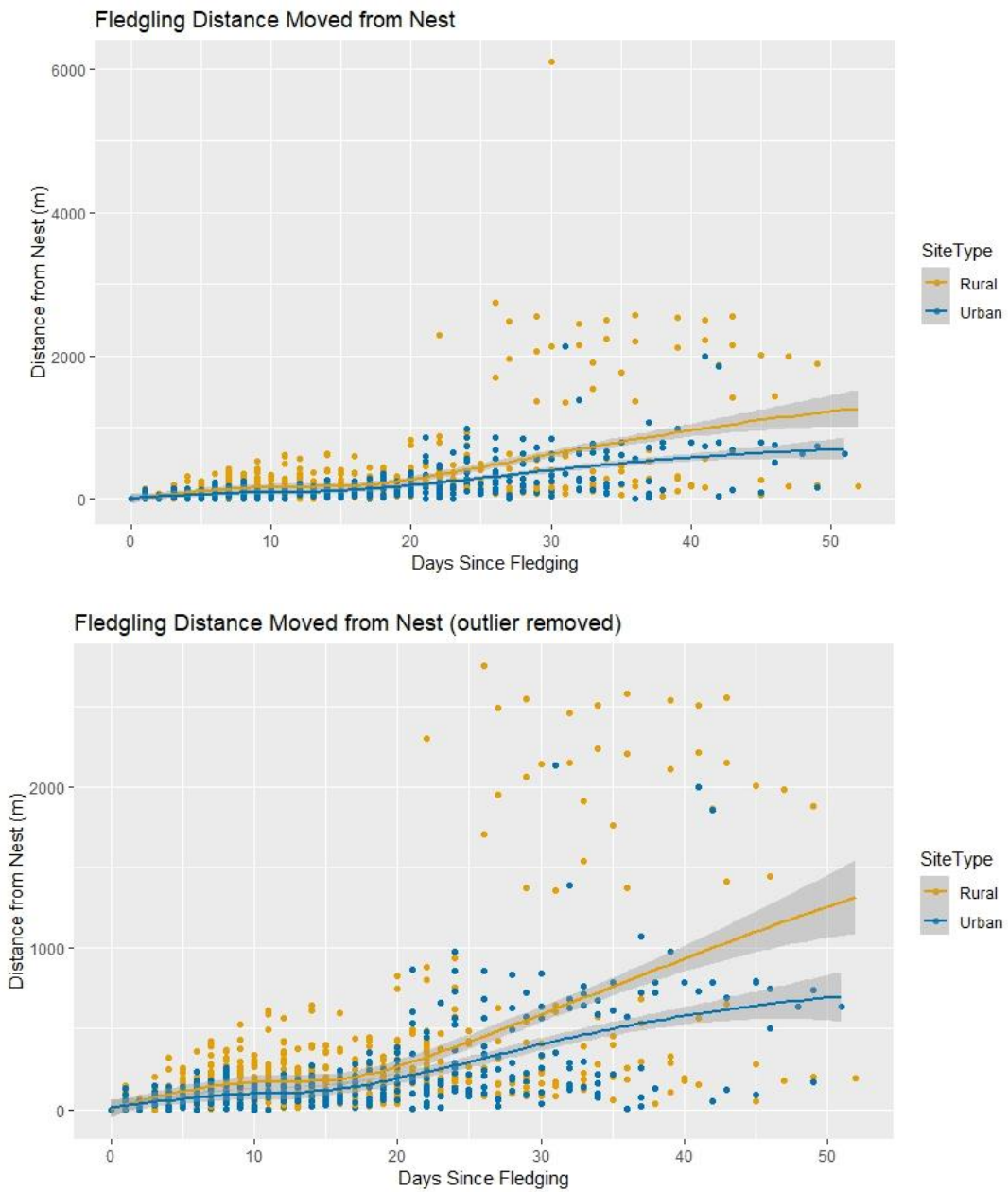


Figure 4.5: Distance from nest by number of days post-fledge for urban and rural birds with outlier (top) and without outlier (bottom). LOESS curves plotted.

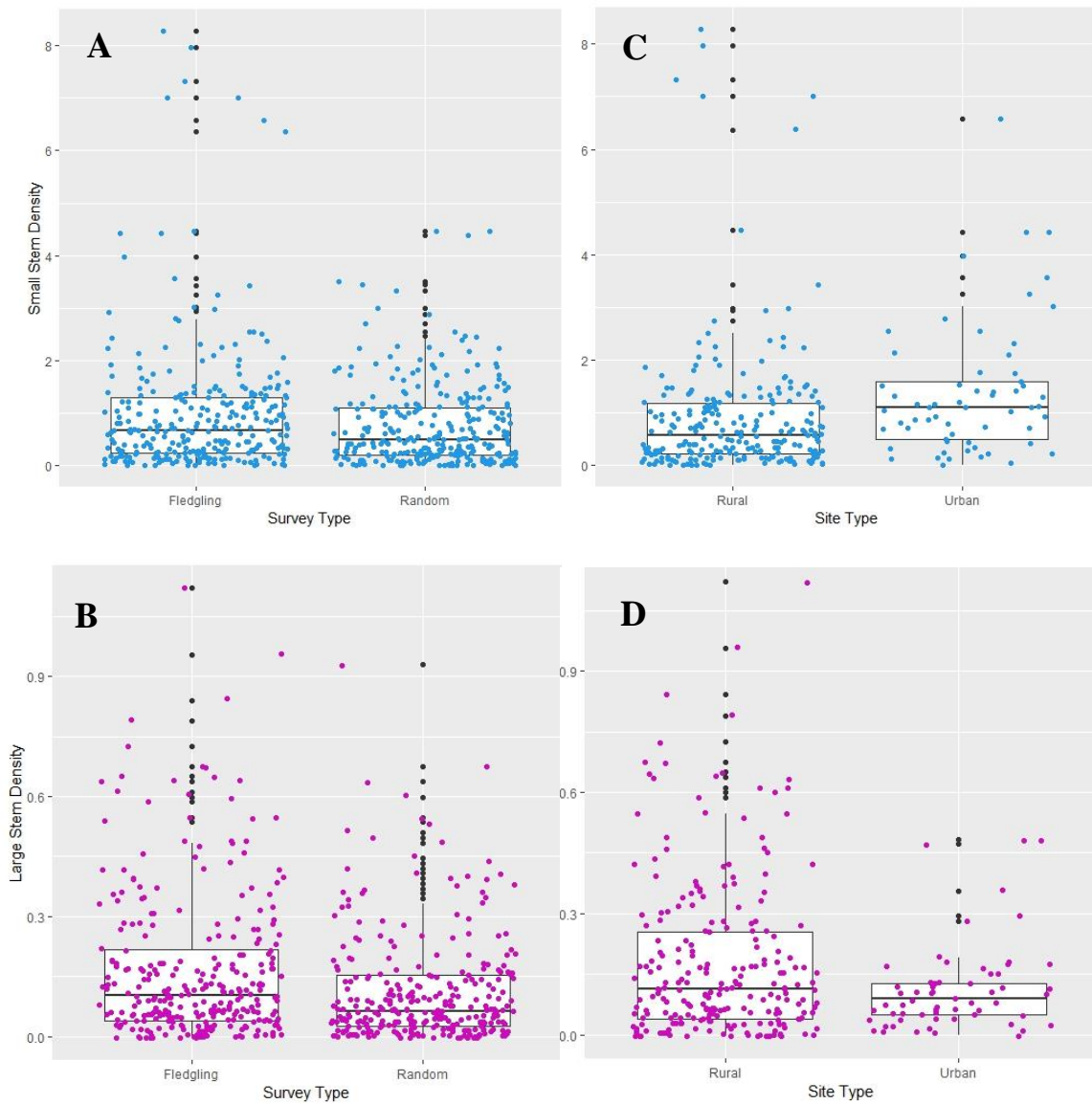


Figure 4.6: Stem density of small (a, c) and large (b,d) stems by survey type (a, b) and site type (used points only; c,d). Colored dots are individual survey points (jitter applied), black points are box plot outliers.

