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Fear, Parental Behavior, and Community Structure in Residential Lands

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FEAR, PARENTAL BEHAVIOR, AND COMMUNITY STRUCTURE IN RESIDENTIAL LANDS

A Dissertation Presented

by

AARON M. GRADE

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DEDICATION

For Clare, who has always shown me the importance of a sliver of light in the dark.

FRONTISPIECE

House Wren at nest box, illustration by Marc Maignan

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This achievement is shared with you all!

ABSTRACT

FEAR, PARENTAL BEHAVIOR, AND COMMUNITY STRUCTURE IN RESIDENTIAL LANDS

SEPTEMBER 2020

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In an urbanizing world, residential lands present an opportunity for conservation of biodiversity right in our backyards. Informed conservation necessitates a mechanistic understanding of how development influences animal populations and communities. Birds nesting in residential lands are less productive in urban yards than rural yards. Urban yards also have higher densities of potential predators, but lower *per capita* predation, indicating that direct predation is not entirely responsible for lack of productivity. I suggest that fear effects, also known as non-lethal effects, could be a mechanism by which predators exert indirect influence on bird parental behavior and nestling condition in urban yards. I investigated how fear of adult-consuming predators interacts with urbanization to affect parental behavior and nestling condition in residential yards across an urban gradient in western Massachusetts. We conducted a predator playback experiment on nesting house wrens (*Troglodytes aedon*), measuring nestling condition and parental behavior. We found that nestlings exposed to predator playbacks and in urban yards had reduced mass compared nestlings exposed to control playbacks and in rural yards. To varying degrees across the gradient, predator playbacks suppressed provisioning rates and brooding durations. Nestling age, clutch size, habitat structure, and microclimate were also related to provisioning rates and brooding durations. In an associated study, we examined the relationship between landscape-scale and parcel-scale features and mammal community structure by deploying camera traps in the same yards. Many mammal species are potential nest and/or adult-consuming predators of house wrens, so changes in the mammal community could alter trophic dynamics and influence fear effects across the gradient. Mammalian community composition varied significantly across the urban gradient, and species richness responded non-linearly to urbanization, with peak richness in the suburbs and in yards with larger mean tree diameters. These results, coupled with fear's influence on bird parental behavior and nestling condition, highlight the importance of considering both direct and indirect effects of trophic dynamics in urban systems.

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CHAPTER 1

INTRODUCTION

Our planet is experiencing a human-driven extinction crisis, resulting in the loss of biodiversity (Ceballos *et al*. 2015). Simultaneously, the human population is growing, and there is movement from rural areas into cities and suburbs worldwide (United Nations 2014). These trends are driving patterns of urbanization and land-use conversion, especially in residential lands, resulting in wildlife habitat loss, degradation, and fragmentation (McKinney 2006). To inform effective conservation of the natural world, researchers and managers alike are recognizing the need to understand the dynamics of residential lands, and to maximize ecosystem function and biodiversity in this ever-growing land-use (McKinney 2002). Conservation of biodiversity in residential lands not only helps to foster landscape connectivity and species populations, it also improves the quality of life for billions of people now living in cities and suburbs (Brown and Grant 2005, Lerman and Warren 2011).

In my dissertation research, I focused on the complex and often counterintuitive ways that ecological communities respond to and interact with urbanization (Shochat *et al*. 2010). *My central thesis was that current models of urban population and community dynamics are underestimating the influence of top-down trophic effects by often failing to account for fear effects.* Fear of predators, a known and well documented non-lethal effect of predation (Cresswell 2008), affects animal behavior and has cascading outcomes on offspring, populations, and communities (LaManna and Martin 2016). Urban and suburban areas are characterized by altered trophic dynamics; humans input resources from the bottom-up, extirpate apex predators, and introduce non-native species (Faeth *et al*. 2005). These changes result in mesopredator release, and a phenomenon called the predation paradox – high population densities of potential nest and adult-consuming predators in urban and suburban areas, yet low *per capita* predation rates (Fischer *et al*. 2012). The presence of numerous potential predators, apart from direct risk of predation, may be influencing animal behavior and reproductive outcomes through fear effects. In my dissertation, I incorporate fear effects into the web of interactions and mechanisms that a common passerine bird, the house wren (*Troglodytes aedon*; Fig. 1), faces while nesting in residential backyards across an urban gradient (Fig. 2).

In **Chapter 1**, I tested the influence of fear on nestling condition using experimental playback of adult-consuming predators. When we introduced a realistic exposure of additional predators, nestling mass decreased by roughly 10% – the same magnitude of change seen across the urban gradient without the introduced fear effects. With these results, we demonstrated that fear could have a significant additive effect on nestling condition in residential lands across an urban gradient. In **Chapter 2**, we assessed how fear and urbanization influenced parental behavior via provisioning and brooding. We found that fear and urbanization influenced provisioning and brooding, and the degree and direction of response depended on the modulating factors of nestling age and clutch size as well as habitat structure and microclimate. Introduction of fear effects significantly suppressed provisioning across the urban gradient. In contrast, older nestlings exposed to control playbacks were provisioned more often in rural yards than in urban yards. With the results of these chapters, we decreased nestling condition to the ultimate mechanism of fear and the proximate mechanism of parental behavior. Several mammal species are opportunistic nest or adult-consuming predators of birds, so shifts in mammal communities could have implications for fear effects in residential lands. In **Chapter 3**, we explored how mammal communities changed across varying degrees of urbanization in residential yards. We found a non-linear relationship between mammalian species richness and urbanization, with peak richness in the suburbs. Urbanization at the landscape-scale was the best predictor of mammal species richness and community composition overall, although at the parcel-scale, average tree diameters were positively associated with species richness. Mammal community diversity and composition were related to urbanization across multiple spatial scales, with possible implications for trophic dynamics, predation, and fear effects.

Residential lands make up a large portion of urban areas across human-dominated landscapes. As the world urbanizes, managers, policymakers, and residents have the opportunity to make science-informed land management decisions at landscape and parcel scales to maximize biodiversity and to support populations of threatened species. Residential lands are often overlooked in discussions about conservation, but they represent our most salient connection to the natural world.

Figure 1. The house wren (*Troglodytes aedon*) served as a model passerine species to examine the effects of urbanization and fear on nesting (photo by AMG).

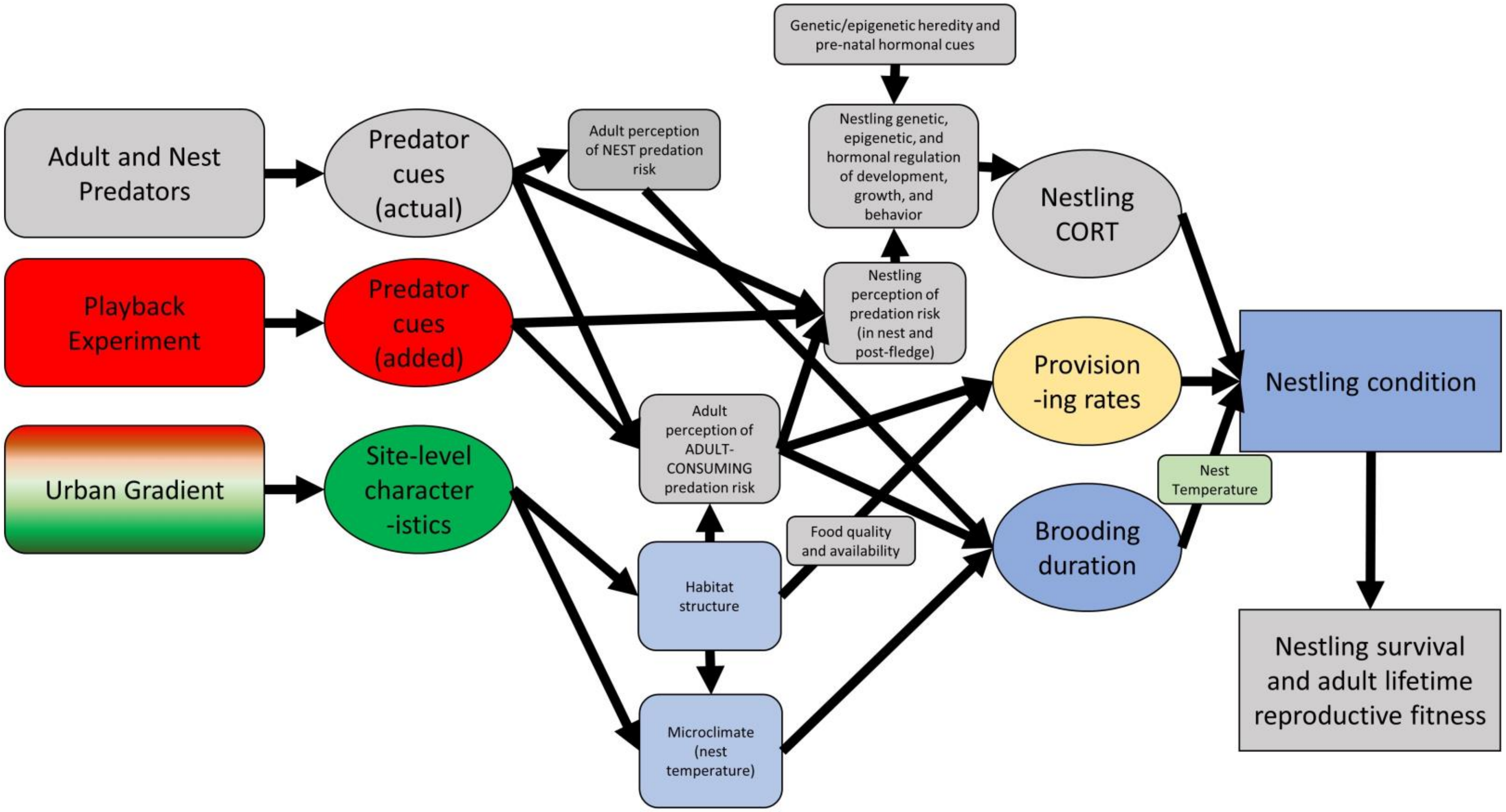

Figure 2. Conceptual diagram of the hypothesized interactions and mechanisms influencing passerine nesting in residential backyards across urban gradients. Gray boxes represent aspects that were not directly measured in our study system. Our playback experiment (red rectangle) added adult-consuming predator cues in a system that already contained adult-consuming and nest predators (gray rectangle, top left), as well as an urban gradient with site-level characteristics (red to green gradient rectangle, bottom left). These three factors, already present adult and nest predators, playback experiment, and urban gradient, influenced aspects of reproduction such as nestling hormones (CORT), provisioning rates, and brooding durations through direct and indirect effects such as behavior in response to risk, habitat structure, microclimate, food availability, and temperature. Genetic and epigenetic factors also influenced

nestling growth and hormonal regulation. These interactions and behaviors resulted in changes in nestling condition, nestling survival, and adult lifetime reproductive fitness.

CHAPTER 2

PERILOUS CHOICES: LANDSCAPES OF FEAR FOR ADULT BIRDS REDUCED NESTLING CONDITION IN RESIDENTIAL YARDS ACROSS AN URBAN GRADIENT

Abstract

Predator fear effects influence parental investment in many species. In non-urban systems, passerines often respond to nest predator cues by reducing parental investment, resulting in smaller and lighter nestlings. In contrast, results of exposure to adult-consuming predators remain unresolved. Since trophic interactions in urban areas are highly altered, it is unclear how passerines respond to fear effects in these human altered landscapes. Nestlings of passerines in urban areas also tend to be smaller and lighter than their rural counterparts and are often exposed to high densities of potential predators, yet experience lower *per capita* predation, a phenomenon called the “predation paradox.” We suggest that in urban habitats, fear effects could be a significant mechanism influencing nestling condition in birds, despite lowered predation rates. We manipulated the exposure of parent birds to adult-consuming predator risk in residential yards across a gradient of urbanization to determine the relative influence of urbanization and fear on nestling condition. We found that nestlings had reduced mass in nests when adults were exposed to predator playbacks as well as in more urban areas, though these effects were additive and not interactive. Despite lower *per capita* predation rates in urban areas, fear effects from increased predator densities may influence passerine fitness through reduced

nestling condition. As urban development expands, biodiversity conservation hinges on a deeper mechanistic understanding of the effects of urbanization on reproductive outcomes.

Introduction

Fear of predators is a significant ecological mechanism that has consequences at the individual (Werner *et al*. 1983, Skelly 1992, Creel *et al*. 2005, Fontaine and Martin 2006), population (Sinclair and Arcese 1995, Creel *et al*. 2005, Zanette *et al*. 2011), and community levels (Kotler 1984, Werner and Anholt 1996, Hua *et al*. 2013). Fear effects, also called non-lethal or non-consumptive effects of predation, are manifested primarily through behavioral changes in response to cues of perceived predation risk (Abrams 1984, Cresswell 2008, Grade and Sieving 2016). Thus, fear effects could be influencing animal demography across human-altered landscapes (e.g., suburbs, cities), which are characterized by high densities of potential predators yet low *per capita* predation rates (Fischer *et al*. 2012). To maximize lifetime reproductive success, breeding adults adjust investment in current reproduction (e.g., provisioning of young) versus self-maintenance and vigilance, and this tradeoff may vary across gradients of human-alteration as a function of levels of fear (Fig. 3; also see Lima 1993, Ghalambor and Martin 2000, Fontaine and Martin 2006, Blumstein 2006). However, given the mismatch between predator densities and predation rates in urban settings, the question remains as to whether animal responses to fear effects significantly influences reproductive outcomes.

Passerines are adept at detecting (Lohr *et al*. 2003), communicating (Magrath *et al*. 2007, Courter and Ritchison 2010), and modifying behavior (Huang *et al*. 2012) in response to even slight changes to landscapes of fear. Experiments conducted on passerines in intact natural systems have shown that in the presence of nest predator cues, breeding birds reduce their reproductive investment by changes in behavior (Zanette *et al*. 2011, Huang *et al*. 2012, Hua *et al*. 2014, Malone *et al*. 2017) or clutch size (Doligez and Clobert 2003, Eggers *et al*. 2006, Zanette *et al*. 2011, Martin 2011). Over time, these individual behaviors could have population-level effects on demography (Pangle *et al*. 2007, Martin 2011) and evolution (Blumstein 2006, Cresswell 2008). In a given breeding season, birds presented with nest predator cues respond rapidly by reducing provisioning rates – a proximate mechanism that can result in reduced nestling mass and condition (Eggers *et al*. 2006, Zanette *et al*. 2011, Martin 2011, Hua *et al*. 2014). This strategy reduces current reproductive investment when the chance of nest failure is high to increase likelihood of adult survival and future reproductive opportunities (Ghalambor and Martin 2000, Fontaine and Martin 2006).

The effects of fear were the subject of a recent critique in which the authors argued that previous studies have overstated the influence of fear on prey demography (Peers *et al*. 2018). Peers *et al*. (2018) rightly suggests that this ecological mechanism requires further exploration with carefully designed *in situ* experiments. Additionally, despite the preponderance of *nest predator* fear effects studies in passerines, few studies have experimentally tested the effect of *adult-consuming* (i.e., predators known to consume breeding-age birds) predator cues on reproductive investment. A small number of previous studies present conflicting responses to this type of threat (Ghalambor and Martin 2000, Malone *et al*. 2017). In fact, Malone *et al*. (2017) argue that shifting patterns of fear effects (nestling vs. adult mortality) may yield different reproductive outcomes. Passerines behaviorally respond to predator cues in short time scales (Lima 1993, Creel and Christianson 2008). Therefore, it is likely that adult-consuming predator cues indirectly influence reproductive outcomes through changes in parental behavior, though it is unclear whether the exposure to these cues typically results in increased or decreased reproductive investment (Ghalambor and Martin 2000, Hua *et al*. 2013, 2014, Malone *et al*. 2017). Given their salience, predator cues may have direct implications for reproductive outcomes, and their effects require further empirical investigation in a variety of study systems, especially in systems with altered trophic dynamics such as urban habitats (Faeth *et al*. 2005).

Patterns of passerine reproductive success across urban gradients are well-described, but the ecological processes behind these patterns remain uncertain (McKinney 2002, Chace and Walsh 2006, Chamberlain *et al*. 2009, Pennington and Blair 2012, Rodewald *et al*. 2013). Studies have described a predation paradox in urban and suburban environments – despite increased density of potential predators with more urbanization, urban systems typically have decreased *per capita* predation (Shochat 2004, Ryder *et al*. 2010, Fischer *et al*. 2012). In areas of increased urbanization, clutch sizes are typically smaller and nestlings in poorer condition (Newhouse *et al*. 2008, Chamberlain *et al*. 2009, Evans *et al*. 2011). Despite relaxed predation in urban systems, passerine reproductive outcomes shift in a direction consistent with an increased risk of predation

(Fig. 3; also see Chamberlain *et al.* 2009; Malone *et al.* 2017). In these systems, fear effects may misrepresent actual predation risk and may serve as a significant ecological mechanism in urban habitats (Shochat *et al*. 2004, Bonnington *et al*. 2013). Although studies have tested the effects of fear in urban versus rural greenspace (e.g., Malone *et al.* 2017), no study to our knowledge has assessed how fear affects nestling condition across urban gradients in response to fear of adult-consuming (versus nest) predators. In addition, behavioral response to fear is understudied in residential lands. Residential lands are a prominent and growing land use type comprising almost half of urban green spaces, and have highly altered trophic dynamics and widespread conservation implications (Lerman and Warren 2011, Lerman *et al*. 2012, Goddard *et al*. 2017).

We designed an experimental cue-addition playback study to test how fear of adult-consuming predators affects nestling condition. We hypothesized that introduction of adult-consuming predator cues would significantly reduce nestling body condition. We used the cue-addition method because it randomizes exposure to supplementary predator cues without eliminating existing predation risk (Hua *et al*. 2013). This maintains the natural lethal and non-lethal effects in the system while controlling for their presence by adding fear cues evenly across the urban gradient. We focused on adult-consuming predator cues because the majority of fear effects studies for birds have focused on nest predators (Martin 2011; Hua *et al.* 2014 but see Ghalambor and Martin 2000). Implementing studies in a variety of ecosystems and utilizing experimental designs that examine different aspects of fear will result in a more generalizable understanding of fear effects in the field of ecology.

Materials and Methods

Study system

We conducted a predator playback experiment on house wrens (*Troglodytes aedon*) by deploying nest boxes in 38 single-family residential yards across a gradient of urbanization in western Massachusetts, United States. All manipulations and measurements were permitted and approved by the University of Massachusetts Amherst IACUC #2015-0052, Commonwealth of Massachusetts banding permit #025.16BB, and United States federal banding permit #23140. House wrens are common, highly territorial, and their nesting ecology is well understood across much of their expansive range (Johnson 2014). They also nest readily in backyard nest boxes and are present across a wide degree of urbanization, avoiding only the most urban or forested areas (Newhouse *et al*. 2008). House wrens often have two clutches of eggs per breeding season and lay anywhere between two and ten eggs per clutch (Johnson 2014). In our study system, house wrens regularly laid a second clutch in the same nest box as the first clutch, even when the first nest failed (AG pers. obs.). Males and females both provision (i.e., feed) nestlings, though only females incubate eggs and brood nestlings (Fontaine and Martin 2006).

Our study area in western Massachusetts is characterized by large tracts of mixed deciduous-coniferous forests interspersed with agricultural land and urban development of various housing densities. Overall, our residential yard study sites were spread across an urban gradient, which included high-density suburban, low-density suburban, and rural forested and agricultural landscapes, but precluded the densest urban city centers as well as interior forested lands (Fig. 4). Our urban gradient was centered on Springfield, the third largest city in Massachusetts, and we developed a generalizable index of urbanization using methods similar to those outlined in Rodewald *et al.* (2013). We generated a 1-km area buffer around each study site (i.e., landscape-scale suitable for this sized passerine; see Rodewald *et al.* 2013; Evans *et al.* 2015) using ArcMap version 10.5 (ESRI, Inc.) and used reduced classifications of land cover from the Massachusetts 2005 land-use data layer (MassGIS 2018) to determine area (m^2) of each land cover type. For this analysis, we included the following reduced categories: forest, open land, low-density residential, high-density residential, and commercial land cover types. We conducted a principal components analysis (PCA) of the cover types surrounding study sites using R program version 3.2.3 (R Core Team 2019). Only the first two principal components had an eigenvalue greater than one, and therefore were considered for inclusion as an axis of variation (Manly *et al*. 2016).

The first principal component explained 49.6% of the variation in land cover surrounding the sites and had an eigenvalue of 2.48. It loaded negatively on forest, open land, and low-density residential land cover types, and positively on high-density residential and commercial land cover types (see Appendix A Table 8 and Fig. 16 for detailed results). We used the first principal component as an urban index for our subsequent analyses since it aligned with urban versus rural land cover types (Rodewald *et al*. 2013) and had the most proportion of variance explained. Sites on our urban index scale were centered around 0 and spanned from -3 (most rural) to + 3 (most urban).

Playback recordings

To test for fear effects of adult-consuming predators, we generated several replicate playback recordings for a playback experiment (Zanette *et al*. 2011, Hua *et al*. 2013). Each nest was exposed to only one treatment type, either predator or control. All predator treatment recordings contained *both* the calls of a regionally common diurnal predator, Cooper's hawk (*Accipiter cooperii*), timed to play during the day, and the calls of a regionally common nocturnal predator, eastern screech owl (*Megascops asio*). Both species are known to depredate adult house wrens, but rarely nestlings of cavity-nesting birds (Johnson 2014, Dorset *et al*. 2017). The control recordings all contained calls of two harmless and regionally common bird species with similar call structures to both predators (Zanette *et al*. 2011). Downy woodpecker (*Picoides pubescens*) served as the hawk control and played during the day, and mourning dove (*Zenaida macroura*) served as the owl control, and therefore played at night (Hua *et al*. 2013). We obtained exemplar call recordings of each species from the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, macaulaylibrary.org) and Xeno-Canto (xeno-canto.org), and selected recordings from the northeastern United States when possible. Using the program Audacity version 2.2.2 (audacity.sourceforge.net), we generated 30 s (for hawks and hawk control) and 60 s (for owl and owl control) exemplar call clips. We applied noise reduction, maximum amplitude, and normalized amplitude to 90% (Zanette *et al*. 2011, Hua *et al*. 2013).

We generated complete recordings (three days long) by creating 24 hour-long tracks for both predator treatment and control playbacks. Each of these 24 hour-long tracks contained either a combination of hawk and owl calls, or a combination of the woodpecker and dove control calls. We inserted randomly selected exemplar clips at randomly selected time intervals within one-hour blocks. The rest of each track contained silence. We kept the rate per hour of the exemplar clips consistent between control and treatment tracks and determined call rates and times of day based on the known activity patterns of the hawk and owl species in the study system (AG pers. obs.). Due to this protocol, the mourning dove calls (i.e., control for owls) followed the typical nocturnal pattern of owl calls (see Appendix A Table 9 for playback recording timing and rates). We built portable playback speaker units using mini portable Bluetooth speakers (Easy Acc Model LX-839) and MP3 players (Sandisk Clipjam MP3 Player 8 gb) that we housed in plastic containers covered in camouflage fabric, and placed on top of 1.5 m garden stakes (see Appendix A Fig. 15 for schematic diagram of assembly).

