

Perilous choices: landscapes of fear for adult birds reduces nestling condition across an urban gradient

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Abstract. Predator fear effects influence reproductive outcomes in many species. In non-urban systems, passerines often respond to predator cues by reducing parental investment, resulting in smaller and lighter nestlings. Since trophic interactions in urban areas are highly altered, it is unclear how passerines respond to fear effects in 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—the predation paradox. We suggest fear effects in urban habitats could be a significant mechanism influencing nestling condition in birds, despite lowered predation rates. We manipulated exposure of nesting 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 nestlings had reduced mass in nests exposed to predator playbacks as well as in more urban areas. 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 how urbanization affects reproductive outcomes.

Key words: behavior; birds; fear effects; house wren; non-lethal effects; *Troglodytes aedon*; urban gradient; urbanization.

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INTRODUCTION

Fear of predators is a significant ecological mechanism that has consequences at the individual (Werner et al. 1983, Creel et al. 2005), population (Sinclair and Arcese 1995, Creel et al. 2005, Zanette et al. 2011), and community levels (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 (Cresswell 2008). 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 respond to perceived risk by adjusting investment in current reproduction (e.g., provisioning of young) vs. self-maintenance and vigilance, and this trade-off may vary across gradients of human alteration as a function of levels of fear (Fig. 1; also see Lima 1993, Ghalambor and Martin 2000,

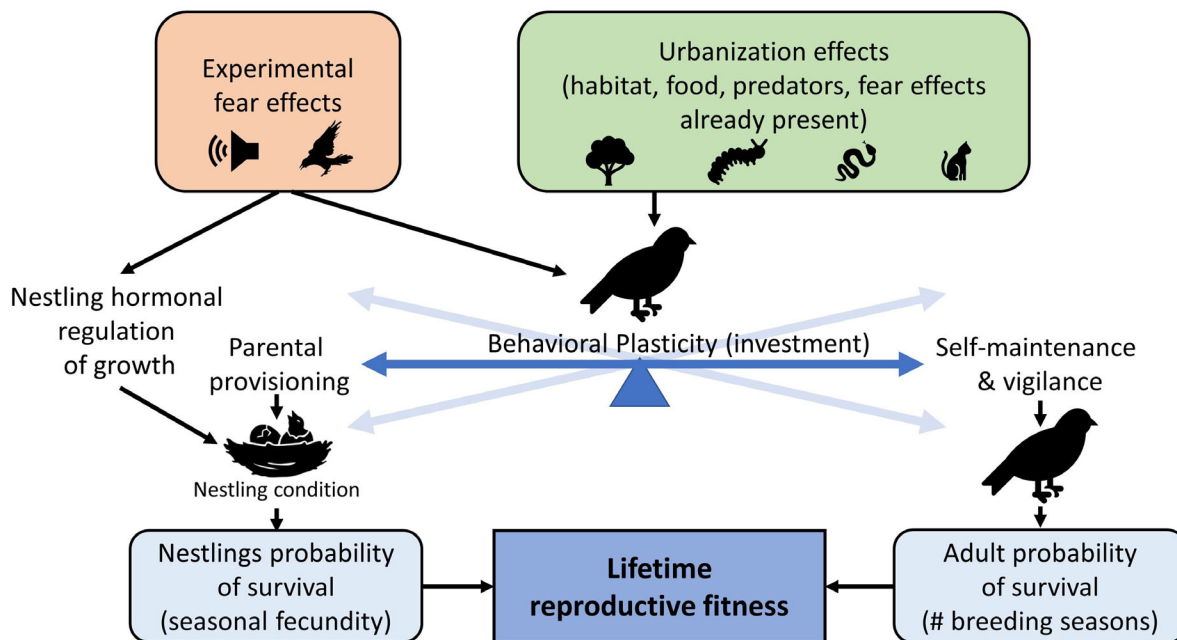


Fig. 1. We experimentally added fear effects of adult-consuming predators (red rectangle, top left) to an urban gradient system in which urbanization effects were already present (green rectangle, top right). Across the gradient of urbanization, habitat, food resources, nest predators, and adult-consuming predators all influence parental investment (behavioral plasticity) of breeding birds (blue balancing scale). The investment prioritizes either 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.

