

Interacting with hummingbirds at home: Associations with supplemental feeding, plant diversity, plant origin, and landscape setting

Timothy D. Meehan*, Kathy Dale, Geoffrey S. Lebaron, John Rowden, Nicole L. Michel, Chad B. Wilsey, Gary M. Langham

National Audubon Society, 225 Varick Street, New York, NY 10014, USA

ARTICLE INFO

Keywords:

Community science
Hummingbird
Native plant
Plant diversity
Urban wildlife

ABSTRACT

Several organizations run wildlife-gardening programs designed to mitigate the biodiversity loss and disconnect between humans and wildlife that commonly accompanies urbanization. The National Audubon Society runs the Plants for Birds and the Hummingbirds at Home programs that, like others, recommend homeowners to establish diverse assemblages of native plants with supplemental feeders. Here, we use plant and hummingbird data from the Hummingbirds at Home program to determine whether common wildlife-gardening recommendations correlate with intended outcomes. Our results showed that, after statistically controlling for several variables related to observer effort and geography, the relative occurrence and relative frequency of hummingbird sightings during patch surveys was positively related to the (1) presence of hummingbird feeders in a patch, (2) number of nectar-provisioning flowering-plant taxa in a patch, (3) degree to which nectar-provisioning flowering-plants in a patch were endemic to the conterminous USA, and (4) lack of impervious surface (a common proxy for urban development) in the surrounding landscape. These results support previous studies that showed how recommendations from wildlife-gardening programs associate with intended outcomes, but do so across an exceptionally broad, national extent that varies enormously in physical and biological geography.

1. Introduction

Urbanization is a defining characteristic of the Anthropocene (Biermann et al., 2016). For the first time in history, more than half of the human population lives in an urban setting (Grimm et al., 2008). Habitat changes associated with urbanization are contributing to dramatic changes in the distribution and abundance of biodiversity (McDonald, Kareiva, & Forman, 2008; McKinney, 2008). The disconnection of people from nature that accompanies urbanization is leading to an extinction of human experiences with nature (Miller, 2005; Soga & Gaston, 2016). Subsequently, disconnected individuals are expected to be less likely to conserve natural resources, leading to a further divergence between humans and nature (Cannon, 1999; Dunn, Gavin, Sanchez, & Solomon, 2006).

Given the magnitude and potential negative impacts of urbanization on biodiversity and human experience, there is increasing interest in making urban areas more wildlife-friendly. Residential yards comprise a sizable fraction of urban areas (Cannon, 1999; Goddard, Dougill, & Benton, 2010; Goddard, Ikin, & Lerman, 2017), accounting for over

30% of some urban landscapes (Belaire, Whelan, & Minor, 2014). Creating wildlife-friendly habitat in residential yards has the potential to temper biodiversity loss and increase interactions between humans and wildlife (Goddard et al., 2010, 2013). Several programs have been developed by non-governmental conservation organizations to encourage homeowners to participate in wildlife-friendly gardening (Goddard et al., 2017). For example, the Xerces Society for Invertebrate Conservation (XSIC, <https://xerces.org/guidelines/>), Royal Society for the Protection of Birds (RSPB, <http://www.rspb.org.uk/hfw/>), National Wildlife Federation (NWF, <http://www.nwf.org/backyard/>), and National Audubon Society (NAS, <https://www.audubon.org/plantsforbirds/>) all conduct programs that provide extensive resources to homeowners interested in gardening in ways that benefit invertebrate and vertebrate wildlife communities.

Wildlife-gardening programs have several recommendations in common. First, many programs recommend establishing diverse plant assemblages, under assumptions that diverse assemblages will have varied biophysical tolerances and phenologies, and thus provide diverse resources to wildlife throughout the year (e.g., Evans, Newson, &

* Corresponding author.

E-mail addresses: tmeehan@audubon.org (T.D. Meehan), kdale@audubon.org (K. Dale), glebaron@audubon.org (G.S. Lebaron), jrowden@audubon.org (J. Rowden), nmichel@audubon.org (N.L. Michel), cwilsey@audubon.org (C.B. Wilsey), glangham@audubon.org (G.M. Langham).