Playback experiment

We deployed nest boxes in each backyard from April – May (prior to the start of breeding) and monitored them from May – August 2017 and 2018. We monitored nest boxes for signs of house wren nest building and continued monitoring until house wrens completed laying eggs. We only conducted the playback experiment at one nest box at a time per yard. We used stratified-random selection across the urban gradient to determine which nests received treatment versus control playback, ensuring even sampling. This experimental randomization also allowed us to parse out added fear effects (i.e., experimental playbacks) from existing effects of urbanization, which included fear effects already present in the system. We began the playback experiment at each nest after the last egg was laid to induce fear effects on incubation and nestling stages. This eliminated pre-incubation playback effects (e.g., clutch size or nest site selection). We placed the playback units five meters away, facing the nest box. We calibrated the playback amplitudes before each deployment to a peak amplitude of 78.2 (± 2) dBA at one-meter using a decibel meter (Dr. Meter Sound Level Meter Model MS-10). We chose close proximity and low volume for playbacks to mitigate community-level effects seen in some fear effects playback studies (Hua *et al*. 2013) as well as to maintain realism of predator cues (Peers *et al*. 2018). We rotated the portable playback speakers in and out of the yards at three-day intervals to avoid habituation to playbacks. We ended playbacks after four rotations, when nestlings typically fledge the nest. In the event of a re-nest in the same yard in the same year, we tested the second clutch with the same treatment type (either predator or control) as the first clutch and accounted for re-nests (i.e., brood-order as a covariate) and repeated measures (site as a random effect) in the statistical models.

Nestling measurements

To assess nestling body condition, we marked each individual nestling with non-toxic colored permanent markers on their tarsi to track individual growth over the course of the experiment (Cheng and Martin 2012). Every three days, we measured each nestling’s mass using a digital scale (AWS AC Pro-200; ± 0.01 g) from age 0 – 6 days, and a spring scale from age 9 – 15 days (Pesola Micro #20060, ± 0.05 g). Older nestlings were a significant force-fledge risk and young nestlings were as light as 0.75 g, making the use of the two measurement instruments necessary for safe and accurate measurements. To ensure accuracy and consistency in measurements, we calibrated the scales regularly with a standard weight, and compared scales to an accuracy of ± 0.05 g, and nestling mass at 12 days old (used in the fear effects analysis) was only measured with the spring scale. In addition to mass, we measured right wing chord, and tail length to the nearest mm.

Statistical Analyses

All statistical analyses were performed in R program version 3.2.3 (R Core Team 2019). We evaluated whether playback treatment or urbanization affected nestling body condition at 12-days of age. We chose 12-days since it was the measurement just prior to nestling fledging and the day of average nestling asymptotic mass derived by the nestling growth analysis (Cheng and Martin 2012; Sofaer *et al.* 2013; see Appendix A for nestling growth curve analysis and results; see Appendix A Fig. 17 for growth curves by playback type). We included only successful nesting attempts in our analyses. Using each growth metric as a response variable (mass, wing chord, and tail), we generated global generalized linear mixed models (GLMMs) using the *nlme* package (Pinheiro *et al.* 2017). These GLMMs included the following hypothesized variables: playback type, urban index, playback type x urban index, and the following covariates: clutch size, brood-order, and nest year. We included nest-nested-in-site (hereafter, Nest | Site) as a random effect to account for multiple individual nestlings within nests and multiple nests within sites (Zuur *et al.* 2009). The covariates were uncorrelated and were compared for fit in a maximum likelihood model selection framework.

We compared ecologically plausible combinations of the fixed effects variables with each other and the global model (Burnham and Anderson 2003). We used the *AICcmodavg* package (Mezerolle 2017) to find corrected Akaike's information criterion, AIC_c (Akaike 1973) values to select best supported models. We considered any model with $\Delta AIC_c < 2$ than the model with the lowest AIC_c value to be equally supported (Burnham and Anderson 2003). We used the *visreg* package (Breheny *et al.* 2017) along with the *ggplot2* package (Wickham 2016) to generate partial model residual regression plots.

Results

We obtained measurements for n = 59 successful nests (n = 28 in 2017 and n = 31 in 2018) and n = 288 nestlings at 30 sites (see Supporting Information). In our analysis, we only included nests that successfully fledged nestlings, and some nests that could not be measured at day 12 were also excluded. Nest failure rates were low, not correlated with urbanization, and were primarily caused by house sparrow (*Passer domesticus*) or house wren competitive antagonism for nest box access (AG pers. obs.). There was only one confirmed instance of nest predation - by black bear (*Ursus americanus*) - and four confirmed instances of nest abandonment, including two confirmed instances of adult female mortality by wounds caused by domestic housecat (*Felis catus*; AG pers. obs.).

We found a significant effect of predator playbacks and urbanization on 12-day nestling mass. Exposure to predator playbacks resulted in nestlings that were on average 10.4% or 1.14 g lighter compared to nestlings exposed to control playbacks (SE = 0.31, t_5

= -3.72, P = 0.01; Fig. 5). Nestlings in more urbanized settings were lighter compared to nestlings in more rural settings (β = -0.23, SE = 0.11 t_{16} = -2.09, P = 0.05; Fig. 6). Brood order (first or second brood) and clutch size were also included in two of the selected models, although they were not statistically significant (Appendix A Table 16; for a full list of candidate models, see Appendix A Table 15 and Table 16). We found no effect of playbacks or urbanization on wing chord or tail length, although we did find an effect of year (β_{2018} = -6.83, SE = 1.46 t_5 = -4.66, P = < 0.01; i.e., 17% smaller in 2018) on 12-day nestling wing chord.

Discussion

The addition of adult-consuming predator cues had a strong effect on 12-day nestling mass, as did urbanization. Nestling mass just prior to fledging is a significant measure of condition and probability of survival post-fledging, and thus a critical point in development (Monrós *et al*. 2002, Cox *et al*. 2014). There was no significant interaction term between urbanization and fear effects (Appendix A Table 15), indicating that the effects of fear in this system were not mediated by degree of urbanization despite clear reductions in 12-day nestling mass across the gradient.

Our experimental results demonstrate fear as an additive driver influencing nestling condition across an urban gradient, but the mechanistic drivers behind fear’s influence on nestling condition remain unclear. Playback-induced fear could be acting to mediate parental behavior through the evolutionary tradeoff between parental investment and self-maintenance (Fig. 3). Alternatively, fear cues could be acting on nestling development directly through hormonal mediation of morphometric growth tradeoffs. For example, nestlings may allocate energy to wing growth for predator avoidance, rather than to mass (Cheng and Martin 2012). Whether the response is at the parental and/or nestling level, our experiment resulted in dramatic reductions in nestling condition with exposure to predator cues. The effects of fear on bird productivity is understudied in urban systems, and most urban nesting ecology studies focus on survival and predation of adults or nestlings (Chamberlain *et al*. 2009, Ryder *et al*. 2010, Rodewald *et al*. 2013, Evans *et al*. 2015). Suburban and urban areas are characterized by high densities of potential nest and adult-consuming predators, yet low per-capita predation (i.e., the predation paradox; (Fischer *et al*. 2012). Thus, research focusing on the effects of predators on urban avian productivity may be underestimating the true impact of predator presence if researchers only consider per-capita predation rates, and not abundance and densities of potential predators.

On its own, differences in nestling condition with fear and urbanization does not directly address proximate causes, such as reduced provisioning rate or food quality. In the following discussion, we suggest two potential proximate mechanisms for fear effects based on the preponderance of fear effects literature: (1) differences in nestling provisioning by adults and (2) nestling stress-induced hormonal responses regulating body condition development. Further, we found through our experiment that urbanization acted as a separate and additive ultimate driver of nestling condition. Thus, based on urban ecology literature, we suggest two additional proximate mechanisms for urban effects: (1) resource availability and (2) existing nest and adult predators in the system.

Fear effects: Parental investment or nestling hormones?

Given the dramatic and separate effect of fear in this system, it appears likely that reduced nestling mass was the result of shifts in investment from parenting to self-maintenance (Fig. 3). When predator risk environments increase, reducing provisioning effort may increase survival probability of adults while still allowing them to successfully rear offspring, even if offspring are in poorer condition (Fig. 3). The provisioning of nestlings in house wrens requires multiple trips per hour from foraging locations to the nest by both parents (Fontaine and Martin 2006). This heightened activity makes adults more conspicuous to predators (Ghalambor *et al.* 2013). A reduction in provisioning rate or time spent searching for high quality food for nestlings can reduce nestling growth, but may also reduce overall chances of predation (Ghalambor *et al.* 2013, Hua *et al.* 2014).

When exposed to an increased predation environment, nestlings in our experiment had reduced mass, but not reduced size. If this change in mass was due to reduced parental investment via lower provisioning rates, then lighter nestlings in risky environments possibly invested more energy in growing wing chord and tail length at the expense of mass (Cheng and Martin 2012). Though an evolutionary tradeoff from the adult perspective is the most likely explanation based on findings from past fear effects studies (see Zanette *et al.* 2011; Ghalambor *et al.* 2013), an alternative explanation is that nestling hormones were altered in response to predator cues (e.g., upregulation or downregulation of corticosterone; Tilgar *et al.* 2010, Ibáñez-Álamo *et al.* 2011). Nestlings exposed to stressful environments have higher baseline secretion levels of glucocorticoid hormones such as corticosterone (CORT; Tilgar *et al.* 2010), and chronically elevated CORT levels could influence development and body condition in nestling passerines, including morphometric tradeoffs between growth and mass (Tilgar *et al*. 2010, Ibáñez-Álamo *et al*. 2011). It is possible that adult CORT levels were also influenced by predator fear, and this could have been further exacerbated by urban effects, such as elevated levels of ambient background noise (Grade and Sieving 2016, Davies *et al*. 2017).

Cavity nesting species, such as house wrens, experience relatively low rates of nest predation at the nestling stage, but are vulnerable to adult-consuming predators once they fledge the nest (Ghalambor and Martin 2000). Thus, investing in tail and flight feather growth at the expense of mass may allow nestlings to better escape adult-consuming predators such as cats, owls, and hawks upon fledging the nest (Cheng and Martin 2012). We exposed nestlings in our experiment to playback cues from incubation until fledging. Nestlings were also potentially exposed to secondary cues of predation risk, such as alarm and scolding calls from their parents and other nearby individuals. It is unclear which of these proximate mechanisms are responsible for differences in nestling mass, and we suggest future physiological studies link nestling CORT levels with nestling development in response to fear effects.

Urban effects: Resource availability or predator abundance?

Our findings of reduced nestling mass in urban yards is a pattern found across species in urban systems (Newhouse *et al*. 2008, Chamberlain *et al*. 2009). In addition to the top-down influence of predators, bottom-up differences in resource availability is often related to reduced nestling condition (Chace and Walsh 2006, Newhouse *et al*. 2008, Chamberlain *et al*. 2009). Adult birds feed their nestlings arthropod sources of food for high protein (Birkhead *et al*. 1999, Wilkin *et al*. 2009). Studies have shown reductions in arthropod biodiversity, abundance, and quality in yards surrounded by higher levels of urbanization (McIntyre 2000, Narango *et al*. 2017). It is possible that the more urban yards had lower arthropod biomass, which resulted in lower nestling mass. We did not measure arthropod biomass in our study system, although research in other urban systems has linked reductions in nestling condition and availability of quality arthropod food resources in urban yards (Seress *et al*. 2018, Narango *et al*. 2018).

In addition to bottom-up factors, top-down trophic effects of predators might also be influencing nestling mass via fear effects that were *already present* in the system. These fear effects are possibly higher in more urban yards since urban yards are characterized by high densities of both nest and adult-consuming predators, and urban areas in general support high densities of mesopredator species (Crooks and Soule 1999, Shochat *et al.* 2006, Fischer *et al.* 2012; see also Chapter 3) that are often opportunistic nest predators (Crooks and Soule 1999, Sorace and Gustin 2009, Rodewald and Kearns 2011). Although some studies have reported reduced nest predation despite elevated predator densities in urban habitats (i.e., the predation paradox; Shochat *et al.* 2006; Ryder *et al.* 2010; Rodewald and Kearns 2011; Fischer *et al.* 2012), others suggest that predation is highest during the post-fledging stage, resulting in lower reproduction in urban areas (Crooks and Soule 1999, Ausprey and Rodewald 2011, Shipley *et al*. 2013). In urban settings, there are also higher population densities of some adult-consuming predators such as domestic housecats (Baker *et al.* 2005; Sims *et al.* 2008), which kill billions of birds annually in the United States alone (Loss *et al*. 2013). Some raptors also specialize on depredating urban songbirds (Mannan and Boal 2004, Chace and Walsh 2006, Rullman and Marzluff 2014). Despite these top-down trophic pressures, there is little empirical evidence that urban environments constitute ecological traps for nesting passerines via lethal effects of predation (but see Leston and Rodewald 2006; Stracey and Robinson 2012a). We suggest that the presence of additional predators in urban areas influence prey through fear effects. Through our cue-addition experiment, we found a similar magnitude of nestling mass reductions by introducing predators as we saw across the urban gradient alone.

Future directions: The value of mechanistic experiments in urban systems

Our experiment demonstrated fear as mechanism for decreased nestling condition in urban systems. Few urban ecological studies use experimental approaches to isolate potential mechanisms underlying observed patterns, but the results of such studies lead to novel inferences and a deeper understanding of the processes behind patterns (Felson and Pickett 2005, Shochat *et al*. 2006). Though it is challenging to conduct these manipulative experiments in human-dominated systems, they are critical for establishing causal inference (Shochat *et al*. 2006, Stracey and Robinson 2012b). If models of passerine demography fail to account for fear effects, they likely underestimate the full effect of predator presence. Further experimental research can determine whether the net effect of predators is additive or compensatory – for example, offset by predators' influence on mesopredators. Either way, fear effects are a highly plausible mechanism for differences in avian nestling condition seen across urban gradients (Chamberlain *et al*. 2009). Our work demonstrates that altered predator-prey interactions in urban systems can have complex and difficult to foresee impacts on reproduction. Thus, increasing urbanization worldwide may have greater consequences on wildlife communities than previously thought.

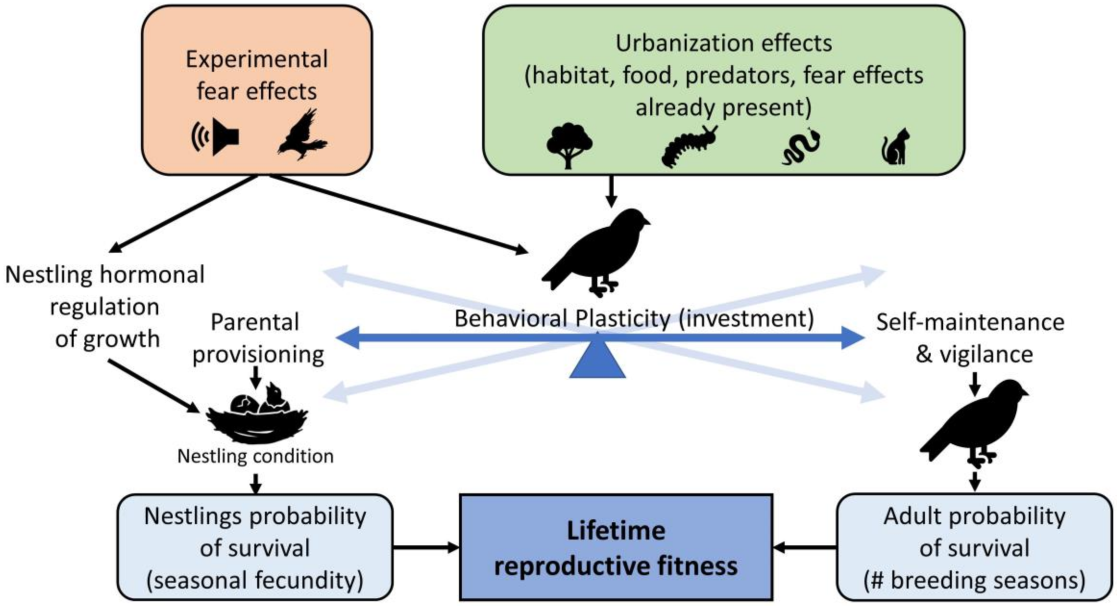

Figure 3. We experimentally added fear effects of adult-consuming predators (red rectangle, top left) to an urban gradient system in which urbanization effects were already present (green rectangle, top right). Across the gradient of urbanization, habitat, food resources, nest predators, and adult-consuming predators all influence parental investment (behavioral plasticity) of breeding birds (blue balancing scale). The investment either prioritizes investment in self-maintenance and vigilance, which increases the adult probability of survival (blue rectangle, bottom right), or parental provisioning, which increases nestling condition and nestling probability of survival (blue rectangle, bottom left). The balance of these investments is fine-tuned over evolutionary time to maximize lifetime reproductive fitness (blue rectangle, bottom center) by responding to environmental cues. By adding fear effects into a system with cues already present (i.e., cue-added study), we were able to detect which direction and to what degree the added cues push the parental investment of breeding birds.

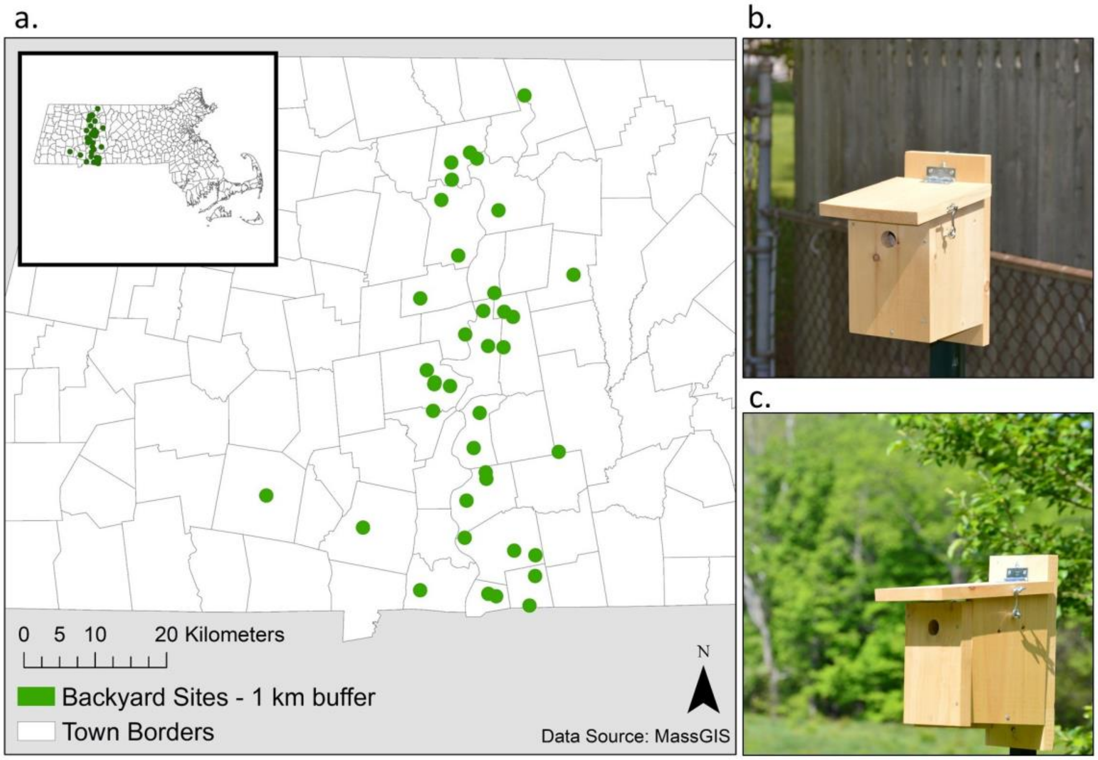

Figure 4. (a) Study sites were located in residential yards in western Massachusetts, USA, along an urbanization gradient. These example nest boxes were placed in urban (b) and rural (c) yards.

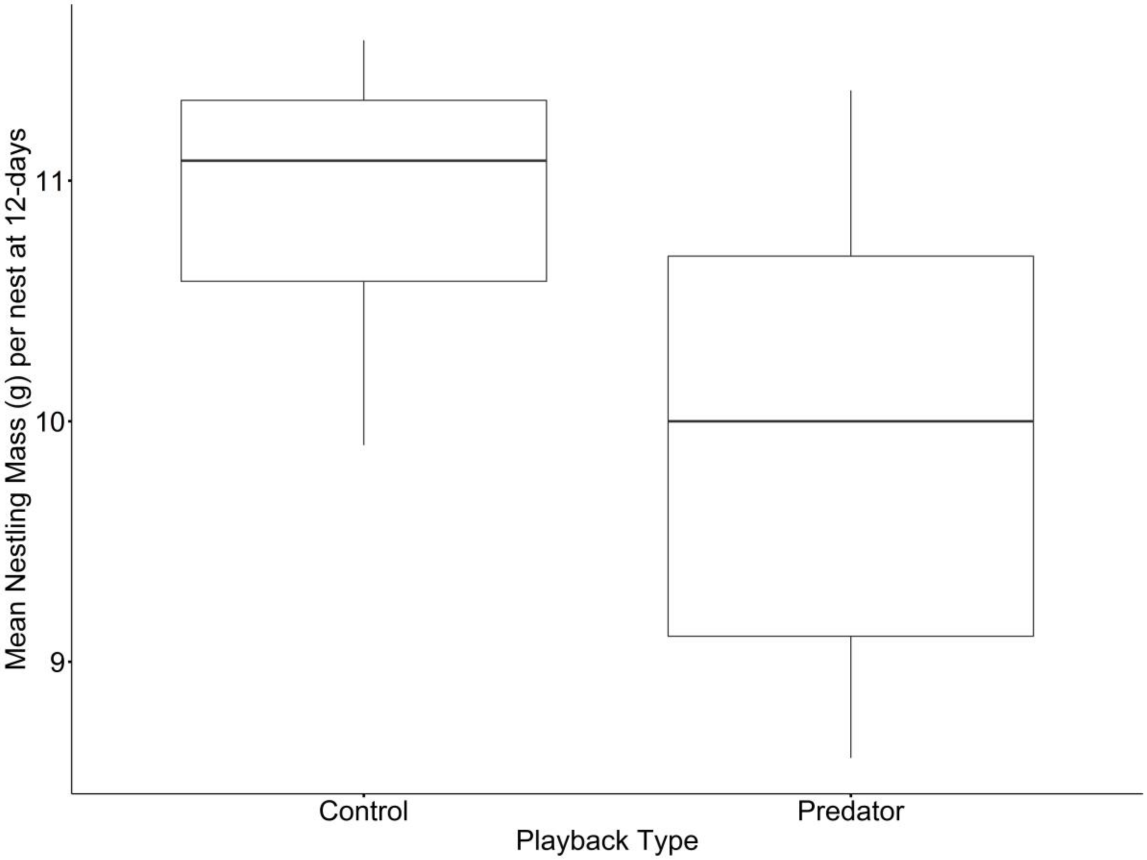

Figure 5. Playback treatment effects for 12-day nestling mass (g). Mean nestling mass taken at the nest level. Residuals generated from generalized linear mixed model (GLMM) with playback and urbanization as fixed effects and Nest nested in Site as random effects. Error bars are standard error.