Fontaine and Martin 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 influence reproductive outcomes.

Passerines are adept at detecting (Lohr et al. 2003), communicating (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 (Huang et al. 2012, Hua et al. 2014) or clutch size (Martin 2011, Zanette et al. 2011). Over time, these individual behaviors could have population-level effects on demography (Pangle et al. 2007) and evolution

(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 (Martin 2011, Zanette et al. 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). Alternatively, nestlings themselves may respond to predator cues with hormonal regulation (Tilgar et al. 2010) and morphometric growth trade-offs (Cheng and Martin 2012) to maximize their chance of survival when they leave the nest.

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 suggest 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 (but see Ghalambor and Martin 2000, Hua et al. 2014, Malone et al. 2017). Adult-consuming predators, such as hawks, are often present in higher densities in urban areas (Rullman and Marzluff 2014). 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). 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, Malone et al. 2017). It is also unclear to what extent nestling response to predator cues influences nestling growth. 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). Here, we focus how predation risk on adults influences nesting behavior, which is an understudied mechanism in fear effects research.

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, Rodewald et al. 2013). Studies have described a predation paradox in urban and suburban environments—despite increased density of potential nestling and adult-consuming predators with more urbanization, urban systems typically have decreased per capita predation (Ryder et al. 2010, Fischer et al. 2012, Rullman and Marzluff 2014).

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. 1; also see Chamberlain et al. 2009).

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 vs. rural greenspace (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 (vs. 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).

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.

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, USA. 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 2020). 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 2020). 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 (Aaron Grade, *personal observation*). 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. 2). 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) and used reduced classifications of land cover from the Massachusetts 2005 land-use data layer (John 2018) to determine area (m²) 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 S1: Table S1 and Fig. S2). We used the first principal component as an urban index for our subsequent analyses since it aligned with urban vs. 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). A second principal component explained less of the variation (25.0% and eigenvalue of 1.25) and loaded positively on forest and negatively on open land, likely describing the agricultural vs. forested matrix of undeveloped land in western Massachusetts. We did not include this PC since differences between these land types were not the main focus of our experiment.

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 (Dorset et al. 2017). Although eastern screech owls are primarily nocturnal, small diurnal songbirds, including cavity nesters, often respond to screech owl calls as a threat and exhibit alarm calls and mobbing behavior (Dolby and Grubb 1998, Templeton and Greene 2007, Sieving et al. 2010). During pilot playback testing, we observed house wren adults exhibit scolding calls, fleeing, and