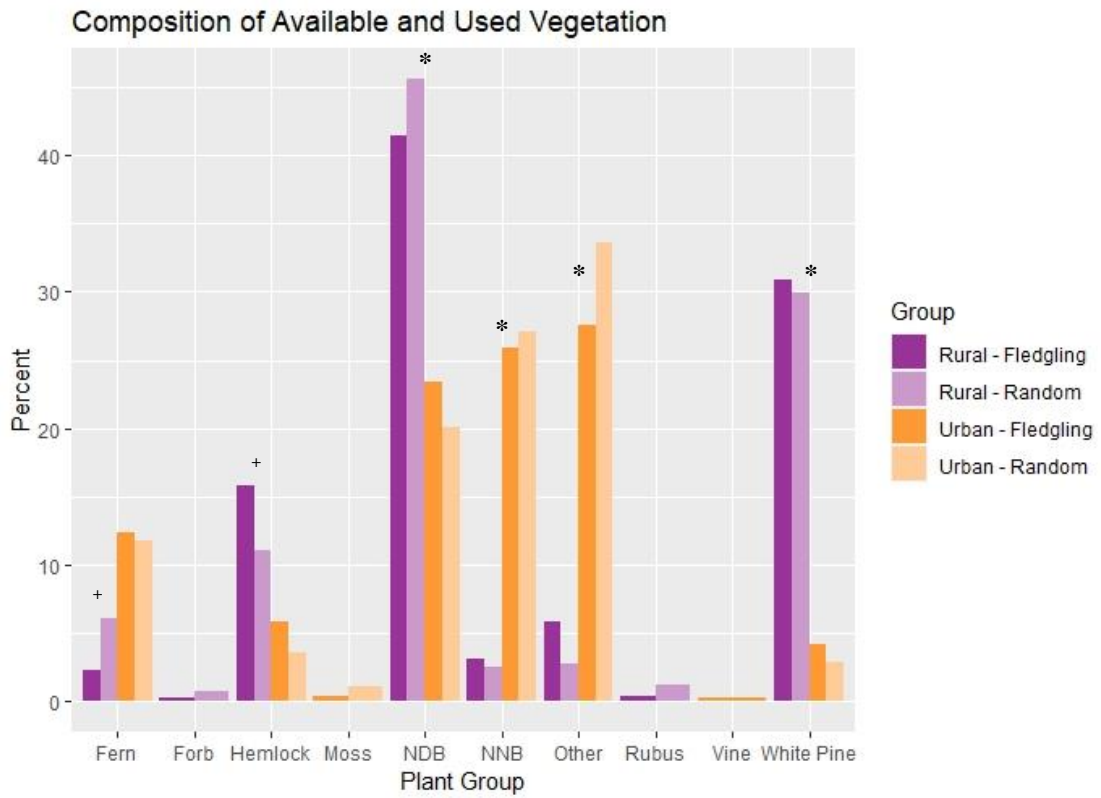


Figure 4.7: Plant composition (percent of all pole contacts) use and availability for fledglings. NDB = native deciduous broadleaf, NNB = non-native broadleaf.
 * = significantly different ($p < 0.05$) chi squared test between available urban and rural points;
 + = significantly different ($p < 0.05$) between fledgling and random points

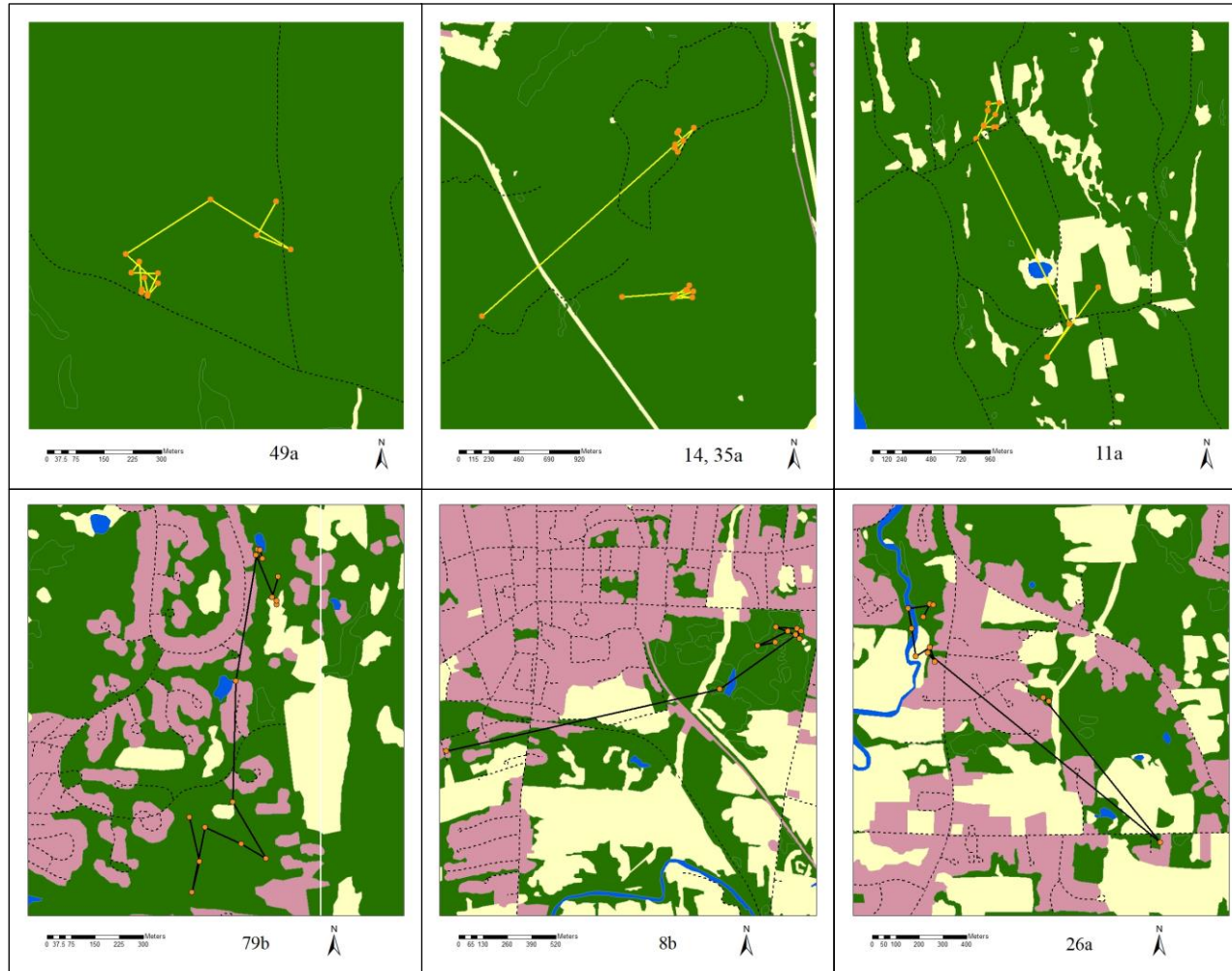


Figure 4.8: Examples of dispersal movements over time by individual fledglings in rural (top) and suburban (bottom) sites. Note that the scale bar changes for each bird's image. Radio tag number(s) / letter(s) of the fledgling(s) is under each map.

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CHAPTER 5

CONCLUSIONS

Avian conservation in urbanized landscapes is vital, both for wildlife and people. Birds perform numerous ecosystem services (Whelan et al. 2015) and delight the humans who share their neighborhoods (Belaire et al. 2015, USDOJ et al. 2016), but many species are experiencing population declines (Rosenberg et al. 2019). Yet, birds utilize many human dominated areas, including urban and suburban forest patches, and these habitats can have important conservation value (Fischer and Lindenmayer 2002, Wintle et al. 2019).

In this dissertation, I investigated avian success, during the breeding season, in urban and suburban forest patches (hereafter, suburban sites) and larger swaths of forest (hereafter, rural sites) in western Massachusetts. I first looked at the abundance of a suite of bird species. I then investigated the nest survival, fledgling survival, fledgling movement, and predator community for a declining neotropical migrant, the Wood Thrush (*Hylocichla mustelina*). My overall findings suggest important conservation value of suburban forest patches for Wood Thrush, as well as provide evidence of the “predation paradox”- a phenomenon that describes an increase of abundance or density of predators in urbanized areas, yet no increase in actual predation rates (Fischer et al. 2012) in the study landscape.

In the first research chapter (ch. 2), I found that some of the general trends in the urban ecology literature were supported by my work, but not for every species. Previous literature suggested that neotropical migrants are more likely to be negatively affected by urbanization than residents or short distance migrants (Chace and Walsh 2006, Kark et al.

2007) and that insectivores are more likely to be negatively affected by urbanization than omnivores (Chace and Walsh 2006; Kark et al. 2007; Croci, Butet, and Clergeau 2008; Hensley et al. 2019). Using point counts and N-mixture models, I found that neotropical migrants, and, to a lesser extent, insectivores, were more likely to be negatively associated with urbanization than short distance migrants/residents and omnivores (respectively). However, not all species followed this pattern. Wood Thrush, for example, had a neutral response to urbanization. Comparing between two landscapes: one with low-mid density suburban (and some agricultural) matrix and an associated forested preserve, the other with mid- to high intensity urban/suburban matrix and an associated forested preserve demonstrated that, while the overall patterns remained the same between the two landscapes, several species were negatively associated with the higher density matrix landscape. This supports the concept of species “filtering” from the regional species pool in urbanized areas (Aronson et al. 2014, Hensley et al. 2019). I suggest that relying on generalizations about response to urbanization based on species traits can likely be useful for general avian conservation, but for conservation of particular species, it is important to have species-specific data. This is particularly true for sensitive or declining species, some of which may be able to succeed in suburban or urban habitat patches. My results also indicate the need for further study for two other species: the Eastern Wood-pewee (*Contopus virens*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), both of which are declining species that did not display a negative association with urbanization in this study. Finally, further research on which factors make some urban forest patches more hospitable to a wider array of species than others may be key to increasing the conservation value of forest patches.