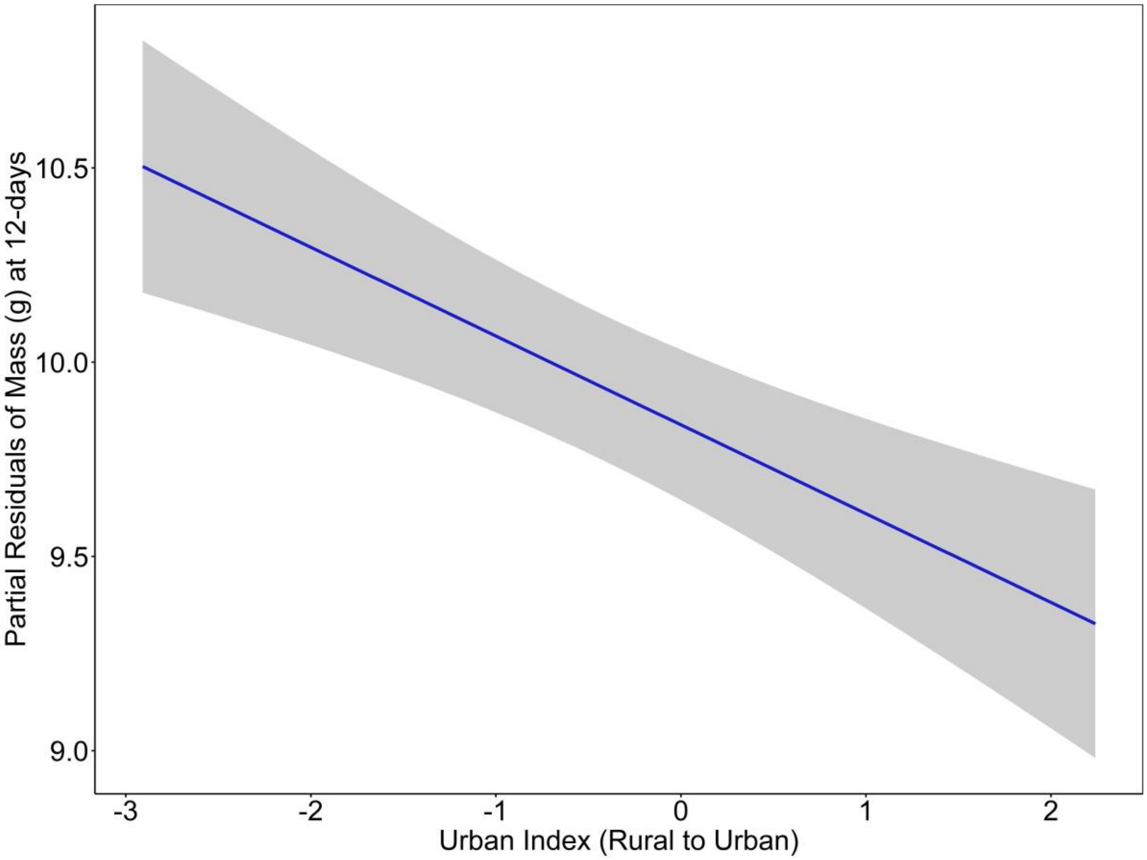

Figure 6. Urbanization effects on partial model residuals for 12-day nestling mass (g). Residuals generated from generalized linear mixed model (GLMM) with playback and urban index as fixed effects and Nest nested in Site as random effects. Ribbon is standard error.

CHAPTER 3

AVIAN PROVISIONING AND BROODING ARE INFLUENCED BY FEAR OF PREDATORS ACROSS AN URBAN GRADIENT

Abstract

Understanding how bird productivity is influenced by human development is a major challenge facing conservation in an urbanizing world. Birds are less productive in urban areas than in rural areas, but there is no consensus on the causal mechanisms. Parental investment across urban gradients is well studied, and birds exhibit behavioral plasticity in response to environmental cues such as habitat, food availability, and microclimate. Fear effects of predators, also known as non-lethal effects, are underexplored as a mechanism influencing parental investment and behavioral plasticity in response to urbanization, although urban areas have higher densities of nest and adult-consuming predators than rural areas. It is also unclear how fear in response to adult-consuming predator cues, rather than nest predator cues, influences parental investment. We conducted a predator playback experiment on house wrens nesting in residential yards across an urban gradient to identify how fear of adult-consuming predators alters parental behavior. We monitored adult provisioning and brooding, habitat structure of the yards, and microclimate at the nests. We found increased provisioning in control nests in more rural areas for older nestlings, and a suppression of provisioning visits across ages and regardless of urbanization when the parents were exposed to additional predator cues. Brooding duration decreased with increased clutch size and in more rural areas not

exposed to predators, although microclimate and exposure to predator playbacks changed the directionality of the relationship between urbanization and brooding duration, suggesting a complex response by brooding females to shifts in male parental care, predation risk, and conditions at the nest. These differences in provisioning and brooding align to our previous findings that nestlings exposed to predator playbacks and nestlings in more urban yards are significantly lighter than nestlings exposed to control playbacks and in more rural yards. Taken together, these findings suggest that fear may be a significant ultimate mechanism that influences parental behavior in residential yards across urban gradients. Fear could be compounding the influence of urbanization on bird productivity by interacting with other features of urban yards, such as habitat structure and microclimate, and modulating factors such as clutch size and nestling age. We postulate that fear effects are a key missing component in our understanding of bird nesting ecology across urban gradients and may be an important mechanism influencing bird productivity in urban areas.

Introduction

Urbanization influences bird productivity, resulting in population and community differences across urban gradients (Chamberlain *et al*. 2009, Ryder *et al*. 2010). Passerine productivity is lower in urban areas compared to rural areas (Chamberlain *et al*. 2009, Ryder *et al*. 2010, Warren and Lepczyk 2012), but the mechanisms that cause reductions in productivity are still up for debate (Chace and Walsh 2006, Shochat *et al*. 2006, Vaugoyeau *et al*. 2016). Plasticity in parental behavior is one such potential mechanism, and is a common response to urbanization (Chamberlain *et al*. 2009). Parental plasticity could include reductions in clutch sizes (Kuranov 2009), differential female versus male parental investment (Johnson and Kermott 1993, Bowers *et al*. 2014), reduced provisioning and brooding rates (Newhouse *et al*. 2008), and ultimately, reduced productivity (Chamberlain *et al*. 2009, Ryder *et al*. 2010, Stracey and Robinson 2012a). Residential lands, in particular, are abundant across gradients of urbanization, and are the focus of research on how urban development influences passerine behavioral plasticity in parenting (Ryder *et al*. 2010, Lerman and Warren 2011, Evans *et al*. 2015, Narango *et al*. 2018). Passerine parental investment tends to be lower in more urban yards, although the results of individual studies across gradients of urbanization have been mixed (Chace and Walsh 2006, Newhouse *et al*. 2008, Chamberlain *et al*. 2009, Marini *et al*. 2017, Seress *et al*. 2018). Despite this focus on nest productivity in yards, few studies have experimentally manipulated features of residential lands to test for the relative contributions of these features on parental behavior and nest productivity (Shochat *et al*. 2006).

Habitat structure and microclimate are aspects of urbanization that can influence parental behavior. Parental responses to habitat and microclimate include changes in clutch sizes (Kuranov 2009), female versus male parental investment (Johnson and Kermott 1993, Bowers *et al*. 2014), provisioning and brooding rates (Newhouse *et al*. 2008), and ultimately, productivity (Chamberlain *et al*. 2009, Ryder *et al*. 2010, Stracey and Robinson 2012a). Urban yards have more impervious surface cover, high-input management of turfgrass, and more non-native plants than rural yards (Loram *et al*. 2007, Lerman and Warren 2011, Pearse *et al*. 2018). These differences in habitat structure indirectly influence productivity by altering the abundance and nutritional quality of invertebrate resources for nestling provisioning in residential yards (Lerman *et al*. 2018, Seress *et al*. 2018, Narango *et al*. 2018). Differences in microclimate have both direct and indirect effects on productivity. Higher surface temperatures from the urban heat island affect alter microclimate, which influences plant and insect phenology (Oke 1995, Seress *et al*. 2018). Microclimate directly alters the required amount of parental brooding by reducing the need for altricial nestling temperature regulation prior to feather development (Johnson and Best 1982, Dawson *et al*. 2005, Greño *et al*. 2008).

We suggest that fear of predators (i.e., non-lethal effects of predation; Cresswell 2008, Martin 2011) is a potential ultimate mechanism that could play an significant role in driving proximate changes in parental investment. The effects of predator fear on parental investment and behavior, also known as non-lethal effects of predation (hereafter, fear effects), have received less attention than habitat structure and microclimate in urban systems. This is despite fear being identified as a significant ultimate evolutionary mechanism that alters parental investment in a variety of ecosystems for a diverse set of taxa (Skelly 1992, Lima 1998, Creel *et al*. 2005, Blumstein 2006, Pangle *et al*. 2007, Cresswell 2008, Møller 2010, Matassa *et al*. 2016, Dudeck *et al*. 2018). Indeed, in systems with high predation pressure, the magnitude of fear effects may exceed the magnitude of direct predation (Creel *et al*. 2005, Blumstein 2006, Martin 2011, LaManna and Martin 2016, but see Peers *et al*. 2018). Passerines exposed to cues of high predation risk reduce provisioning visits and alter brooding duration (Fontaine and Martin 2006, Ghalambor *et al*. 2013). Urban areas often have higher population densities of both nest and adult-consuming predators (Rodewald and Kearns 2011, Stracey and Robinson 2012b, Fischer *et al*. 2012, Rullman and Marzluff 2014), thus it is likely that birds in urban yards are exposed to a higher “dose” of predator cues than rural yards.

Plasticity in parental behavior responds rapidly to perceived predation risk derived from sensory cues detected in the environment (Sieving *et al*. 2010, Hua *et al*. 2014). On average, passerines exposed to cues of high predation risk reduce provisioning visits and brooding durations (Fontaine and Martin 2006, Ghalambor *et al*. 2013). However, when comparing parental response across species and study systems, the direction and magnitude of response is not straightforward and depends on a variety of factors. For example, life history of the species mediates fear effects; more fecund and shorter lived species tend to prioritize nest success over individual safety (Ghalambor and Martin 2000, Ghalambor *et al*. 2013, Dorset *et al*. 2017). Response to fear varies by stage of the nest (i.e., eggs, nestlings, or fledglings; Paclík *et al*. 2012, Dorset *et al*. 2017, Dudeck *et al*. 2018) and whether or not the nest is the first attempt of the season (Dorset *et al*. 2017). Parental behavioral response also differs by sex of the parent. Males are more likely to reduce overall parental effort with increased predation risk, while females may compensate for male reductions with decreased brooding and increased provisioning (Moks and Tilgar 2014, Dorset *et al*. 2017). Notwithstanding the multitude of research on fear effects in non-urbanized systems, the relative contribution of fear to plasticity in parental behavior across urban gradients remains unclear.

In a previous study (see Chapter 1), we conducted a playback experiment in residential yards across an urban gradient to test for the influence of two ultimate mechanisms – fear effects and urbanization – on differences in nestling condition. We tested for fear effects of adult-consuming predators rather than nest predators because there are few studies of fear effects by adult-consuming predators (Ghalambor and Martin 2000, Hua *et al*. 2014, Ibáñez-Álamo *et al*. 2015). Life history theory suggests responses to adult-consuming predators could be dependent on context and species' "pace of life" (Ghalambor and Martin 2000, Hua *et al*. 2014, Sepp *et al*. 2018). By randomizing experimental playback treatments across a gradient of urbanization, we separated the relative contributions of our *added* fear cues from the effects of urbanization (including fear effects) that were already present (Hua *et al*. 2014).When we conducted this playback experiment, we found that urban nests and nests that were exposed to predator playback treatments had up to a 10% reduction in nestling mass, and that fear effects were additive and not mediated by urbanization (see Chapter 1). Here, we examine how urban gradient, habitat, microclimate, and fear effects influenced brooding and provisioning in this same playback experiment. We hypothesized introducing adult-consuming predator cues would alter provisioning rates and brooding durations. We predicted provisioning and brooding would decrease when the parents were exposed to predator playbacks versus control playbacks, and across the urban gradient, and that other factors, such as nestling age and clutch size, would influence the magnitude or possibly the direction of responses. We also predicted habitat structure and microclimate would relate to differences in provisioning and brooding. Our experimental design allowed us to see whether these effects were additive or compensatory, and to what extent the addition of fear cues altered provisioning and brooding behavior.

Materials and Methods

Study system

We deployed nest boxes in 38 residential yards across an urban gradient in western Massachusetts, United States (see Chapter 1). Residents of the sites were community scientists participating in Neighborhood Nestwatch, a Smithsonian Migratory Bird Center study of avian survival and nesting ecology (Ryder *et al*. 2010, Evans *et al*. 2015). We designed the nest boxes specifically for our study species, the house wren (*Troglodytes aedon*), and the cavity size excluded most other cavity-nesting bird species. All experimental activities were approved by the University of Massachusetts Amherst IACUC #2015-0052, Commonwealth of Massachusetts banding permit #025.16BB, and United States federal banding permit #23140.

Urban Gradient

Land cover surrounding our residential study sites varied from rural low-density residential areas to suburban high-density residential areas. A matrix of mixed deciduous-coniferous forest and agriculture dominated non-residential land cover (Fig. 7). To characterize the urban gradient into a single urban index suitable for the region, we first calculated the total square areas (m^2) of major land cover types (forest, open lands, low-density residential, high density residential, and commercial; MassGIS 2018, mass.gov/orgs/massgis-bureau-of-geographic-information) within a 1-km buffer of each study site (landscape-scale for small passerines (Evans *et al*. 2015) using ArcMap version 10.5 (ESRI, Inc.). We then conducted a principal component analysis (PCA) of these land use values (Rodewald *et al*. 2013). We selected the first principal component (49.6% of the variation, eigenvalue = 2.48) as our urban index (Manly *et al*. 2016). The urban index principal component loaded positively on high-density residential and commercial, and negatively on forest, open land, and low-density residential land uses. Urban index values for our sites ranged from -3 (most rural) to +3 (most urban) and were centered at 0 (suburban). See Chapter 1 for detailed descriptions and tables of the urban index.

Predator cue playback experiment

We monitored the nest boxes during the house wren breeding season, May – August 2016 – 2018. Once egg laying ended (i.e., beginning of incubation), we exposed nests to playbacks of either predator or control acoustic cues (bird calls) to test for effects of fear on parental behavior across the urban gradient (Zanette *et al*. 2011). We tested each nest with only one treatment type (predator or control treatments; Hua *et al*. 2014). To avoid indirect long-term effects of playback, we targeted the playbacks at specific nests and began playback exposure at each nest within three days of egg laying. To avoid habituation, we rotated the playback exposures at each nest in a three-days-on followed by three-days-off pattern for four total playback rotations, which coincided with nestling fledge day.

Each portable playback unit was approximately 1 m tall, set up 5 m away, faced each nest box, and had a recording of mostly silence interspersed with bird calls at natural timings and volume (peak amplitude 78.2 ± 2 dBA at 1 m). Each predator playback included both calls of a local diurnal predator (Cooper's hawk, *Accipiter cooperii*) timed to play during the day and calls of a local nocturnal predator (eastern screech owl, *Megascops asio*) timed to play at night. Control playbacks incorporated harmless bird calls that had similar acoustic structures to the predator calls. Downy woodpecker (*Picoides pubescens*) calls served as hawk controls and were played during the day, and mourning dove (*Zenaida macroura*) calls served as owl controls and were thus played at night. See Chapter 1 for detailed methods of playback set up and recording calibration procedures.

Provisioning visitation rates and brooding durations

We monitored parental behavior with two video recordings on active nests. To select which nests were monitored on which days, we used stratified random selection to prioritize an even sampling of playback treatments and urban gradient locations. Each nest camera (Lightdow LD6000, ZLY Technology Co. Ltd.) was deployed between 0800 and 1000 prior to any other surveys or nest checks on the property. The camera was mounted on a tripod and placed 1 m on the side of the nest to better capture cavity entries and exits. Once the camera was deployed, we immediately left the area until the videography had ceased. Due to equipment battery limitations, each video recording was 48 min 28 s long, and the house wren adults typically continued their interrupted parental activities within 1 – 2 min after deployment (AG pers. obs.).

We tagged and quantified parental behaviors within the videos using program JWatcher version 0.9 (Blumstein *et al*. 2000). Two observers (blind to treatment and urban gradient) observed each video and tagged each moment that an adult house wren entered or exited the cavity hole of the nest box. Since nestlings were typically fed within the nest box, a provisioning visit was presumed when an adult entered and then exited the nest box cavity (Newhouse *et al*. 2008). Although observers also indicated if a house wren appeared to be carrying a food item, it is possible that the wrens sometimes carried food that was not visible, so we assumed all visits included provisioning (Newhouse *et al*. 2008, Bowers *et al*. 2014). In addition to provisioning visit counts, the observers considered any visit longer than 1 min in length as brooding activity. Observers recorded nestling brooding duration (min) from that subset of visits (Johnson and Best 1982, Newhouse *et al*. 2008, Dorset *et al*. 2017). We compared observer results for precision between observers, and we used the means of each variable from the two observers for subsequent analyses.

Internal and external nest temperatures

We assessed internal and external nest temperatures using Thermachron temperature loggers (Model DS1921G, OneSolution Pty. Ltd.). We deployed external temperature loggers prior to the breeding season (April – May only 2017 – 2018), hung on wire filament directly under each nest box, and suspended in inverted plastic cups for weather protection (Vierling *et al*. 2018; Appendix B Fig. 18a-b). We verified through data exploration that the use of clear plastic cups did not result in a significant temperature spike from solar radiation, and that there all iButtons were deployed similarly across the urban gradient. We deployed internal temperature loggers at the beginning of egg incubation (May – August 2016 – 2018) and attached them using wire filament into the internal side of the nest cup about 1 cm down from the top of the cup with the top facing towards the center of the nest (Vierling *et al*. 2018). We buried the logger in approximately 2 mm of nest material to prevent disturbance by the metallic shine (Appendix B Fig. 18b). To balance data collection with battery life, the external temperature loggers recorded a temperature every hour and the internal temperature loggers recorded a temperature every 24 min.

We calculated external and internal mean, minimum, maximum, and standard deviation of temperatures for all years and all nests combined (hereafter, *global-level temperatures*; Vierling *et al*. 2018). To assess the relationship between temperature and urban index and temperature and habitat measures, we calculated the above temperature variables externally and internally for all nests and years combined at each site (hereafter, *site-level temperatures*).

Habitat surveys

We accounted for variation in residential yard habitat by conducting a habitat survey for each site once at the end of breeding season (2016 – 2018). We counted anthropogenic resources (e.g., flower gardens) parcel-wide and standardized the resource availability by dividing counts by parcel size (ha) to account for parcel size variation. We also quantified vegetative structural features, including ground cover, stem density, tree height, diameters, species, and proportion of hardwood trees, in three replicate 11.3 m radius plots at each parcel. The first plot was centered on the house wren nest box, the second plot was in the center of the yard, and the third plot location was in a random direction 50 m from the other two plots (Lerman *et al*. 2014, *i-Tree Software Suite* 2018). Prior to use for analysis, we reduced the number of habitat variables by eliminating any variable that was determined to be collinear (> |0.5| correlation coefficient) to a priority variable (Table 1). We determined priority variables based on information on house wren habitat and foraging preferences (Newhouse *et al*. 2008, Johnson 2014; Table 1).

Statistical analyses

We used R program version 3.2.3 (R Core Team 2019) for all statistical analyses and an *a priori* probability value cutoff of $p \leq 0.05$ for significance testing. Due to the nature of our experimental design, we developed a hypothesis-driven model selection approach for determining the influence of predictor variables on provisioning visits and brooding duration. Our main hypothesized predictors were playback treatment type (control versus predator) and urbanization (urban index). We also included microclimate (temperature metrics at the nest) and the habitat variables (Table 1) as covariates for each response variable.

We assessed the relationship between number of provisioning visits and urban index, playback treatment, and other covariates (Table 2) with backward stepwise selection of generalized linear mixed effects models. Exploratory analysis indicated that the data were Poisson distributed, and we set “nest” as a random effect since we repeatedly measured provisioning visits at the nest level. We built the models using the *glmer* function in the R package *lme4* (Bates *et al*. 2020), set the optimizer to bound optimization by quadratic approximation (BOBYQA), and the maximum number of iterations to 200,000. We selected the top model by first producing a global model with all hypothesized predictor variables, covariates, and interaction terms, and then removed least significant terms for each subsequent model, comparing the competing models at each step via ANOVA (Appendix B Table 17). To test for the effects of microclimate and habitat, we ran a separate stepwise selection procedure that included all the above variables, plus the habitat metrics (Table 2 and Appendix B Table 17). Finally, to test for the effects of microclimate, we ran another stepwise selection procedure that excluded the habitat metrics but included all the other variables as well as temperature variables (Table 2 and Appendix B Table 17).

In a similar manner, we assessed the relationship between mean brooding duration and urban index, playback treatment, and other covariates (Table 3). We built a series of models with relevant combinations of variables and interaction terms with the *glmmTMB* function in the R package *glmmTMB* (Magnusson *et al*. 2020; Appendix B Table 18). After exploratory analysis, we set a gaussian link function, nest as a random effect, log-transformed mean brooding duration, and used corrected Akaike's information criterion model selection for finite sample sizes (AIC_c) to select the best supported models out of a set of hypothesized variable combinations (Burnham and Anderson 2003, Burnham *et al*. 2011). We considered any model with $\Delta AIC_c < 2$ than the model with the lowest AIC_c value to be equally supported (Burnham and Anderson 2003). To test for the effects of microclimate, we ran a second selection procedure that included all the above variables as well as the temperature variables (Table 3 and Appendix B Table 19).

We also assessed the relationship between microclimate and urbanization, and microclimate and habitat. We ran a series of simple linear models in program R for each of the site-level temperature variables as response variables and urban index as the predictor variable (Zuur *et al*. 2009). To select the best fit model for habitat and temperature, we used the model selection approach used for the brooding duration, but with a series of simple linear models for each habitat variable (see Table 1).

Results

We had a total of 84 successful videography trials across 55 nests at 30 of the sites. We excluded several of the videography trials from the analysis due to interruptions or equipment failure, including one instance of active nestling depredation (nest box takeover) by house sparrow (*Passer domesticus*) while filming. The best fit model for provisioning visits included playback treatment, urban index, nestling age, and clutch size (Appendix B Table 20), and had the following structure: $playback \times urban\ index \times age + clutch\ size$, with nest as a random effect. Nests with larger clutches had significantly more visits (β = 0.19, SE = 0.06, $z_{54} = 3.33$, $P = 0.000883$), and there was a significant relationship between provisioning visits and the interaction between urban index and age (β = -0.04, SE = 0.01, $z_{54} = -2.51$, $P = 0.012255$; Fig. 8). When we added the habitat covariates or microclimate covariates into the selection procedure, the best fit models for provisioning visits did not include either habitat or microclimate.

The best fit model for brooding duration included playback treatment, urban index, clutch size, and nestling age (Appendix B Table 21), and had the following structure: $playback \times urban\ index \times clutch\ size + age$, with nest as a random effect. More rural nests had significantly longer brooding durations (β = -0.68, SE = 0.28, z_{47} = -2.39, P = 0.0167), as did nests with younger nestlings (β = -0.04, SE = 0.02, z_{47} = -2.54, P = 0.011). There were also significant relationships between brooding duration and the interaction between playback treatment and urban index (β = 0.87, SE = 0.38, z_{54} = 2.28, P = 0.0229), urban index and clutch size (β = 0.13, SE = 0.05, z_{54} = 2.48, P = 0.0131), and playback treatment, urban index, and clutch size (β = -0.17, SE = 0.07, z_{54} = -2.36, P = 0.0183; Fig. 9). When we added the microclimate covariates into the selection procedure, the best fit model for brooding duration included playback treatment, urban index, standard deviation external temperature, and clutch size (Appendix B Table 22), and had the following structure: $playback \times urban\ index \times standard\ deviation\ external\ temperature + \ clutch\ size$, with nest as a random effect. Nests exposed to predator playbacks had significantly shorter brooding durations (β = -2.43, SE = 1.15, z_{20} = -2.103 P = 0.0355), as did nests with larger clutch sizes (β = -0.20, SE = 0.04, z_{20} = -4.68, P = < 0.001; Fig. 10). Brooding durations were mediated by clutch size; with larger clutches, there were shorter mean brooding durations. When nests with smaller clutches were exposed to control playbacks, mean brooding duration decreased with increased urbanization, whereas mean brooding duration stayed about the same across the gradient when nests were exposed to predator playbacks. With larger clutches, mean brooding durations were lower, and the changes in mean brooding durations across the gradient were negligible.