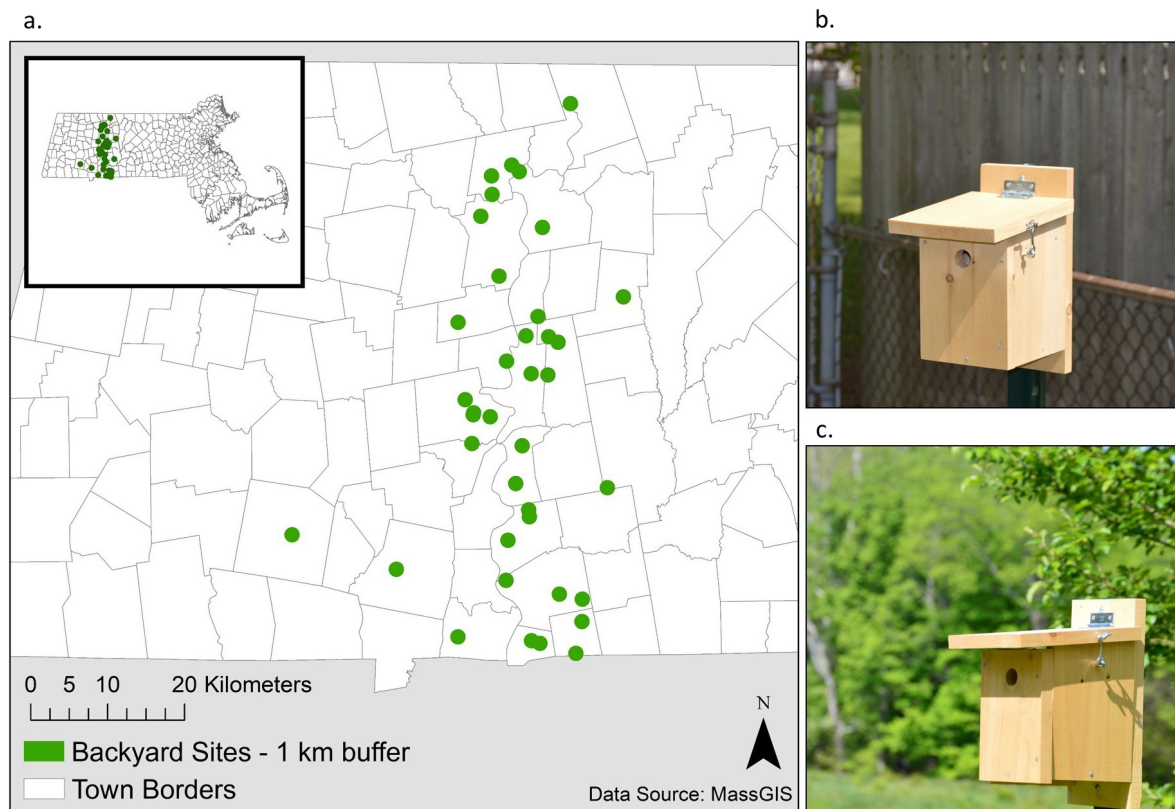


Fig. 2. (a) Study sites were located in residential yards in western Massachusetts, USA, along an urbanization gradient. These example nest boxes were placed in urban (b) and rural (c) yards.

mobbing behavior in response to both Cooper's hawk and eastern screech owl calls, suggesting that they perceive these birds of prey as predator threats. 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-h long tracks for both predator treatment and control playbacks. Each of these 24-h 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, *personal observation*). Due to this protocol, the mourning dove calls (i.e., control for owls) followed the typical nocturnal pattern of owl calls (see Appendix S1: Table S2 for

autoplay 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 S1: Fig. S1 for schematic diagram of assembly).

Playback experiment

We deployed nest boxes in each backyard from April to May (prior to the start of breeding) and monitored them from May to 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 vs. 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 $78.2 (\pm 2)$ 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 to 6 d and a spring scale from age 9 to 15 d (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 d 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 d of age. We chose 12 d since it was the measurement just prior to nestling fledging and the day of average nestling asymptotic mass derived by the nestling growth analysis (Sofaer et al. 2013). See Appendix S1 for nestling growth curve analysis and results and Appendix S1: Fig. S3 for results of 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 $\times$ 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 (Meze-rolle 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, although we present all models with $\Delta AIC_c < 2$ for consideration in supplementary tables (Burnham and Anderson 2003). After model selection, we then assessed variable significance using a cutoff of $P \leq 0.05$. We used the visreg package (Breheny and Burchett 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 Appendix S1). 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, *personal observation*). 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, *personal observation*).

We found a significant effect of predator playbacks and urbanization on 12-d 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. 3). Nestlings in more urbanized settings were lighter compared to nestlings in more rural settings ($\beta = -0.23$, $SE = 0.11$, $t_{16} = -2.09$, $P = 0.05$; Fig. 4). 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 S1: Table S8; for a full list of candidate models, see Appendix S1:

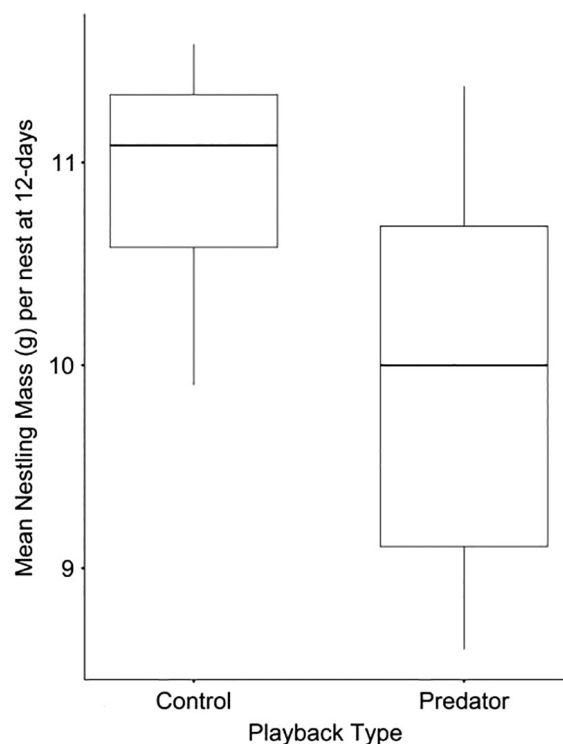


Fig. 3. Playback treatment effects (predator and control) for 12-d nestling mass (g). Mean nestling mass taken at the nest level.

