THE TRAITS THAT PREDICT FOREST BIRD RESPONSES TO URBANIZATION INTENSITY

by

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A thesis submitted to the faculty of
The University of North Carolina at Charlotte
in partial fulfillment of the requirements
for the degree of Master of Science in
Earth Sciences

Charlotte

2018

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ABSTRACT

GRANT DEAN PATON. The traits that predict forest bird responses to urbanization intensity (Under the direction of DR. SARA A. GAGNÉ)

As humans continue moving to urban areas, there is a growing need to understand the effects of urban intensification on native wildlife populations. Forest species in remnant habitat are particularly vulnerable to urban intensification, but the mechanisms behind these effects are poorly understood. Through generalized linear modeling and multi-model inference, I used occurrence data for 58 forest species derived from 16,541 forested point counts from the Second Pennsylvania Breeding Bird Atlas, urbanization intensity and other landscape metrics derived from circular radii of ten different sizes surrounding count locations, and species trait data to determine the role that biological traits play in forest birds' response to urbanization intensity and scale of effect. Of the twenty species traits analyzed, clutch size, fledglings per nest, frugivory, and sedentarism had positive relationships with species' responses to urbanization intensity, with fledglings per nest and sedentarism being the most influential predictors. Cavity nesting, clutch size, flock size, frugivory, granivory, omnivory, and wingspan had positive relationships with scale of effect, with frugivory being the most influential predictor. This research suggests that frugivorous, sedentary forest bird species with large reproductive outputs are the most equipped to survive in urban areas, and that species' dietary habits have the greatest impact on the size of landscape they require. These findings can be used to inform forest bird biodiversity and land conservation programs in urban areas.

DEDICATION

This work is dedicated to my Opa, William A. Paton Jr., who passed away after 92 loving and compassionate years during its completion.

ACKNOWLEDGMENTS

I would like to thank Andrew Wilson, Daniel Brauning, Robert Mulvihill, and all those that contributed to the Second Pennsylvania Breeding Bird Atlas. Without their thorough work and willingness to provide us with their hard-earned data, this project would not have been possible. I would also like to thank Alexandra Shoffner for her vital contributions to the geospatial component of this research. I am thankful for my committee members for their time and feedback, and especially so for my advisor, Dr. Sara Gagné, for her endless patience and attention to detail. Finally, I would like to thank everyone in the Department of Geography and Earth Sciences for the knowledge and support they have given me.

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CHAPTER 1: INTRODUCTION

The 21st century will be defined by the expansion of urban development. Fifty-four percent of the world's population lived in urban areas in 2014, with 66% expected to be doing so by 2050 (United Nations 2014). As a result, total urban area is projected to grow by at least 430,000 km^2 by 2030, an increase of 139% (Seto et al. 2011).

Expanding urban centers often fragment natural areas, imperiling native species. Much of the research in this regard has been focused on the effects of urbanization on forest breeding birds. Proximity to and intensity of surrounding urban development affect the abundance of generalist species in forest patches (Klingbeil and Willig 2016, Posa and Sodhi 2006, Suarez-Rubio et al. 2011). For example, the abundance of blue jays (*Cyanocitta cristata*) – a generalist forest species – was over three times greater in forests surrounded by medium-intensity housing than in those surrounding low-intensity housing (Kluza et al. 2000). Conversely, urbanization has particularly strong negative effects on the abundances of specialist and forest interior species (Dunford and Freemark 2004, Pidgeon et al. 2007, Vignoli et al. 2013, Minor and Urban 2010). For example, the density of ovenbirds (*Seiurus aurocapilla*) in forests amongst medium-intensity housing was over 50% lower than that in forests surrounded by low-intensity housing (Kluza et al. 2000). Species can be affected by urbanization at varying spatial scales, and the scale at which landscape effects are strongest is known as the scale of effect (Jackson and Fahrig 2015). Studies on urban bird populations that take landscape scale into effect are lacking, and many studies that do consider spatial scale focus on the landscapes within 1 km of their study site only, despite the possibility that birds may regularly cover larger distances (Evans et al. 2009, Lee and Carroll 2014, Rodewald and Shustack 2008, Trammell et al. 2011).

Urbanization can affect forest species in habitat patches by altering movement success, resource availability, and the intensity and frequency of disturbances both overall and at habitat edges (Kennedy et al. 2010). More intense urbanization may increase the effective isolation of forest patches, making the resources within those patches more difficult to access (Chace and Walsh 2006, Meffert and Dziock 2013). Increasing urbanization may also lead to increased dispersal mortality. Sources of dispersal mortality in urban areas include collisions with buildings, the leading anthropogenic cause of death for birds in North America (Erickson et al. 2005), and predation by domestic cats, estimated in one study to be responsible for roughly one bird fatality per cat per week in southeastern Michigan (Lepczyk et al. 2004). Urban areas may also be a source of novel or more resources, favoring species in remnant habitat that can take advantage of these opportunities (Planillo et al. 2015, Rodewald et al. 2011). Examples include raptor species being more abundant around busy roadways because of the availability of roadkill (Planillo et al. 2015) and increased abundances of species that commonly visit bird feeders in neighborhoods with higher densities of feeders (Fuller et al. 2008). Conversely, the replacement of native habitat with developed land cover in urban areas may make native food sources rarer, imperiling species that have limited dietary or nesting options (Croci et al. 2008). Urban areas may also favor species that respond positively to forest edges and those that are less sensitive to human disturbance

(Ditchkoff et al. 2006, Mason et al. 2007). For example, the width of forested corridors in urban areas can limit the species that are found there, favoring edge tolerant species over forest-interior species (Mason et al. 2007). Declines in abundance for some forest bird species can be explained by the increase in anthropogenic noise that accompanies human development, particularly among songbirds (Bayne et al. 2008, Goodwin and Shriver 2011). The higher temperatures and increased pollution associated with urban development may also serve as disturbances for forest birds (Aronson et al. 2014, Jackson et al. 2011, Lewis et al. 2013, Loss et al. 2009).

Species traits are useful in elucidating the importance of these potential mechanisms in structuring bird communities. For forest bird species, traits associated with high urban abundances include an omnivorous diet, a medium or high nesting height, sociality, parental involvement in nest construction, long duration in nest after hatching, and cavity nesting (Croci et al. 2008, Pidgeon et al. 2007, Møller 2013). Omnivory may indicate a more generalized feeding behavior, potentially enabling a forest species to utilize anthropogenic food sources, such as trash and non-native vegetation (Jokimäki and Suhonen 1998). Medium to high nesting heights may ensure that forest bird nests are less exposed to disturbances from humans, such as landscaping alterations, parental flushing due to an approaching person (Kosinski 2001, Wang et al. 2008), or from nest predators. Bird species that live in medium- or large-sized groups may gain the advantage of learning urban survival strategies from other group members (Liker and Bokony 2009). Biparental involvement in nest construction may result in more stable nests that can better withstand urban disturbances (Jose et al. 1998). Species that spend longer periods of time in the nest before fledging may require lower daily resource needs than faster-growing species, making them more suited to a potentially resource-depleted urban area (Croci et al. 2008, Hemborg et al. 2001). Cavity nesting could better protect a species' young from urban predators and other disturbances, such as strong winds or rains (Kark et al. 2007).