When we added temperature metrics into the model selection, standard deviation of temperatures significantly influenced brooding duration, but this response was mediated by playback (Fig. 10). This resulted in a significant relationship between brooding duration and the interaction between playback treatment, urban index, and standard deviations of external temperature ($\beta = -1.09$, SE = 0.28, $z_{20} = -3.92$, $P = < 0.001$; Fig. 10). In nests with low variance in temperatures, brooding durations increased from rural to urban nests when the nests were exposed to predator playbacks. In contrast, brooding decreased from rural to urban nests when nests were exposed to control playbacks, which represents the prediction of decreased brooding rates in urban areas.

With our temperature loggers, we monitored 71 nests at 36 sites over three breeding seasons. We obtained n = 51,295 external temperature measures and n = 73,464 internal temperature measures throughout the experiment. Mean global-level temperatures were 22.1 °C (SD 5.9 °C) for external and 27.3 °C (SD 6.2 °C) for internal (Table 4). We found no significant differences in external or internal site-level temperature measures (mean, maximum, minimum, or standard deviation) across the urban gradient. When we assessed the relationship between habitat variables and temperature, we found that larger average tree DBH (diameter at breast height in cm) resulted in significantly lower mean external temperatures ($\beta = -0.03$, SE = 0.01, $t_{28} = -2.09$, $P = 0.0454$) and reduced standard deviations of external temperatures ($\beta = -0.05$, SE = 0.01, $t_{28} = -3.08$, $P = 0.00457$). Additionally, higher numbers of flower beds per hectare significantly reduced the standard deviations of external temperatures ($\beta = -0.04$, SE = 0.02, $t_{28} = 2.264$, $P = 0.0315$). Proportion of shrub cover, proportion of hardwood versus softwood trees, and number of vegetable gardens per hectare had no significant relationships to internal or external temperature of nests.

Discussion

Our results provide evidence that provisioning may be a proximate mechanism that links fear with reduced parental investment. Differences in provisioning rates were consistent to our observations of reduced nestling mass in nests exposed to predator playbacks and nests in urban yards (Chapter 1). Both provisioning and brooding were influenced by fear effects and urbanization. At all nestling ages and across the urban gradient, provisioning visits were suppressed by the introduction of predator cues (Fig. 8; orange line). In contrast, nests exposed to control playbacks had fewer provisioning visits in urban yards than rural ones, but only when nestlings were older (Fig. 8; blue line). The effects of fear on parental behavior also appeared to differ with nestling age. In particular, the older the nestlings, the more the parental investment differed across the urban gradient and in response to playback. In effect, our experiment added predator cues to rural yards that are likely already present in urban yards, demonstrating how fear effects alone may suppress provisioning.

For house wrens in particular, the magnitude of fear-driven suppression of older nestling provisioning is surprising. House wrens, compared to other small passerines, have a relatively fast “pace of life” (i.e., more r than K selected), larger clutch sizes, higher nestling mortality, and shorter life spans. (Bowers *et al*. 2014, Dorset *et al*. 2017). Thus, one would expect parental investment to increase as nestlings aged to maximize current reproductive success over reducing self-risk, thus ensuring higher lifetime reproductive fitness (Ghalambor and Martin 2000, Bowers *et al*. 2014, Dorset *et al*. 2017). This life history tradeoff could explain why fear effects did not reduce provisioning rates at the early stages of the nests (Newhouse *et al*. 2008, Paclík *et al*. 2012, Dudeck *et al*. 2018). It is possible that lowering provisioning rates in the late-stage may serve to reduce conspicuousness of the nest itself, and the soon-to-fledge nestlings inside, rather than to mitigate parental self-risk (Dawson *et al*. 2005, Yoon *et al*. 2017). Fledglings, particularly when in poor condition, are highly vulnerable to aerial ambush predators such as hawks and owls (Ausprey and Rodewald 2011, Cox *et al*. 2014). (Dudeck *et al*. 2018) found that nestlings of parents exposed to fear effects have lower rates of survival post-fledge. Fear may compound the already poor nestling condition in urban yards due to low invertebrate food availability and quality (Narango *et al*. 2017). These compounding effects may further reduce productivity through mortality in the vulnerable post-fledge stage.

There were several interacting relationships between brooding duration and clutch size, temperature, urbanization, and fear effects. Given these interactions, decreased brooding durations in more urban nests exposed to control playbacks (Fig. 9; blue line) may be due to a combination of microclimatic conditions and a provisioning-brooding tradeoff, rather than fear effects. Although in our study we did not detect a difference in temperatures across the gradient, the urban heat island effect generally leads to higher temperatures, especially higher minimum temperatures (Oke 1973, 1995). Higher minimum temperatures would require less brooding effort (Kendeigh and Baldwin 1928, Finke *et al*. 1987, Martin and Ghalambor 1999). As external temperature standard deviations, and therefore variance, increases to high levels, brooding duration remained flat across the gradient in control playback nests (Fig. 10; blue line) and increased in predator playback nests (Fig. 10; orange line). This provides evidence that across the urban gradient, a combination of foraging time (leading to less time for brooding), mitigation of predation risk, and the need to thermoregulate nestlings all shift brooding durations. The relationship between brooding and fear effects are still unclear. When exposed to predator playbacks, brooding durations increased across the urban gradient in nests with low fluctuations (i.e., standard deviations) in temperatures (Fig. 10; orange line), which may be indicative of a strong anti-predator response compounded by urbanization (i.e., more time in the nest results in fewer trips to-and-from the nest). In contrast, nests exposed to control playbacks had a reduction in brooding durations across the urban gradient (Fig. 10; blue line). In the absence of fear effects, urban females may spend more time on provisioning when faced with reduced male investment and/or reduced food resource availability (Newhouse *et al*. 2008, Dorset *et al*. 2017).

Nests with small clutches exposed to predator playbacks appeared to have higher variability rather than across-the-board reductions in brooding duration. In contrast, nest with large clutches did not exhibit much difference in brooding duration, regardless of urbanization or predator playbacks. Brooding durations were likely stabilized by clutch size because a larger group of nestlings is better able to maintain the required temperature

(Finke *et al*. 1987, Martin and Ghalambor 1999, Dawson *et al*. 2005, Pipoly *et al*. 2020). Following that trend, nests with eight nestlings, the maximum found in our system, had the lowest brooding durations in urban yards and when exposed to predators, which could be a due to a combination of large-group thermoregulation and predator effects. Our findings suggest clutch size, urbanization, and fear of nest predators may play a greater role in brooding duration than fear of adult-consuming predators (Dawson *et al*. 2005, Ghalambor *et al*. 2013, Dorset *et al*. 2017).

Mismatches in female versus male parental nest investment may also be driving differences in provisioning rates and brooding durations. Brooding duration is inversely related to provisioning visits in house wrens (Dawson *et al*. 2005, Yoon *et al*. 2017), especially since the female is the sole brooder while females and males are both required to provision nestlings (Johnson and Kermott 1993, Newhouse *et al*. 2008, Yoon *et al*. 2017, Dorset *et al*. 2017). Level of male house wren parental investment is contingent on availability and quality of invertebrate food resources, which is likely low in more urban yards (Seress *et al*. 2018, Narango *et al*. 2018), and males are more likely to reduce provisioning effort for nests with lower chances of success (Yoon *et al*. 2017, Dorset *et al*. 2017). Female wrens, in contrast, have been shown to compensate for reduced male investment by provisioning more at the cost of reduced brooding (Johnson and Kermott 1993, Yoon *et al*. 2017, Dorset *et al*. 2017). Smaller territory sizes for house wrens in urban yards (Newhouse *et al*. 2008, Ryder *et al*. 2010, Juarez *et al*. 2020) also increases the possibility of territoriality-driven conspecific nest predation, or nest predation by house sparrows, which are both a common occurrence (Johnson and Kermott 1993, Martin and Ghalambor 1999, Ghalambor *et al*. 2013, Johnson 2014). Female house wrens brood nests for longer in areas with increased risk of nest predation, to reduce nest conspicuousness and to guard the nest (Johnson and Kermott 1993, Martin and Ghalambor 1999, Dorset *et al*. 2017). We did observe some house wren pairs using a "relay" method of feeding nestlings in which the male foraged and passed food to the female, who did not appear to immediately swallow the food item, but instead appeared to feed the nestlings with the item (AG pers. obs.). This behavior allowed the female to remain at the nest for a longer period of time while the male foraged (Johnson and Kermott 1993, Martin and Ghalambor 1999).

Microclimate (temperature metrics) outside and inside the nests was not significantly related to the urban gradient, but this may be a function of our sample size. While the study sites spanned a gradient from rural to high-density suburban, all were situated in residential yards and therefore had relatively homogenous local habitat structures (i.e., turfgrass, trees, shrubs; Pearse *et al*. 2018, but see Rudd *et al*. 2002, Loram *et al*. 2007, Lerman and Warren 2011). Nevertheless, some local habitat features were associated with the wren's parental behaviors. Size and maturity of trees and abundance of flower beds influenced means or standard deviations of temperatures, and in turn, standard deviations of temperatures were significantly linked to brooding durations. This finding adds to an abundance of research that green space, particularly trees and gardens, mitigate heat (Edmondson *et al*. 2016) and have cascading effects on animal behavior and productivity in residential yards (Ackley *et al*. 2015, Pipoly *et al*. 2020).

Although we did not find evidence of an urban heat island effect in our study system at the nest scale, it is possible that the urban heat island effect could be present at landscape or neighborhood scales (Oke 1995). This mismatch in scale implies that the urban heat island may not affect nest temperature regulation, but instead affect larger-scale ecological processes, such as invertebrate resource availability across the gradient (Sattler *et al*. 2010, Seress *et al*. 2018). We did not include failed nests in our analyses, and some nest failures appeared to be due to hypothermia and subsequent abandonment (AG pers. obs.; Dawson *et al*. 2005).

Future directions

We used an experimental approach to link reductions in provisioning and brooding to fear effects and urbanization. Differences in provisioning across the urban gradient were mediated by fear, demonstrating the power of fear in influencing passerine parental investment in residential yards, with consequences for nestling body condition (Chapter 1). This experiment provides compelling evidence that fear-induced changes in provisioning is a significant mechanism at play in urban environments. Remaining questions include the full fitness consequences of these effects, or how other factors, such as food resources, interact with fear to drive differences in avian productivity. Manipulating other features of urbanization with experimental studies across urban gradients, particularly on residential lands, will elucidate the key ultimate causes and proximate mechanisms influencing avian productivity. Cumulative experimental evidence will lead to a better understanding of how animal behavioral plasticity responds to urbanization and land-use change.

Table 1. Table of relevant habitat features that were measured, sampling method, type of measure, and whether they were included in final model selection analyses (features in bold). See Appendix B for the variable selection and inclusion protocol.

Feature	Sampling	Type	Analysis
Urban index (urban gradient)	1-km buffer	Urbanization	Included
Number of flower gardens / ha	Parcel-wide	Food source	Included*
Number of vegetable gardens / ha	Parcel-wide	Food source	Included**
Number of compost piles / ha	Parcel-wide	Food source	Correlated**
Canopy height (m)	11.3 m plots	Vegetative structure	Excluded†
Shrub cover (m^2)	11.3 m plots	Vegetative structure	Included††
Total shrub species	11.3 m plots	Vegetative structure	Correlated ††
Percent hardwoods (vs. softwoods)	11.3 m plots	Vegetative structure	Included
Average tree DBH (cm)	11.3 m plots	Vegetative structure	Included

Table 2. List of hypothesized predictor variables and potential covariates for provisioning visits for inclusion in model selection (See Appendix B Table 17 for list of considered models). The second selection procedure included habitat variables plus the variables included for the first selection procedure. The third selection procedure included microclimate variables plus the variables included for the first selection procedure and did not include habitat variables.

Variable	Type	Description
Playback treatment	Predictor	Fear of predators (predator or control)
Urban index	Predictor	Urbanization gradient (rural to urban)
Clutch size	Covariate	Number of nestlings
Nestling age (days)	Covariate	Age of nestlings since hatch day 0
Habitat variables included in second selection procedure		
Shrub cover (m^2)	Covariate	Represents understory density
% hardwood versus softwood trees	Covariate	Represents tree/forest composition
Mean tree diameter at breast ht. (cm)	Covariate	Represents size/maturity of trees
Number of vegetable gardens / ha	Covariate	Provides possible invertebrate resources
Number of flower beds / ha	Covariate	Provides possible invertebrate resources
Microclimate variables included in third selection procedure		
Mean external temperatures	Covariate	°C
Maximum external temperatures	Covariate	°C
Minimum external temperatures	Covariate	°C
Standard deviation external temperatures	Covariate	°C

Table 3. List of hypothesized predictor variables and potential covariates for brooding duration for inclusion in model selection (See Appendix B Table 18 for list of considered models). The second selection procedure included microclimate plus the variables included for the first selection procedure.

Variable	Type	Description
Playback treatment	Predictor	Fear of predators (predator or control)
Urban index	Predictor	Urbanization gradient (rural to urban)
Clutch size	Covariate	Number of nestlings
Nestling age (days)	Covariate	Age of nestlings since hatch day 0
Nest year	Covariate	Year of nest (2016, 2017, or 2018)
Microclimate variables included in second selection procedure		
Mean external temperatures	Covariate	°C
Maximum external temperatures	Covariate	°C
Minimum external temperatures	Covariate	°C
Standard deviation external temperatures	Covariate	°C

Table 4. Global-level mean, standard deviation, and range of temperatures (°C) of all temperature measurements recorded on iButtons placed external to the nest box during the 2017 – 2018 field seasons, and internal to active house wren nests in the nest boxes during the 2016 – 2018 field seasons. Means and standard deviations were computed by averaging temperatures within and then among nests. Minimum and maximum temperatures are absolute relative temperatures, and the differences between the internal and external measures are also included.

iButton Location	Mean	SD	Min	Max
External to nest	22.1	5.9	9.7	40.6
Internal	27.3	6.2	11.4	40.8
Difference (internal – external)	5.2	0.3	1.7	0.2

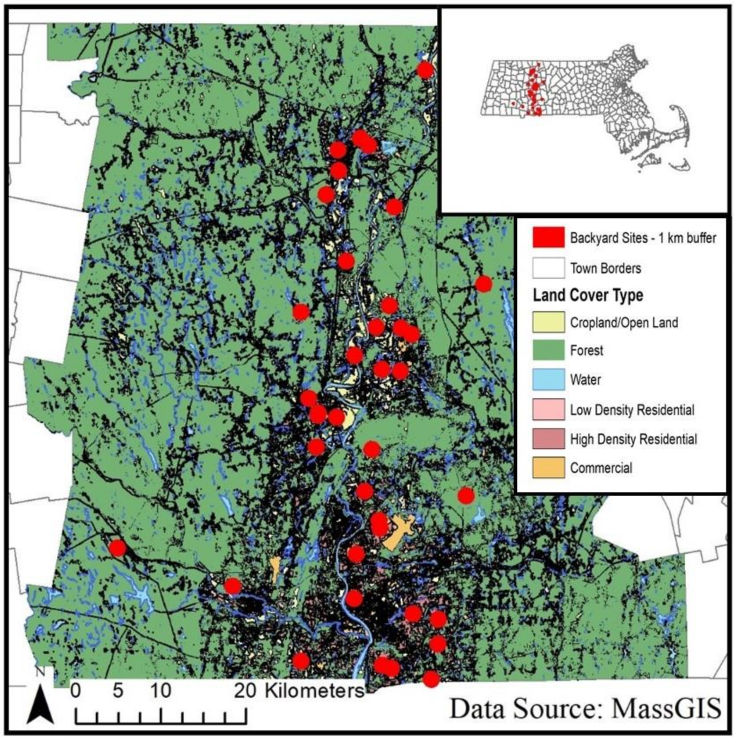

Figure 7. Nest boxes were distributed in residential yards across western Massachusetts. Landscape-scale urban index was calculated based on land-use categories within a 1-km buffer (red dots) surrounding each residential yard.

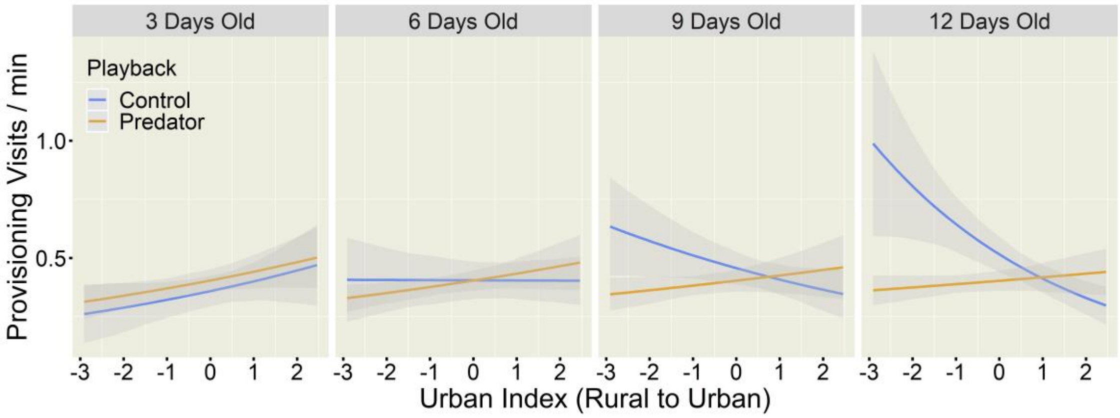

Figure 8. Relationship between urban index (rural to urban) and provisioning visits / min by four different ages (in days), demonstrating the playback x urban index x age interaction. Provisioning visits back transformed from Poisson distribution. Residuals generated from generalized linear mixed model (GLMM) with nest as random effect. Error ribbons (gray) are standard error (generated via bootstrapping with n = 100 iterations).

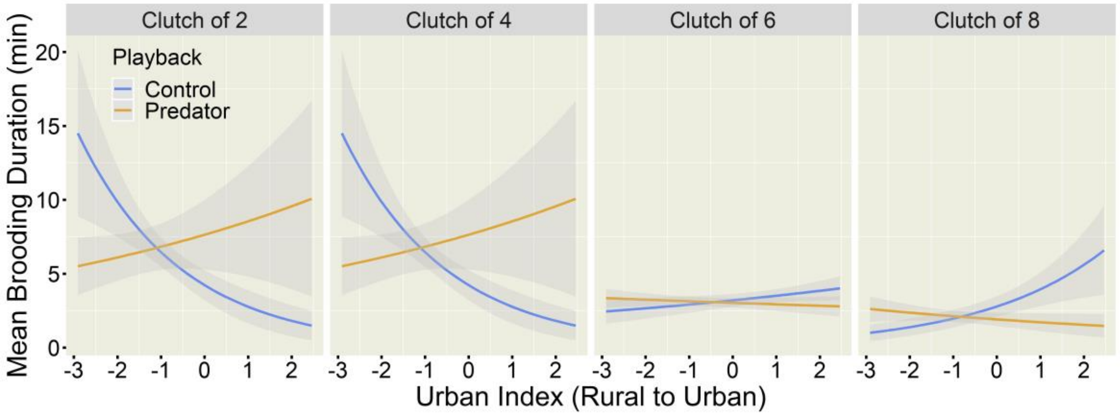

Figure 9. Relationship between urban index (rural to urban) and mean brooding duration (min) by four different clutch sizes, demonstrating the playback x urban index x clutch size interaction. Mean brooding duration (min) back transformed from Poisson distribution. Residuals generated from generalized linear mixed model (GLMM) with nest as random effect. Error ribbons (gray) are standard error.

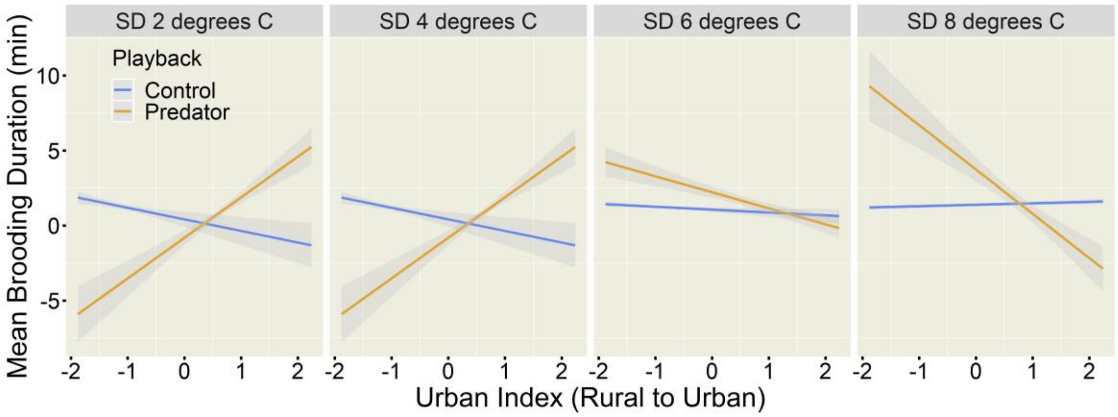

Figure 10. Relationship between urban index (rural to urban) and mean brooding duration (min) by four different standard deviations of external nest box temperatures (°C), demonstrating the playback x urban index x standard deviation external temperature interaction. Mean brooding duration (min) back transformed from Poisson distribution. Residuals generated from generalized linear mixed model (GLMM) with nest as random effect. Error ribbons (gray) are standard error

CHAPTER 4

MANAGING YARDS FOR MAMMALS: MAMMAL SPECIES RICHNESS PEAKS IN THE SUBURBS AND IN YARDS WITH LARGER TREES

Abstract

As human populations grow and urbanize, residential land-use represents significant potential wildlife habitat. Diverse mammal communities can be found across all levels of urbanization, but it is unclear how mammal community diversity and composition vary across urban gradients. Residential land-use represents a large proportion of private lands in urban areas and could provide connectivity between patches of green space. We conducted a camera trapping study in residential yards across an urban gradient to assess the relative contributions of landscape-scale land-use and parcel-scale land management to predicting mammal community diversity and composition. At the landscape-scale we found that species richness peaks in the suburbs and tapers off at the rural and urban ends of the gradient, and that urban gradient was a greater predictor of species richness and composition than parcel-level features. At the parcel-scale, average tree diameters were positively correlated with species richness. Our findings highlight that suburban yards have an overlap of species that occupy urban and rural areas, a pattern seen in other taxonomic groups. Although landscape-scale features may be more important filters of species composition in yards than habitat management by residents, retaining mature trees in yards could lead to greater yard biodiversity. Presence or absence of a species in residential yards is primarily mediated by factors out of individual residents' control, but residential yards still provide useful resources or

threatening disturbances for mammal species. Managing both resources and disturbances in yards, such as trees, bird feeders, and outdoor cats, may facilitate use and movement through yards to surrounding patches of intact habitat. Informed residential yard management remains an important tool for urban wildlife management in an era of global change.

Introduction

The human population is growing and shifting away from rural areas and into cities and suburbs – by 2050, 66% of the world population will live in urban areas (UN 2014). These trends drive worldwide patterns of habitat loss, fragmentation, and urban sprawl that result in changes to community composition (McKinney 2002, 2006). Urban areas, particularly residential lands, are highly heterogenous at multiple scales, and habitat quality often varies based on land management at the parcel-scale (Lerman and Warren 2011, Lerman *et al*. 2018). By understanding how patterns and processes from the landscape-scale to the parcel-scale influence wildlife, residential lands could be managed to maximize connectivity of fragmented wildlands in human-dominated landscapes (Rudd *et al*. 2002, Gallo *et al*. 2017).