Table S9 for subset of selected models). We found no effect of playbacks or urbanization on wing chord or tail length.

DISCUSSION

The addition of adult-consuming predator cues had a strong effect on 12-d 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 (Cox et al. 2014). There was no significant interaction term between urbanization and fear effects (Appendix S1: Table S8), indicating that the effects of fear in this system were not mediated by degree of urbanization despite clear reductions in 12-d nestling mass across the gradient.

Our experimental results demonstrate fear as an additive driver influencing nestling condition across an urban gradient, but the proximate mechanisms behind fear's influence on nestling

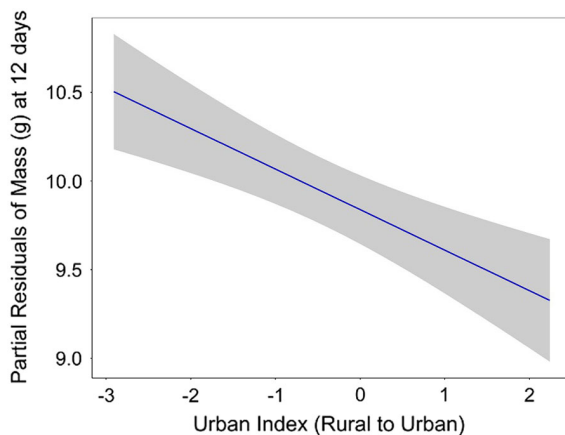


Fig. 4. Urbanization effects on partial model residuals for 12-d nestling mass (g). Residuals generated from generalized linear mixed model (GLMM) with playback and urban index as fixed effects and Nest nested in Site as random effects. Ribbon is standard error.

condition remain unclear. Playback-induced fear could be acting to mediate parental behavior through the evolutionary trade-off between parental investment and self-maintenance (Fig. 1). Alternatively, fear cues could be acting on nestling development directly through hormonal mediation of morphometric growth trade-offs. For example, nestlings may allocate energy to wing growth for predator avoidance, rather than to mass (Freed 1981, 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 are 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. 1). 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. 1). 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 trade-off from the adult perspective is the most likely explanation based on findings from past fear effects studies (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 trade-offs between growth and mass (Tilgar et al. 2010). 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). Elevated adult CORT levels have been associated with increased boldness behaviors in some urban bird populations, (Atwell et al. 2012) which may also influence foraging and parental behaviors (Uchida et al. 2019).

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 (Freed 1981, 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 are 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 (Wilkin et al. 2009). Studies have shown reductions in arthropod biodiversity, abundance, and quality in yards surrounded by higher levels of urbanization (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 (Narango et al. 2018, Seress 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 (Shochat et al. 2006, Fischer et al. 2012) that are often opportunistic nest predators (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; 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 (Shipley et al. 2013). In urban settings, there are also higher population densities of some adult-consuming predators such as domestic housecats (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 (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 (Stracey and Robinson 2012a). We suggest that the presence of additional predators in urban areas influences 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 (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.