Despite these insights, there is much to gain in our understanding of forest bird trait variation associated with urbanization. First, we do not know whether traits associated with urbanization success in birds in general, such as sedantariness, large clutch size, multiple clutches per year, high nesting height, large body size, wingspan, and brain size (Brown and Graham 2015, Conole and Kirkpatrick 2011, Croci et al. 2008, Evans et al. 2011, Jokimäki et al. 2016, Kark et al. 2007), also characterize abundant forest bird species in urban landscapes. Second, we have no direct evidence of associations between forest birds and species responses to urbanization. Existing research assumes that traits characteristic of abundant forest bird species in urban landscapes are associated with a positive response to urbanization, but no study has directly tested this contention. Third, we do not know whether traits have any association with species' scales of effect of urbanization. To our knowledge, no studies have attempted to connect urbanization scales of effect to species traits. Knowledge of the degrees to which a variety of traits are linked to species responses to urbanization and scales of effect will significantly improve our understanding of the mechanisms underlying urbanization effects on forest bird communities.

The objective of the present research was to add to our understanding of what mechanisms influence forest bird responses to urbanization intensity by analyzing traits associated with differing urbanization success in forest birds, others seen for birds in general, and exploratory variables not previously tested. Using a large point count dataset from the Second Pennsylvania Breeding Bird Atlas (Wilson et al. 2012), I estimated the effect of urbanization intensity in landscapes of multiple scales on the individual occurrences of 58 forest bird species, controlling for other potentially important explanatory variables such as forest amount and configuration, local habitat quality, and species detectability. For each species, I chose the largest effect among scales as a measure of both its response to urbanization and its scale of effect of urbanization. I then tested for the influence of species traits, including flock size, frugivory, and sedentariness (Table 1) on species responses to urbanization and scales of effect using phylogenetic regressions and meta-analyses.

CHAPTER 2: METHODS

2.1. Study Area

Pennsylvania is approximately 120,000 km^2 in area between 39.0° and 42.5°N and 74.0° and 81°W in the northeastern United States (Figure 1). Elevations are typically 300 to 400 m, except for where the state is bisected by the Appalachian and Allegheny mountain ranges with a maximum elevation of approximately 980 m, and the southeastern corner of the state, which approaches sea level (Carter and Provorse 1996). Pennsylvania’s main climatic regions are the Humid Continental and the Humid Subtropical regions, with the Humid Continental climate occurring in the northern half of the state as well as along the Appalachian Mountains (Kottek et al. 2006). Land cover is predominantly forest cover, dominated by red and white oak, with agricultural activity occurring in the lower elevations, namely in southeastern and western regions (Fry et al. 2011, Rhoads and Block 2005). Average population density in Pennsylvania is 100 people/km^2, with roughly 65% of the population residing in the Philadelphia or Pittsburgh metropolitan areas (United States Census Bureau 2016). By 2040, Pennsylvania’s population is expected to grow by 11% to approximately 14.1 million people, with most of the growth expected in the Philadelphia metropolitan area and the center of the state (Behney et al. 2014)

2.2. Second Pennsylvania Breeding Bird Atlas

The Second Pennsylvania Breeding Bird Atlas (PBBA) was conducted statewide by 2,000 staff and volunteers between 2004 and 2009 (Wilson et al. 2012). Volunteers surveyed each of 4,937 ‘blocks’, each approximately 25 km^2 in area, looking for species presence, and evidence of breeding. Within each survey block, trained staff conducted eight point counts each, for a total of 33,763 counts in the state during which 176 species were observed. Count locations were selected by random placement of a point within a block, with adjustments made to locate the points on the nearest non-highway road at least 400m away from other points. Each point was surveyed once during the five-year Atlas period between May 25 and July 4. Observers recorded the species of each bird heard or seen within two distance bands of the point (< 75 m and > 75 m) during a 6 minutes and 15 seconds span between 5 and 10 am, provided there was little to no rain and light to no wind. Observers also recorded the survey start time, evidence of recent land cover change, and dominant local habitat type at points.

2.3. Forest Birds

From the 176 species detected during PBBA point counts, we excluded species that had the following characteristics: 1) hybrid species; 2) irregular breeder in the state; 3) raptor; 4) waterfowl; and 5) occurrence at fewer than 30 count locations. The forest dependency of each of the remaining 101 species was assessed by comparing the cumulative distribution of a species’ counts across all 33,763 count locations, to the cumulative distribution of forest amount in landscapes at each scale using Kolmogorov-Smirnov (KS) tests of no difference (Figure 2). We classified species as forest-dependent if they were found disproportionally in landscapes dominated by forests or occurred in proportion to forest amount.

2.4. Species Traits

I collected data on the wingspan, body size, dietary habits (frugivory, granivory, omnivory), foraging height, sedentariness, nesting height, clutch size, number of fledglings per clutch, number of clutches per year, duration in the nest, cavity nesting, parental involvement, sociality, song attributes, brain size, and dispersal distance of each forest-dependent species (Table 1). I also collected data on brain size and dispersal distance, although these variables were not analyzed further due to a lack of species-specific data. With the exception of song attributes, I gathered species trait data using the information in respected field guides or other sources (Kaufman 2001, Rodewald 2015). I averaged values between sexes and across sources for continuous traits, and used the most commonly referenced state for categorical traits. For song attributes, I recorded song frequency (Hz), song length, and song range (the difference between a song's lowest and highest frequencies). I measured song variables by analyzing species recordings from the Cornell Lab of Ornithology (Rodewald 2015) with the sonographic analysis tools available in the linguistics software Praat (Boersma and Weernink 2018). Song frequencies averaged 416.33 Hz ± 86.63, song lengths averaged 1.96 seconds ± 1.56, and song ranges averaged 175.45 Hz ± 134.83.

2.5. Landscape Definition and Selection

I defined landscapes as circular areas centered on point count locations that were surrounded by >50% forest cover – composed of the Deciduous, Mixed, and Evergreen Forest classes of the National Land Cover Database (NLCD, Fry et al. 2011) – within a 0.2 km radius (Fig. 1). I restricted my selection of count locations in this way to maximize the likelihood that observed forest species were indeed breeding in forest.

Landscapes were of ten different radii: 0.2, 0.5, 1, 2, 4, 6, 8, 10, 12, and 16 km. These scales were chosen to cover a wide range of over one order of magnitude at a high density to more accurately assess each species' scale of effect (Jackson and Fahrig 2015). For each forest bird species, I selected the landscapes within the species' range (Fig. 1). To determine species ranges, I used block occurrence probabilities from the PBBA for each species, calculated through simple conditional autoregressive models accounting for observer effort and landscape covariates (Wilson et al. 2017). I then spatially interpolated occurrence probabilities for each species using kriging in ArcGIS (ESRI 2016, Oliver and Webster 1990, Wilson et al. 2012). I classified blocks with an interpolated occurrence probability ≥ 0.2 as lying within the species' range. An occurrence probability of 0.2 translates into seeing the species in a given location once every five years on average – the duration of the PBBA. This conservative range estimate is also equivalent to predicted species presence in at least the given location's survey block or one of the four neighboring survey blocks with contiguous boundaries.

2.6. Urbanization Intensity and other Explanatory Variables

In this section, I outline the measurement of urbanization intensity and other explanatory variables that was completed in a prior study (Shoffner 2016). Urbanization intensity was quantified as the first component from a principal component analysis of six variables: the proportional area of landscapes in each of the four Developed classes of the NLCD, area-weighted average population density in landscapes, and area-weighted average housing density in landscapes. Landscape averages of population and housing densities from the 2010 US Census (United States Census 2015) were weighted by census block area.