In the second research chapter (ch. 3), RMark survival analysis showed that Wood Thrush are not just present in the suburban sites, but are breeding successfully. This is a hopeful sign for the conservation value of suburban forest patches for Wood Thrush. I also found that the general patterns associated with the “predation paradox” (more potential predators, yet no difference in nest survival; Fischer et al. 2012) could be observed for Wood Thrush in this study system. The most common predator taxa documented depredate Wood Thrush nests were sciurids and raptors. Hypotheses for mechanisms of the predation paradox involving predator composition changes and/or consumption of anthropogenic food subsidies by predators (Fischer et al. 2012) may be supported by this work. Additional work is needed to help flesh out mechanisms for the predation paradox, particularly research on raptor abundance in urbanized areas.

In the third research chapter (ch. 4), using radio-telemetry and RMark survival analysis, I found that survival of Wood Thrush during the post-fledging life stage was comparable between suburban and rural study sites. The fledgling life stage is both understudied (Ausprey and Rodewald 2011, Cox et al. 2014) and demographically important (Donovan and Thompson 2001, Cox et al. 2014), and these results are some of the first to compare Wood Thrush post-fledging survival between suburban and rural forests. This gives further support for the Wood Thrush’s ability to thrive in (at least some) suburban forest patches, and, when combined with potential predator findings from chapter three, lends further support for the predation paradox. Comparing the distance moved from the nest by fledgling Wood Thrushes, using generalized linear mixed models, demonstrated that fledglings from rural sites moved farther than fledglings from suburban sites. This warrants further research regarding possible barriers to

movement for fledglings in suburban or urban areas (see Fink 2003). Investigation of older fledglings is also necessary to investigate possible anthropogenic hazards (Adalsteinsson et al. 2018). Comparing habitat use between suburban and rural fledglings showed that fledglings in both types of sites used denser stems than would be expected from availability, and fledglings used a higher proportion of open land cover as they aged. Finally, I found that force-fledging and being left outside the nest after radio-tagging had a negative effect on survival (see Schlossberg et al. 2018), and, with my collaborators, I developed techniques to minimize its occurrence.

I note the importance of context in this research. I conducted this work in urban and suburban forest patches, and suggest that these results be primarily compared with other studies conducted in habitat patches, as opposed to urban or suburban matrix. Also, the matrix surrounding the forest patches in chapter 3 and 4 was primarily low- to mid-intensity suburban development, and caution should be exercised when comparing these findings to those with densely populated urban matrix. Connectivity between forest patches is not something that I quantified in this dissertation but is likely relevant to the conservation value of forest patches (Wintle et al. 2019). Lastly, variation in both the predator community and the prevalence of nest parasitism are apparent throughout the Wood Thrush's range (Hoover and Brittingham 1993, Farnsworth and Simons 2000, Williams and Wood 2002, Rodewald and Kearns 2011), and may account for differences in findings between this dissertation and research in other parts of the Wood Thrush's range.

Overall, I found very hopeful signs that suburban forest patches can support successful populations of Wood Thrush. While changes in potential predator community

and changes in post-fledging movement indicate differences in habitat and/or behavior in suburban forest patches, Wood Thrushes seem to be able to survive and even thrive in these study areas. Given the extent and intensity of development in the northeastern U.S. (Potapov et al. 2022), as well as the high amount of wildland-urban interface (Radeloff et al. 2005), the relatively high nest and fledgling survival that I found for Wood Thrush is notable. I suggest that managers aiming to conserve this species in urbanized landscapes look at remnant forest patches, especially relatively mesic patches with potential for connectivity to other forested and open lands. Protecting these spaces, improving connectivity between such spaces with corridors that can be used by fledglings, and engaging the public in the process may have great value for the Wood Thrush, as well as for other species. The Wood Thrush, with its melodic song, may even serve as an ambassador for forest dwelling species near urban areas.

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APPENDIX A: CONDENSED GIS LAND USE CATEGORIES

Categories of land use cover from MassGIS (2005) which were condensed into the three composite land use categories used in this dissertation.

Forested (FORE): Forest (3), Forested Wetland (37)

Non-Forested Open (NFOP): Cropland (1), Pasture (2), Non-Forested Wetland (4), Open Land (6), Participation Recreation (7), Powerline/Utility (24), Golf Course (26), Cemetery (34), Orchard (35), Nursery (36), Very Low Density Residential (38), Brushland/Successional (40)

Non-Forested Developed (NFDE): Mining (5), Spectator Recreation (8) , Water-Based Recreation (9), Multi-Family Residential (10), High Density Residential (11), Medium Density Residential (12), Low Density Residential (13), Commercial (15), Industrial (16), Transitional (17), Transportation (18), Waste Disposal (19), Urban Public / Institutional (31), Junkyard (39)

APPENDIX B: N-MIXTURE MODEL INCLUSION CRITERIA VALUES FOR

ALL SPECIES (CHAPTER 2)

i. Number of observations (males only) for each species in each of the four study areas and in each of the two years of the study. Note that the number of observations is equal to or greater than the number of confirmed individuals. * = counted as predator on predator point count surveys.

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
American Goldfinch	<i>Spinus tristis</i>	2013	Northern	Urban	2
American Goldfinch	<i>Spinus tristis</i>	2014	Northern	Rural	1
American Goldfinch	<i>Spinus tristis</i>	2014	Northern	Urban	1
American Goldfinch	<i>Spinus tristis</i>	2014	Southern	Rural	1
American Goldfinch	<i>Spinus tristis</i>	2014	Southern	Urban	1
American Redstart	<i>Setophaga ruticilla</i>	2013	Northern	Rural	47
American Redstart	<i>Setophaga ruticilla</i>	2013	Northern	Urban	1
American Redstart	<i>Setophaga ruticilla</i>	2014	Northern	Rural	79
American Redstart	<i>Setophaga ruticilla</i>	2014	Northern	Urban	9
American Redstart	<i>Setophaga ruticilla</i>	2014	Southern	Rural	1
American Robin	<i>Turdus migratorius</i>	2013	Northern	Rural	5
American Robin	<i>Turdus migratorius</i>	2013	Northern	Urban	5
American Robin	<i>Turdus migratorius</i>	2013	Southern	Urban	5
American Robin	<i>Turdus migratorius</i>	2014	Northern	Rural	9
American Robin	<i>Turdus migratorius</i>	2014	Northern	Urban	7
American Robin	<i>Turdus migratorius</i>	2014	Southern	Rural	1
American Robin	<i>Turdus migratorius</i>	2014	Southern	Urban	11
Baltimore Oriole	<i>Icterus galbula</i>	2013	Northern	Rural	3
Baltimore Oriole	<i>Icterus galbula</i>	2013	Northern	Urban	1
Baltimore Oriole	<i>Icterus galbula</i>	2013	Southern	Urban	7
Baltimore Oriole	<i>Icterus galbula</i>	2014	Northern	Urban	5
Baltimore Oriole	<i>Icterus galbula</i>	2014	Southern	Rural	1
Baltimore Oriole	<i>Icterus galbula</i>	2014	Southern	Urban	4
Black-and-white Warbler	<i>Mniotilta varia</i>	2013	Northern	Rural	9
Black-and-white Warbler	<i>Mniotilta varia</i>	2014	Northern	Rural	12
Black-and-white Warbler	<i>Mniotilta varia</i>	2014	Northern	Urban	2
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	2014	Northern	Rural	1
Blackburnian Warbler	<i>Setophaga fusca</i>	2013	Northern	Rural	2
Blackburnian Warbler	<i>Setophaga fusca</i>	2014	Northern	Rural	3
Black-capped Chickadee	<i>Poecile atricapillus</i>	2013	Northern	Rural	11
Black-capped Chickadee	<i>Poecile atricapillus</i>	2013	Northern	Urban	24
Black-capped Chickadee	<i>Poecile atricapillus</i>	2013	Southern	Rural	1
Black-capped Chickadee	<i>Poecile atricapillus</i>	2014	Northern	Rural	12