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LITERATURE CITED

- Akaike, H. 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika* 60:255–265.
- Atwell, J. W., G. C. Cardoso, D. J. Whittaker, S. Campbell-Nelson, K. W. Robertson, and E. D. Ketterson. 2012. Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology* 23:960–969.
- Bonnington, C., K. J. Gaston, and K. L. Evans. 2013. Fearing the feline: Domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *Journal of Applied Ecology* 50:15–24.
- Breheny, P., and W. Burchett. 2017. Visualization of regression models using visreg. *R Journal* 9:56.
- Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York, New York, USA.
- Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74:46–69.
- Chamberlain, D. E., A. R. Cannon, M. P. Toms, D. I. Leech, B. J. Hatchwell, and K. J. Gaston. 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* 151:1–18.
- Cheng, Y.-R., and T. E. Martin. 2012. Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *American Naturalist* 180:285–295.
- Courter, J. R., and G. Ritchison. 2010. Alarm calls of tufted titmice convey information about predator size and threat. *Behavioral Ecology* 21:936–942.
- Cox, W. A., F. R. Thompson, A. S. Cox, and J. Faaborg. 2014. Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *Journal of Wildlife Management* 78:183–193.
- Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Cresswell, W. 2008. Non-lethal effects of predation in birds. *Ibis* 150:3–17.
- Dolby, A. S., and T. C. Grubb. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behaviour* 56:501–509.
- Dorset, E. E., S. K. Sakaluk, and C. F. Thompson. 2017. Behavioral plasticity in response to perceived predation risk in breeding house wrens. *Evolutionary Biology* 44:227–239.
- Evans, B. S., T. B. Ryder, R. Reitsma, A. H. Hurlbert, and P. P. Marra. 2015. Characterizing avian survival along a rural-to-urban land use gradient. *Ecology* 96:1631–1640.
- Evans, K. L., D. E. Chamberlain, B. J. Hatchwell, R. D. Gregory, and K. J. Gaston. 2011. What makes an urban bird? *Global Change Biology* 17:32–44.
- Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marusch. 2005. Trophic dynamics in urban communities. *BioScience* 55:399–407.