Other explanatory variables included forest amount, forest configuration, agriculture amount, mean elevation, elevation range, and dominant local land cover. Forest amount was the proportional area of landscapes in the NLCD Forest cover class – Deciduous, Mixed, or Evergreen – that best matched each forest species' habitat affinity. The forest configuration of landscapes was also quantified for each NCLD Forest cover class using the patch density and clumpiness index metrics (McGarical et al. 2012). For generalist forest species or those for which lack a habitat affinity was unknown, the total of all Forest cover classes was used to estimate forest amount and configuration. Agriculture amount was the proportional area of landscapes in the NLCD Cultivated Crops and Pasture/Hay classes. Mean elevation over each landscape was calculated using a publicly available digital elevation model raster for the state of Pennsylvania (PA DNCR 2006). Landscape heterogeneity was measured using two variables: elevation range in the landscape, and Shannon's Diversity Index. Local habitat type and evidence of recent land use were recorded by surveyors at the time and location of the PBBA point counts as measures of local habitat quality. For species detectability variables, I used day, year, start time of the point count, and observer identity, which were all recorded by PBBA surveyors.

2.7. Analyses

I tested for the influence of species traits on the magnitude, direction, and scale of effect of forest bird responses to urbanization intensity in two steps. First, I used logistic regressions and multi-model inference to estimate the effect of urbanization intensity on the occurrence of each forest bird species at each scale. Models also included forest amount, forest configuration, agriculture amount, variables describing landscape heterogeneity, variables decribing local habitat quality, and species detectability. I chose this analytical approach because it produces unbiased estimates of true effect sizes even if explanatory variables are highly correlated, i.e., $r = .90$ (Smith et al. 2009). In my case, the absolute value of correlations between urbanization intensity and other explanatory variables averaged 0.218 (minimum $|r| = 0.000572$, maximum $|r| = 0.632$). To further ensure that multicollinearity did not influence urbanization intensity effect sizes, I divided explanatory variables by their partial standard deviations. As a result, urbanization intensity effect sizes are independent of the multicollinearity structure of any given model and therefore could be sensibly averaged across models (Cade 2015).

For each species and each landscape scale, I used Akaike's Information Criterion (AIC) to evaluate models that included every possible combination of explanatory variables. I calculated the full model-averaged effect size of urbanization intensity and its unconditional variance using the best ($\Delta_i \leq 2$) models of each species' occurrence at each scale (Anderson & Burnham 2002). The scale of effect of urbanization intensity for each species was the scale at which urbanization intensity has the largest absolute effect on its occurrence.

Second, I determined the effects of species traits on species' urbanization intensity effect sizes and scales of effect using multi-model inference. Species effect sizes were weighted by their inverse variance to account for the varying precision of estimates

(Cooper et al. 2009). In order to determine whether species relatedness would violate model assumptions, I first performed univariate phylogenetic regressions each trait using randomly selected Ericson backbone trees from the online service BirdTree (www.birdtree.org, Jetz et al. 2012). For each trait, I estimated their λ values, the degree to which a trait's effect on urbanization intensity response or scale of effect is attributable to species interrelatedness. If λ is not significantly different from 0, then the results of a phylogenetic regression are the same as those from a standard regression. No traits exhibited a phylogenetic signal significantly different from 0. I chose the traits that explained the most variation in effect sizes or scales of effect, i.e., their models had the highest adjusted R^2 values, to include in subsequent models. For urbanization intensity response, I also analyzed all the traits that had a value for each species to maximize the possibility of observing trait associations. Selected traits were transformed in the same manner as the variables used in models to estimate the effects of urbanization intensity described above. I built models that included all possible combinations of selected traits and ranked them using AIC. I calculated the full model-averaged effect size of each trait and its unconditional variance for the best ($\Delta_i \leq 2$) models to estimate the trait's effect on species responses to urbanization intensity.

CHAPTER 3: RESULTS

3.1. Forest Bird Responses to Urbanization Intensity

I estimated the effect of urbanization intensity on the occurrence of 58 of 60 forest-dependent bird species. Two species, the Black-billed Cuckoo (*Coccyzus erythrophthalmus)* and the Yellow-rumped Warbler (*Setophaga coronata)*, were too rare to permit estimation of regression parameters. The average urbanization intensity effect size across species was -0.36 ± 0.49 (SE), with effect sizes ranging between -1.49 ± 0.50 (SE) and 0.90 ± 0.20 (SE) (Table 2). The average scale of urbanization intensity effect across species was 4.87 ± 5.95 (SE) (Table 2). Scales of urbanization intensity effect occurred at each of the ten scales we examined. Half of the species were most sensitive to urbanization intensity at scales ≤ 1 km.

3.2 Effects of Species Traits on Urbanization Intensity Responses

I selected seven traits that each explained a relatively large proportion of the variance in urbanization intensity effect sizes across species to include in multivariate models: cavity nesting, clutch size, fledglings per nest, frugivory, granivory, omnivory and sedentarism (Table 3). I retained these seven variables for further analysis. Four of these traits were included in the five best models of species responses to urbanization intensity (Table 4). Species with larger clutch sizes or more fledglings per nest that are frugivorous or sedentary are more positively affected by urbanization intensity (Table 5, Figures 3 & 4)

I also performed an analysis that included all the traits containing a value for each species to maximize the chances of observing trait associations. This subset of traits was nearly identical to that of the best predicting univariate traits on urbanization intensity response: body mass, cavity nesting, clutch size, frugivory, granivory, omnivory and sedentarism. Five of these traits were included in the seven best models of species responses to urbanization intensity (Table 6). Cavity nesting species with larger clutch sizes that are frugivorous, granivorous, or sedentary are more positively affected by urbanization (Table 7).

3.3. Effects of Species Traits on Scales of Effect

I selected eleven traits that each explained a relatively large proportion of the variance in scales of effect across species to include in multivariate models: cavity nesting, clutch size, duration in nest, flock size, foraging height, frugivory, granivory, lifespan, omnivory, sedentarism, and wingspan (Table 8). I retained these eleven variables for further analysis. Seven of these traits were included in the eleven best models of species responses to urbanization intensity (Table 9). Cavity nesting species with larger clutch sizes that live in larger flocks, are frugivorous, granivorous, or omnivorous, or have larger wingspans are more sensitive to urbanization at bigger scales (Table 10). The best-performing predictive model was a univariate regression of frugivory on scale of effect (Figure 5).

CHAPTER 4: DISCUSSION

The traits influencing forest bird species responses to urbanization intensity, in descending order of effect sizes, are fledglings per nest, sedentarism, clutch size, and frugivory. The traits influencing forest bird scales of effect, in descending order of effect sizes are frugivory, granivory, omnivory, cavity nesting, clutch size, flock size, and wingspan. In this section I will describe the possible mechanisms behind the observed species trait associations with urbanization intensity response and scale of effect, as well as compare the results of this experiment to those of other studies, and discuss the management implications of my research.

The number of fledglings per nest that a forest bird species has was the strongest influencing trait on their response to urbanization intensity. Controlling for clutch size, fledging 2-3 young per nest is enough to counteract the negative effects of urbanization intensity and enable species to start to positively respond to urban environments. The importance of fledgling success suggests that reproductive capability is the most important factor for forest birds to succeed in urban areas. Previous studies have indicated varying reproductive outputs in birds along rural-urban gradients (Peach et al. 2008, Rodewald et al. 2011, Ryder et al. 2010) with the general results being that species lay fewer eggs in more urban environments but have higher levels of nest survival. Forest species that are naturally more efficient at raising their young may be able to capitalize on this urban phenomenon more than species that struggle to fledge their chicks.