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
Black-capped Chickadee	<i>Poecile atricapillus</i>	2014	Northern	Urban	20
Black-capped Chickadee	<i>Poecile atricapillus</i>	2014	Southern	Rural	3
Black-capped Chickadee	<i>Poecile atricapillus</i>	2014	Southern	Urban	3
Black-capped Chickadee	<i>Poecile atricapillus</i>	2013	Southern	Urban	1
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	2013	Northern	Rural	22
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	2013	Southern	Rural	1
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	2014	Northern	Rural	25
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	2014	Southern	Rural	4
Black-throated Green Warbler	<i>Setophaga virens</i>	2013	Northern	Rural	10
Black-throated Green Warbler	<i>Setophaga virens</i>	2013	Northern	Urban	4
Black-throated Green Warbler	<i>Setophaga virens</i>	2014	Northern	Rural	34
Black-throated Green Warbler	<i>Setophaga virens</i>	2014	Northern	Urban	7
Black-throated Green Warbler	<i>Setophaga virens</i>	2014	Southern	Rural	2
Blue Jay*	<i>Cyanocitta cristata</i>	2013	Southern	Urban	1
Blue Jay*	<i>Cyanocitta cristata</i>	2014	Southern	Urban	1
Blue Jay*	<i>Cyanocitta cristata</i>	2013	Northern	Rural	3
Blue-headed Vireo	<i>Vireo solitarius</i>	2013	Southern	Rural	1
Blue-headed Vireo	<i>Vireo solitarius</i>	2013	Northern	Rural	1
Blue-winged Warber	<i>Vermivora cyanoptera</i>	2014	Northern	Rural	2
Brown Creeper	<i>Certhia americana</i>	2014	Northern	Urban	1
Brown Creeper	<i>Certhia americana</i>	2014	Southern	Rural	1
Brown Creeper	<i>Certhia americana</i>	2014	Southern	Urban	3
Brown-headed Cowbird	<i>Molothrus ater</i>	2014	Southern	Urban	2
Brown-headed Cowbird	<i>Molothrus ater</i>	2013	Southern	Rural	1
Carolina Wren	<i>Thryothorus ludovicianus</i>	2013	Northern	Urban	7
Carolina Wren	<i>Thryothorus ludovicianus</i>	2013	Southern	Urban	4
Carolina Wren	<i>Thryothorus ludovicianus</i>	2014	Northern	Urban	5
Carolina Wren	<i>Thryothorus ludovicianus</i>	2014	Southern	Urban	9
Cedar Waxwing	<i>Bombycilla cedrorum</i>	2013	Southern	Urban	2
Cedar Waxwing	<i>Bombycilla cedrorum</i>	2014	Northern	Rural	1
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	2013	Northern	Rural	24
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	2014	Northern	Rural	49

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	2014	Northern	Urban	1
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	2014	Southern	Rural	1
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	2014	Southern	Urban	1
Chipping Sparrow	<i>Spizella passerina</i>	2013	Northern	Urban	2
Chipping Sparrow	<i>Spizella passerina</i>	2013	Southern	Rural	1
Chipping Sparrow	<i>Spizella passerina</i>	2013	Southern	Urban	1
Chipping Sparrow	<i>Spizella passerina</i>	2014	Northern	Rural	4
Chipping Sparrow	<i>Spizella passerina</i>	2014	Northern	Urban	1
Chipping Sparrow	<i>Spizella passerina</i>	2014	Southern	Urban	3
Common Grackle*	<i>Quiscalus quiscula</i>	2014	Southern	Urban	1
Common Grackle*	<i>Quiscalus quiscula</i>	2013	Southern	Urban	5
Common Yellowthroat	<i>Geothlypis trichas</i>	2013	Northern	Rural	29
Common Yellowthroat	<i>Geothlypis trichas</i>	2013	Northern	Urban	15
Common Yellowthroat	<i>Geothlypis trichas</i>	2013	Southern	Urban	2
Common Yellowthroat	<i>Geothlypis trichas</i>	2014	Northern	Rural	54
Common Yellowthroat	<i>Geothlypis trichas</i>	2014	Northern	Urban	30
Common Yellowthroat	<i>Geothlypis trichas</i>	2014	Southern	Urban	3
Downy Woodpecker	<i>Dryobates pubescens</i>	2014	Southern	Urban	1
Downy Woodpecker	<i>Dryobates pubescens</i>	2014	Northern	Rural	1
Downy Woodpecker	<i>Dryobates pubescens</i>	2014	Northern	Urban	1
Eastern Phoebe	<i>Sayornis phoebe</i>	2013	Northern	Urban	3
Eastern Phoebe	<i>Sayornis phoebe</i>	2014	Northern	Rural	2
Eastern Phoebe	<i>Sayornis phoebe</i>	2014	Northern	Urban	2
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	2013	Northern	Rural	16
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	2014	Northern	Rural	29
Eastern Wood-pewee	<i>Contopus virens</i>	2013	Northern	Rural	6
Eastern Wood-pewee	<i>Contopus virens</i>	2013	Northern	Urban	14
Eastern Wood-pewee	<i>Contopus virens</i>	2013	Southern	Rural	3
Eastern Wood-pewee	<i>Contopus virens</i>	2013	Southern	Urban	6
Eastern Wood-pewee	<i>Contopus virens</i>	2014	Northern	Rural	6
Eastern Wood-pewee	<i>Contopus virens</i>	2014	Northern	Urban	9
Eastern Wood-pewee	<i>Contopus virens</i>	2014	Southern	Rural	2
Eastern Wood-pewee	<i>Contopus virens</i>	2014	Southern	Urban	17
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	2013	Southern	Urban	1
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	2014	Northern	Urban	2
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	2014	Southern	Urban	1

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
Grey Catbird	<i>Dumetella carolinensis</i>	2013	Northern	Rural	7
Grey Catbird	<i>Dumetella carolinensis</i>	2013	Northern	Urban	22
Grey Catbird	<i>Dumetella carolinensis</i>	2013	Southern	Urban	9
Grey Catbird	<i>Dumetella carolinensis</i>	2014	Northern	Rural	23
Grey Catbird	<i>Dumetella carolinensis</i>	2014	Northern	Urban	35
Grey Catbird	<i>Dumetella carolinensis</i>	2014	Southern	Rural	1
Grey Catbird	<i>Dumetella carolinensis</i>	2014	Southern	Urban	15
Hairy Woodpecker	<i>Dryobates villosus</i>	2013	Southern	Urban	1
Hairy Woodpecker	<i>Dryobates villosus</i>	2014	Southern	Urban	1
Hairy Woodpecker	<i>Dryobates villosus</i>	2014	Northern	Urban	1
Hermit Thrush	<i>Catharus guttatus</i>	2013	Northern	Rural	2
Hermit Thrush	<i>Catharus guttatus</i>	2014	Northern	Rural	2
House Sparrow	<i>Passer domesticus</i>	2013	Northern	Urban	1
House Sparrow	<i>Passer domesticus</i>	2013	Southern	Urban	1
House Sparrow	<i>Passer domesticus</i>	2014	Southern	Urban	3
House Wren	<i>Troglodytes aedon</i>	2013	Northern	Urban	1
House Wren	<i>Troglodytes aedon</i>	2014	Northern	Urban	11
Indigo Bunting	<i>Passerina cyanea</i>	2014	Northern	Rural	1
Indigo Bunting	<i>Passerina cyanea</i>	2014	Northern	Urban	1
Least Flycatcher	<i>Empidonax minimus</i>	2013	Northern	Rural	1
Least Flycatcher	<i>Empidonax minimus</i>	2014	Northern	Rural	12
Louisiana Waterthrush	<i>Parkesia motacilla</i>	2013	Northern	Urban	4
Louisiana Waterthrush	<i>Parkesia motacilla</i>	2014	Northern	Urban	2
Magnolia Warbler	<i>Setophaga magnolia</i>	2013	Northern	Rural	1
Magnolia Warbler	<i>Setophaga magnolia</i>	2014	Northern	Rural	2
Magnolia Warbler	<i>Setophaga magnolia</i>	2014	Southern	Urban	1
Mourning Dove	<i>Zenaida macroura</i>	2013	Northern	Rural	1
Mourning Dove	<i>Zenaida macroura</i>	2013	Northern	Urban	1
Mourning Dove	<i>Zenaida macroura</i>	2014	Northern	Rural	1
Mourning Dove	<i>Zenaida macroura</i>	2014	Northern	Urban	2
Northern Cardinal	<i>Cardinalis cardinalis</i>	2013	Northern	Urban	27
Northern Cardinal	<i>Cardinalis cardinalis</i>	2013	Southern	Urban	2
Northern Cardinal	<i>Cardinalis cardinalis</i>	2014	Northern	Rural	5
Northern Cardinal	<i>Cardinalis cardinalis</i>	2014	Northern	Urban	23
Northern Cardinal	<i>Cardinalis cardinalis</i>	2014	Southern	Urban	22