<https://doi.org/10.1016/j.landurbplan.2020.103774>

Received 21 August 2019; Received in revised form 5 February 2020; Accepted 9 February 2020

Available online 18 February 2020

0169-2046/ © 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Gaston, 2009; Hülsmann, Von Wehrden, Klein, & Leonhardt, 2015; Paker, Yom-Tov, Alon-Mozes, & Barnea, 2014; Salisbury et al., 2015). Second, many programs recommend establishment of native plant assemblages, under assumptions that native plants are adapted to local climatic conditions, and that native plants are preferred resources for herbivorous and nectarivorous invertebrates that comprise important links in local food webs (Burghardt, Tallamy, & Gregory Shriver, 2009; Narango, Tallamy, & Marra, 2017; Paker et al., 2014). Third, in addition to establishing plants, programs commonly encourage adding supplemental resources such as bird feeders, water features, and nesting substrate, under assumptions that these features will both support wildlife and provide a focal point for human-wildlife interactions (e.g., Daniels & Kirkpatrick, 2006; Evans et al., 2009; Fuller, Warren, Armsworth, Barbosa, & Gaston, 2008). While wildlife-gardening programs tend to be focused on the characteristics of individual habitat patches, there is growing recognition that the neighborhood-scale size and arrangement of patches is also an important determinant of urban habitat quality (Belaire et al., 2014; Evans et al., 2009; Hostetler & Holling, 2000), and some programs encourage homeowners to engage their neighbors in wildlife gardening to expand the spatial grain and extent of wildlife resources (e.g., <https://www.audubon.org/plantsforbirds/>).

Efforts by organizations to promote wildlife gardening frequently co-occur with community science efforts to monitor wildlife distribution and abundance (Goddard et al., 2010, 2017). For example, XSIC helps run Bumblebee Watch, RSPB conducts the Big Garden Bird Watch, and NAS runs the Hummingbirds at Home (HAH) program. These community science monitoring programs yield data with the potential to evaluate the effectiveness of wildlife-gardening recommendations (Goddard et al., 2010). The HAH program, in particular, was begun by NAS in 2013 (<https://www.audubon.org/content/hummingbirds-home/>). The program encourages hummingbird enthusiasts across the continental USA to (1) provide wildlife resources, such as diverse assemblages of native plants and supplemental nectar feeders, to attract hummingbirds to their yards and (2) monitor hummingbird visitation.

In this observational study, we use existing gradients in data from the HAH program to ask, specifically, whether the occurrence or frequency of hummingbird sightings in residential yards are related to (1) supplemental feeding, (2) the number of nectar-provisioning flowering-plant taxa, (3) the proportion of nectar-provisioning flowering-plant taxa that are endemic to the USA, or (4) the proportion of a neighborhood that is covered by concrete, asphalt, and other impervious surfaces. The study aimed to assess associations between common wildlife-gardening recommendations and hummingbird sightings at an exceptionally broad, national scale and, by doing so, improve our understanding of the importance and generality of wildlife-gardening recommendations for supporting wildlife and increasing human-wildlife interactions in urban landscapes.

2. Methods

2.1. Data collection

Participation in HAH is facilitated by software that runs on smart phones, tablets, laptops, and desktop computers. The HAH software offers three different protocols for recording observations of plants and hummingbirds. The single-sighting protocol is a simple protocol used to report incidental sightings of hummingbirds. For the nectar-watch protocol, an observer focuses on a single nectar source, recording all visitors to that single source over a timed period. The patch-survey protocol is the source of the hummingbird and plant data used in this analysis, and is structured as follows.

First, a user defines a patch or area to survey. Given that the HAH program is partly oriented toward residential homeowners, and based on anecdotal observations of known participants, it appears that patches mostly comprised residential yards and gardens. We have no way

to know the exact proportions of residential yards, versus home gardens, versus public park gardens. Defining a patch involves giving it a name, assigning it spatial coordinates (usually done using the location services built into a mobile device), and estimating the area of the patch to be monitored. The user can then identify the plant and hummingbird species monitored during the survey, and note the presence of a hummingbird feeder. All nectar-provisioning flowering-plant taxa (hereafter, called plants) are recorded, regardless of hummingbird use. Plants that are not nectar sources are not recorded (e.g., wind-pollinated tree species). Plant identifications are aided by location-specific lists and images provided by the software. Plants are usually identified to species, but sometimes are identified to genus. We use the term taxon in this study to describe both genus and species-level groupings. When a generic and species identification are both reported during the same survey (e.g., *Salvia* spp. and *Salvia splendens*), we considered them to be different plant taxa. Note that we were not able to evaluate the accuracy of plant species identifications by community scientists participating in the program, but expect that estimates of plant morphospecies richness derived from these data will be positively correlated with taxonomic species richness (Oliver & Beattie, 1996; Derraik, Early, Closs, & Dickinson, 2010).