Sedentarism was also a large contributor to forest bird responses to urbanization intensity, basically equivalent in effect size to fledging an additional chick per nest (17.09 vs. 18.09, respectively). This effect is substantial when one considers the entirety of a species' reproductively viable years, and that some species rear multiple broods a year. Sedentarism has been associated with urbanization success in other studies (Croci et al. 2008, Jokimäki and Suhonen 1998, Jokimäki et al. 2016), although this is the first study to my knowledge that has quantified this association and compared it to the association of other species traits. Sedentary species may accomplish this by being able to claim prime nesting habitat before migratory species arrive in the area, or by having a more comprehensive knowledge of urban resources through their continuous presence (Croci et al. 2008, Evans et al. 2011, Kark et al. 2007). Interestingly, several of the sedentary species that responded positively to urbanization (Table 2) are known to cache food supplies for later use, such as the red-breasted and white-breasted nuthatches (*S. canadensis* and *carolinensis*, respectively), American crow (*C. brachyrhynchos*), and black-capped chickadee (*P. atricapillus*). It is possible that food caching better enables these species to respond to the potential resources pressures of urban areas (Kozlovsky et al. 2017) although further research addressing this potential mechanism is needed. Further research is also needed to determine what impact, if any, the predisposal of migratory species to urbanization compared to sedentary species contributes to observed long-term declines in North American migratory bird populations (Robbins et al. 1989).

Clutch size had the third largest trait association with urbanization intensity response. Controlling for fledglings per nest, forest species needed clutch sizes of 4-7 to counteract the negative effects of urbanization and enable species to positively respond to urban environments. Previous research has indicated that as urbanization increases, clutch size tends to decrease (Chamberlain et al. 2009, Rodewald and Shustack 2008) while the number of fledglings per nest, as discussed earlier, is slightly augmented in urban areas. These results underscore that large clutch sizes are not as important for forest birds as is the rate at which these species are able to convert laid eggs into fledglings. Forest species that naturally lay larger clutch sizes may be able to reach the 4-7 egg benchmark even in urban areas where their clutch sizes are reduced.

Frugivorous species responded better to increasing urbanization intensity than granivorous or omnivorous species did. Fruits from common landscaping species such as holly and juniper may contribute to the diets of frugivorous species, making urban environments more resource-rich than native forest (Belaire et al. 2014). Urban areas often lack the long grasses that contribute to granivorous diets, and omnivorous species that prey on insects have their food supply restricted by the abundance of non-native plants and pesticides in urban areas. My findings contradict existing literature regarding frugivory and urbanization success, with other studies indicating a drop in frugivorous species richness in urban environments compared to rural ones (Reis et al. 2012, Silva et al. 2016). Most studies addressing frugivory and urbanization success were conducted in tropical ecosystems however, so these results may not be applicable to temperate forest species like those studied here.

Based on the analysis of species traits with data for all the sample species, cavity nesting and granivory are also associated with urbanization intensity response, but only if fledglings per nest is not controlled for. These traits were not highly correlated in the dataset, so the reason for this is unclear. It is possible that species who nest in cavities may produce more fledglings than those species that do not due to increased protection from environmental disturbances, leading to an increase in urbanization intensity response that is accounted for if fledglings per nest is controlled for, although data in support of this hypothesis is conflicting (Blewett and Marzluff 2005, Kark et al. 2007, Reale and Blair 2008). Similarly, granivorous species may produce more fledglings in urban environments, so the association of granivory with urbanization intensity response is removed if fledglings per nest is controlled for, although I could not find any studies directly relating diet and fledgling success in urban ecosystems to corroborate this hypothesis. Cavity nesting and granivory do show an association with urbanization intensity response, but it is secondary to those of clutch size, fledglings per nest, frugivory, and sedentarism.

The species traits influencing scales of effect of urbanization intensity response in descending order of influence are frugivory, granivory, omnivory, cavity nesting, clutch size, flock size, and wingspan. Frugivorous species were most sensitive to increasing urbanization intensity at scales with radii 2.17 km larger than non-frugivorous species, controlling for the other strongly associated traits. This finding in conjunction with frugivory’s positive association with urbanization intensity response may indicate that while urban areas contain more fruits, these resources may be separated by larger distances in urban areas compared to native forest. Urban green space, either natural or cultivated, is often unequally distributed in urban areas, driven by factors such as community income or racial composition (Heynen et al. 2006) that can also influence floral community structure (Lubbe et al. 2010). The inequitable distribution of urban green space and the plant species within may also explain why granivory and omnivory also resulted in forest bird species using larger landscapes. Cavity nesting species required larger landscapes than open-nesting species, possibly because of a relative lack of suitable trees in urban areas (Blewett and Marzluff 2005). Like frugivory, granivory, and omnivory's impacts on scale of effect, clutch size may increase scale of effect because more offspring require more food to sustain them. Species with large clutches may need to utilize the resources in larger landscapes to provide for their young. Forest species with larger flock sizes may also need to utilize larger landscapes to adequately feed all members of the flock (Maldonado-Coelho and Marini 2004). Wingspan is highly correlated with body size, and larger bird species may require larger landscapes to obtain the amount of resources they require (Haskell et al. 2002, Rytwinski and Fahrig 2012). Few studies have related species traits to scales of effect like this one, making the mechanisms behind these trait-scale relationships difficult to corroborate. More research needs to be done in using biological traits to predict the spatial element of species responses.

From a biodiversity conservation or management perspective, taking species traits into account reveals management strategies that can be adopted to promote urban forest bird populations. Because reproductive output was a substantial contributor to species responses to urbanization intensity, increasing species nesting success is vital to long-term urban success. Fledglings per nest could possibly be augmented in urban areas by management strategies that increase insect populations such as planting native trees or limiting urban pesticide usage. Such practices may increase the protein-rich food supply that nestlings require and result in more nestlings surviving the transition into live outside the nest (Chamberlain et al. 2009, Pollock et al. 2017). Higher proportions of native plants are associated with higher abundances and species richness of bird species, promoting more native species than just those that are more receptive to invasive plants (Burghardt et al. 2009, Chace and Walsh 2006, Day 1995). The average scale of effect I observed was a circular landscape with a radius of 4.87 km (± 5.95), equivalent to an area of roughly 74.51 km^2. Preserving forest fragments of this size would be suitable for the average forest species, but urban forest preserves of this size are highly unlikely and may even exceed the city’s area. This underscores that forest bird species are often operating on larger spatial scales than we realize, meaning that cities should try to preserve as much contiguous forest as possible as well as promote bird-friendly habitat practices among the city’s private landowners. A combination of public and private land management is necessary to preserve and maintain the health of urban forests that are sufficiently large for urban forest birds. Urban conservation and management programs need to consider the species traits influencing forest bird species responses to urbanization intensity as well as their scales of effect to adequately assess which species are in the most need of conservation prioritization.

In conclusion, the forest species best able to cope with increasing urbanization intensity are those that are sedentary, frugivorous, have large clutch sizes, and fledge a larger number of young per nest. Species lacking these biological advantages are potentially at-risk due to urbanization and should be prioritized in urban conservation programs. The largest positive contributor to scale of effect in forest birds is frugivory, although cavity nesting, larger clutch size, large flock size, granivory, omnivory, and wingspan also increase the scale at which forest birds are most sensitive to urbanization intensity to lesser degrees. Urban biodiversity conservation programs need to consider both the species traits of forest birds potentially at risk in urban environments and the scale at which these species are most sensitive to urbanization.