- Felson, A. J., and S. T. Pickett. 2005. Designed experiments: new approaches to studying urban ecosystems. *Frontiers in Ecology and the Environment* 3:549–556.
- Fischer, J. D., S. H. Cleeton, T. P. Lyons, and J. R. Miller. 2012. Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *BioScience* 62:809–818.
- Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434.
- Freed, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? *Ecology* 62:1179–1186.
- Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behaviour* 60:263–267.
- Ghalambor, C. K., S. I. Peluc, and T. E. Martin. 2013. Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biology Letters* 9:20130154.
- Grade, A. M., and K. E. Sieving. 2016. When the birds go unheard: Highway noise disrupts information transfer between bird species. *Biology Letters* 12:20160113.
- Hua, F., R. J. Fletcher, K. E. Sieving, and R. M. Dorazio. 2013. Too risky to settle: Avian community structure changes in response to perceived predation risk on adults and offspring. *Proceedings: Biological Sciences* 280:1–8.
- Hua, F., K. E. Sieving, R. J. Fletcher, and C. A. Wright. 2014. Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behavioral Ecology* 25:509–519.
- Huang, P., K. E. Sieving, and C. M. St Mary. 2012. Heterospecific information about predation risk influences exploratory behavior. *Behavioral Ecology* 23:463–472.
- Ibáñez-Álamo, J. D., O. Chastel, and M. Soler. 2011. Hormonal response of nestlings to predator calls. *General and Comparative Endocrinology* 171:232–236.
- John, P. 2018. MassGIS Data: Land Use (2005). MassGIS (Bureau of Geographic Information).
- Johnson, L. S. 2020. House Wren (*Troglodytes aedon*), version 2.0. In A. F. Poole, editor. *Birds of the world*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <https://birdsoftheworld.org/bow/species/houwre/cur/introduction>
- Lerman, S. B., and P. S. Warren. 2011. The conservation value of residential yards: linking birds and people. *Ecological Applications* 21:1327–1339.
- Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bulletin* 105:1–47.
- Lohr, B., T. F. Wright, and R. J. Dooling. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour* 65:763–777.
- Loss, S. R., T. Will, and P. P. Marra. 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications* 4:1396.
- Malone, K. M., A. C. Powell, F. Hua, and K. E. Sieving. 2017. Bluebirds perceive prey switching by Cooper's hawks across an urban gradient and adjust reproductive effort. *Écoscience* 24:21–31.
- Manly, B. F. J., J. A. N. Alberto, and J. A. N. Alberto. 2016. *Multivariate statistical methods: a primer*. Fourth edition. Chapman and Hall/CRC, New York, New York, USA.
- Martin, T. E. 2011. The cost of fear. *Science* 334:1353–1354.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52:883–890.
- Mezerolle, M. J. 2017. AICcmoavg: Model selection and multimodel inference based on (Q)AIC(c).
- Narango, D. L., D. W. Tallamy, and P. P. Marra. 2017. Native plants improve breeding and foraging habitat for an insectivorous bird. *Biological Conservation* 213:42–50.
- Narango, D. L., D. W. Tallamy, and P. P. Marra. 2018. Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences of the United States of America* 115:11549–11554.
- Newhouse, M. J., P. P. Marra, and L. S. Johnson. 2008. Reproductive success of house wrens in suburban and rural landscapes. *Wilson Journal of Ornithology* 120:99–105.
- Pangle, K. L., S. D. Peacor, and O. E. Johannsson. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology* 88:402–412.
- Peers, M. J. L., et al. 2018. Quantifying fear effects on prey demography in nature. *Ecology* 99:1716–1723.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: linear and nonlinear mixed effects models.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Rodewald, A. D., and L. J. Kearns. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. *Condor* 113:899–907.
- Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2013. Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. *Biological Conservation* 160:32–39.
- Rullman, S., and J. M. Marzluff. 2014. Raptor presence along an urban–wildland gradient: influences of prey abundance and land cover. *Journal of Raptor Research* 48:257–273.
- Ryder, T. B., R. Reitsma, B. Evans, and P. P. Marra. 2010. Quantifying avian nest survival along an urbanization gradient using citizen- and scientist-generated data. *Ecological Applications* 20:419–426.
- Seress, G., T. Hammer, V. Bókony, E. Vincze, B. Preiszner, I. Pipoly, C. Sinkovics, K. L. Evans, and A. Liker. 2018. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecological Applications* 28:1143–1156.
- Shipley, A. A., M. T. Murphy, and A. H. Elzinga. 2013. Residential edges as ecological traps: postfledging survival of a ground-nesting passerine in a forested urban park. *The Auk* 130:501–511.
- Shochat, E., S. B. Lerman, M. Katti, and D. B. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *American Naturalist* 164:232–243.
- Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution* 21:186–191.
- Sieving, K. E., S. A. Hetrick, and M. L. Avery. 2010. The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. *Oikos* 119:264–276.
- Sims, V., K. L. Evans, S. E. Newson, J. A. Tratalos, and K. J. Gaston. 2008. Avian assemblage structure and domestic cat densities in urban environments. *Diversity and Distributions* 14:387–399.
- Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predation-sensitive foraging: the serengeti wildebeest. *Ecology* 76:882–891.
- Sofaer, H. R., P. L. Chapman, T. S. Sillett, and C. K. Ghalambor. 2013. Advantages of nonlinear mixed models for fitting avian growth curves. *Journal of Avian Biology* 44:469–478.
- Sorace, A., and M. Gustin. 2009. Distribution of generalist and specialist predators along urban gradients. *Landscape and Urban Planning* 90:111–118.
- Stracey, C. M., and S. K. Robinson. 2012a. Are urban habitats ecological traps for a native songbird? Season-long productivity, apparent survival, and site fidelity in urban and rural habitats. *Journal of Avian Biology* 43:50–60.
- Stracey, C. M., and S. K. Robinson. 2012b. Does nest predation shape urban bird communities. Pages 49–70 in P. S. Warren, and C. A. Lepczyk, editors. *Urban bird ecology and conservation*. First edition. University of California Press, Berkeley, California, USA.
- Templeton, C. N., and E. Greene. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America* 104:5479–5482.
- Tilgar, V., P. Saag, R. Külavee, and R. Mänd. 2010. Behavioral and physiological responses of nestling pied flycatchers to acoustic stress. *Hormones and Behavior* 57:481–487.
- Uchida, K., K. K. Suzuki, T. Shimamoto, H. Yanagawa, and I. Koizumi. 2019. Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behavioral Ecology* 30:1583–1590.
- Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* 77:157–169.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York, New York, USA.
- Wilkin, T. A., L. E. King, and B. C. Sheldon. 2009. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. *Journal of Avian Biology* 40:135–145.
- Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334:1398–1401.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media, New York, New York, USA.

DATA AVAILABILITY

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.14627790.v2>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3665/full>