Once a patch survey is set up, the user starts a survey timer and records hummingbird visits to each plant taxon. On many occasions, the user opts to provide a count of hummingbird sightings per plant taxon. Users are instructed to record each hummingbird sighting as a new observation, as it is usually not possible to identify individual birds. Given this situation, multiple observations of hummingbirds do not necessarily indicate multiple individuals or reflect local population size. We stress that, when we discuss relative occurrence and relative frequency in this manuscript, readers must interpret these metrics as the occurrence and frequency of hummingbird sightings. Estimating true hummingbird occupancy or abundance is not possible using the HAH patch survey protocol. Indeed, quantifying true occupancy and abundance requires highly-structured sampling protocols (Kery & Schaub, 2011), which would be an enormous undertaking at a national scale.

Upon survey completion, observations are submitted through the HAH application to a centralized relational database. The hummingbird and plant data used in this analysis were extracted from this database, from surveys conducted in the conterminous USA between 1 January 2013 and 31 December 2018. Given that data were entered into the database using software that controls input values, patch survey data were relatively clean, with few misspellings, missing values, or extreme values. In addition to hummingbird and plant data, the software forced all records to include location and effort information used during this study. Unfortunately, it was not possible to identify the observer associated with a given patch survey, so this information could not be used during statistical analysis. The data were a combination of isolated patch surveys conducted only one time at a given location (40%), and a series of patch surveys collected over multiple days or years at a given location (60%). A small fraction (9%) of observations were from the same location during the same day. We dealt with the lack of observational independence due to repeated measures at the same location during statistical analysis.

2.2. Statistical analysis

The goal of this analysis was to explore factors associated with the relative occurrence and relative frequency of hummingbird sightings during HAH patch surveys. These two dependent variables undoubtedly are driven by many methodological, geographical, and biological factors. In this analysis, we explored 12 possible factors using a Bayesian generalized linear mixed model (GLMM), analyzed using the R-INLA package (Rue et al., 2017) for R statistical computing software (Core, 2016). A GLMM was employed because it accommodates response variables that are not normally distributed and allows fixed effects, random smooth effects, and random spatial effects (Blangiardo &

Cameletti, 2015). The structure of the GLMM used in this study can be summarized with the following formula, where variables are grouped by common attributes:

$$f(\text{Hummingbirds}) \sim (\text{Year} + \text{Day}) + (\text{Latitude} + \text{Longitude} + \text{Distance} + \text{Site}) + (\text{Duration} + \text{Area}) + (\text{Feeder presence} + \text{Plant richness} + \text{Proportion endemic} + \text{Impervious surface}).$$

The $f(\text{Hummingbird})$ term on the left side of the GLMM equation represented either the expected relative occurrence of hummingbird sightings on the logit scale (as for logistic regression) or the expected relative count of hummingbird sightings on the natural-log scale (as for Poisson regression). Given the difficulty of identifying hummingbirds in flight to species, our analysis of occurrence and frequency did not incorporate information on hummingbird species. All hummingbird species, sexes, and ages were pooled for this analysis.

The first set of terms on the right side of the GLMM equation accounted for variation in hummingbird relative occurrence and relative frequency that might be attributable to changing conditions for plants and hummingbirds across years and across days of the year. The Year term was a zero-centered, normally-distributed, random intercept per observation year, and Day was a smooth random effect of observation day of the year, modeled as a second-order random walk with normally-distributed residuals (Wang, Ryan, & Faraway, 2018). Both Year and Day terms were assigned penalized complexity priors for dispersion with a prior SD = 1 and an exceedance probability of 0.01 (Simpson, Rue, Riebler, Martins, & Sørbye, 2017). Flexible random effects were selected to model Year and Day effects instead of fixed effects because we wished to account for these variables while avoiding numerous additional fixed-effect parameters that were not directly related to our research questions.