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APPENDIX A: TABLES

Table 1: Alphabetical list of the trait categories that I analyzed, along with the mechanisms by which the traits may influence species responses to urbanization, my predictions of the effect of traits on species responses to urbanization, and relevant literature on the topics

Category	**Mechanisms**	**Predicted Effect of Traits on Species Responses to Urbanization**	**Relevant Literature**
Biparental nestbuilding	Parental involvement in nest construction may make them stronger and more resilient to disturbance	Neutral	Croci et al. 2008 Jose et al. 1998
Body mass (g)	May indicate ability to access widely scattered urban resources, or predation risk by urban predators such as cats	Positive	Conole and Kirkpatrick 2011 Croci et al. 2008 Kark et al. 2007 Møller 2013
Cavity nesting	Cavity-nesting species may be better protected from predators and human disturbances. Such species would also be able to utilize nesting boxes and birdhouses	Positive	Blewett and Marzluff 2005 Croci et al. 2008 Pidgeon et al. 2007
Clutch size	Urbanization may be related to reductions in reproductive output. Large clutch sizes could offset urban fatalities	Positive	Kennedy et al. 2010 Roodbergen et al. 2012 Strasser and Heath 2013
Clutches per year	Multiple clutches in a year could offset urban fatalities	Positive	Kark et al. 2007
Duration in nest	Slow growth of chicks may be more suited for a resource scarce urban ecosystem, however also makes the hatchlings prone to nest predators for a longer period of time	Neutral / Mixed	Croci et al. 2008 Hemborg et al. 2001
Fledglings per clutch	More fledglings per clutch mean more individuals in the population, potentially	Positive	Kark et al. 2007 Vigallon and Marzluff 2005

	offsetting urban fatalities		
Flock size	Social species may have the advantage of learning adaptation strategies from other members of their flock	Positive	Croci et al 2008 Liker and Bokony 2009
Foraging height (m)	Birds that forage at the height of foliage common in urban areas will have more feeding locations, and higher foragers may avoid more urban disturbances	Positive	Kennedy et al. 2010
Frugivory	Fruiting shrubs such as holly are commonly planted in urban green spaces. Ability to utilize these resources could aid urbanization	Positive	Lim and Sodhi 2004
Granivory	Seed-eating species may be able to take advantage of anthropogenic resource subsidies in the form of bird-feeders	Positive	Jokimäki et al. 2016 Marzluff et al. 2016 Meffert and Dziock 2013
Lifespan	Longer-lived species may produce more offspring over the course of their life than shorter-lived species	Positive	Croci et al. 2008
Nesting height (m)	The height at which a species nest influences the type and amount of predators that can access them. Urban nesters may be prone to increased predator activity and human disturbance	Positive	Conole and Kirkpatrick 2011 Kosinski 2001 Møller et al. 2013 Wang et al. 2008
Omnivory	Indicates a flexible diet, and potentially enables a species to utilize anthropogenic resources, such as trash	Positive	Brown and Graham 2015 Jokimäki and Suhonen 1998 Kark et al. 2007

Sedentarism	Species that live year-round in urban areas may be more aware of resource locations within the city than migrants are	Positive for sedentary species	Croci et al. 2008 Evans et al. 2011 Kark et al. 2007
Song qualities (frequency and range in Hz, and length in seconds)	Urban noise pollution can mask certain species' calls, lowering communication potential and reproductive ability	Negative for species whose song frequencies or amplitudes are obscured by urban noise, and for species with long songs	Fuller et al. 2007 Slabbekoorn 2013 Wood and Yezerinac 2006
Territory size (ha)	Species with large territories can draw resources from a larger area, but they may be more at risk of mortality from passing through the urban matrix more frequently. Smaller forest patches in urban environments may also favor species that require less territory	Neutral	Chace and Walsh 2006 Rodewald and Shustack 2008
Wingspan (cm)	Large wingspans can indicate a greater ability to navigate through the matrix	Positive	Croci et al. 2008

Table 2: Examined species, their urbanization intensity responses (UIR) and accompanying standard errors (SE), and their scale of effect (SoE) in km

Species (Common Name)	**Scientific Name**	**UIR**	**SE**	**SoE**
Canada Warbler	*Cardellina canadensis*	-1.49	0.50	1
Black-throated Blue Warbler	*Setophaga caerulescens*	-1.19	0.21	1
Winter Wren	*Troglodytes hiemalis*	-1.16	0.27	1
Louisiana Waterthrush	*Parkesia motacilla*	-1.12	0.18	0.5
Least Flycatcher	*Empidonax minimus*	-1.09	0.21	1
Hermit Thrush	*Catharus guttatus*	-1.06	0.10	2
Pine Warbler	*Setophaga pinus*	-0.95	0.31	16
Magnolia Warbler	*Setophaga magnolia*	-0.91	0.13	1
Yellow-bellied Sapsucker	*Sphyrapicus varius*	-0.87	0.12	8
Mourning Warbler	*Geothlypis philadephia*	-0.86	0.40	0.5
Worm-eating Warbler	*Helmitheros vermivorum*	-0.82	0.32	0.2
Dark-eyed Junco	*Junco hyemalis*	-0.81	0.10	8
Brown Creeper	*Certhia americana*	-0.78	0.23	0.2
Blackburnian Warbler	*Setophaga fusca*	-0.72	0.10	1
Golden-winged Warbler	*Vermivora chrysoptera*	-0.70	0.32	2
Black-throated Green Warbler	*Setophaga virens*	-0.68	0.07	1
Common Raven	*Corvus corax*	-0.66	0.16	2
Ovenbird	*Seiurus aurocapilla*	-0.62	0.05	16
Veery	*Catharus fuscescens*	-0.61	0.06	0.2
Golden-crowned Kinglet	*Regulus satrapa*	-0.58	0.31	2
Yellow-throated Vireo	*Vireo flavifrons*	-0.56	0.14	6
Chestnut-sided Warbler	*Setophaga pensylvanica*	-0.54	0.06	1
Hooded Warbler	*Setophaga citrina*	-0.54	0.13	0.2
Swamp Sparrow	*Melospiza georgiana*	-0.52	0.18	16
Great Crested Flycatcher	*Myiarchus crinitus*	-0.48	0.10	16
Blue-headed Vireo	*Vireo solitarius*	-0.44	0.08	1
Cerulean Warbler	*Setophaga cerulea*	-0.44	0.14	6
Acadian Flycatcher	*Empidonax virescens*	-0.39	0.06	0.2
Scarlet Tanager	*Piranga olivacea*	-0.34	0.04	0.2
Blue-gray Gnatcatcher	*Polioptila caerulea*	-0.32	0.08	0.5
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	-0.31	0.06	0.5
Yellow-billed Cuckoo	*Coccyzus americanus*	-0.29	0.06	1
American Redstart	*Setophaga ruticilla*	-0.28	0.04	0.2
Common Yellowthroat	*Geothlypis trichas*	-0.26	0.03	0.2
Eastern Wood-Pewee	*Contopus virens*	-0.24	0.03	0.2
Pileated Woodpecker	*Dryocopus pileatus*	-0.24	0.07	6
Black-and-white Warbler	*Mniotilta varia*	-0.20	0.07	0.2
Red-eyed Vireo	*Vireo olivaceus*	-0.19	0.02	0.5
Hairy Woodpecker	*Picoides villosus*	-0.18	0.07	0.2

Cedar Waxwing	*Bombycilla cedrorum*	-0.13	0.06	16
Tree Swallow	*Tachycineta bicolor*	-0.12	0.14	2
Ruby-throated Hummingbird	*Archilochus colubris*	-0.06	0.06	6
Prairie Warbler	*Setophaga discolor*	-0.03	0.08	0.2
Red-breasted Nuthatch	*Sitta canadensis*	0.01	0.06	0.5
Purple Finch	*Haemorhous purpureus*	0.02	0.05	10
Black-capped Chickadee	*Poecile atricapillus*	0.03	0.03	10
White-breasted Nuthatch	*Sitta carolinensis*	0.03	0.03	2
Indigo Bunting	*Passerina cyanea*	0.08	0.02	8
Eastern Phoebe	*Sayornis phoebe*	0.09	0.09	16
Yellow-throated Warbler	*Setophaga dominica*	0.13	0.34	4
Chipping Sparrow	*Spizella passerina*	0.17	0.02	0.2
Wood Thrush	*Hylocichla mustelina*	0.19	0.04	10
American Crow	*Corvus brachyrhynchos*	0.22	0.05	16
Tufted Titmouse	*Baeolophus bicolor*	0.25	0.04	16
Northern Flicker	*Colaptes auratus*	0.45	0.08	16
Kentucky Warbler	*Geothlypis formosa*	0.49	0.47	12
Eastern Towhee	*Pipilo erythrophthalmus*	0.74	0.06	16
Northern Parula	*Setophaga americana*	0.90	0.20	1

Table 3: Results from general linear models of the effects of traits on forest-dependent bird species responses to urbanization intensity in Pennsylvania, USA. No traits exhibited a phylogenetic relationship to urbanization intensity response (λ = 0).