There are few studies that compare and contrast how features across multiple spatial scales influence wildlife community composition in human-dominated landscapes, especially in mammals (Shochat *et al*. 2006, Aronson *et al*. 2016). Connectivity and configuration of habitat patches operate on the scale of landscapes, which could vary from 500 m for small-medium-sized mammals (e.g., racoons, *Procyon lotor*; Gallo *et al*. 2017) to multiple kilometers for large mammals (e.g., mountain lions, *Puma concolor*;

Ordeñana *et al*. 2010). At the individual parcel-scale, high levels of heterogeneity represent the outcome of choices made by individual land owners (Lerman and Warren 2011), and result in landscaping design differences (e.g., lawn dominated versus tree dominated; Davies *et al*. 2009, Lerman and Warren 2011, Pearse *et al*. 2018), as well as the presence of human-provided resources (e.g., bird feeders; Reed and Bonter 2018) or human-caused disturbances (e.g., noise pollution; Warren *et al*. 2006). By understanding the relative contributions of landscape-scale and parcel-scale features, we can begin to have a holistic understanding of the processes that filter and shape mammal communities across human-dominated landscapes.

Landscape-scale features and mammal communities

Human development varies in intensity across gradients of urbanization; thus, ecologists have utilized urban gradients as a means to study shifts in biodiversity (Luck and Smallbone 2010). Although many studies have described patterns of wildlife biodiversity across urban gradients, most have targeted birds (Clergeau *et al*. 1998, Shochat *et al*. 2010, Evans *et al*. 2018) and arthropods (Ahrné *et al*. 2009, Sattler *et al*. 2010, Nagy *et al*. 2018), and few have documented how mammals (Crooks 2002, Mahan and O’Connell 2005, Eötvös *et al*. 2018) respond to urbanization (see McKinney 2008, Faeth *et al*. 2011 for reviews by taxa). For most taxa, as urbanization increases, species richness decreases monotonically, while synanthropic species – or species that have adapted to urban settings – increase in population density (Crooks 2002, McKinney 2008, Ahrné *et al*. 2009). In some cases, species richness reaches a peak at intermediate levels of urbanization (i.e., the suburbs; McKinney 2008, Shochat *et al*. 2010). This is particularly true of plants (Deutschewitz *et al*. 2003, Godefroid and Koedam 2003) and birds (Blair 1996, Marzluff and Rodewald 2008). This intermediate peak is often driven by exotic and native plantings in suburban gardens and yards, which provides additional resources for birds and adds to plant biodiversity (Donnelly and Marzluff 2004, Faeth *et al*. 2011, Goddard *et al*. 2013). Within a single land-use type, such as residential lands, the unique structure of human-dominated landscapes introduces extraordinary intra-land-use heterogeneity, where each landowner acts as a parcel-level land manager (Cook *et al*. 2012). Investigating the effects of this intra-land-use heterogeneity is an important avenue of research to uncover some of the processes behind patterns of mammal diversity in human-dominated landscapes (Beninde *et al*. 2015).

Parcel-scale features and mammal communities

Land management at the parcel-scale determines habitat structure, human-built-structure, human-provided resources, and human-caused disturbances within the home range of individual mammals (Goddard *et al*. 2013, Kays and Parsons 2014). Unlike landscape-scale features, parcel-scale (i.e., ownership block) features are often in direct control of individual managers. Parcel size and management regime are typically related to the land-use type of the parcel (Gallo *et al*. 2017). Urban parks, for example, are often on the scale of several hectares and managed by professionals, whereas a residential parcel may be less than one hectare and managed by the resident of the parcel (Lerman and Warren 2011, Pearse *et al*. 2018).

In contrast to studies of plants, birds, and arthropods, the majority of urban mammal community studies have focused on non-residential urban green spaces, such as parks, golf courses, cemeteries, and forest patches. These urban green spaces are typically dominated by omnivorous generalists and meso-predators (Crooks and Soulé 1999, Crooks 2002, Gompper 2002, Gallo *et al*. 2017). Despite the dominance of residential land-use in urban areas (e.g., 21.8% - 26.8% of urban land-use in cities across the United Kingdom; Loram *et al*. 2007), few studies exist of mammal communities in residential yards (but see Kays and Parsons 2014, Malpass *et al*. 2015, Murray and Clair 2017). This limits our ability to have a comprehensive picture of urban wildlife communities in both public and private lands.

Since people live and recreate in residential parcels, yards commonly have human-provided resources that are either intentionally or unintentionally made available to wildlife (Loram *et al*. 2007, Lerman and Warren 2011, Goddard *et al*. 2013, Murray and Clair 2017). Kays and Parsons (2014) found that the mammal species typically found in yards were ones that occasionally entered the yard to utilize human-provided resources, such as eggs in chicken coops. Human-caused disturbances also influence mammalian use of residential yards. Light and noise pollution may drive some species away, while altering the time-of-day activity patterns of others (Stone *et al*. 2009, 2015). Lawn-mowing and children recreating may also act as disturbances to mammals in yards, although the extent of impact from these activities is still unclear. Outdoor domestic dogs (*Canus lupus familiarus*) and house cats (*Felis catus*), due to their association with humans, can also act as a human-caused disturbance (Loss *et al*. 2013, Parsons *et al*. 2016). They introduce human-wildlife conflict (e.g., coyote, *Canis latrans*, depredating pets; Gompper 2002) and outdoor cats, in particular, are estimated to kill 6.2 – 22.3 billion mammals per year in the United States alone (Loss *et al*. 2013). Although impacts of cats and dogs on populations are well-documented, it is unclear if domestic pet presence in yards influences mammals at the community level.

We conducted a camera trapping study to investigate the relative effects of landscape-scale and parcel-scale factors on mammal communities in residential backyards across a human-dominated landscape. Our aim was to assess the relative contributions of landscape-scale and parcel-scale features, and to determine which of these features were associated with changes in mammal community and composition. We hypothesized that species richness, composition, and community similarity would be related to a combination of landscape-scale and parcel-scale features, and that species-specific responses would depend on the species' level of synanthropy.

We also aimed to determine the extent to which presence of domestic cats and dogs influenced mammalian community diversity and composition. We hypothesized that presence of cats would have a greater effect than presence of dogs and that yards in which cat were present would have significantly different species richness and community compositions from those without cats. Using a multi-faceted approach, we measured landscape features as well as human-provided resources, human-caused disturbances, and vegetative structure. Comparing potential factors driving mammalian community structure across spatial scales allowed us to clearly see the relative contributions of landscape-scale factors and parcel-scale management in shaping residential mammal communities.

Materials and Methods

Study system

Our camera trapping effort surveyed mammals in 36 residential yards across an urban gradient in western Massachusetts, United States. Survey efforts were in conjunction with an avian nesting ecology study on the effects of urbanization on house wrens (*Troglodytes aedon*) nesting in the same yards (Chapter 1 and 2) Residential yards were situated throughout western Massachusetts and centered on Springfield, MA (Fig. 11). These sites varied from low-density rural development to high-density suburban development (see Chapter 1 Materials and Methods). Land-use and habitat surrounding the sites were a mixture of residential housing, farmland, recreational areas, and mixed deciduous-coniferous temperate forest. Landscaping practices varied in residential yards. Many were dominated by traditional manicured turfgrass lawn, while others were dominated by either trees and shrubs, “low-mow” unmanaged grass, or gardens. Parcel residents participated in Neighborhood Nestwatch, a Smithsonian Migratory Bird Center community science project with a focus on avian nesting ecology and adult survival (Ryder *et al*. 2010, Evans *et al*. 2015).

Camera trap surveys and photo processing

We implemented a motion-triggered camera trapping survey in the yards to characterize mammal communities. We conducted the camera trap, human-resource/disturbance, and habitat surveys in the residential yards from May – mid-September 2016 – 2018. We deployed two cameras twice per year (once in late spring to early summer, once mid- to late summer) in the yards, and each deployment was for eight days. Due to ongoing participation and recruitment practices, not all yards were utilized for all years. We used a stratified random sampling design to determine dates of deployment for even sampling across the urban gradient.

Each deployment consisted of two Bushnell Trophy Cam or Bushnell Trophy Cam HD camera traps (Bushnell Corporation, Overland Park, KS) with infrared flash, three-picture burst, and 30 s delay between new picture burst triggers (Bondi *et al*. 2010, Erb *et al*. 2012). We treated the two cameras per each deployment as a single coordinated sampling effort (i.e., non-independent and combined) in the analysis. We mounted each camera on 1 m tall garden stakes and angled them slightly downward. In each yard and for each deployment, we situated one camera approximately 2.5 m from a house wren nest box (which was mounted on a 2.5 m metal garden stake) facing the nest box, while we placed the second camera at least 10 m from the nest box camera at another location in the yard that was relatively open, had signs of mammal activity, was adjacent to vegetation cover, and/or was near the edge of the yard boundary, and not aimed towards the nest box (O'Connell *et al*. 2010, Sollmann 2018). Using two cameras per deployment allowed us to capture a larger area of the yard simultaneously, while also treating the nest box and its associated activity as a pseudo- "bait" station to assess potential nest predators.

All photos were imported into and processed using CPW Photo Warehouse Software version 4.3.0.3 (Newkirk 2016). At least two observers examined and identified each photo to species or the most accurate taxonomic level possible. A third observer examined photos with conflicting identifications and determined the correct identification. We set independent detections, or the assumption that the detection of an animal of the same species was a new individual, at 60 min between detection events on the same camera (O'Connell *et al*. 2010, Sollmann 2018). We exported and collated the data for import into R program version 3.6.2 for analysis (R Core Team 2019). Metadata from each camera trapping deployment included site, deployment date, and effort per deployment (total camera trap-hours; hereafter "effort").

Landscape-scale urban index

For each yard, we assessed relevant features at the landscape-scale (Aronson *et al*. 2016). Landscape-scale was defined as a 1-km buffer around the sites, well over the home-range of most mammals surveyed (DeGraaf and Yamasaki 2001, Bowler *et al*. 2017). To account for magnitude of surrounding development on the landscape, we developed an index of urbanization (Rodewald and Kearns 2011). We quantified the degree of urbanization by calculating the square areas (m^2) of major land-cover types (MassGIS 2018) from the MassGIS 2005 digital dataset of land cover using ArcMap version 10.5 (ESRI 2011) in a 1-km area buffer around each study site. Land cover types in this data set are a statewide data layer that was created using semi-automated methods via digital ortho imagery. We converted the vector data into raster data, condensed the land use categories into higher-level basic categories, and then further condensed the cover types into one axis of urbanization via principal component analysis (Rodewald *et al*. 2013, see Chapter 1 and Appendix C Fig. 19 for results of the urban index). Sites on the urban index scale were centered around 0 (i.e., suburban), and spanned from -3 (most rural) to +3 (most urban). The urban index principal component explained 49.6% of the land-cover variation, loading negatively (i.e., more rural) on forest, open land, and low-density residential cover types, and positively (i.e., more urban) on high-density and commercial cover types.

Parcel-scale measures

Plot surveys. We assessed vegetation, built structures, human resources, and human disturbances in each parcel (Fig. 11). We took the detailed vegetative structural measures at three replicate 11.3 m radius plots at each parcel (Martin *et al*. 1996). Since vegetative structure is relatively stable in yards across a two-to-three-year period, we conducted the vegetation survey only once per yard. The first plot was centered on the house wren nest box, the second was in the geographic center of the yard (but at least 20 m away from the nest box), and the third plot location was selected at random and separated from the other two plots by at least 50 m, even if the location was out of the parcel boundary. Following a protocol adapted from iTree version 5 (Lerman *et al*. 2014, *i-Tree Software Suite* 2018), within a 5 m sub-radius of each plot center we estimated woody stem counts and percent ground cover of select categories (e.g., grass, brush, forbs). Within an 11.3 m inclusive radius of the plot center, we noted shrub and tree species names, counts, measured shrub area (m^2) of each shrub and diameter at breast height (DBH) of each tree (Martin *et al*. 1996). Using ocular estimation, we determined percent canopy cover and canopy height within the 11.3 m radius (Martin *et al*. 1996). To analyze the replicate plot survey data, we collated variable measurements from each site by taking the mean of each variable.

Human resources and disturbances. We counted and listed parcel-wide human resources and disturbances, which included: built-structural components (e.g., houses, sheds), transportation features (e.g., roads, road types, vehicles), potential food and water resources (e.g., vegetable and flower gardens, bird feeders, unlidded trash cans, bird baths), and presence/absence of potential disturbance indicators (motion-activated lights, and children's toys). Since human resources and human disturbances are more likely to vary over time, we conducted these surveys once per year in each yard while the study was active and used the mean count of each variable for analysis. To standardize the parcel-wide human resource and disturbance counts, we divided the total count by the parcel size (ha). We used our camera trap data to determine presence/absence of dogs and cats at the site, assuming that outdoor dogs and cats were absent at a site if they were never detected by the camera traps (i.e., assumed naïve detectability).

Statistical Analyses

Variable inclusion. Prior to our analysis, we conducted a variable inclusion procedure to reduce the number of variables to a manageable amount. We examined correlation matrices of related numerical variables (e.g., ground cover variables) to assess collinearity (Zuur *et al*. 2009). We considered two variables with correlation coefficients > |0.5| to be collinear and included only one of the two collinear variables as covariates in future analyses. We chose which covariate to prioritize by reviewing literature on northeastern mammal habitat use; DeGraaf and Yamasaki 2001). From this process, we selected a final set of predictor variables for inclusion as potential covariates in our analyses (Table 5).

Species richness. To assess biodiversity, we calculated species richness using the *diversity* function in the R package *vegan* (Oksanen *et al*. 2019). Due to difficulties of visual identification, we combined all mice (e.g., from the family Muridae) into a mice spp. category, and the two possible species of rabbits (*Sylvilagus floridanus* and *S. transitionalis*) into a rabbit spp. category. We did not include domestic cats or dogs in this analysis, although they were considered as potential human disturbances in later analyses. To confirm adequate sampling effort, we generated species accumulation curves using the *specaccum* function in the R package *vegan* (Oksanen *et al*. 2019), using both random order and rarefaction, 1000 permutations, and weighted by effort.

Exploratory analyses indicated that relationships between variables were non-linear (Eilers and Marx 1996), so we developed a series of generalized additive models (GAMs) using the *GAM* function in the R package *mgcv* (Wood 2019) to evaluate the relative influence of landscape-scale and parcel-scale variables on species richness. Using a hypothesis-driven forward stepwise model selection approach, we compared a series of candidate GAMs that all included effort (to control for differences in survey effort due to equipment failure or blockage of image by vegetation) and urban index as predictors, and iteratively added parcel-level predictors (Table 5) plus ecologically relevant interactions (Zuur *et al*. 2009). Each independent variable was tested as linear and as smoothed using cubic regression splines (Zuur *et al*. 2009). We generated plots using the R packages *ggplot2* (Wickham 2016) and *voxel* (Garcia de la Garza *et al*. 2018).

Variance partitioning analyses. Once we selected the GAM model structure and predictors, we quantitatively assessed the relative contributions of the selected landscape-scale and parcel-scale predictors using the *Hmsc* function in the R package *Hmsc* (Tikhonov *et al*. 2019). The function uses Bayesian Hierarchical Modelling of Species Communities (HMSC) and Gibbs Markov chain Monte Carlo (MCMC) sampling to partition the variance and estimate the proportion of variance explained by the predictors, as well as the remaining residual variance explained by other effects (i.e., random effects of site; Ovaskainen *et al*. 2017).

<u>Community similarity</u>. To test whether communities vary along the urban gradient or with select parcel-scale variables (related to species richness), we conducted Jaccard's similarity index analysis. Jaccard's similarity considers presence-absence and not abundance, to estimate community similarity among sites (Jaccard 1901). We calculated Jaccard's index with non-metric multidimensional scaling (nMDS) in the function *metaMDS* in R package *vegan* (Oksanen *et al*. 2019). We specified two dimensions and ran 100 iterations (Oksanen 2011, Shafii *et al*. 2013). Based on the results of the species richness, we tested for overlap between Jaccard's community similarity and urban index using distance matrices to run a permutational multivariate analysis of variance (MANOVA). We used the function *adonis* in the R package *vegan* (Oksanen *et al*. 2019), specified 200 permutations, and fit a linear model with Jaccard's similarity value as the dependent variable and urban index + effort as independent variables. For visualization, we overlaid species with urban index in two-dimensional ordinal space using the Jaccard's nMDS results and the functions *ordisurf* and *orditorp* in the R package *vegan* (Oksanen *et al*. 2019).

Effects of domestic cats and dogs on mammal communities. To evaluate the effect of domestic pet presence on mammal communities across the urban gradient, we split each site into either cats present (i.e., at least one cat captured on cameras during all surveys at the site, although most sites in which cats were present had more than one individual cat) or cats absent (i.e., no cats captured on cameras during all surveys at the site). We used a separate variable to indicate dogs present versus dogs absent based on the camera trap data. Collinearities between cat/dog presence and urban gradient could have confounded our results. Thus, we ran two generalized linear models that ruled out a significant relationship between urbanization and cat/dog presence-absence (cats, z = 1.04, *P* = 0.3003; and dogs, z = -0.15, *P* = 0.881). We then tested for differences in species richness between sites with or without cats/dogs using generalized mixed models (GLMM) with the function *lme* in R package *nlme* (Pinheiro *et al*. 2017), setting effort as a random effect, categorical cat/dog presence-absence variables as the independent variable, and species richness as the dependent variable (Zuur *et al*. 2009). Finally, we used the categorical cat/dog presence-absence variables to assess the influence of cats and dogs on Jaccard’s community similarity, using the same methods outlined above (*Community similarity*) for testing for the effects of urbanization.

We ranked the ratios of species presence when cats were also present to see if there was a pattern between the predator-prey relationship of the mammalian species and what species tended to be present in yards that also had cats. We calculated the ratio as:

$$\frac{\alpha_{smp}}{\alpha_{scp}} \Big/ \frac{\alpha_{sma}}{\alpha_{sca}} \qquad (1)$$

where $\alpha_{smp} =$ proportion of sites in which the mammal species is present, $\alpha_{scp} =$ proportion of sites in which cats are present $\alpha_{sma} =$ proportion of sites in which the mammal species is absent, and $\alpha_{sca} =$ proportion of sites in which cats are absent. A higher ratio value indicates greater likelihood that species is present when cats are also present. We statistically assessed these relationships for each species with chi-square tests of matrices of site of cat-presence-by-species-presence, since cats are known to be predators of small to medium-sized mammals (Loss *et al*. 2013).

Results

Relative effects of landscape-scale and parcel-scale features on species richness

During the spring and summer of 2016 – 2018, we deployed camera traps at a total of 36 residential backyard sites, logged a total effort of 119.91 camera-days, and identified 14 wild mammal species/species categories and two domestic species; cats and dogs (Table 6). Not all sites had cameras for every year. In our assessment of species richness, the selected GAM model had an adjusted $R^2 = 0.4$, 47.9% deviance explained, with the predictor variables urban index (smoothed, $F = 1.79$, $P \leq 0.001$) as well as average tree DBH (diameter at breast height in cm; smoothed, $F = 0.755$, $P = 0.018$), and effort (linear, $F = 1.279$, $P = 0.211$) (Fig. 12). When we partitioned the variance of urban index, average tree DBH, and the remaining random effects for site for each mammal species/species categories, we found that urban index generally explained a higher proportion of the variance than average tree DBH or random effects, although the relative proportions differed by species (Fig. 13). In the case of coyotes, mice, and deer, average tree DBH explained a higher proportion of the variance than urban index.

Effects of landscape-scale and parcel-scale features on community similarity

We assessed the effects of the selected features, urban index (landscape-scale) and average tree DBH (parcel-scale) on community similarity. There was a significant relationship between Jaccard's similarity and urban index ($F_{1,35}$ = 2.66, R^2 = 0.069, P = 0.005), but the relationship between similarity and mean tree DBH was not significant ($F_{1,35}$ = 0.68, P = 0.781). A stress plot indicated good preservation of similarity/dissimilarity when the data were condensed into two-dimensional space (Oksanen 2011, Shafii *et al*. 2013). Eastern gray squirrel (*Sciurus carolinensis*) and eastern chipmunk (*Tamias striatus*) separated from the rest of the species, occupying the more urban space in the ordination; opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), rabbit (*Sylvilagus floridanus* plus *S. transitionalis*), red fox (*Vulpes vulpes*), and mouse (Family Muridae) occupied the suburban space, and skunk (*Mephitis mephitis*), gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), black bear (*Ursus americanus*), and white-tailed deer (*Odocoileus virginianus*) occupied the suburban to more rural space in the ordination (Fig 14).

Effects of cats and dogs on mammal communities

Out of the 36 sites, 20 had cats present and 20 had dogs present. There was no significant relationship between presence-absence of cats (t = 2.01, P = 0.052) or dogs (t = 0.59, P = 0.557) and species richness. There was no significant community dissimilarity at sites that were occupied by cats versus sites where cats were absent ($F_{1,35}$ = 1.21, P = 0.284). Generally, potential prey species of cats (e.g., eastern gray squirrel) were less likely to be present in yards occupied with cats, while potential predator species (e.g., gray fox) were more likely to be present to be in yards occupied with cats (Table 7). This descriptive observation was only statistically significant for two mammal species via chi-square tests. We has no *a priori* prediction for Bear association with cats, but they were significantly more likely to be present in yards in which cats were never detected ($\chi^2_{1,35} = 5.00$, $P = 0.025$), while red fox, a potential cat predator species, were significantly more likely to be present in yards occupied by cats ($\chi^2_{1,35} = 6.92$, $P = 0.009$).

Discussion

We found that urbanization at the landscape-scale had a strong relationship to the structure of mammal communities. Decades of research indicates that macro-scale features filter and shape wildlife community structure in human-dominated landscapes across many geographical regions and taxa (Blair 1996, McKinney 2008, Aronson *et al*. 2016, Gallo *et al*. 2017), but there is little research that compares the relative contributions of macro-scale urbanization and micro-scale parcel management across human-dominated landscapes. Therefore, we compared the relative contributions of landscape and parcel-scale features and found that although landscape-scale urbanization was the primary predictor of mammal community structure, average tree size, a parcel-scale habitat feature, was strongly related to species richness in the residential yards. Taken together, these findings highlight the importance of land-use context on the landscape scale as well as parcel-level management to mammal community structure.

Landscape-scale filters mammal communities

After regional climate and biogeography, land-use composition at the landscape scale represent the highest order of species filtering across human-dominated regions (Aronson *et al*. 2016). In our study system, the most influential feature on mammal community structure was an urban index that had land-use ranging from low density housing, forest, and agriculture in rural settings to high density residential and commercial districts in urban settings. Previous studies have highlighted that forest specialist mammals are more likely to utilize residential yard resources if they have access to large forest patches nearby (Kays and Parsons 2014, Murray and Clair 2017). In New England, medium-to-large sized mammals, such as coyotes or foxes, have home ranges that exceed the size of an average residential parcel (DeGraaf and Yamasaki 2001). Forest specialists also require specific natural features, such as rocky outcroppings for dens, for suitable habitation (DeGraaf and Yamasaki 2001). Therefore, presence of a species in a yard, especially if it requires intact forested habitat, may depend on landscape context, regardless of the yard's available resources.