The second set of terms on the right side of the GLMM equation accounted for spatial variation in hummingbird relative occurrence and relative frequency that might be attributable to variable conditions for plants and hummingbirds across the continent, regions, and locales. Here, Latitude and Longitude were fixed effects to accommodate continental gradients in hummingbird sightings due to biogeographic factors. Distance was a geostatistical random effect to model spatial structure in the dependent variables across neighboring survey sites. Site was a random intercept per patch location that accounted for unexplained variation at the local level, and allowed for repeated observations from a single site. The fixed effects were assigned vague normal priors, with a mean = 0 and an SD = 1000, so that prior distributions had minimal impact on posterior distributions and parameter inference. The geostatistical spatial effect had a Matérn structure (Blangiardo & Cameletti, 2015) and was given a penalized complexity prior with an SD = 1 and an exceedance probability of 0.01 (Krainski et al., 2018). The Site effect was a zero-centered, normally-distributed, random intercept, as described above for Year.

The third set of terms on the right side of the GLMM equation accounted for the effects of variable observer effort on measures of hummingbird relative occurrence and relative frequency. Duration (min) was a smooth random effect of survey duration and Area (m²) was a smooth random effect of survey area. The smooth Duration and Area effects were modeled with a second-order random walk, specified as described above for Day. Flexible random effects were selected to model effort-related variation instead of fixed effects because we wished to account for these variables while avoiding numerous additional fixed-effect parameters that were not directly related to our research questions. Note that survey area reported by observers could have reflected all or a portion of a discrete landscape patch. The patch survey data did not include sufficient information to differentiate between these two different interpretations of this variable; incidentally, both survey area and patch size are expected to have a positive effect on occurrence and relative frequency (Cotton, 2007).

Finally, the fourth set of terms on the right side of the GLMM equation were the focal fixed effects, added to evaluate associations between hummingbird relative occurrence and relative frequency and the four habitat characteristics commonly promoted by wildlife-gardening programs. Feeder presence was a dichotomous fixed effect of the presence or absence of a hummingbird feeder. Plant richness was a fixed effect for the number of nectar-provisioning flowering-plant taxa observed. Proportion endemic was a fixed effect of the continuous proportion that represented the degree to which nectar-provisioning flowering-plant taxa were endemic to the conterminous USA. Impervious surface was a fixed effect of a continuous proportion that represented the fraction of area within 1 km of a patch survey that was covered by impervious surface (e.g., buildings, roads, and parking lots; Arnold & Gibbons, 1996). These four fixed effects were parameterized as described above for Latitude. We determined if a plant taxon was endemic to the conterminous USA using the Plants Database (<https://plants.sc.egov.usda.gov/>), maintained by the Natural Resources Conservation Service of the US Department of Agriculture (USDA; <https://plants.sc.egov.usda.gov/java/>). The proportion of impervious surface within 1 km of a surveyed patch was computed with a Geographic Information System (GIS) using the Urban Imperviousness product from the 2016 National Land Cover Database (NLCD), provided by the Multi-Resolution Land Characteristics Consortium (<https://www.mrlc.gov/>). These habitat variables were modeled as fixed effects because they were considered focal variables for which we wanted to infer about the general direction and size of effects. Initial analyses explored the possibility of interacting effects of these four variables. We found negligible, non-crossover interactions that did not confound main effects and contributed little to model fit, and thus did not consider them further.

We computed Spearman correlation coefficients between pairs of independent variables and found that coefficients fell between -0.16 and 0.42, suggesting that multicollinearity was not a serious problem during model analysis. All variables were centered on the mean and scaled by standard deviations before analysis to aid computation and interpretation of parameter estimates, and to attain standardized beta coefficients that allowed us to compare the relative magnitude of continuous fixed effects (Schielzeth, 2010). The magnitudes of effects were also judged using predictions from the models, illustrated in the figures. The probabilities associated with parameter values were assessed using marginal posterior distributions from the GLMM. We derived our conclusions from analysis results of the full model, as model variables were not strongly correlated and because variable selection methods for complex hierarchical models are still an active and disputed area of research (Hooten & Hobbs, 2015).