Variable	λ ML	95% CI	*β*	Residual df	Adjusted R^2
Biparental Nestbuilding	0	NA - .28	12.48	52	-0.02
Cavity Nesting	0	NA - .25	48.34	54	0.01
Clutch	0	NA - .29	21.96	56	0.03
Clutches per Year	0	NA - .33	26.19	50	-0.01
Duration in Nest	0	NA - .29	1.64	54	-0.01
Fledglings per Nest	0	NA - .42	26.78	28	0.08
Flock Size	0	NA - .38	0.52	32	-0.03
Foraging Height	0	NA - .26	-2.05	38	-0.02
Frugivory	0	NA - .36	32.14	56	0.00
Granivory	0	NA - .21	63.41	56	0.06
Lifespan	0	NA - .27	3.70	54	-0.01
Mass	0	NA - .28	0.05	55	-0.01
Nesting Height	0	NA - .30	1.76	51	-0.01
Omnivory	0	NA - .28	44.16	56	0.01
Sedentarism	0	NA - .20	53.23	54	0.02
Song Frequency	0	NA - .30	-0.01	47	-0.02
Song Length	0	NA - .28	1.95	47	-0.02
Song Range	0	NA - .36	-0.03	47	-0.02
Territory	0	NA - .79	0.00	36	-0.03
Wingspan	0	NA - .39	0.56	54	-0.01

Table 4: Best predicting models of species traits on urbanization intensity response using subset of top-performing univariate traits

Model	**K**	**AIC**	**Δ**	**w**
Fledglings per nest	3	362.15	0	0.30
Clutch size	3	362.53	0.38	0.25
Sedentarism	3	363.03	0.88	0.19
Fledglings per nest + sedentarism	4	363.76	1.61	0.13
Fledglings per nest + frugivory	4	363.82	1.67	0.13

K: number of estimated parameters, *AIC*: Akaike's Information Criterion, *Δ*: AIC (best) – AIC (model), *w*: Akaike weight, the probability of being the best model given the observed data and evaluated models

Table 5: Unconditional model averages and standard errors of traits in the best predictive models (Δ AIC < 2) of species traits on urbanization intensity responses, based on subset of most predictive traits

Variable	**Effect Size**	**SE**
Intercept	-51.09	22.28
Clutch size	7.61	15.87
Fledglings per nest	18.09	21.16
Frugivory	4.67	18.14
Sedentarism	17.09	33.63

Table 6: Best predicting models of species traits on urbanization intensity response using subset of traits for which there was a known value for every species studied. These results should be considered secondary to those of the trait subset in Tables 4 and 5, as data availability was the deciding factor of this subset rather than predictive power.

Model	**K**	**AIC**	**Δ**	**w**
Granivory	3	716.48	0	0.27
Cavity nesting + granivory	4	717.60	1.12	0.15
Clutch size + granivory	4	717.65	1.18	0.15
Granivory + sedentarism	4	718.14	1.67	0.12
Sedentarism	3	718.36	1.88	0.10
Frugivory + Granivory	4	718.36	1.89	0.10
Clutch size	3	718.39	1.91	0.10

K: number of estimated parameters, *AIC*: Akaike's Information Criterion, *Δ*: AIC (best) – AIC (model), *w*: Akaike weight, the probability of being the best model given the observed data and evaluated models

Table 7: Unconditional model averages and standard errors of traits in the best predictive models (Δ AIC < 2) of species traits on urbanization intensity responses, based on subset of traits with data for all species

Variable	**Effect Size**	**SE**
Intercept	-57.83	22.36
Cavity nesting	6.01	20.17
Clutch size	4.92	11.63
Frugivory	2.057	11.67
Granivory	46.24	36.38
Sedentarism	9.24	24.98

Table 8: Results from general linear models of the effects of traits on forest-dependent bird species scales of effect to urbanization intensity in Pennsylvania, USA. No traits exhibited a phylogenetic relationship to urbanization intensity response ($\lambda = 0$).

Variable	λ ML	95% CI	β	Residual df	Adjusted R^2
Biparental Nestbuilding	0	NA - .31	-0.51	52	-0.02
Cavity Nesting	0	NA - .28	2.03	54	0.00
Clutch	0	NA - .52	0.81	56	0.01
Clutches per Year	0	NA - .32	0.35	50	-0.02
Duration in Nest	0	NA - .26	0.11	54	0.00
Fledglings per Nest	0	NA - .37	0.37	28	-0.03
Flock Size	0	NA - .31	0.21	32	0.08
Foraging Height	0	NA - .40	-0.26	38	0.03
Frugivory	0	NA - .25	3.09	56	0.05
Granivory	0	NA - .28	4.11	56	0.10
Lifespan	0	NA - .25	0.39	54	0.03
Mass	0	NA - .30	0.00	55	-0.01
Nesting Height	0	NA - .30	0.01	51	-0.02
Omnivory	0	NA - .31	4.59	56	0.09
Sedentarism	0	NA - .30	2.56	54	0.02
Song Frequency	0	NA - .57	0.01	47	-0.00
Song Length	0	NA - .66	-0.55	47	-0.00
Song Range	0	NA - .72	0.00	47	-0.02
Territory	0	NA - .45	-0.00	36	-0.02
Wingspan	0	NA - .29	0.06	54	0.01

Table 9: Best performing models of species traits on scale of effect using subset of top-performing univariate traits

Model	**K**	**AIC**	**Δ**	**w**
Frugivory	3	168.33	0	0.13
Frugivory + granivory	4	168.82	0.49	0.10
Wingspan	3	168.91	0.58	0.10
Clutch size + frugivory	4	168.99	0.66	0.09
Granivory	3	169.23	0.90	0.08
Flock size + frugivory	4	169.41	1.08	0.07
Omnivory	3	169.41	1.08	0.07
Granivory + wingspan	4	169.48	1.15	0.07
Cavity nesting + frugivory	4	169.50	1.17	0.07
Cavity nesting	3	169.88	1.55	0.06
Frugivory + wingspan	4	170.17	1.84	0.05
Flock size + wingspan	4	170.28	1.95	0.05
Omnivory + wingspan	4	170.30	1.97	0.05

K: number of estimated parameters, *AIC*: Akaike's Information Criterion, *Δ*: AIC (best) – AIC (model), *w*: Akaike weight, the probability of being the best model given the observed data and evaluated models

Table 10: Unconditional model averages and standard errors of traits in the best predictive models (Δ AIC < 2) of species traits on scale of effect, based on subset of most predictive traits

Variable	**Effect Size**	**SE**
Intercept	0.60	3.30
Cavity nesting	0.37	1.27
Clutch size	0.10	0.41
Flock size	0.08	0.27
Frugivory	2.17	2.71
Granivory	0.81	1.77
Omnivory	0.55	1.93
Wingspan	0.04	0.09