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
Northern Flicker	<i>Colaptes auratus</i>	2014	Southern	Urban	1
Northern Parula	<i>Setophaga americana</i>	2014	Northern	Rural	5
Northern Parula	<i>Setophaga americana</i>	2014	Northern	Urban	1
Other		2013	Southern	Rural	3
Other		2014	Southern	Rural	3
Other		2014	Southern	Urban	3
Ovenbird	<i>Seiurus aurocapilla</i>	2013	Northern	Rural	78
Ovenbird	<i>Seiurus aurocapilla</i>	2013	Northern	Urban	31
Ovenbird	<i>Seiurus aurocapilla</i>	2013	Southern	Rural	12
Ovenbird	<i>Seiurus aurocapilla</i>	2014	Northern	Rural	114
Ovenbird	<i>Seiurus aurocapilla</i>	2014	Northern	Urban	49
Ovenbird	<i>Seiurus aurocapilla</i>	2014	Southern	Rural	14
Ovenbird	<i>Seiurus aurocapilla</i>	2014	Southern	Urban	2
Pine Warb. Or Chipping Sp		2013	Northern	Rural	7
Pine Warb. Or Chipping Sp		2013	Northern	Urban	3
Pine Warb. Or Chipping Sp		2014	Northern	Rural	9
Pine Warb. Or Chipping Sp		2014	Northern	Urban	9
Pine Warbler	<i>Setophaga pinus</i>	2013	Northern	Rural	23
Pine Warbler	<i>Setophaga pinus</i>	2013	Northern	Urban	10
Pine Warbler	<i>Setophaga pinus</i>	2013	Southern	Rural	1
Pine Warbler	<i>Setophaga pinus</i>	2013	Southern	Urban	1
Pine Warbler	<i>Setophaga pinus</i>	2014	Northern	Rural	43
Pine Warbler	<i>Setophaga pinus</i>	2014	Northern	Urban	7
Pine Warbler	<i>Setophaga pinus</i>	2014	Southern	Rural	1
Pine Warbler	<i>Setophaga pinus</i>	2014	Southern	Urban	5
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	2013	Southern	Urban	1
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	2014	Southern	Urban	5
Red-eyed Vireo	<i>Vireo olivaceus</i>	2013	Northern	Rural	65
Red-eyed Vireo	<i>Vireo olivaceus</i>	2013	Northern	Urban	39
Red-eyed Vireo	<i>Vireo olivaceus</i>	2013	Southern	Rural	23
Red-eyed Vireo	<i>Vireo olivaceus</i>	2013	Southern	Urban	3
Red-eyed Vireo	<i>Vireo olivaceus</i>	2014	Northern	Rural	106
Red-eyed Vireo	<i>Vireo olivaceus</i>	2014	Northern	Urban	40
Red-eyed Vireo	<i>Vireo olivaceus</i>	2014	Southern	Rural	33
Red-eyed Vireo	<i>Vireo olivaceus</i>	2014	Southern	Urban	6
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	2014	Northern	Urban	1

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	2013	Northern	Rural	1
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	2013	Northern	Urban	8
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	2014	Northern	Urban	3
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	2014	Southern	Urban	2
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	2014	Northern	Rural	1
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2013	Northern	Rural	7
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2013	Northern	Urban	12
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2013	Southern	Rural	2
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2013	Southern	Urban	4
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2014	Northern	Rural	19
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2014	Northern	Urban	10
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	2014	Southern	Urban	3
Scarlet Tanager	<i>Piranga olivacea</i>	2013	Northern	Rural	9
Scarlet Tanager	<i>Piranga olivacea</i>	2013	Northern	Urban	6
Scarlet Tanager	<i>Piranga olivacea</i>	2013	Southern	Rural	8
Scarlet Tanager	<i>Piranga olivacea</i>	2013	Southern	Urban	4
Scarlet Tanager	<i>Piranga olivacea</i>	2014	Northern	Rural	20
Scarlet Tanager	<i>Piranga olivacea</i>	2014	Northern	Urban	9
Scarlet Tanager	<i>Piranga olivacea</i>	2014	Southern	Rural	6
Scarlet Tanager	<i>Piranga olivacea</i>	2014	Southern	Urban	2
Song Sparrow	<i>Melospiza melodia</i>	2013	Northern	Rural	1
Song Sparrow	<i>Melospiza melodia</i>	2013	Northern	Urban	5
Song Sparrow	<i>Melospiza melodia</i>	2014	Northern	Rural	2
Song Sparrow	<i>Melospiza melodia</i>	2014	Northern	Urban	5
Tufted Titmouse	<i>Baeolophus bicolor</i>	2013	Northern	Urban	9
Tufted Titmouse	<i>Baeolophus bicolor</i>	2013	Southern	Rural	2
Tufted Titmouse	<i>Baeolophus bicolor</i>	2013	Southern	Urban	8
Tufted Titmouse	<i>Baeolophus bicolor</i>	2014	Northern	Rural	1
Tufted Titmouse	<i>Baeolophus bicolor</i>	2014	Northern	Urban	22
Tufted Titmouse	<i>Baeolophus bicolor</i>	2014	Southern	Urban	8
Unknown/unconfirmed		2013	Northern	Rural	3
Unknown/unconfirmed		2013	Southern	Urban	2
Unknown/unconfirmed		2014	Northern	Rural	5
Unknown/unconfirmed		2014	Northern	Urban	1
Unknown/unconfirmed		2014	Southern	Rural	2
Veery	<i>Catharus fuscescens</i>	2013	Northern	Rural	25
Veery	<i>Catharus fuscescens</i>	2013	Northern	Urban	3

Species	Scientific Name	Survey Year	Region	Site Type	Number Obs.
Veery	<i>Catharus fuscescens</i>	2013	Southern	Rural	3
Veery	<i>Catharus fuscescens</i>	2013	Southern	Urban	1
Veery	<i>Catharus fuscescens</i>	2014	Northern	Rural	34
Veery	<i>Catharus fuscescens</i>	2014	Northern	Urban	5
Veery	<i>Catharus fuscescens</i>	2014	Southern	Rural	7
White-breasted Nuthatch	<i>Sitta carolinensis</i>	2013	Southern	Urban	2
White-breasted Nuthatch	<i>Sitta carolinensis</i>	2013	Northern	Urban	3
White-breasted Nuthatch	<i>Sitta carolinensis</i>	2014	Northern	Rural	1
White-breasted Nuthatch	<i>Sitta carolinensis</i>	2014	Northern	Urban	2
Winter Wren	<i>Troglodytes hiemalis</i>	2013	Northern	Urban	1
Winter Wren	<i>Troglodytes hiemalis</i>	2014	Northern	Urban	1
Wood Thrush	<i>Hylocichla mustelina</i>	2013	Northern	Rural	13
Wood Thrush	<i>Hylocichla mustelina</i>	2013	Northern	Urban	13
Wood Thrush	<i>Hylocichla mustelina</i>	2013	Southern	Urban	8
Wood Thrush	<i>Hylocichla mustelina</i>	2014	Northern	Rural	20
Wood Thrush	<i>Hylocichla mustelina</i>	2014	Northern	Urban	22
Wood Thrush	<i>Hylocichla mustelina</i>	2014	Southern	Rural	4
Wood Thrush	<i>Hylocichla mustelina</i>	2014	Southern	Urban	5
Yellow Warbler	<i>Setophaga petechia</i>	2013	Northern	Rural	12
Yellow Warbler	<i>Setophaga petechia</i>	2014	Northern	Rural	9
Yellow Warbler	<i>Setophaga petechia</i>	2014	Northern	Urban	1
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	2013	Northern	Rural	1

ii. Total and percent of all plots per year that each species was observed, males only. See A for scientific names. * = counted as predator on predator point count surveys.

Species	Survey Year	Number Plots	Percent Plots
American Goldfinch	2013	2	3.33
American Goldfinch	2014	4	5.00
American Redstart	2013	16	26.67
American Redstart	2014	36	45.00
American Robin	2013	14	23.33
American Robin	2014	23	28.75
Baltimore Oriole	2013	9	15.00
Baltimore Oriole	2014	9	11.25
Black-and-white Warbler	2013	8	13.33
Black-and-white Warbler	2014	11	13.75
Black-billed Cuckoo	2014	1	1.25
Blackburnian Warbler	2013	1	1.67
Blackburnian Warbler	2014	2	2.50
Black-capped Chickadee	2013	22	36.67
Black-capped Chickadee	2014	31	38.75
Black-throated Blue Warbler	2013	12	20.00
Black-throated Blue Warbler	2014	19	23.75
Black-throated Green Warbler	2013	8	13.33
Black-throated Green Warbler	2014	26	32.50
Blue Jay*	2013	2	3.33
Blue Jay*	2014	1	1.25
Blue-headed Vireo	2013	2	3.33
Blue-winged Warbler	2014	1	1.25
Brown Creeper	2014	4	5.00
Brown-headed Cowbird	2013	1	1.67
Brown-headed Cowbird	2014	2	2.50
Carolina Wren	2013	8	13.33
Carolina Wren	2014	12	15.00
Cedar Waxwing	2013	2	3.33
Cedar Waxwing	2014	1	1.25
Chestnut-sided Warbler	2013	16	26.67
Chestnut-sided Warbler	2014	26	32.50
Chipping Sparrow	2013	4	6.67
Chipping Sparrow	2014	8	10.00
Common Grackle*	2013	1	1.67
Common Grackle*	2014	1	1.25
Common Yellowthroat	2013	21	35.00
Common Yellowthroat	2014	44	55.00
Downy Woodpecker	2014	3	3.75