3. Results

In total, there were 4081 patch surveys reported from 744 unique locations across the conterminous USA (Fig. 1) from 2013 through 2018 (Fig. S1A). Hummingbirds were observed during 78% of these patch surveys and were not observed during 22% of these surveys. There was a subset of 2767 patch surveys where hummingbird frequency was also recorded. During these observations, median hummingbird frequency was 3 individuals (minimum = 1, maximum = 116). The total number of nectar-provisioning flowering-plant taxa recorded was 350. Of these taxa, 64% were endemic to the conterminous USA, 29% were introduced, and 7% were generic taxa where geographic origins could not be determined. Table S1 lists the 46 plant taxa that were observed during 100 or more patch surveys, along with raw proportions of patch surveys where hummingbirds visited each plant taxon. We consider these proportions as very rough estimates of hummingbird use because they could be confounded by several contextual variables shown to affect hummingbird visitation, as described in the modeling results, below.

Across the 4081 patch surveys, median observation day of the year was 211 (approximately 30 July; Fig. S1B), observation duration was

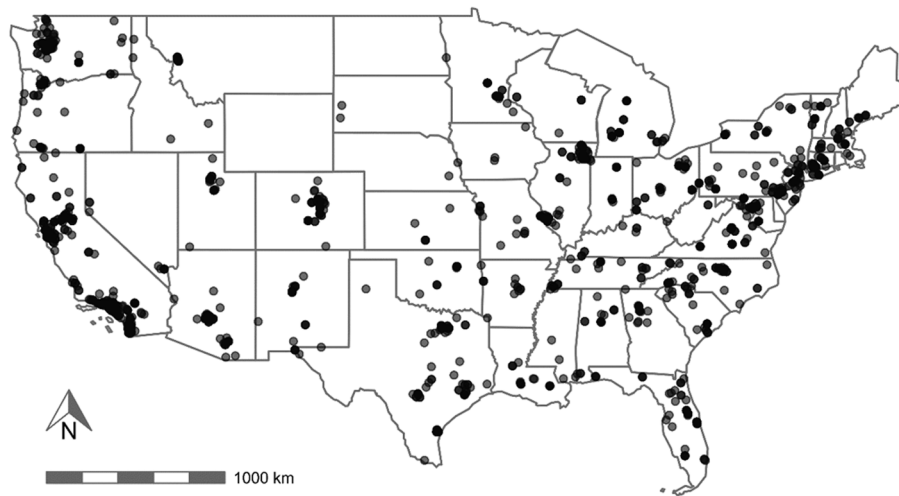


Fig. 1. Map of 4081 patch surveys conducted at 744 locations between 2013 and 2018 by volunteers with the National Audubon Society Hummingbirds at Home program. Location points are partially transparent to help illustrate where they are most concentrated.

20 min (Fig. S1C), and observation area was 93 m² (Fig. S1D). A hummingbird feeder was present during 80% and not present during 20% of the patch surveys (Fig. S1E). Median plant richness was 2 taxa (Fig. S1F), median proportion of endemic plant taxa was 0.33 (Fig. S1G), and median proportion of the neighborhood with impervious surface was 0.29 (Fig. S1H).

Regarding GLMM results, the relative occurrence of hummingbird sightings varied across years (Table 1, Table S2, Fig. S2A), peaked during the summer (Fig. S2B), and increased with the duration of an observation (Table 1, Table S2, Fig. S2C). Relative occurrence varied considerably by site (Table 1, Table S2), decreased with latitude (Table 1, Table S2), did not clearly relate to longitude (Table 1, Table S2), and exhibited moderate spatial structure with a range of 0.34° latitude or longitude, or approximately 40 km (Table 1, Table S2).

After statistically accounting for effort and geography, relative occurrence of hummingbird sightings increased with the presence of a hummingbird feeder (Table 1, Table S2, Fig. 2A) and increased with the number of plant taxa in a patch (Table 1, Table S2, Fig. 2B). The magnitude of the feeder effect was stronger than that of plant richness, but both appeared biologically meaningful (Table 1, Fig. 2). The

Table 1

Characteristics (posterior medians with lower and upper 95% credible limits) of the relative occurrence and relative frequency models, including standardized coefficients of fixed effects, the standardized distance associated with the spatial range, and the standard deviations associated with random effects. Effect definitions are given in the text.