APPENDIX B: FIGURES

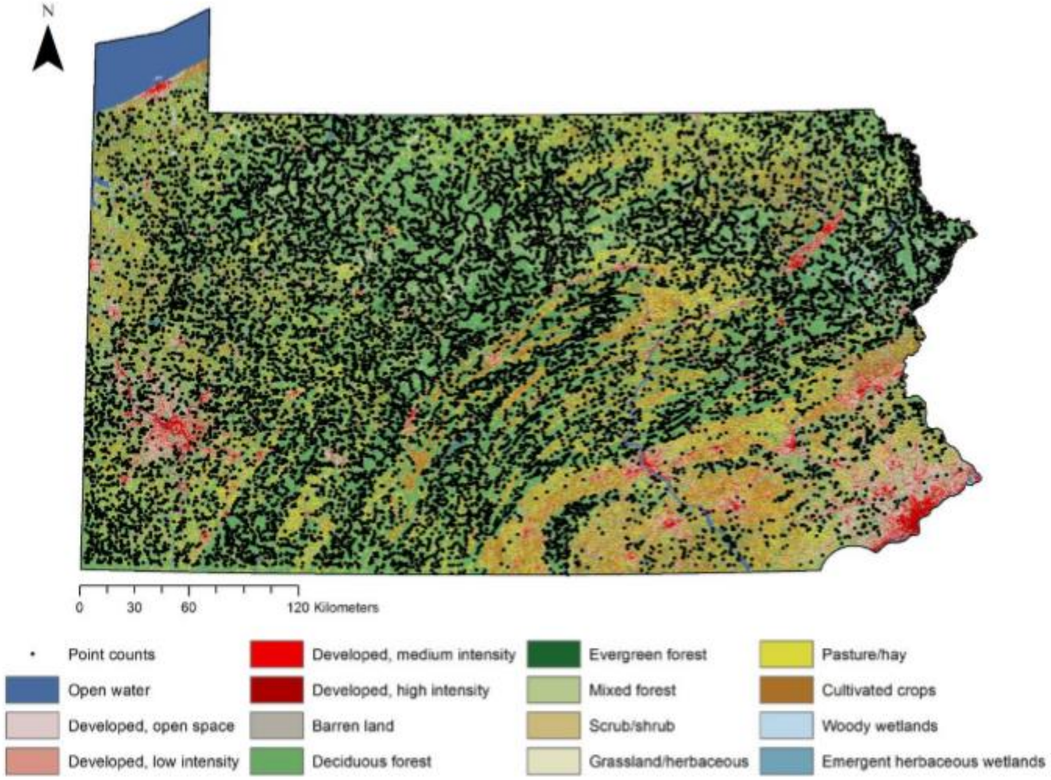

Figure 1: Land cover classes of Pennsylvania from 2006 National Land Cover Database and forested point count locations from the 2nd Pennsylvania Breeding Bird Atlas (n = 16563). Cartography from Shoffner (2016).

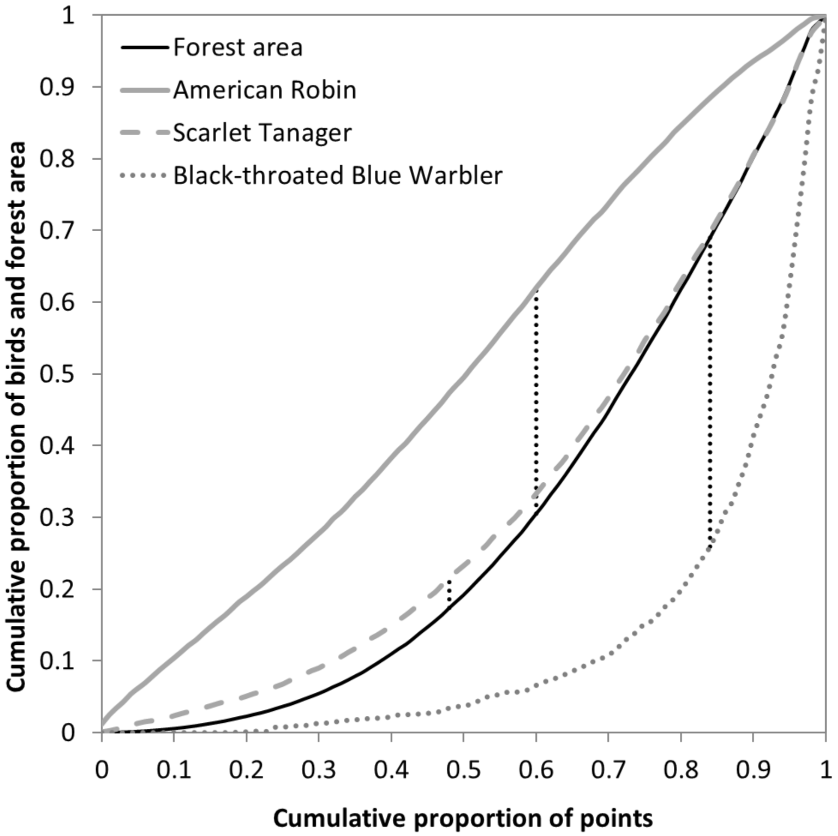

Figure 2: Example of classification of species into habitat association guilds based on cumulative distribution of bird counts and cumulative distribution of forest cover in landscapes surrounding count locations (N = 33,763 points). This example is for landscapes of 1-km radius. Dotted black lines represent the largest deviance between the species curve and the forest curve, as measured by *D*, the Kolmogorov-Smirnov test statistic. The Black-throated Blue Warbler (*Setophaga caerulescens*) was found disproportionately in heavily forested landscapes (*D* = 0.43, *p* < 0.001), and the Scarlet Tanager (*Piranga olivacea*) occurred in proportion to forest extent (*D* = 0.04, *p* = 0.851) therefore they are both classified as “forest-dependent” species. By contrast, the American Robin (*Turdus migratorius*) was found disproportionately in sparsely forested landscapes (*D* = -0.31, *p* < 0.001) and is therefore classified as an “edge/open country” species.