Species	Survey Year	Number Plots	Percent Plots
Eastern Phoebe	2013	3	5.00
Eastern Phoebe	2014	4	5.00
Eastern Towhee	2013	9	15.00
Eastern Towhee	2014	19	23.75
Eastern Wood-pewee	2013	22	36.67
Eastern Wood-pewee	2014	27	33.75
Great Crested Flycatcher	2013	1	1.67
Great Crested Flycatcher	2014	3	3.75
Grey Catbird	2013	19	31.67
Grey Catbird	2014	42	52.50
Hairy Woodpecker	2013	1	1.67
Hairy Woodpecker	2014	2	2.50
Hermit Thrush	2013	2	3.33
Hermit Thrush	2014	2	2.50
House Sparrow	2013	2	3.33
House Sparrow	2014	2	2.50
House Wren	2013	1	1.67
House Wren	2014	9	11.25
Indigo Bunting	2014	2	2.50
Least Flycatcher	2013	1	1.67
Least Flycatcher	2014	5	6.25
Louisiana Waterthrush	2013	3	5.00
Louisiana Waterthrush	2014	2	2.50
Magnolia Warbler	2013	1	1.67
Magnolia Warbler	2014	3	3.75
Mourning Dove	2013	2	3.33
Mourning Dove	2014	3	3.75
Northern Cardinal	2013	16	26.67
Northern Cardinal	2014	32	40.00
Northern Flicker	2014	1	1.25
Northern Parula	2014	5	6.25
Other	2013	2	3.33
Other	2014	6	7.50
Ovenbird	2013	32	53.33
Ovenbird	2014	60	75.00
Pine Warb. Or Chipping Sp	2013	7	11.67
Pine Warb. Or Chipping Sp	2014	13	16.25
Pine Warbler	2013	20	33.33
Pine Warbler	2014	31	38.75
Red-bellied Woodpecker	2013	1	1.67
Red-bellied Woodpecker	2014	4	5.00

Species	Survey Year	Number Plots	Percent Plots
Red-eyed Vireo	2013	48	80.00
Red-eyed Vireo	2014	63	78.75
Red-headed Woodpecker	2014	1	1.25
Red-winged Blackbird	2013	3	5.00
Red-winged Blackbird	2014	5	6.25
Rose-breasted Grosbeak	2013	17	28.33
Rose-breasted Grosbeak	2014	24	30.00
Scarlet Tanager	2013	19	31.67
Scarlet Tanager	2014	30	37.50
Song Sparrow	2013	5	8.33
Song Sparrow	2014	7	8.75
Tufted Titmouse	2013	16	26.67
Tufted Titmouse	2014	24	30.00
Unknown/unconfirmed	2013	5	8.33
Unknown/unconfirmed	2014	8	10.00
Veery	2013	19	31.67
Veery	2014	29	36.25
White-breasted Nuthatch	2013	4	6.67
White-breasted Nuthatch	2014	3	3.75
Winter Wren	2013	1	1.67
Winter Wren	2014	1	1.25
Wood Thrush	2013	19	31.67
Wood Thrush	2014	29	36.25
Yellow Warbler	2013	8	13.33
Yellow Warbler	2014	8	10.00
Yellow-bellied Sapsucker	2013	1	1.67

iii. Species observed but not included in A and B (i.e., no males counted), per year. * = counted as predator on predator point count surveys.

Survey Year	Species	Scientific Name
2013	American Crow*	<i>Corvus brachyrhynchos</i>
2014	American Crow*	<i>Corvus brachyrhynchos</i>
2013	American red squirrel*	<i>Tamiasciurus hudsonicus</i>
2014	American red squirrel*	<i>Tamiasciurus hudsonicus</i>
2014	Barred Owl*	<i>Strix varia</i>
2013	Blue-gray Gnatcatcher	<i>Poliopitila caerulea</i>
2014	Blue-gray Gnatcatcher	<i>Poliopitila caerulea</i>
2014	Cooper's Hawk*	<i>Accipiter cooperii</i>
2013	Eastern chipmunk*	<i>Tamias striatus</i>
2014	Eastern chipmunk*	<i>Tamias striatus</i>
2013	Eastern gray squirrel*	<i>Sciurus carolinensis</i>
2014	Eastern gray squirrel*	<i>Sciurus carolinensis</i>
2014	Eastern Screech-owl*	<i>Megascops asio</i>
2013	Great Blue Heron	<i>Ardea herodias</i>
2013	Pileated Woodpecker	<i>Dryocopus pileatus</i>
2014	Pileated Woodpecker	<i>Dryocopus pileatus</i>
2013	Red-breasted Nuthatch	<i>Sitta canadensis</i>
2014	Red-breasted Nuthatch	<i>Sitta canadensis</i>
2014	Red-tailed Hawk*	<i>Buteo jamaicensis</i>
2013	Ruby-throated Hummingbird	<i>Archilochus colubris</i>
2014	Ruby-throated Hummingbird	<i>Archilochus colubris</i>
2014	Ruffed Grouse	<i>Bonasa umbellus</i>
2013	Wild Turkey	<i>Meleagris gallopavo</i>
2014	Wild Turkey	<i>Meleagris gallopavo</i>

**APPENDIX C: SIGNIFICANCE TESTS AND LOADINGS OF PRINCIPAL
COMPONENTS (CHAPTER 2)**

Variables: basal area of all trees (>10 cm DBH; BA), basal area of small trees (10-22 cm DBH for softwoods, 10-30 cm for hardwoods; BASmallTrees), [following Degraaf and Chadwick (1987) to categorize large vs small trees], percent basal area of conifers (PercentBAConif), density of small stems (≤ 2.5 cm in diameter at knee height; SmStem1m), and density of large stems (>2.5 and ≤ 8 cm in diameter at knee height; LgStem1m).

i. Importance of components:

	PC1	PC2	PC3	PC4	PC5
Variance(eigenvalue)	1.374166	1.148408	1.040519	0.838562	0.598345
Proportion of Variance	0.274833	0.229682	0.208104	0.167712	0.119669
Cumulative Proportion	0.274833	0.504515	0.712619	0.880331	1
Broken-stick value	2.283333	1.283333	0.783333	0.45	0.2

ii. Randomization test of eigenvalues:

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	1.374	1.148	1.041	0.839	0.598
P-value	0.203	0.314	0.127	0.697	0.938

iii. Eigenvectors:

	PC1	PC2	PC3	PC4	PC5
BA	-0.422	0.597	0.238	0.419	0.482
BASmallTrees	0.358	0.497	-0.528	0.422	-0.409
PercentBAConif	-0.717				-0.692
SmStem1m	-0.359	0.102	-0.75	-0.446	0.317
LgStem1m	-0.227	-0.619	-0.313	0.668	0.142

APPENDIX D: FULL RESULTS TABLES FOR N-MIXTURE MODELS (CHAPTER 2)

i. Tabulated results table by species and year:

Supported parameters were within 2 AICc of the top model; strongly supported parameters were within 2 AICc of the top model and did not have zero in their 95% confidence intervals.

INT = interaction term parameter; PC1 = first vegetation principal component

Direction: S = southern landscape (i.e. Springfield + Facing Rock); U = urban/suburban type (i.e. Amherst + Springfield); variables supported but not strongly supported are in parentheses; x = parameter changes directions among models for L (landscape) or T (type)

For GOF (goodness of fit): U = underdispersed, OK = fit is satisfactory with at least one error distribution

For Black-capped Chickadee 2013: Type is highly supported only when using a Poisson error distribution (at 95% CI), but the GOF is only OK under Negative Binomial error distribution.

Species	Year	Supported Parameters	Strongly Supported Params	Direction	GOF
Gray Catbird	2013	Landscape, Type, INT, PC1	Type	(S-), U+	OK
Gray Catbird	2014	Landscape, Type, INT, PC1	Landscape, Type	S-, U+	OK
Ovenbird	2013	Landscape, Type, INT, PC1	Landscape, Type	S-, U-	OK
Ovenbird	2014	Landscape, Type, INT	Landscape, Type	S-, U-	U
Red-eyed Vireo	2013	Landscape, Type, INT, PC1	Landscape, Type	S-, U-	U
Red-eyed Vireo	2014	Landscape, Type, INT	Type, INT	(S-) U-	U
American Redstart	2013	Landscape, Type, PC1	Type, PC1	(S-) U-	OK
American Redstart	2014	Landscape, Type, INT, PC1	Landscape, Type, PC1	S-, U-	OK
Common Yellowthroat	2013	Landscape, Type, INT, PC1	Landscape	S- (U-)	OK
Common Yellowthroat	2014	Landscape, Type, INT, PC1	Landscape, Type	S-, U-	OK
Wood Thrush	2013	Landscape, Type, INT	None	(S-, Tx)	OK
Wood Thrush	2014	Landscape, Type, PC1	None	(S-, U-)	OK

Species	Year	Supported Parameters	Strongly Supported Params	Direction	GOF
Chestnut-sided Warbler	2014	Landscape, Type, INT	Landscape, Type	S-, U-	OK
Northern Cardinal	2014	Landscape, Type, INT	Type	(Lx) U+	OK
Veery	2013	Landscape, Type, INT	Landscape, Type	S-, U-	OK
Veery	2014	Landscape, Type, INT, PC1	Type	(S-) U-	OK
Black-throated Green Warbler	2014	Landscape, Type, INT, PC1	Landscape, Type	S-, U-	OK
Scarlet Tanager	2014	Type, Landscape, PC1	Type	(S-) U-	OK
Eastern Wood-pewee	2014	Landscape, Type, INT, PC1	Type	(S+) U+	OK
Rose-breasted Grosbeak	2014	Landscape, Type, INT	Landscape	S- (U-)	OK
Tufted Titmouse	2014	Landscape, Type, PC1	Type	(S-) U+	OK
Black-capped Chickadee	2013	Landscape, Type	Landscape, Type*	S- (U+)	OK
Black-capped Chickadee	2014	Landscape, Type, PC1	Landscape	S- (U+)	OK
23 data sets (15 species)					

ii. Full results table:

Spp = Species; Yr = Year (2013 or 2014); Error D = error distribution used (Poisson, Negative binomial, or Zero-inflated poisson); GOF = goodness of fit

*=No 0 in 95% confidence interval; + = No 0 in 90% confidence interval; ^{NA} = NaN values

Variables: OTime, ODate, QTime, QDate; Type, Landscape, PC1, Landscape*Type

All models within 2 AIC of top models are reported, in order. Underlined detection parameters are the ones used in the model. The top detection variable was used in the model regardless of its significance. Parameter directions are consistent across top models unless specified. Goodness of fit (GOF) is for top model unless specified. For bird species abbreviations, see table 2.1.