| Model characteristic | Relative occurrence model | | | Relative frequency model | | |
|----------------------------|---------------------------|-------|-------|--------------------------|-------|-------|
| | Median | LCL | UCL | Median | LCL | UCL |
| Feeder presence | 1.77 | 1.41 | 2.15 | 0.41 | 0.31 | 0.51 |
| Plant richness | 0.24 | 0.07 | 0.40 | 0.09 | 0.07 | 0.12 |
| Proportion endemic | 0.12 | -0.03 | 0.27 | 0.09 | 0.05 | 0.13 |
| Impervious surface | -0.07 | -0.35 | 0.19 | -0.20 | -0.30 | -0.11 |
| Latitude | -0.25 | -0.48 | -0.03 | -0.12 | -0.23 | 0.00 |
| Longitude | -0.26 | -0.53 | 0.01 | -0.35 | -0.50 | -0.20 |
| Spatial range for Distance | 0.64 | 0.09 | 6.27 | 1.45 | 0.40 | 5.48 |
| SD for Distance | 0.14 | 0.01 | 0.70 | 0.46 | 0.27 | 0.73 |
| SD for Site | 2.43 | 2.07 | 2.87 | 0.70 | 0.63 | 0.77 |
| SD for Year | 0.31 | 0.14 | 0.67 | 0.10 | 0.05 | 0.29 |
| SD for Day | 0.65 | 0.31 | 1.24 | 0.51 | 0.33 | 0.82 |
| SD for Duration | 0.20 | 0.04 | 0.70 | 0.39 | 0.21 | 0.74 |
| SD for Area | 0.13 | 0.02 | 0.61 | 0.07 | 0.01 | 0.38 |

relative occurrence of sightings was not clearly related to the proportion of plants that were endemic to the conterminous USA or the proportion of a neighborhood covered by impervious surface (Table 1, Table S2).

The relative frequency of hummingbird sightings also varied across years (Table 1, Table S2, Fig. S1E), peaked during the summer (Fig. S1F), and increased with the duration of an observation (Table 1, Table S2, Fig. S1G). Relative frequency varied considerably by site (Table 1, Table S2) but did not vary strongly by latitude (Table 1, Table S2). There was a longitudinal gradient (Table 1, Table S2) and strong spatial structure in relative frequency, with a range of approximate 1.45° latitude or longitude, or approximately 160 km (Table 1, Table S2).

After statistically accounting for effort and geography, relative frequency of hummingbird sightings increased with the presence of a hummingbird feeder (Table 1, Table S2, Fig. 3A), increased with the number of plant taxa in a patch (Table 1, Table S2, Fig. 3B), increased with the proportion of plants that were endemic to the conterminous USA (Table 1, Table S2, Fig. 3C), and decreased with the proportion of a neighborhood covered by impervious surface (Table 1, Table S2, Fig. 3D). Of those four effects, the effect of feeders was strongest, the effect of impervious surface was intermediate, and the effects of plant richness and endemism were weakest (Table 1, Table S2, Fig. 3).

4. Discussion

Across the conterminous USA, the likelihood of residential hummingbird sightings depends on many factors. After statistically controlling for several factors related to effort and geography, we found that the relative occurrence of hummingbird sightings increased with the presence of hummingbird feeders and the number of nectar-provisioning flowering-plant taxa in a patch. Given hummingbird occurrence, the relative frequency of hummingbird sightings increased with the presence of hummingbird feeders, the number of nectar-provisioning flowering-plant taxa in a patch, the proportion of nectar-provisioning flowering-plant taxa that were endemic to the conterminous USA, and the lack of impervious surface within 1 km of a patch.

The garden characteristics associated with hummingbird relative occurrence and frequency mirrored common recommendations of wildlife-gardening programs: to establish large patches of diverse, endemic plants, and encourage neighboring homeowners to do the same. Results from this study provide correlative evidence that these recommendations will indeed bring intended benefits, such as increased prevalence of wildlife and increased human-wildlife interactions. These recommendations stem from considerable prior research on urban