The importance of landscape context is borne out by our finding that suburban yards had the highest level of predicted and measured species richness. Suburban yards, by definition, are embedded within a heterogenous matrix of land use that includes both wildland and more dense human development. Urban yards often have limited forest and agriculture nearby and are surrounded by more residential and commercial land. In contrast, rural yards tend to be surrounded by other low-density residential developments, as well as larger tracts of forest and agricultural land. With this heterogeneity, suburbs have an intermediate combination of proximity to natural areas and high densities of anthropogenic resources, which may draw mammals occupying adjacent wildlands into the backyard (Kays and Parsons 2014, Newsome *et al*. 2015).

Surprisingly, the more rural end of the gradient also exhibited a decline in species richness, presumably by losing more urban-dwelling species such as opossum (Fig. 14). Rural residences are often surrounded by continuous wildlands, with housing at a far lower density than in the suburbs. Therefore, available resources at the wildland urban interface are often limited in density as well (Blair 1996, Shochat 2004, Rodewald *et al*. 2011, Bar-Massada *et al*. 2014). This lack of patchiness may preclude the need for mammals to disperse through or utilize the relatively “unfriendly” backyards at the rate seen in more developed areas.

Communities were also significantly dissimilar based on degree of urbanization. Our results indicated that community composition varied within residential land-use across the urban gradient. Predictably, large-bodied, wide-ranging, and interior forest species, such as gray fox, were more associated with rural sites, while synanthropic species, such as eastern gray squirrel, were more urban-associated (Goad *et al*. 2014). This distribution of species indicates that while there were few urban-dwelling species found in rural areas and few urban-avoiding species found in urban areas, both sets of species are occasionally found in the suburbs. Though we did not directly quantify species interactions, this shift in community composition likely has implications for trophic dynamics, especially between predators and their prey, such as fox and rabbit (Fischer *et al*. 2012, Jokimäki *et al*. 2020; but see Eötvös *et al*. 2018). For example, our camera trap captured an instance of a red fox depredating a groundhog in a suburban yard (Appendix C Fig. 20).

Parcel-scale average tree diameters increase mammal species richness

The most important parcel-scale feature to mammalian species richness was mean tree diameter. Species richness increased monotonically, adding roughly one additional mammal species for each increase of 15 cm in mean diameter (Fig. 12b). Other measures of forest structure, such as percent log cover, shrub cover (an indication of understory complexity that was highly correlated with stem density), number of trees within the 11.3 m radius, and canopy height, were not significantly related to species richness (see Appendix C Table 23. for full list of measured vegetation variables). Whether deciduous or coniferous trees dominate the yard was also not significantly related to species richness.

It appears that increasing mean tree diameter in a given yard leads to an increase in mammal species richness, regardless of location along the urban gradient, or what tree species are present. Tree diameters are often directly related to both tree maturity and tree height, and are common metrics of forest structure that relate closely to mammalian species richness in forests of the eastern United States (Hansen *et al*. 1991, DeGraaf and Yamasaki 2001, Schmid-Holmes and Drickamer 2001). It is important to note, however, that stem and shrub densities (i.e., complex understory) are often related to an increase in small mammal species richness, which is hard to capture with camera traps (Miller and Getz 1977, Adler 1985). Therefore, our findings coupled with previous research indicates that residents should retain their mature trees to maximize mammal species richness, while also keeping a complex understory in the less managed areas of the yard to promote small mammal species diversity.

The anthropogenic resources and most of the habitat factors we measured did not significantly influence mammal community structure in the residential backyards. It is possible that many mammal species only utilize backyards on rare occasions and for specific resources, since the yards are often smaller than an individual's home range (DeGraaf and Yamasaki 2001). Although species richness did not appear to be related to parcel-level management practices, it is possible that there could have been a difference in species-specific abundances. In other studies, abundance of a species, and not occupancy, has been more tightly linked to anthropogenic resource availability (Prange *et al*. 2003). Abundance was metric that we were unable to assess using our study design (Erb *et al*. 2012) for which we prioritized increasing the number of sites over increasing the amount of replicate surveys at each site. This allowed us to get a better picture of species richness across the region, at the expense of accurate estimates of abundance (see Royle and Nichols 2003, Bowler *et al*. 2017, Sollmann 2018, Ehlers Smith *et al*. 2018).

Effects of cat and dog presence on mammal communities

We did not find any significant effect of cats or dogs on mammal diversity or community composition. Although we did not find a significant effect of presence of cats on species richness and community dissimilarity there was a possible trend of higher species richness in yards occupied by cats. We also found a positive correlation between cat and red fox presence. Perhaps cat presence could be attracting predators, such as foxes (Shochat 2004, Ordeñana *et al*. 2010, Kays *et al*. 2015). By design, camera trap surveys target medium to large-sized mammals (e.g., chipmunk and larger), which cats rarely prey upon (Loss *et al*. 2013). Since camera traps studies are unable to identify many small mammal species (e.g., mice and voles), we suggest future research augment camera traps with live trapping in yards to better capture the influence of cat presence on small mammal communities and populations (Bondi *et al*. 2010, Elizondo and Loss 2016).

Future directions: Multi-scale filters and human-dominated landscapes

We aimed to compare the relative effects of landscape-scale and parcel-scale features on mammal communities, and found that urbanization at the landscape-scale, and not parcel-level management, was the major contributor to species richness and community composition. At the parcel-level, tree size alone was a significant predictor of species richness, and the influence of cat and dog presence in the yards was inconclusive. Mammal species richness peaked in the suburbs, a pattern that could represent the intersection of urban-dwelling and urban-avoiding species ranges.

Urban areas are characterized by high levels of habitat heterogeneity both within and among land-use types (Aronson *et al*. 2016b, 2017, Gallo *et al*. 2017). Our study demonstrates the need for more research that compares community composition within the same land-use type. To inform effective management, future studies should continue to investigate the multi-scale patterns and process that determine drivers of species diversity and composition in human-dominated areas. Urbanization will continue to expand into and fragment intact wildlands. Effective conservation of mammal species requires that we address the realities of an urbanizing world.

Table 5. List of potential predictor variables selected for inclusion in the models. See Appendix C Table 23 for full list of variables.

Variable	Units	Scale
Urban Index	Scale	Landscape (1-km)
Number of vegetable gardens / acre	Count/ha	Parcel
Number of fruit trees / acre	Count/ha	Parcel
Number of bird feeders / acre	Count/ha	Parcel
Number of pet food receptacles / acre	Count/ha	Parcel
% log cover (on ground)	Percentage	Parcel (mean of 3 plots)
Canopy height	M	Parcel (mean of 3 plots)
Shrub cover	m^2	Parcel (mean of 3 plots)
Number of trees in plot	Count	Parcel (mean of 3 plots)
Mean tree diameter at breast height (DBH)	Cm	Parcel (mean of 3 plots)
Proportion hardwood versus softwood trees	Percentage	Parcel (mean of 3 plots)

Table 6. Summary statistics of all mammal species that were detected by camera traps during the study, with common names and Latin names. Total detections at all sites for all years was under the assumption that a detection event > 60 min apart was a new individual. Proportion of sites (out of 36) that species were present represents a raw detection proportion and does not account for false absences or total effort.

Species Common Name	Species Latin Name	Total Detections	Proportion of sites species were present
American red squirrel	*Tamiasciurus hudsonicus*	13	0.11
Black bear	*Ursus americanus*	5	0.11
Common raccoon	*Procyon lotor*	111	0.64
Coyote	*Canis latrans*	6	0.17
Domestic cat	*Felis catus*	223	0.72
Domestic dog	*Canis lupus familiaris*	196	0.36
Eastern chipmunk	*Tamias striatus*	1019	0.89
Eastern gray squirrel	*Sciurus carolinensis*	1248	0.94
Gray fox	*Urocyon cinereoargenteus*	19	0.31
Groundhog	*Marmota monax*	90	0.22
Mouse spp.	Family Muridae	24	0.31
Rabbit spp.	*Sylvilagus floridanus* and *S. transitionalis*	223	0.78
Red fox	*Vulpes*	28	0.33
Striped Skunk	*Mephitis mephitis*	79	0.72
Virginia opossum	*Didelphis virginiana*	102	0.67
White-tailed deer	*Odocoileus virginianus*	19	0.22

Table 7. Mammal species surveyed, trophic relationship of species to cats, and ratio of species presence when cats are also present versus absent when cats are also absent. Ratio = (proportion of sites that species is present / proportion of sites that cats are present) / (proportion of sites that species is absent/proportion of sites that cats are absent) Higher ratio values indicate greater likelihood that species is present when cat is also present. Species listed by shortened common names (see Table 6).

Species Common Name	Trophic relationship to cats	Present when cats are also present ratio
Bear	N/A	0.33
Red squirrel	Possible prey	1
Deer	N/A	1.67
Skunk	N/A	2.25
Raccoon	N/A	2.29
Mouse	Possible prey	2.67
Gray squirrel	Possible prey	2.78
Chipmunk	Possible prey	3
Opossum	N/A	3
Rabbit	Possible prey	3.67
Coyote	Possible predator	5
Groundhog	N/A	7
Gray fox	Possible predator	10
Red fox	Possible predator	10

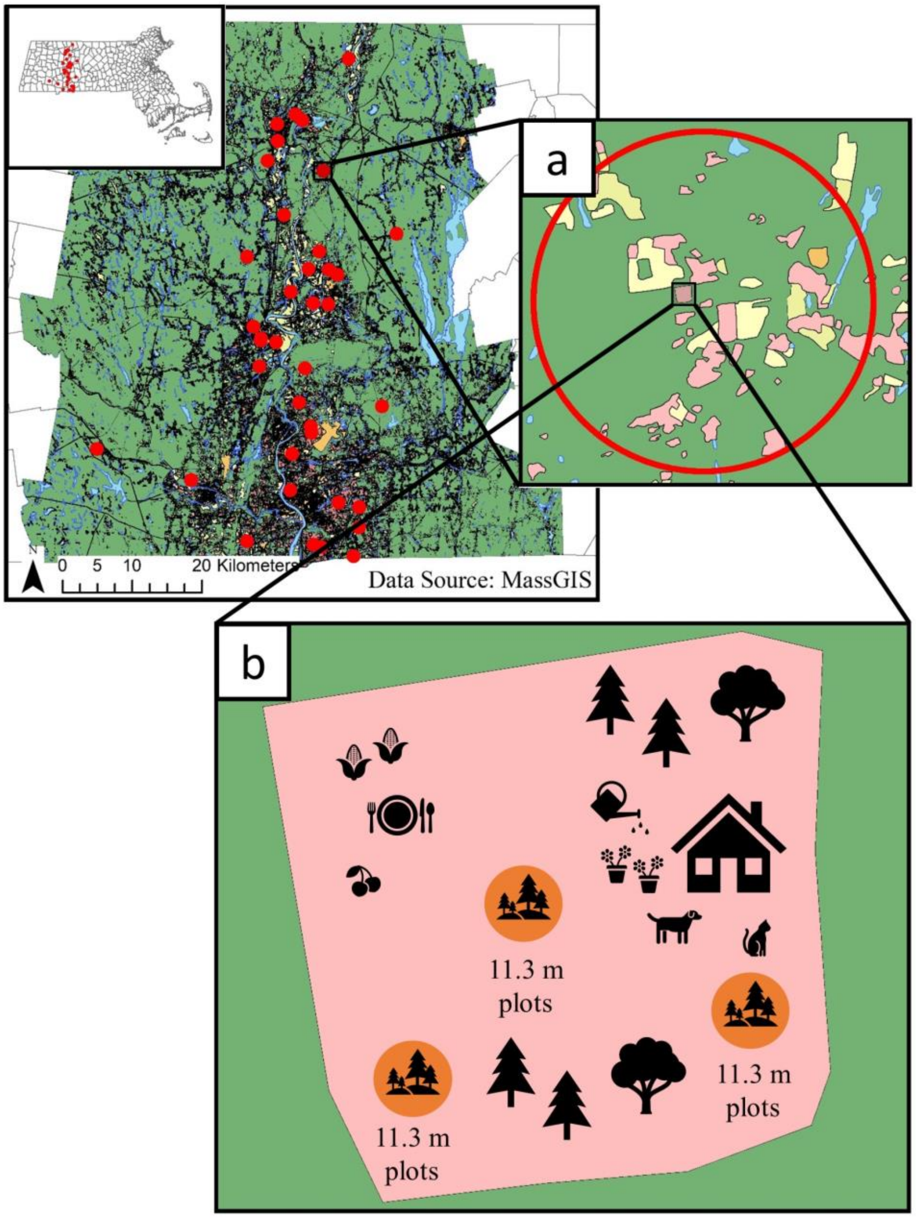

Figure 11. Cameras were deployed in residential yards across western Massachusetts (Study Region). (a) Landscape-scale urban index was calculated based on land-use categories within a 1-km buffer surrounding each residential yard (Landscape-scale). (b) Parcel-scale features were measured with parcel-wide counts (Parcel-scale; counts) standardized by parcel-size in ha. These features included food resources, water resources, and gardens. Detailed vegetation and built-structural measures were assessed within 3 replicate 11.3 m plots (orange circles) within the parcel, with the mean of selected measures used for final analyses. Presented locations at the multiple scales were shifted from true locations to protect participant anonymity.

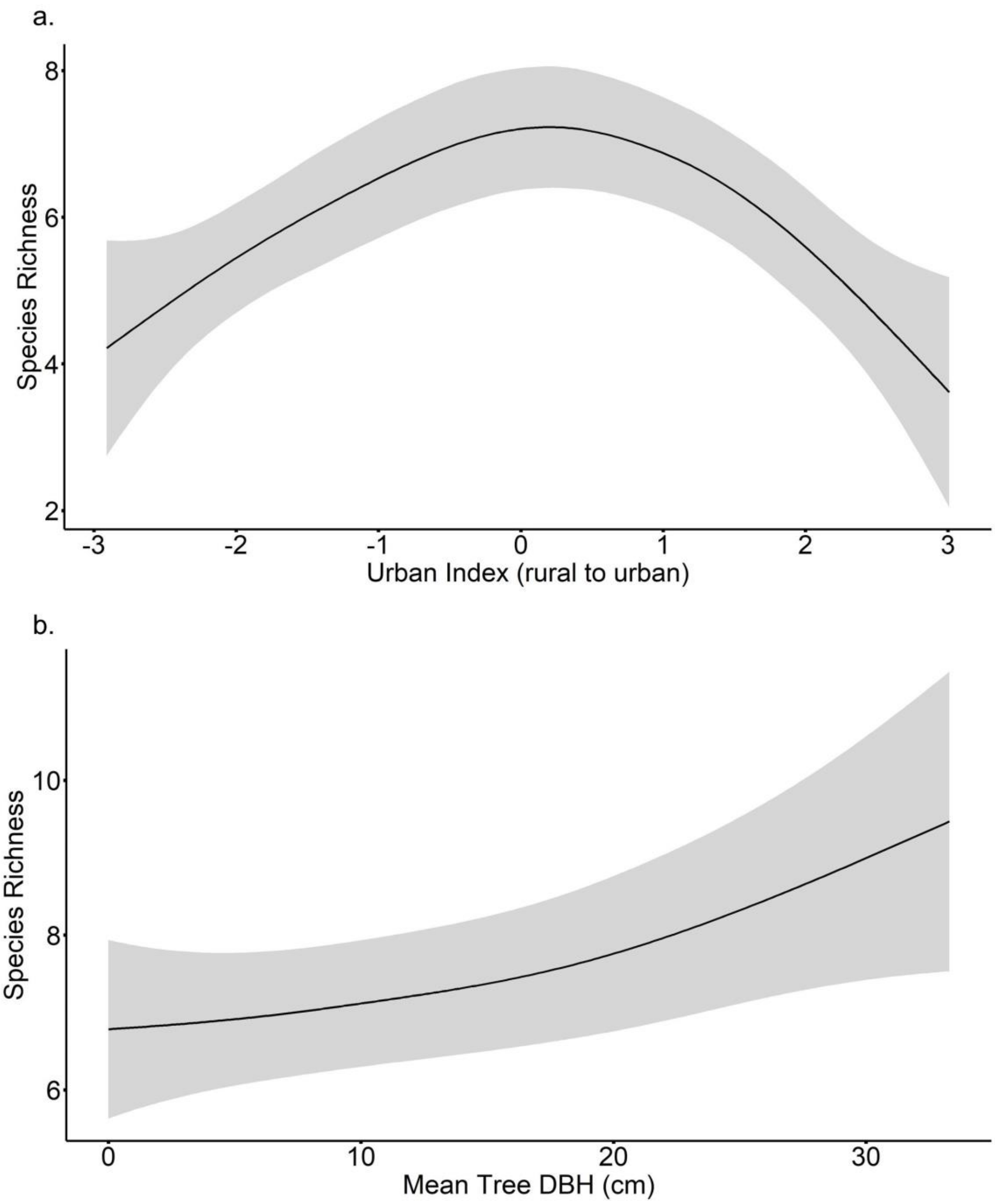
a.
Species Richness
8
6
4
2
-3
-2
-1
0
1
2
3
Urban Index (rural to urban)
b.
Species Richness
10
8
6
0
10
20
30
Mean Tree DBH (cm)

Figure 12. Species richness by (a) urban index and (b) mean tree diameter at breast height (cm).

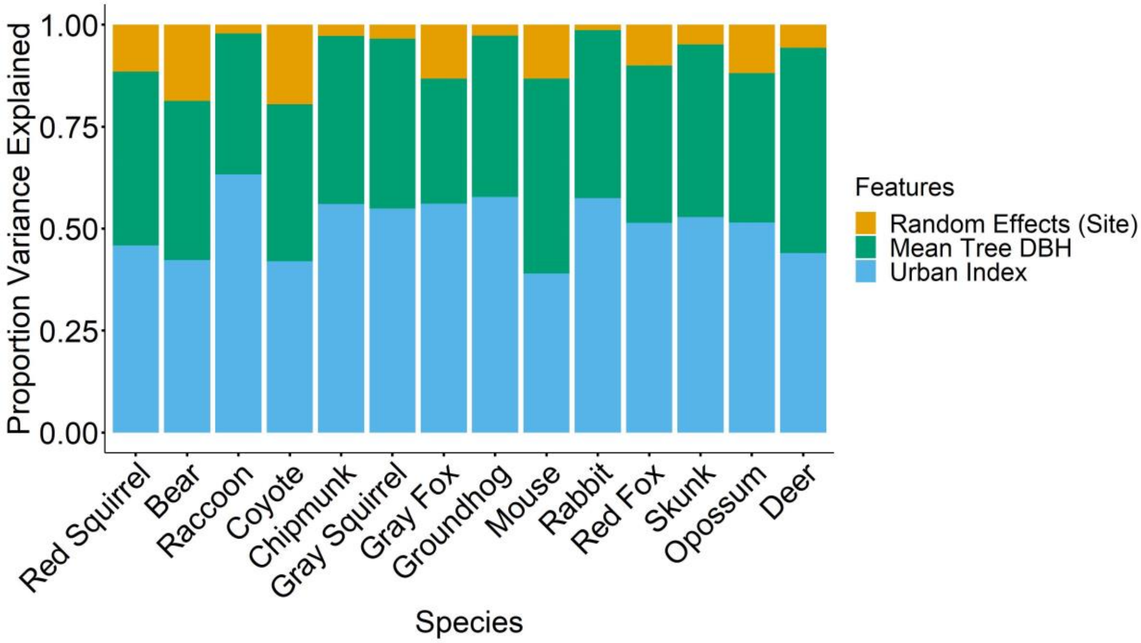

Figure 13. Proportion of variance explained for species-specific occurrence at sites. Variance partitioned by: Random effects of site (orange), mean tree diameter at breast height (DBH in cm; green), and (3) urban index value (blue).

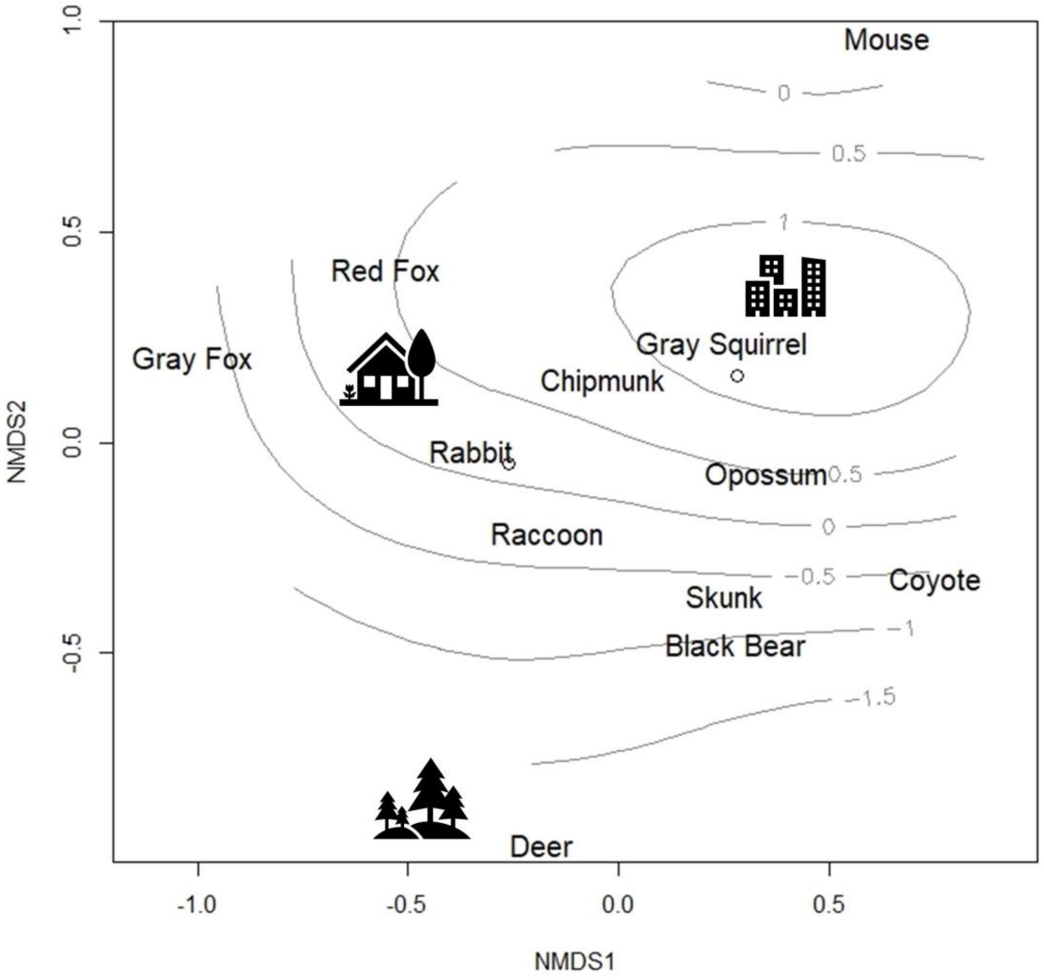

Figure 14. Species disbursed across the urban gradient in two-dimensional ordinal space via NMDS. Isoclines indicate urban index values spanning from more urban (positive values) in the center and extending out into suburban and rural (negative values) on the edges. Values were calculated only for species with sufficient sample size, and thus excluded groundhog and red squirrel.