Spp	Yr	Error D	Top detection model	Environmental model	Parameter directions	GOF	Notes
GRCA	13	Pois	<u>OTime</u>	Type*; Landscape_Type*; Landscape.Type*; Type*.PC1	Urban+, Southern-	0.537	
GRCA	14	Pois	<u>NullDet</u> , QTime, OTime	Landscape*.Type*; Landscape*.Type+.PC1; Landscape+_Type.PC1; Landscape+_Type; Landscape*.PC1+	Urban+, Southern-	0.786	
OVEN	13	Pois	<u>NullDet</u> , ODate	Landscape*_Type*; Landscape*_Type*.PC1; Landscape*.Type*.PC1	Urban-, Southern-	0.581	
OVEN	14	Pois	<u>NullDet</u>	Landscape*_Type*, Landscape*.Type*	Urban-, Southern-	0.994	
		NegBin	Same	Same	Same	Same	
		ZIP	Same	Same	Same	0.986	
REVI	13	Pois	<u>NullDet</u> , ODate	Landscape*.Type*.PC1; Landscape_Type; Landscape*.Type*; Landscape_Type+.PC1	Urban-, Southern-	0.998 (for top model and for Landscape.Type)	
		NegBin	Same	Landscape*.Type*.PC1; Landscape*.Type*; Landscape_Type; Landscape_Type+.PC1	Same	Same (both models)	
		ZIP	Same	Same as NegBin	Same	0.996 (for both models)	
REVI	14	Pois	<u>OTime</u> .ODate, ODate, NullDet	Landscape_*Type*	Urban- (Southern-)	0.998	Some NaNs for dispersion values (not sure what that means)
		NegBin	<u>OTime</u> .ODate, ODate, NullDet, OTime	Same	Same	Same	
		ZIP	Same as NegBin	Same	Same	Same	

Spp	Yr	Error D	Top detection model	Environmental model	Parameter directions	GOF	Notes
AMRE	13	Pois	<u>QTime.ODate</u> , <u>OTime</u> , NullDet, <u>ODate</u>	Landscape.Type*.PC1*	Urban- (Southern-)	0.627	
AMRE	14	Pois	<u>NullDet</u> , <u>QTime</u> , <u>ODate</u> , <u>OTime</u> , <u>QTime.ODate</u>	Landscape*.Type*.PC1*; Landscape*_Type*.PC1*	Urban-, Southern-	0.964	
COYE	13	Pois	<u>NullDet</u>	Landscape_Type; Landscape*; Landscape_Type+.PC1; Landscape*.Type; Landscape*.PC1	(Urban-), Southern-	Top model: 0.2; Landscape model: 0.212	
COYE	14	Pois	<u>NullDet</u>	Landscape*.Type+; Landscape_Type*; Landscape*; Landscape*.Type*.PC1	Urban-, Southern-	0.766	
WOTH	13	Pois	<u>QDate</u> , <u>ODate</u> , <u>NullDet</u>	Landscape_Type	(Type changes direction w/ interaction, Southern-)	0.188	
WOTH	14	Pois	<u>ODate</u> , <u>OTime.ODate</u>	Landscape; Type; PC1; Landscape.Type; Landscape.PC1; Type.PC1	(Urban-, Southern-)	0.224	Note estimate sizes
CSWA	14	Pois	<u>NullDet</u>	Landscape*_Type*; Landscape*.Type*	Urban-, Southern-	Landscape_Ty pe: 0.97 Landscape.Ty pe: 0.954	
NOCA	14	Pois	<u>NullDet</u> , <u>ODate</u> , <u>QDate</u>	Type*; Landscape.Type*; Landscape_Type*	Urban+ (Landscape changes direction w/ interaction)	0.565	
VEER	13	Pois	<u>NullDet</u> , <u>QDate</u>	Landscape*.Type*; Landscape*_Type*	Urban-, Southern-	0.559	
VEER	14	Pois	<u>NullDet</u> , <u>ODate</u>	Landscape.Type*; Type*; Landscape_Type*; Landscape.Type*.PC1	Urban- (Southern-)	Top: 0.874; Type: 0.888	

Spp	Yr	Error D	Top detection model	Environmental model	Parameter directions	GOF	Notes
BTNW	14	Pois	<u>ODate</u> , NullDet, QDate	Landscape*.Type*; Landscape*_Type*; Landscape*.Type*.PC1	Urban-, Southern-	0.838	
SCTA	14	Pois	<u>NullDet</u> , OTime	Type*; Landscape.Type*; Type*.PC1	Urban-, (Southern-)	0.685	
EAWP	14	Pois	<u>NullDet</u> , null, OTime, ODate	Landscape+.Type*; Type*; Landscape_Type; Landscape+.Type*.PC1	Urban+, (Southern+)	0.78	
RBGR	14	Pois	<u>NullDet</u> , ODate	Landscape*; Landscape_Type; Landscape*.Type	(Urban-), Southern-	0.403	
TUTI	14	Pois	<u>ODate</u> , QDate	Type*; Landscape.Type*; Type*.PC1; Landscape.Type*.PC1	Urban+, (Southern-)	0.555	
BCCH	13	Pois	<u>NullDet</u>	Landscape*.Type*	Urban+, Southern-	0.018	
		NegBin	<u>NullDet</u>	Landscape*.Type+; Landscape*	(Urban+), Southern-	Top: 0.0479; Landscape: 0.0619	
BCCH	14	Pois	null, <u>NullDet</u>	Landscape*; Landscape*.Type; Landscape*.PC1	(Urban+), Southern-	0.567	

APPENDIX E: TAXA OBSERVED ON TRAIL CAMERAS AND AT NON WOOD THRUSH NESTS (CHAPTER 3)

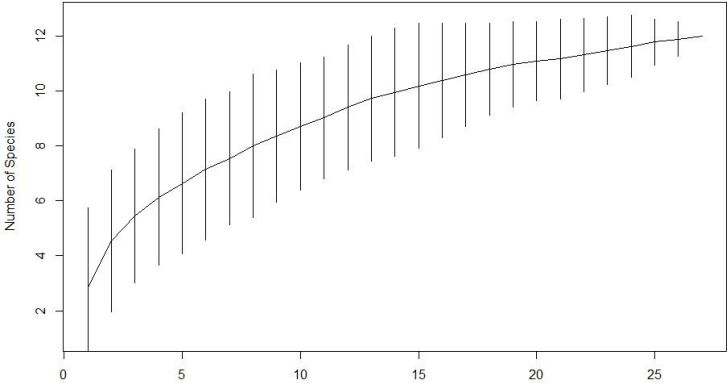
Taxa identified on trail camera surveys. Left: species counted as predators; right: species not counted as predators.

Species	Scientific Name
American Crow	<i>Corvus brachyrhynchos</i>
American Red Squirrel	<i>Tamiasciurus hudsonicus</i>
Black Bear	<i>Ursus americanus</i>
Blue Jay	<i>Cyanocitta cristata</i>
Bobcat	<i>Lynx rufus</i>
Coyote	<i>Canis latrans</i>
Domestic Cat	<i>Felis catus</i>
Eastern Chipmunk	<i>Tamias striatus</i>
Eastern Gray Squirrel	<i>Sciurus carolinensis</i>
Fisher	<i>Pekania pennanti</i>
Gray Fox	<i>Urocyon cinereoargenteus</i>
Jumping Mouse	<i>Zapodidae</i>
Northern Flying Squirrel	<i>Glaucomys sabrinus</i>
Raccoon	<i>Procyon lotor</i>
Red Fox	<i>Vulpes vulpes</i>
Striped Skunk	<i>Mephitis mephitis</i>
Virginia Opossum	<i>Didelphis virginiana</i>