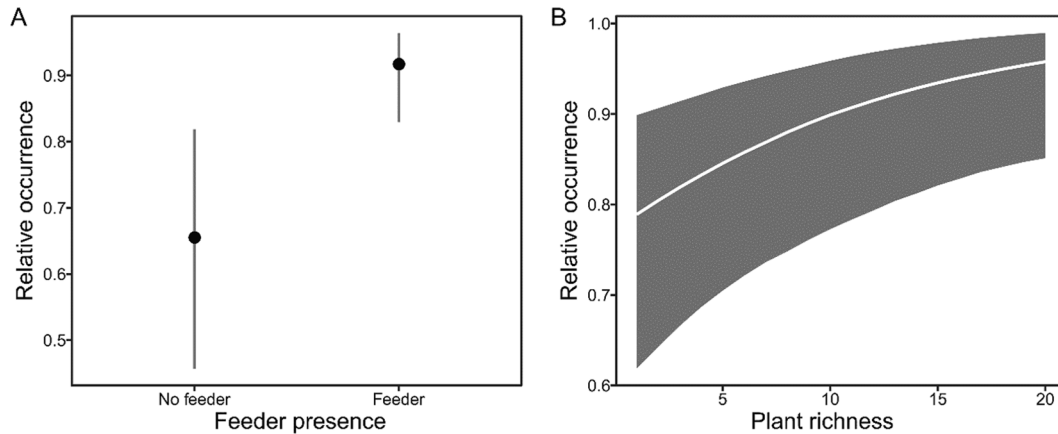


Fig. 2. Select predictors of hummingbird relative occurrence. Plots showing the effects, with 95% credible intervals, of (A) hummingbird feeders and (B) the number of nectar-provisioning flowering-plant taxa in a patch on the expected probability of seeing a hummingbird during an otherwise average patch survey.

biodiversity (Burghardt et al., 2009; Daniels & Kirkpatrick, 2006; Fuller et al., 2008; Lerman & Warren, 2011), much of which has occurred at similar spatial grains (i.e., yards) but much smaller spatial extents (i.e., cities). Our results add to existing evidence, but do so for an exceptionally large spatial extent (i.e., national). Adding to existing evidence is not trivial given that, in some cases, generalized wildlife-gardening recommendations have proven ineffective (Gaston, Smith, Thompson, & Warren, 2005). Contributing evidence across a national extent has value because many wildlife-gardening programs are

administered at national scales (Goddard et al., 2010), and because it is not given that simple recommendations can be effective across large extents that encompass numerous, diverse biomes (Paker et al., 2014).

Conclusions from this study are based on the relative occurrence and relative frequency of hummingbird sightings. It is possible that the relative occurrence of sightings is proportional to the true occupancy of hummingbirds near a survey patch. However true occupancy can only be estimated after estimating detection probability, which was not possible using data from the HAH patch survey protocol. Similarly, it is