APPENDICES

APPENDIX A

SUPPLEMENTAL MATERIALS FOR CHAPTER 2

Supplemental Materials and Methods

Effects of playback and urbanization on nestling growth

We assessed whether playback treatment or urbanization influenced nestling growth by using nestling growth measures (mass, right wing chord, and tail) over time to parameterize individual growth curves for each nestling. Based on a previous House Wren nestling growth study (Zach 1982) we used the following logistic growth function (Sofaer *et al*. 2013) for the fixed effects structure of the models:

$$M_t = \frac{A}{1 + e^{(K(L-t))}} \quad (1)$$

where $M_t =$ growth metric (in g or mm) at age t (days), $A =$ asymptote of the growth curve (in g or mm), $e =$ natural logarithm constant, $K =$ growth rate constant, and $L =$ inflection point of the curve (days) of the logistic curve. We adapted the formula, code, and methods from Sofaer *et al*. (2013) to select from multiple candidate models containing all plausible random effects structures. We then parameterized each growth curve in a non-linear mixed effects model using the *nlme* package in R (Pinheiro *et al*. 2017). We excluded from all analyses any nestlings that died, did not complete the experimental treatment, or had obvious measurement errors. Possible random effects structures included either nest, nestling, or nestling-nested-in-nest as random effects on either one, two, or all three of the parameters (A, K, and/or L), as these parameters were repeatedly measured and could covary at the nest, nestling, or nestling-nested-in-nest (hereafter, Nestling | Nest) levels. We used the *AICcmodavg* package in R (Mezerolle 2017) to find corrected Akaike's information criterion, AIC_c (Akaike 1973) values to select best supported models. We considered any model with $\Delta AIC_c < 2$ than the model with the lowest AIC_c value to be equally supported (Burnham and Anderson 2003).

Once we selected the optimal model structure for each growth metric, we used the resulting coefficients for either A, K, and/or L (whichever variables varied based on the random effects structure) from each nestling growth curve as response variables to evaluate whether playback treatment or urbanization affected nestling growth. Using the coefficients of either A, K, and/or L for mass, right wing chord, and tail as predictor variables, we compared a series of linear mixed effects-models (LMMs) in a maximum likelihood model selection framework (Burnham *et al*. 2011). We used corrected Akaike's information criterion, AIC_c (Akaike 1973) to select best supported models.

We began with a global LMM for each response variable that included the following fixed effects (predictor variables): playback treatment, urban index, and their interaction term, as well as potentially confounding variables (clutch size, clutch-order – i.e., first or second clutch of the year at a site, and nest year). We included nest-nested-in-site (hereafter, Nest | Site) as a random effect to account for multiple individual nestlings within nests and multiple nests within sites (Zuur *et al*. 2009). We compared ecologically plausible (based on study system knowledge) combinations of the fixed effects variables with each other and the global model (Burnham and Anderson 2003). Models that had $\Delta AIC_c < 2$ more than the model with the lowest AIC_c value were considered equally supported (Burnham and Anderson 2003). We used the *visreg* package in R (Breheny *et al*. 2017) along with the *ggplot2* package in R (Wickham 2016) to generate plots.

Supplemental Results

Effects of playback and urbanization on nestling growth

Out of $n = 38$ sites, we were able to complete the playback experiment and obtain enough measurements to fit the growth curves for $n = 30$ sites, $n = 59$ nests, and $n = 288$ nestlings. The mean clutch size of the nests was 5.7 (SE = 0.04) and nestlings typically fledged on day 15. The growth curve for mass had Nestling | Nest as a random effect on asymptote (A) and inflection (L) and had a mean asymptote of 10.56 g (SE = 0.13, $t_{572} = 79.36$, $P < 0.001$), inflection point of 4.34 days (SE = 0.14, $t_{572} = 30.87$, $P < 0.001$), and growth rate constant (K) of 0.52 (SE = 0.02, $t_{572} = 29.52$, $P < 0.001$; Fig. 17). The growth curve for wing chord had Nestling | Nest as a random effect on asymptote (A) and inflection (L) and had a mean asymptote of 49.03 mm (SE = 1.36, $t_{572} = 35.92$, $P < 0.001$), inflection point of 8.31 days (SE = 0.21, $t_{572} = 39.31$, $P < 0.001$), and growth rate constant (K) of 0.28 (SE = 0.01, $t_{572} = 35.33$, $P < 0.001$). The growth curve for tail had Nestling | Nest as a random effect on inflection (L) and had a mean asymptote of 18.48 mm (SE = 0.27, $t_{569} = 66.42$, $P < 0.001$), inflection point of 10.83 days (SE = 0.19, $t_{569} = 58.05$, $P < 0.001$), and growth rate constant (K) of 0.59 (SE = 0.01, $t_{572} = 40.16$, $P < 0.001$).

We found no significant effects of predator playback and urbanization on any of the nestling growth curves. The selected model for the asymptote (A) of mass had clutch size as the sole fixed effect ($\beta = -0.15$, SE = 0.06, $t_{28} = -2.45$, $P = 0.02$, Appendix A Table

10). The best fit model included the intercept only model for inflection point (L) of mass (Appendix A Table 11). The selected model for the asymptote (A) of wing chord included only nest year as a fixed effect (Appendix A Table 12), indicating that the asymptotic wing chord was larger in 2017 than in 2018 ($\beta = 7.12$, SE = 1.23, $t_{28} = -5.81$, $P < 0.001$). The best fit model included the intercept only model for inflection point (L) of wing chord (Appendix A Table 13) or the inflection point (L) of tail (Appendix A Table 14).

Supplemental Tables and Figures

Table 8. Results of principle component analysis (PCA) for land cover area (m^2) within 1-km buffer of study sites. Each principle component is presented with loadings by land-cover type, eigenvalues, and proportion of variance explained. PC1 (bolded) had the highest eigenvalue and PC2 was the only other eigenvalue over one. PC1 was selected as the best PC for the urbanization index based on the loadings, statistics, and knowledge of the study region.

Land-cover Type	PC1	PC2	PC3	PC4	PC5
Forest	**-0.510**	0.364	-0.423	-0.115	-0.665
High-density Residential	**0.548**	0.095	0.440	-0.369	-0.602
Commercial	**0.484**	-0.266	-0.484	0.598	-0.322
Open Land	**-0.117**	-0.801	-0.253	-0.521	-0.100
Low-density Residential	**-0.439**	0.383	0.574	0.472	-0.330
Statistics					
Eigenvalues	**2.480**	1.252	0.688	0.433	0.147
Proportion Variance Explained	**0.496**	0.250	0.138	0.087	0.029

Table 9. Playback recordings were generated by creating hour-long tracks by time (e.g., 0600 – 0700, 0700 – 0800, etc.) and assembling 24 tracks into a 24 hour-long track. We created 16 replicates of these 24-long hour tracks, using the call lengths and rates described in this table below. 8 of these 24-hour long tracks contained only treatment call types and the other 8 contained only control call types. The period of the day and time of day determined the call length and rates of each treatment type and control counterpart for a given hour-long time period. Treatment types were hawk (Cooper's Hawk *Accipiter cooperii)* and owl (Eastern Screech Owl *Megascops asio*), and their control counterparts were woodpecker (for hawk; Downy Woodpecker *Picoides pubescens*) and mourning dove (for owl; Mourning Dove *Zenaida macroura*). Call lengths included natural spacing between call notes. Call rates were how many times per hour calls were inserted. Calls were inserted at random times within hour-long blocks.

Period of Day	Time of Day	Treatment Type / Control Counterpart	Call Length	Call Rate
Dawn to morning	0600 – 1000	Hawk	30 s	3/hr
		Owl	60 s	6/hr
Morning to afternoon	1001 – 1600	Hawk	30 s	2/hr
		Owl	None	None
Dusk to night	1601 – 1800	Hawk	30 s	4/hr
		Owl	None	None
Night to late night	1801 – 2100	Hawk	None	None
		Owl	60 s	6/hr
Late night to overnight	2101 – 0300	Hawk	None	None
		Owl	60 s	2/hr
Overnight to dawn	0300 – 0600	Hawk	None	None
		Owl	60 s	3/hr

Table 10. Maximum likelihood estimation of full model set of generalized linear mixed models (GLMMs) testing for effects of playback and urbanization on the asymptote (***A***) parameter of nestling mass (g) growth curves. All models have the random effects structure of Nest | Site. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. For bolded models, * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
clutch size*	**5**	**424.99**	**0**	**0.29**
urbanization + clutch size*	**6**	**426.51**	**1.52**	**0.14**
playback + clutch size*	**6**	**426.86**	**1.87**	**0.11**
urbanization + clutch size + clutch-order	7	427.57	2.57	0.08
playback + urbanization + clutch size	7	428.31	3.32	0.06
1 (Intercept)	4	428.37	3.38	0.05
urbanization	5	429.07	4.08	0.04
clutch-order	5	429.2	4.21	0.04
playback + urbanization + clutch size + clutch-order	8	429.3	4.31	0.03
playback	5	430.1	5.11	0.02
playback x urbanization + clutch size	8	430.12	5.13	0.02
urbanization + clutch-order	6	430.31	5.32	0.02
nest year	5	430.33	5.34	0.02
playback + urbanization	6	430.64	5.65	0.02
playback + clutch-order	6	430.84	5.85	0.02
playback x urbanization + clutch size + clutch-order	9	431.18	6.19	0.01
playback + urbanization + clutch-order	7	431.82	6.83	0.01
playback x urbanization	7	432.04	7.05	0.01
1 + playback x urbanization + clutch size + clutch-order + nest year	10	432.21	7.22	0.01
playback x urbanization + clutch-order	8	433.28	8.29	0

Table 11. Maximum likelihood estimation of full model set of generalized linear mixed models (GLMMs) testing for effects of playback and urbanization on the inflection (***L***) parameter of nestling mass (g) growth curves. All models have the random effects structure of Nest | Site. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. For bolded models, * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
1 (Intercept)*	**4**	**95.53**	**0**	**0.19**
playback	**5**	**96.79**	**1.26**	**0.1**
nest year	**5**	**97.01**	**1.48**	**0.09**
clutch size	**5**	**97.52**	**1.99**	**0.07**
urbanization	5	97.54	2.01	0.07
clutch-order	5	97.55	2.02	0.07
playback + clutch-order	6	98.8	3.28	0.04
playback + clutch size	6	98.81	3.28	0.04
playback + urbanization	6	98.81	3.29	0.04
clutch size + nest year	6	98.83	3.31	0.04
playback x urbanization	7	98.88	3.35	0.04
nest year + clutch-order	6	99.04	3.51	0.03
urbanization + clutch size	6	99.53	4	0.03
clutch size + clutch-order	6	99.55	4.02	0.03
urbanization + clutch-order	6	99.56	4.04	0.03
playback + urbanization + clutch-order	7	100.84	5.31	0.01
playback + urbanization + clutch size	7	100.84	5.31	0.01
clutch size + clutch-order + nest year	7	100.87	5.34	0.01
playback x urbanization + clutch size	8	100.89	5.37	0.01
playback x urbanization + clutch-order	8	100.91	5.39	0.01
urbanization + clutch size + clutch-order	7	101.56	6.03	0.01

playback + clutch size + clutch-order + nest year	8	102.18	6.65	0.01
playback + urbanization + clutch-order + nest year	8	102.31	6.78	0.01
playback + urbanization + clutch size + clutch-order	8	102.87	7.34	0
playback x urbanization + clutch size + clutch-order	9	102.93	7.41	0
1 + playback x urbanization + clutch-order + clutch size + nest year	10	104.53	9.01	0

Table 12. Maximum likelihood estimation of full model set of generalized linear mixed models (GLMMs) testing for effects of playback and urbanization on the asymptote (***A***) parameter of wing chord (mm) growth curves. All models have the random effects structure of Nest | Site. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. For bolded models, * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
nest year*	**5**	**4052.2**	**0**	**0.98**
1 + playback x urbanization + clutch size + clutch-order + nest year	10	4059.67	7.47	0.02
clutch size	5	4074.01	21.81	0
playback + clutch size	6	4075.4	23.2	0
urbanization + clutch size	6	4076.03	23.83	0
1 (Intercept)	4	4076.83	24.63	0
playback + urbanization + clutch size	7	4077.43	25.23	0
urbanization + clutch size + clutch-order	7	4077.66	25.46	0
playback	5	4078.55	26.35	0
playback x urbanization + clutch size	8	4078.57	26.36	0
clutch-order	5	4078.6	26.4	0
urbanization	5	4078.65	26.44	0
playback + urbanization + clutch size + clutch-order	8	4079.01	26.81	0
playback x urbanization + clutch size + clutch-order	9	4080.21	28	0
playback + clutch-order	6	4080.28	28.08	0
urbanization + clutch-order	6	4080.3	28.1	0
playback + urbanization	6	4080.42	28.22	0
playback + urbanization + clutch-order	7	4082.05	29.85	0
playback x urbanization	7	4082.18	29.98	0
playback x urbanization + clutch-order	8	4083.85	31.64	0

Table 13. Maximum likelihood estimation of full model set of generalized linear mixed models (GLMMs) testing for effects of playback and urbanization on the inflection point (***L***) parameter of wing chord (mm) growth curves. All models have the random effects structure of Nest | Site. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. For bolded models, * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
1 (Intercept)*	**4**	**-1479.13**	**0**	**0.14**
nest year	**5**	**-1479.05**	**0.09**	**0.13**
urbanization	**5**	**-1478.87**	**0.27**	**0.12**
playback	**5**	**-1477.41**	**1.72**	**0.06**
clutch size + nest year	**6**	**-1477.23**	**1.9**	**0.05**
clutch-order	**5**	**-1477.15**	**1.98**	**0.05**
clutch size	5	-1477.11	2.02	0.05
nest year + clutch-order	6	-1477.06	2.08	0.05
playback + urbanization	6	-1477	2.14	0.05
urbanization + clutch size	6	-1476.87	2.26	0.04
urbanization + clutch-order	6	-1476.84	2.29	0.04
playback x urbanization	7	-1475.98	3.15	0.03
playback + clutch-order	6	-1475.41	3.72	0.02
playback + clutch size	6	-1475.39	3.74	0.02
clutch size + clutch-order + nest year	7	-1475.24	3.89	0.02
clutch size + clutch-order	6	-1475.12	4.01	0.02
playback + urbanization + clutch-order + nest year	8	-1475.1	4.03	0.02
playback + urbanization + clutch size	7	-1474.98	4.15	0.02
playback + urbanization + clutch-order	7	-1474.97	4.16	0.02
urbanization + clutch size + clutch-order	7	-1474.84	4.29	0.02

playback x urbanization + clutch-order	8	-1473.95	5.19	0.01
playback x urbanization + clutch size	8	-1473.95	5.19	0.01
playback + clutch size + clutch-order + nest year	8	-1473.47	5.66	0.01
playback + urbanization + clutch size + clutch-order	8	-1472.95	6.18	0.01
1 + playback x urbanization + clutch size + clutch-order + nest year	10	-1472.15	6.98	0
playback x urbanization + clutch size + clutch-order	9	-1471.9	7.23	0

Table 14. Maximum likelihood estimation of full model set of generalized linear mixed models (GLMMs) testing for effects of playback and urbanization on the inflection point (***L***) parameter of tail (mm) growth curves. All models have the random effects structure of Nest | Site. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. For bolded models, * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
1 (Intercept) *	**4**	**-1479.13**	**0**	**0.14**
nest year	**5**	**-1479.05**	**0.09**	**0.13**
urbanization	**5**	**-1478.87**	**0.27**	**0.12**
playback	**5**	**-1477.41**	**1.72**	**0.06**
clutch size + nest year	**6**	**-1477.23**	**1.9**	**0.05**
clutch-order	**5**	**-1477.15**	**1.98**	**0.05**
clutch size	5	-1477.11	2.02	0.05
nest year + clutch-order	6	-1477.06	2.08	0.05
playback + urbanization	6	-1477	2.14	0.05
urbanization + clutch size	6	-1476.87	2.26	0.04
urbanization + clutch-order	6	-1476.84	2.29	0.04
playback x urbanization	7	-1475.98	3.15	0.03
playback + clutch-order	6	-1475.41	3.72	0.02
playback + clutch size	6	-1475.39	3.74	0.02
clutch size + clutch-order + nest year	7	-1475.24	3.89	0.02
clutch size + clutch-order	6	-1475.12	4.01	0.02
playback + urbanization + clutch-order + nest year	8	-1475.1	4.03	0.02
playback + urbanization + clutch size	7	-1474.98	4.15	0.02
playback + urbanization + clutch-order	7	-1474.97	4.16	0.02
urbanization + clutch size + clutch-order	7	-1474.84	4.29	0.02

playback x urbanization + clutch-order	8	-1473.95	5.19	0.01
playback x urbanization + clutch size	8	-1473.95	5.19	0.01
playback + clutch size + clutch-order + nest year	8	-1473.47	5.66	0.01
playback + urbanization + clutch size + clutch-order	8	-1472.95	6.18	0.01
1 + playback x urbanization + clutch size + clutch-order + nest year	10	-1472.15	6.98	0
playback x urbanization + clutch size + clutch-order	9	-1471.9	7.23	0

Table 15. Maximum likelihood estimation of full model set of generalized linear mixed models (GLMMs) testing for effects of playback and urbanization on nestling mass (g) at 12-days. All models have the random effects structure of Nest | Site. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$ (all models with $\Delta AIC_c < 4$ shown here; k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight). * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$. See Table 16 for selected model parameter estimates.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
playback* + urbanization*	**6**	**289.76**	**0**	**0.26**
playback*	**5**	**291.15**	**1.38**	**0.13**
playback* + urbanization‡ + clutch-order	**7**	**291.45**	**1.68**	**0.11**
playback* + clutch size	**6**	**291.71**	**1.95**	**0.1**
playback + urbanization + clutch size	7	291.86	2.1	0.09
playback x urbanization	7	291.94	2.17	0.09
playback + clutch-order	6	292.2	2.43	0.08
playback + urbanization + clutch size + clutch-order	8	293.62	3.86	0.04
playback x urbanization + clutch-order	8	293.66	3.9	0.04
playback x urbanization + clutch size	8	294.2	4.44	0.03
playback x urbanization + clutch size + clutch-order	9	296	6.24	0.01
1 (Intercept)	4	296.7	6.94	0.01
clutch-order	5	297.63	7.86	0.01
urbanization	5	297.87	8.11	0
clutch size	5	298.1	8.34	0
1 + playback x urbanization + clutch size + clutch-order + nest year	10	298.39	8.63	0
nest year	5	298.88	9.12	0
urbanization + clutch-order	6	299.33	9.57	0

urbanization + clutch size	6	299.81	10.05	0
urbanization + clutch size + clutch-order	7	300.82	11.06	0

Table 16. Model parameter estimates (fixed effects ± SE, standard error; random effects variances ± SD, standard deviation) for best supported generalized linear mixed models (models a - d) testing for effects of playback and urbanization on nestling mass (g) at 12-days.

(a) playback + urbanization

Fixed effects	Estimate ± SE	df	t value	P-value
1 (Intercept)	10.98 ± 0.24	79	45.74	< 0.001
playback (predator)	-1.14 ± 0.31	5	-3.72	0.0138
urbanization	-0.23 ± 0.11	16	-2.09	0.0532

Random effects	Variance ± SD
site (Intercept)	0.083 ± 0.288
nest (Intercept)	0.239 ± 0.489
nest (Residual)	0.671 ± 0.819

(b) playback

Fixed effects	Estimate ± SE	df	t value	P-value
1 (Intercept)	10.91 ± 0.25	79	43.27	< 0.001
playback (predator)	-1.03 ± 0.30	5	-3.41	0.019

Random effects	Variance ± SD
site (Intercept)	0.237 ± 0.486
nest (Intercept)	0.183 ± 0.428
nest (Residual)	0.673 ± 0.820

(c) playback + urbanization + clutch-order

Fixed effects	Estimate ± SE	df	t value	P-value
1 (Intercept)	10.90 ± 0.26	79	41.79	< 0.001
playback (predator)	-1.11 ± 0.31	4	-3.55	0.0238
urbanization	-0.21 ± 0.11	16	-1.85	0.0822
clutch-order (2nd clutch)	0.27 ± 0.35	4	0.79	0.4744

Random effects	Variance ± SD

site (Intercept)	0.051 ± 0.226			
nest (Intercept)	0.258 ± 0.508			
nest (Residual)	0.670 ± 0.818			
(d) playback + clutch size				
Fixed effects	Estimate ± SE	df	t value	P-value
1 (Intercept)	11.83 ± 0.63	79	18.91	< 0.001
playback (predator)	-0.93 ± 0.29	4	-3.19	0.0333
clutch size	-0.18 ± 0.11	4	-1.54	0.1983
Random effects	Variance ± SD			
site (Intercept)	0.383 ± 0.619			
nest (Intercept)	0.051 ± 0.227			
nest (Residual)	0.672 ± 0.820			

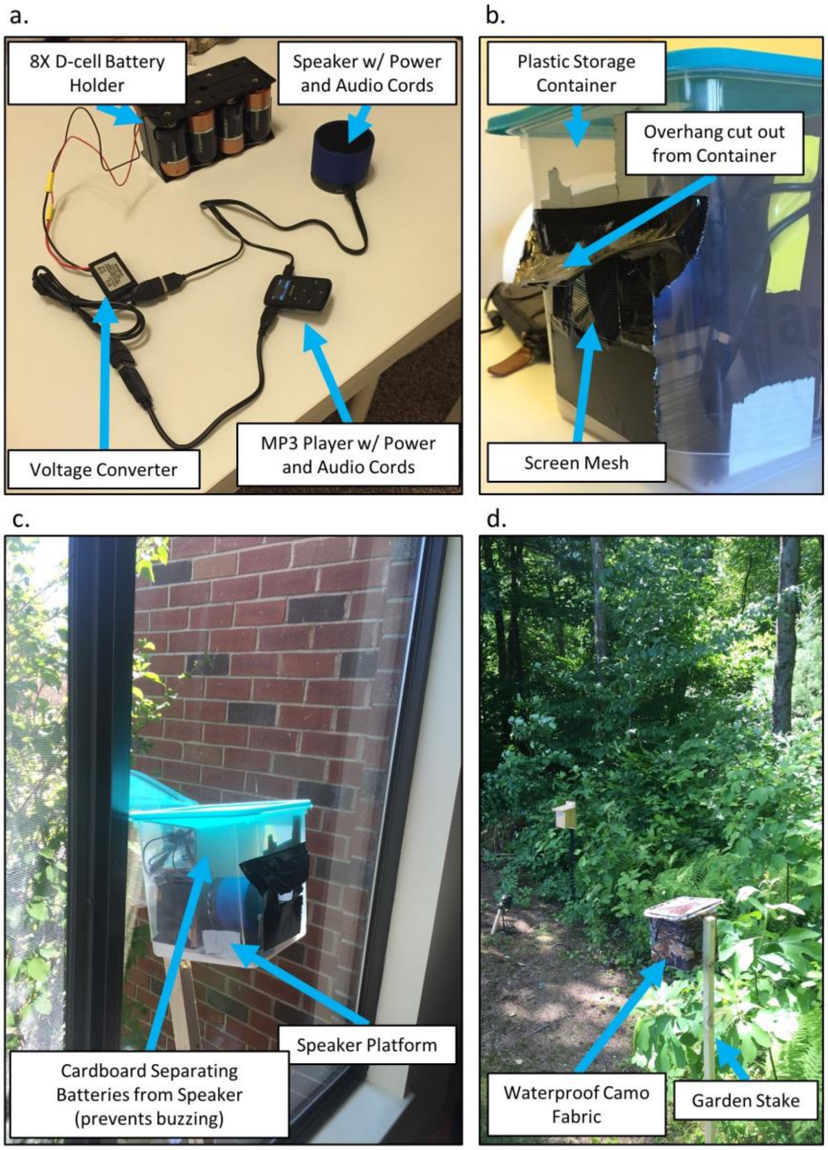

Figure 15. Schematic diagram of portable playback speaker unit assembly. (a) Shows internal electrical components along with (b) container, (c) mount, and (d) set up in situ. Portable playback speaker units last approximately 3.5 days with 8 rechargeable D-cell batteries and audio playing at our calibrated amplitude, rates, and duration. Speaker units were rotated every 3 days.