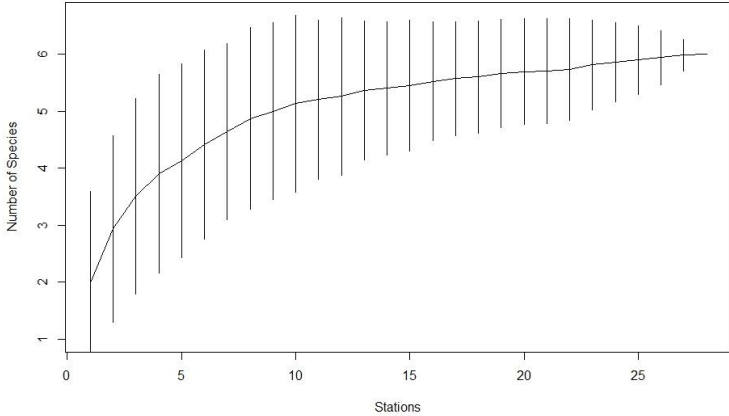
Species	Scientific Name
Domestic Dog	<i>Canis familiaris</i>
Cottontail Rabbit	<i>Sylvilagus spp.</i>
Human	<i>Homo sapiens home so</i>
Moose	<i>Alces alces;</i>
Porcupine	<i>Erethizon dorsatum</i>
Turkey Vulture	<i>Cathartes aura</i>
White-tailed deer	<i>Odocoileus virginianus</i>
Wild Turkey	<i>Meleagris gallopavo</i>
Wood Thrush	<i>Hylocichla mustelina</i>
Woodchuck	<i>Marmota monax</i>

APPENDIX F: SPECIES ACCUMULATION CURVES FOR PREDATOR POINT COUNT SURVEYS (CHAPTER 3)

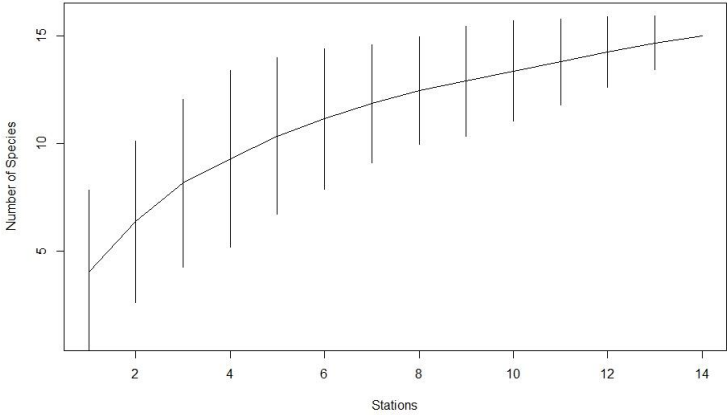
Species Accumulation on Urban Point Counts



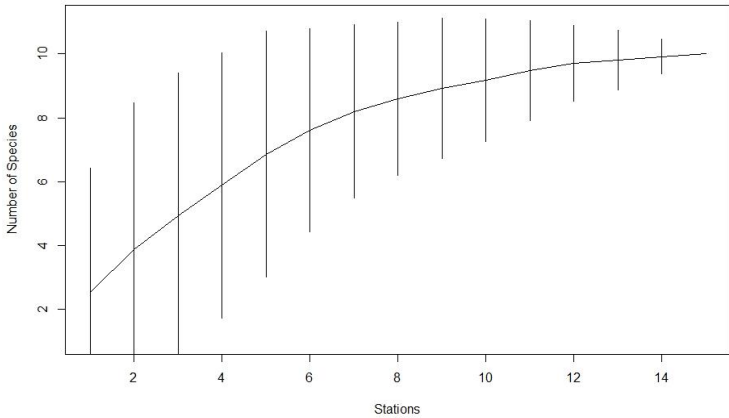
Species Accumulation on Rural Point Counts



Species Accumulation on Urban Trail Cameras



Species Accumulation on Rural Trail Cameras



APPENDIX G: PLANT TAXA IN COMPOSITE VEGETATION GROUPS (CHAPTER 4)

Plant taxa included in composite groups for vegetation composition analysis. Note that forb and rubus spp. were separate categories for the urban vs rural composition analysis, but not for the random vs used composition analysis. *Chestnut was included in the “Other” category because it was unclear whether the observer recorded American chestnut (*Castanea dentata*; native) or horse-chestnut (*Aesculus hippocastanum*; introduced).

Native deciduous broadleaf (NDB)	Non-native Broadleaf (NNB)	Other
Alder spp (<i>Alnus</i>)	Barberry (<i>Berberis thunbergii</i>)	Apple (<i>Malus domestica</i>)
Ash spp (<i>Fraxinus</i>)	Buckthorn, common (<i>Frangula alnus</i>)	Bittersweet (<i>Celastrus orbiculatus</i>)
Aspen, quaking (<i>Populus tremuloides</i>)	Buckthorn, glossy (<i>Rhamnus cathartica</i>)	Cherry spp (not black; <i>Prunus</i>)
Basswood, American (<i>Tilia americana</i>)	Euonymus, winged (<i>Euonymus alatus</i>)	Chestnut*
Beech, American (<i>Fagus grandifolia</i>)	Honeysuckle (<i>Lonicera</i>)	Crabapple (<i>Malus</i> spp)
Birch, black (<i>Betula lenta</i>)	Knotweed, Japanese (<i>Fallopia japonica</i>)	Dead branch(es)
Birch, gray (<i>Betula populifolia</i>)	Maple, Norway (<i>Acer platanoides</i>)	Debris
Birch, yellow (<i>Betula alleghaniensis</i>)	Olive, autumn (<i>Elaeagnus umbellata</i>)	Elderberry (<i>Sambucus canadensis</i>)
Birch, white (<i>Betula papyrifera</i>)	Privet (<i>Ligustrum</i> spp)	Forb spp / herbaceous
Blueberry (<i>Vaccinium</i> spp)	Rose, multiflora (<i>Rosa multiflora</i>)	Graminoid spp
Cherry, black (<i>Prunus serotina</i>)		Grapevine (<i>Vitis</i> spp)
Dogwood (flowering; <i>Benthamidia florida</i>)		Maple spp (<i>Acer</i> spp)
Dogwood (<i>Swida</i> spp)		Mountain laurel (<i>Kalmia</i> spp)
Elm spp (<i>Ulmus</i>)		Pine, red (<i>Pinus resinosa</i>)
Hickory spp (<i>Carya</i>)		Pine spp (<i>Pinus</i>)
Holly, winterberry (<i>Ilex verticillata</i>)		Poison ivy (<i>Toxicodendron radicans</i>)
Ironwood (<i>Ostrya virginiana</i>)		<i>Rubus</i> spp
Maple, red (<i>Acer rubrum</i>)		<i>Spirea</i>
Maple, striped (<i>Acer pensylvanicum</i>)		Spruce, Norway (<i>Picea abies</i>)
Maple, sugar (<i>Acer saccharum</i>)		UnIDed woody
Musclewood (<i>Carpinus caroliniana</i>)		Viburnum, maple-leaf (<i>Viburnum acerifolium</i>)
Oak, black (<i>Quercus velutina</i>)		Vine (groundnut; <i>Viburnum acerifolium</i>)
Oak, red (<i>Quercus rubra</i>)		Vine (virgins bower; <i>Clematis virginiana</i>)
Oak [red oak group; black, red, or scarlet (<i>Quercus coccinea</i>) oak]		Virginia creeper (<i>Parthenocissus quinquefolia</i>)
Oak, white (<i>Quercus alba</i>)		Yew (<i>Taxus</i>)
Serviceberry spp (<i>Amelanchier</i>)		
Spicebush (<i>Lindera benzoin</i>)		
Witch-hazel (<i>Hamamelis virginiana</i>)		

APPENDIX H: RESIDUALS AND P-VALUES FROM CHI SQUARED POST HOC TESTS (CHAPTER 4)

Hemlock = eastern hemlock, NDB = native deciduous broadleaf, NNB = non-native broadleaf, Rub = rubus spp. See appendix F for plant species included in NDB, NNB, and Other categories.

i. Rural birds only:

		Fern	Forb	Hemlock	White Pine	NDB	NNB	Other	Rub
Fledgling	Residuals	-5.336933	-2.028019	3.621853	0.5429402	-2.237542	0.91639	3.842517	-2.48268
Fledgling	p values	0.000002	0.680933	0.00468	1	0.404015	1	0.001948	0.208638
Random	Residuals	5.336933	2.028019	-3.621853	-0.5429402	2.237542	-0.91639	-3.84252	2.482678
Random	p values	0.000002	0.680933	0.00468	1	0.404015	1	0.001948	0.208638

ii. All fledgling resight locations (i.e., “used”):

		Fern	Hemlock	White Pine	NDB	NNB	Other
Rural	Residuals	-0.2265546	3.635156	10.58962	2.00389	-18.2728	-6.770613
Rural	p values	1	0.003334	0	0.540982	0	0
Urban	Residuals	0.2265546	-3.635156	-10.5896	-2.00389	18.2728	6.770613
Urban	p values	1	0.003334	0	0.540982	0	0

iii. All random locations (i.e., “available”)

		Fern	Hemlock	White Pine	NDB	NNB	Other
Rural	Residuals	2.412719	2.52743	9.951285	4.720556	-18.8262	-7.48863
Rural	p values	0.190008	0.137881	0	0.000028	0	0
Urban	Residuals	-2.41272	-2.52743	-9.951285	-4.72056	18.82622	7.488625
Urban	p values	0.190008	0.137881	0	0.000028	0	0