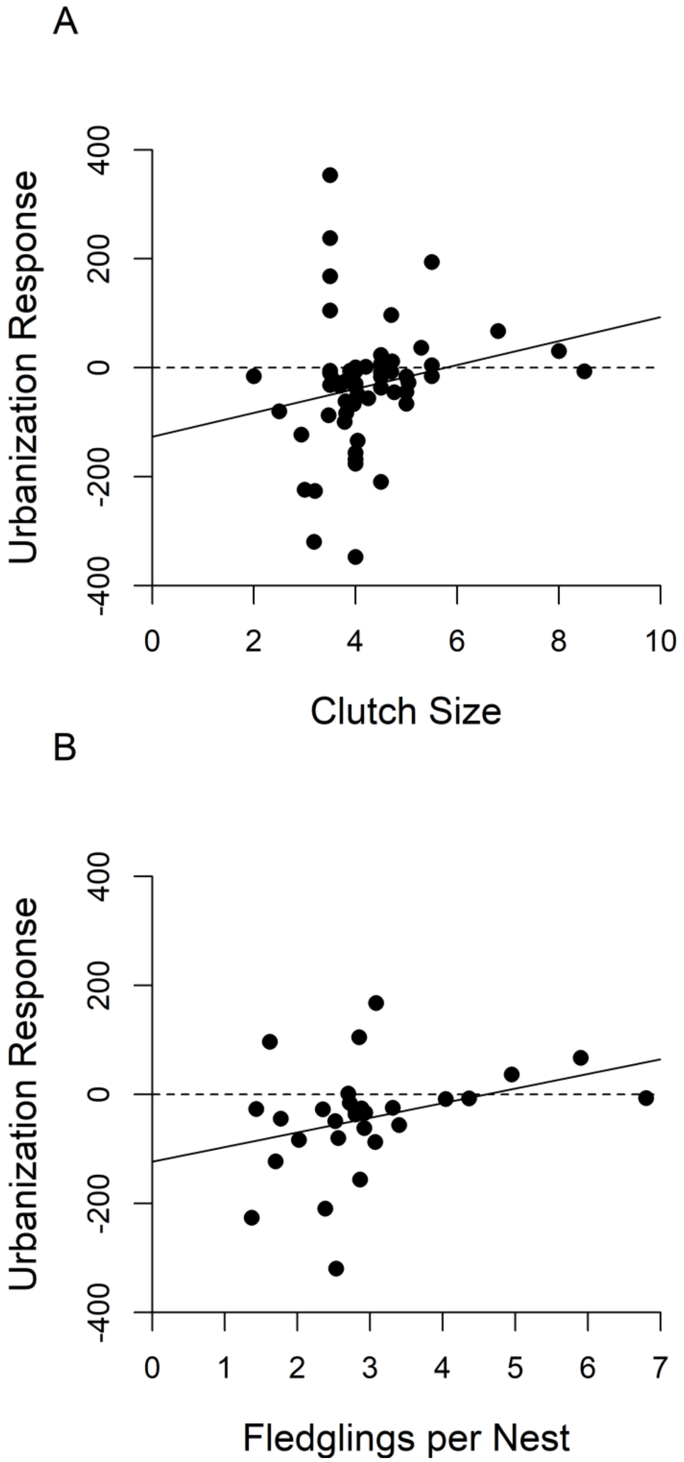

Figure 3: The effects of clutch size (A) and fledglings per nest (B) on forest-dependent bird species responses to urbanization intensity in Pennsylvania, USA. Clutch size had an effect size of 7.606 ± 15.872, and fledglings per nest had an effect size of 18.088 ± 21.164

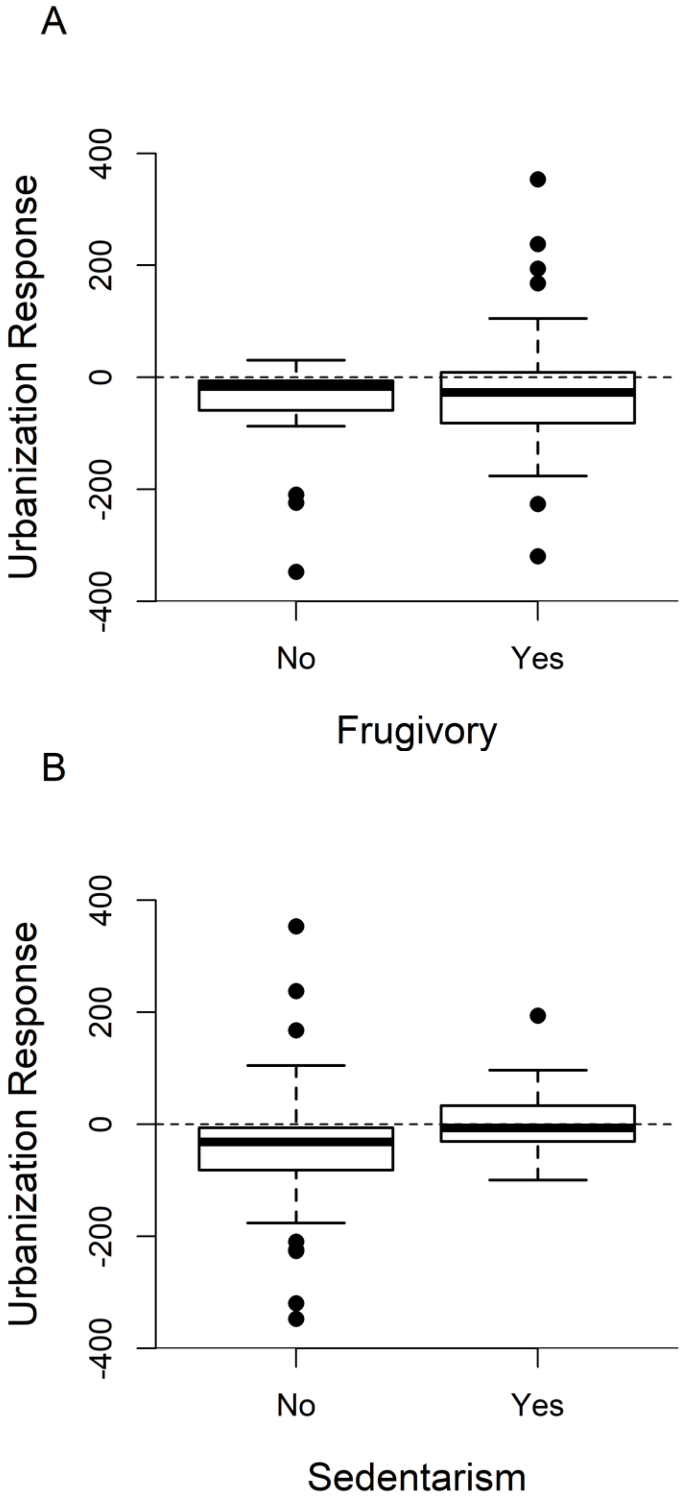

Figure 4: The effects of frugivory (A) and sedentarism (B) on forest-dependent bird species responses to urbanization intensity in Pennsylvania, USA. Frugivory had an effect size of 4.688 ± 18.144, and sedentarism had an effect size of 17.091 ± 33.632.

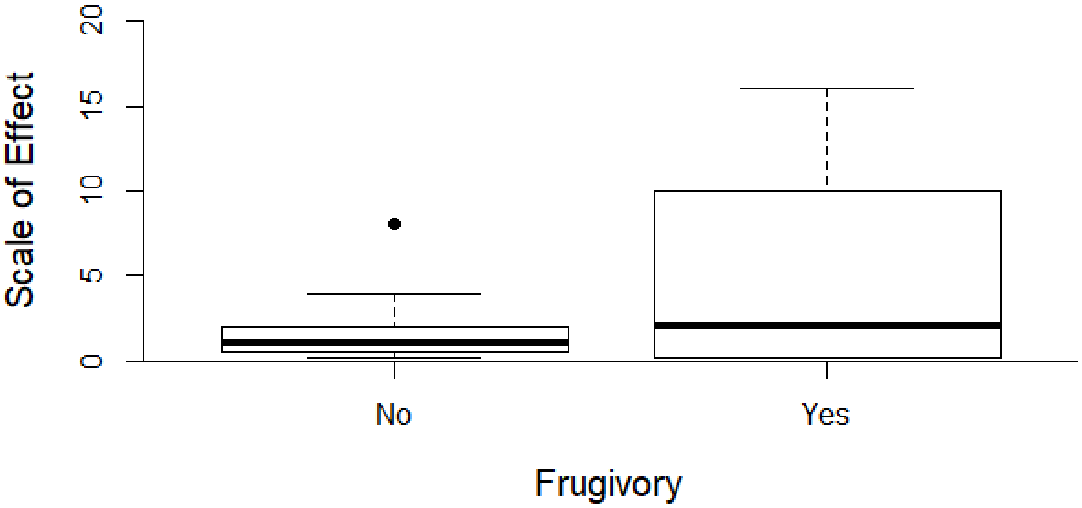

Figure 5: Best predictive model of traits on scale of effect (km) ($\beta = 4.112 \pm 1.493$, $p < .01$). Frugivory was also the best predicting trait on scale of effect based on multi-model inference and model averaging