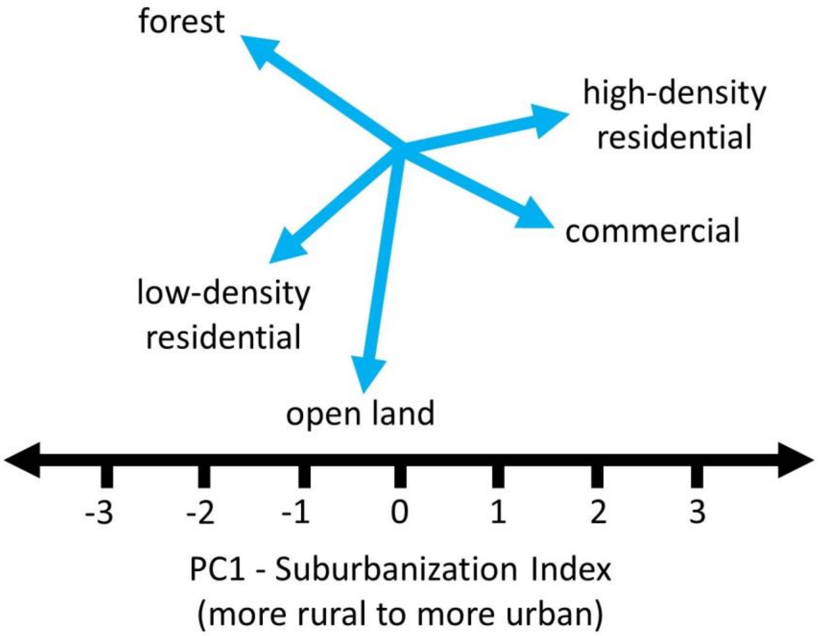

Figure 16. Visualization of PC1 and PC2 biplot for principle component analysis of land-cover type area (m^2) within a 1-km radius of all study sites. PC1 axis is the only axis shown for ease of visualization. PC1 was selected as the urbanization index, with more negative values signifying more rural sites and more positive values signifying more urban sites. PC2 appears to represent open land versus forested and/or residential development.

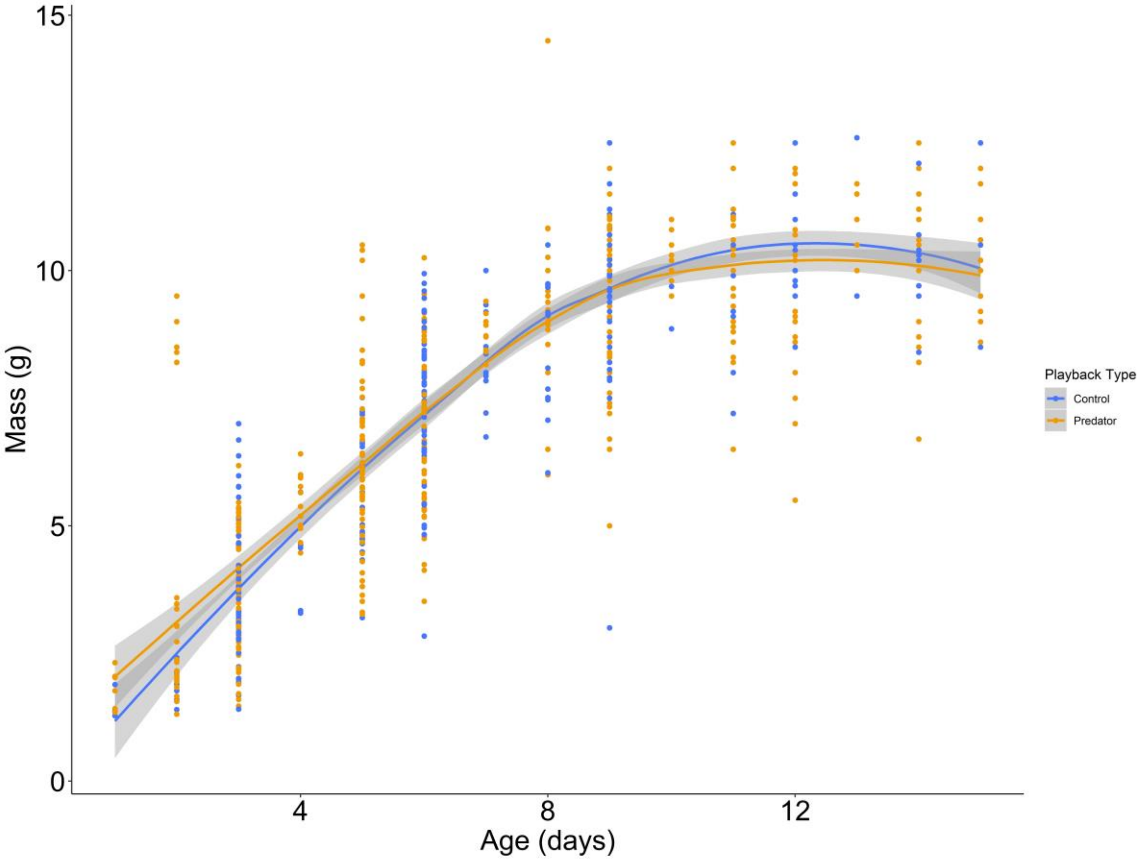

Figure 17. Growth curves for nestling mass (g) by age (days) split by control (blue) and predator (orange) playback type. Points are individual measurements, lines are means, and gray area are confidence intervals.

APPENDIX B

SUPPLEMENTAL MATERIALS FOR CHAPTER 3

Supplemental Materials and Methods

Protocol for reduction, selection, and inclusion of habitat feature variables

Features were reduced and a subset was selected for inclusion (indicated as “Included” in Analysis column). Sampling took place either at a 1-km buffer (landscape-scale), parcel-wide counts (standardized by parcel size in hectares) and mean of three 11.3 m plots within the parcel. Feature types included urbanization (land-use PCA), human-provided food source, and vegetative structure. Variables that were counted parcel-wide at the parcel-scale were compared via correlation, and one variable was included in any set of variables with $r \geq |0.5|$ (indicated in the Analysis column by matching * symbols). The average of each feature was taken from the three plots measured at the 11.3 m and 5 m radii. The features measured at the 11.3 m radius were compared via correlation, and one variable was included in any set of variables with $r \geq |0.5|$ (indicated in the Analysis column by matching † symbols. Some variables were eliminated based on low sample size, or knowledge of house wren foraging habitat requirements in the system (indicated by “Excluded” in the Analysis column). In the case where variables were correlated, the included variable was selected based on the relevance of that variable to house wren foraging habitat requirements in the system.

Supplemental Results

Supplemental Tables

Table 17. Fixed effects structures for candidate models for stepwise selection of generalized linear mixed models (GLMMs) testing for the relationship between playback and urbanization and number of nestling provisioning visits. Non-habitat covariates were tested first, then the habitat covariates and then temperature variables were stepwise selected from the best fit model. All models have nest as a random effect and a Poisson distribution. The best supported model (bolded) was selected from candidate models using hypothesis-driven backwards stepwise selection and ANOVA comparisons with each iteration. The playback variable was included in models as well as its interactions terms even in cases that playback or interaction terms had non-significant p-values. Due to the experimental design, playback had to be included to maximize model fit and covariate term significance. Step: model step, df: degrees of freedom, AIC: Akaike's information criterion, χ^2: chi-square test statistic (from ANOVA tests comparing a model step with a previous step), χ^2 p-value is the chi-squared test p-values. * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$. See Table 20 for selected model parameter estimates.

Step	Fixed Effects Structure	df	AIC$_c$	χ^2	χ^2 p-value
1	**(playback x (urban index x age‡)*)‡ + clutch size***	**10**	**805.1**	**NA**	**NA**
2a	playback x age + (urban index x age)‡ + clutch size*	8	806.9	5.84	0.054
2b	playback + urban index + age + clutch size*	6	807.3	10.18	0.0375$_{S1}$
2c	playback x age + urban index + clutch size*	7	808.2	9.11	0.0279$_{S1}$
2d	playback + urban index x age + clutch size*	7	807.3	8.14	0.0431$_{S1}$
2e	(playback x (urban index‡ x age*)*)‡	9	813.1	10.00	0.0016$_{S1}$
Steps with habitat variables included					
1	**(playback x (urban index x age‡)*)‡ + clutch size***	**10**	**805.1**	**NA**	**NA**
2	(playback x (urban index x age‡) *)* + clutch size* + shrub cover + percent hardwood +	15	716.4	NA	Failed

	mean tree DBH + vegetable gardens + flower beds				
3a	(playback x (age‡ x urban index)*)* + clutch size* + shrub cover + percent hardwood + mean tree DBH + flower beds	14	714.4	0.01	0.93
3b	((playback x [age*)‡ x urban index] *)‡ + clutch size* + shrub cover + mean tree DBH + flower beds	13	810.5	0.66	0.88
3c	((playback x [age*)‡ x urban index] *)‡ + clutch size* + shrub cover + mean tree DBH	12	808.5	0.61	0.73
3d	((playback x [age*)‡ x urban index] *)‡ + clutch size* + mean tree DBH	11	806.7	0.40	0.53
Steps with temperature variables included					
1	((playback* x urban index)* x age) * + clutch size + mean temp + max temp + min temp + SD temp	14	163.2	NA	NA
2a	((playback* x urban index) * x age) * + clutch size + max temp + min temp + SD temp‡	**13**	**161.3**	**0.03**	**0.86**
2b	((playback* x urban index)* x age) * + max temp + min temp + SD temp	12	159.7	0.43	0.81
2c	((playback* x urban index) * x age) * + max temp + SD temp	11	160.0	2.81	0.42
2d	playback x urban index x max temp + age x SD temp	9	161.2	7.92	0.16
2e	((playback x [urban index*)* x max temp]*)* + age + SD temp	11	163.2	0	1
2f	((playback x [urban index*)* x SD temp] *)* + age + max temp	11	152.2	0	1
3a	((playback$^{\pm}$ x [urban index*)* x max temp] *)* + SD temp‡	10	154.3	0	1
3b	(playback x [urban index*)* x max temp]*)*	9	154.7	1.48	0.92
4a	(playback x [urban index*)* x SD temp]*)* + max temp	10	150.2	0	1

4b	((playback* x [urban index)* x SD temp]*)*	9	149.4	0	1
5a	((playback* x [urban index)* x age]*)* + clutch size	9	154.7	0	1
5b	**((playback* x urban index‡)* x age)***	**9**	**156.8**	**2.10**	**<0.001**

Table 18. Maximum likelihood estimation of hypothesized candidate set of Poisson distributed generalized linear mixed models (GLMMs) testing for the relationship between playback and urbanization and brooding duration (see Table 2 for full variable list). All models have the nest as a random effect. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$ and maximum number of statistically significant predictors. The playback variable was included in models as well as its interactions terms even in cases that playback or interaction terms had non-significant p-values. Due to the experimental design, playback had to be included to maximize model fit and covariate term significance. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$. See Table 21 for selected model parameter estimates.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
((playback x [urban index*)* x clutch size] *)* + age*	**10**	**282.17**	**0.00**	**0.45**
playback x urban index + clutch size*	6	282.54	0.37	0.38
((playback‡ x [urban index)‡ x clutch size]‡)‡	9	286.16	3.99	0.06
playback x urban index x age + clutch size*	10	286.33	4.16	0.06
((playback‡ x [urban index*)* x clutch size]*)* + age* + nest year	12	286.84	4.67	0.04
playback x urban index + age*	6	291.65	9.48	0.00
playback x urban index x age	9	295.75	13.58	0.00
playback x urban index x nest year + age* + clutch size*	15	300.84	18.67	0.00

Table 19. Maximum likelihood estimation of hypothesized candidate set of Poisson distributed generalized linear mixed models (GLMMs) testing for the relationship between playback and urbanization and brooding duration, including temperature variables (see Table 2 for full variable list). All models have the nest as a random effect. Best supported models (bolded) selected from candidate models using maximum likelihood estimation with $\Delta AIC_c < 2$ and maximum number of statistically significant predictors. The playback variable was included in models as well as its interactions terms even in cases that playback or interaction terms had non-significant p-values. Due to the experimental design, playback had to be included to maximize model fit and covariate term significance. k: number of parameters, AIC_c: corrected Akaike's Information Criterion, ΔAIC_c: difference from lowest AIC_c model, w: AIC_c weight. * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$. See Table 22 for selected model parameter estimates.

Fixed Effects Structure	k	AIC_c	ΔAIC_c	W
playback* x urban index + min temp x clutch size + age	10	59.62	0.00	0.40
((urban index‡ x [playback*)* x SD temp‡]*)* + clutch size*	**11**	**60.10**	**0.48**	**0.32**
playback* x urban index + mean temp x clutch size* + age	10	60.64	1.03	0.24
((playback x [urban index*)* x clutch size‡]*)* + age	11	65.56	5.94	0.02
(playback* max temp) * x urban index + clutch size	11	68.52	8.90	0.00
playback x urban index + min temp + clutch size*	11	68.68	9.06	0.00
playback x urban index x mean temp + clutch size*	11	71.02	11.40	0.00
((playback x [urban index*)* x clutch size‡]*)* +age + max temp	12	77.32	17.70	0.00
mean temp + max temp + min temp + SD temp	12	68.90	19.28	0.00
(playback x urban index) ‡ x min temp) ‡ + clutch size* + age	12	80.75	21.14	0.00
(playback* x max temp) * x urban index + clutch size* + age	12	81.89	22.27	0.00
playback x urban index x mean temp + clutch size* + age	12	83.80	24.19	0.00

Table 20. Selected model parameters for provisioning visits. Model parameter estimates (fixed effects ± SE, standard error; random effects variances ± SD, standard deviation) for best supported generalized linear mixed model testing for relationship between playback and urban index and provisioning visits. * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Log(provisioning visits) = playback x urban index x age + clutch size			
Fixed effects	Estimate ± SE	z value	P-value
1 (Intercept)	1.69 ± 0.36	4.64	< 0.001*
playback (predator)	0.24 ± 0.29	0.84	0.399
urban index	0.22 ± 0.16	1.39	0.165
age	0.04 ± 0.02	1.92	0.055‡
clutch size	0.19 ± 0.06	3.33	< 0.001*
playback x urban index	-0.12 ± 0.19	-0.61	0.542
playback x age	-0.04 ± 0.02	-1.63	0.104
urban index x age	-0.04 ± 0.01	-2.51	0.012*
playback x urban index x age	0.03 ± 0.02	1.84	0.066‡
Random effects	Variance ± SD		
nest (Intercept)	0.2541 ± 0.5041		

Table 21. Selected model parameters for brooding duration. Model parameter estimates (fixed effects ± SE, standard error; random effects variances ± SD, standard deviation) for best supported generalized linear mixed model testing for relationship between playback and urban index and brooding duration. * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Log(brooding duration) = playback x urban index x clutch size + age			
Fixed effects	Estimate ± SE	z value	P-value
1 (Intercept)	1.98 ± 0.37	5.33	< 0.001*
playback (predator)	0.91 ± 0.59	1.56	0.119
urban index	-0.68 ± 0.28	-2.39	0.017*
clutch size	-0.07 ± 0.07	-0.97	<0.333
age	-0.04 ± 0.02	-2.54	0.01*
playback x urban index	0.87 ± 0.38	2.28	0.023*
playback x clutch size	-0.16 ± 0.11	-1.48	0.139
urban index x clutch size	0.13 ± 0.05	2.48	0.013*
playback x urban index x clutch size	-0.17 ± 0.07	-2.36	0.018*
Random effects	Variance ± SD		
nest (Intercept)	0.0000 ± 0.0000		

Table 22. Selected model parameters for brooding duration including temperature. Model parameter estimates (fixed effects ± SE, standard error; random effects variances ± SD, standard deviation) for best supported generalized linear mixed model testing for relationship between playback and urban index and provisioning visits. * indicates variables with $p < 0.05$, ‡ indicates $p < 0.10$.

Log(brooding duration) = playback x urban index x SD temp + clutch size

Fixed effects	Estimate ± SE	z value	P-value
1 (Intercept)	1.10 ± 0.72	1.52	0.1288
playback (predator)	-2.43 ± 1.15	-2.10	0.0355*
urban index	-1.06 ± 0.59	-1.79	0.0731‡
SD temp	0.16 ± 0.09	1.79	0.0742‡
clutch size	-0.20 ± 0.04	-4.68	< 0.001*
playback x urban index	5.66 ± 1.39	4.09	<0.001*
playback x SD temp	0.60 ± 0.23	2.56	0.0104*
urban index x SD temp	0.14 ± 0.08	1.91	0.0567‡
playback x urban index x SD temp	-1.09 ± 0.28	-3.92	<0.001*
Random effects	**Variance ± SD**		
nest (Intercept)	0.0000 ± 0.0000		
residual	0.0076 ± 0.0275		

Supplemental Figures

Figure 18. iButton temperature loggers were placed both external and internal to nests. (a) Suspended plastic up containing hanging external iButton, (b) external iButton suspended by wire filament, and (c) internal iButton wired into side of nest cup (exposed for visibility).

APPENDIX C

SUPPLEMENTAL MATERIALS FOR CHAPTER 4

Supplemental Materials and Methods

Protocol for reduction, selection, and inclusion of habitat feature variables

Features were reduced and a subset was selected for inclusion (indicated as "Included" in Analysis column, Table 23). Sampling took place either at a 1-km buffer (landscape-scale), parcel-wide counts (standardized by parcel size in hectares), the mean of three 11.3 m plots within the parcel, and the proportion cover or stem density in a 5 m subplot within the three 11.3 m plots. Feature types included urbanization (land-use PCA), human-provided food source, human-provided water source, vegetative structure, or built structure. Variables that were counted parcel-wide at the parcel-scale were compared via correlation, and one variable was included in any set of variables with $r \geq |0.5|$ (indicated in the Analysis column by matching * symbols, Table 23). The average of each feature was taken from the three plots measured at the 11.3 m and 5 m radii. The features measured at the 11.3 m radius were compared via correlation, and one variable was included in any set of variables with $r \geq |0.5|$ (indicated in the Analysis column by matching † symbols, Table 23). Features measured at the 5 m radius were condensed via principle component analysis and plotted on a biplot. The biplot indicated strong covariation between ground cover variables in either the cut grass (i.e., managed lawn) or logs (i.e., woodland) direction. Cut grass and logs were negatively correlated with $r \geq |0.5|$ (indicated in the Analysis column by matching $ symbols, Table 23), thus we used log cover as a proxy of ground cover, with low values of logs indicating managed lawn (e.g., correlated with pavement, buildings), and high values of logs indicating woodland (e.g., correlated with litter, moss). Some variables were eliminated based on low sample size, or knowledge of mammalian habitat requirements in the system (indicated by Eliminated in the Analysis column, Table 23). In the case where variables were correlated, the included variable was selected based on the relevance of that variable to mammalian habitat requirements in the system.

Supplemental Tables

Table 23. Full list of considered landscape-scale and parcel-scale features for consideration in mammal community analyses. Full explanation of selection and inclusion protocol above.

Feature	Scale	Sampling	Type	Analysis
Urban index (urban gradient)	Landscape-scale	1-km buffer	Urbanization	Included
Number of flower gardens / ha	Parcel-scale	Parcel-wide	Food source	Included*
Number of vegetable gardens / ha	Parcel-scale	Parcel-wide	Food source	Included**
Number of fruit trees / ha	Parcel-scale	Parcel-wide	Food source	Included***
Number of bird feeders / ha	Parcel-scale	Parcel-wide	Food source	Included
Number of compost piles / ha	Parcel-scale	Parcel-wide	Food source	Correlated**
Number of pet food receptacles / ha	Parcel-scale	Parcel-wide	Food source	Included****
Number of unlidded trash cans / ha	Parcel-scale	Parcel-wide	Food source	Eliminated*****
Number of outdoor grills / ha	Parcel-scale	Parcel-wide	Food source	Correlated *****
Number of bird baths / ha	Parcel-scale	Parcel-wide	Water source	Correlated *
Number of pools / ha	Parcel-scale	Parcel-wide	Water source	Eliminated
Number of pet water receptacles / ha	Parcel-scale	Parcel-wide	Water source	Correlated ****
Number of water features / ha	Parcel-scale	Parcel-wide	Water source	Correlated ***
Canopy height (m)	Parcel-scale	11.3 m plots	Vegetative structure	Included†
Shrub cover (m^2)	Parcel-scale	11.3 m plots	Vegetative structure	Included††

Total shrub species	Parcel-scale	11.3 m plots	Vegetative structure	Correlated[††]
Number of trees	Parcel-scale	11.3 m plots	Vegetative structure	Included
Number of tree species	Parcel-scale	11.3 m plots	Vegetative structure	Correlated[†]
Percent hardwoods (vs. softwoods)	Parcel-scale	11.3 m plots	Vegetative structure	Included
Average tree DBH (cm)	Parcel-scale	11.3 m plots	Vegetative structure	Included
Total stem density (stems / m^2)	Parcel-scale	5 m subplots	Vegetative structure	Included
Cut grass ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	Correlated[$]
Grown grass ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Shrub ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Brush ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Forb ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Moss ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Litter ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Grass ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Logs ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	Included[$]
Bare/dirt/sand ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Rock ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Water ground cover (m^2)	Parcel-scale	5 m subplots	Vegetative structure	PCA reduced
Building/fence ground cover (m^2)	Parcel-scale	5 m subplots	Built structure	PCA reduced
Pavement ground cover (m^2)	Parcel-scale	5 m subplots	Built structure	PCA reduced

Supplemental Figures

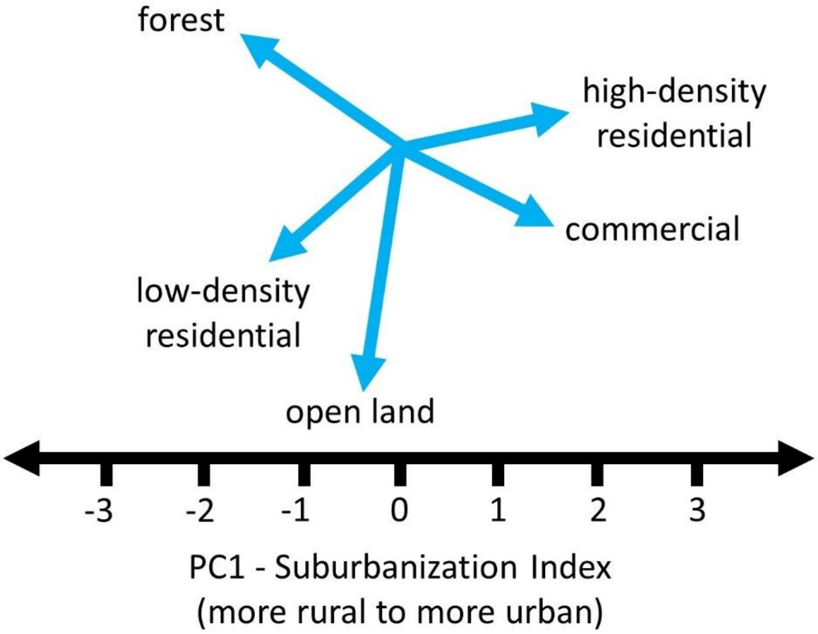

Figure 19. Visualization of PC1 and PC2 biplot for principle component analysis of land-cover type area (m^2) within a 1-km radius of all study sites. PC1 axis is the only axis shown for ease of visualization. PC1 was selected as the urbanization index, with more negative values signifying more rural sites and more positive values signifying more urban sites. PC2 appears to represent open land versus forested and/or residential development.

Figure 20. A red fox depredating a groundhog in a suburban backyard in Amherst, MA.

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