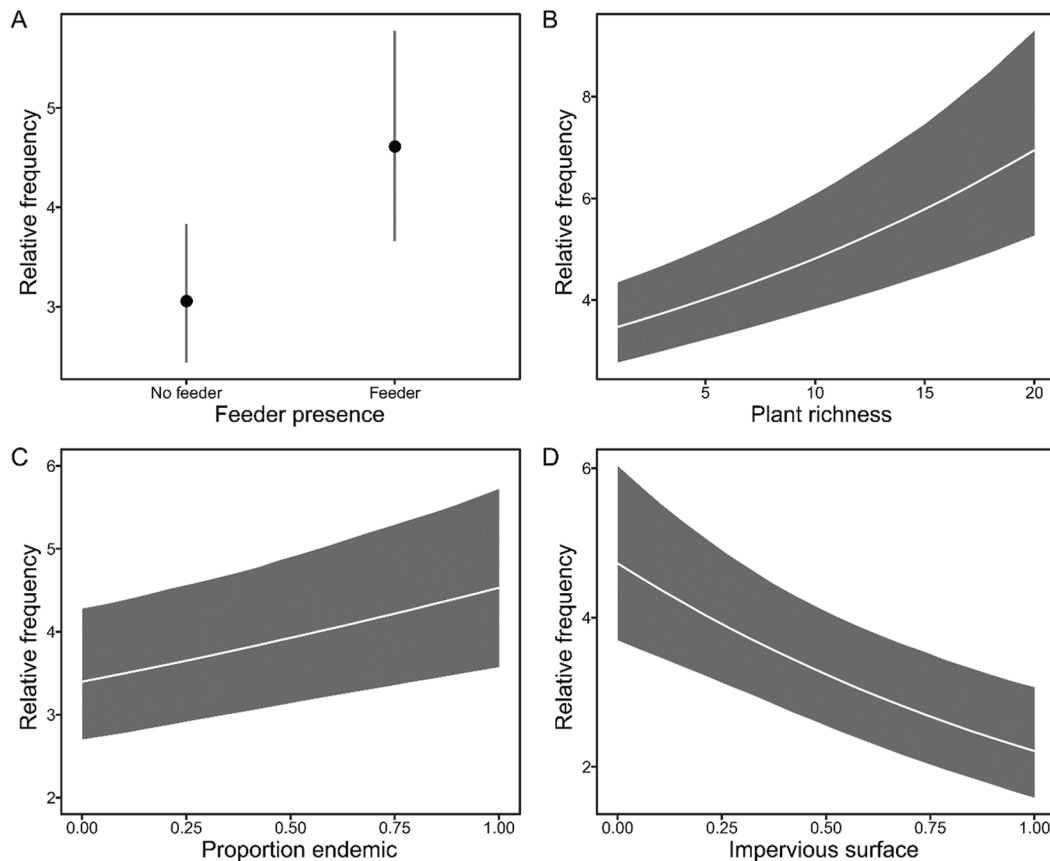


Fig. 3. Select predictors of hummingbird relative frequency. Plots showing the effects, with 95% credible intervals, of (A) hummingbird feeders, (B) the number of nectar-provisioning flowering-plant taxa in a patch, (C) the proportion of nectar-provisioning flowering-plant taxa that are endemic to the conterminous USA, and (D) the proportion of the neighborhood (within 1 km of a patch) that is covered in impervious surfaces such as concrete or asphalt, on the expected number of hummingbirds observed during an otherwise average patch survey.

possible that relative frequency of sightings is somewhat correlated with local hummingbird abundance. Unfortunately, the strength of that correlation is not known. Since this study did not measure detection probabilities, estimates of true abundance are not possible. However, we note that several other studies have established links between providing supplemental resources and increased wildlife productivity, survivorship, occurrence, and abundance (Cox & Gaston, 2018; Greig, Wood, & Bonter, 2017). Supplemental resources in this case could comprise sugar water and nectar provided by feeders and diverse assemblages of nectar-provisioning flowering plants, but also could include herbivorous and nectarivorous arthropods that are critical components of hummingbird diets (Remsen, Stiles, & Scott, 1986) and could occur at higher biomasses in diverse plant communities dominated by native plants (Zuefle, Brown, & Tallamy, 2008; Bezemer, Harvey, & Cronin, 2014).

Other limitations on inference from this study, besides those concerning detection probabilities, relate to the data originating from a large community science program. While community science datasets allow novel scientific investigations, often at unprecedented spatial and temporal scales, they also may include heterogeneity and bias related to variable observer characteristics and effort (Dickinson, Zuckerman, & Bonter, 2010). Specific to this study, we were not able to evaluate the accuracy of plant species identification, although we expect that the morphospecies richness estimates by volunteers were proportional to taxonomic richness and were useful for understanding differences in habitat characteristics (e.g., Oliver & Beattie, 1996; Derraik et al., 2010). Second, it was not clear to what extent observers recorded true patch area versus the area of a patch observed. While both characteristics are expected to positively correlate with hummingbird occurrence and relative frequency (Cotton, 2007), interpretation of this parameter remains somewhat ambiguous. Third, hummingbird surveys by community scientists varied considerably in terms of the area surveyed and the amount of time spent surveying. We were able to account for much of this heterogeneity by including effort variables in the statistical model, a common approach when analyzing community science data (Dickinson et al., 2010). Finally, this study used hummingbird observations by community scientists across existing gradients in garden characteristics as a means to evaluate wildlife-gardening recommendations. Observations were opportunistic and garden treatments were not randomly assigned in advance, as might be done in smaller-scaled, controlled experiments. Thus inference is based on correlation, which does not necessarily indicate causation (Altman & Krzywinski, 2015).

While links between garden characteristics and true hummingbird occupancy and abundance are tenuous, there is little doubt about the link between garden characteristics and human-wildlife interactions demonstrated in this study. Observers in gardens that supplied nectar feeders, had diverse assemblages of endemic plants, and resided in greener neighborhoods, were more likely to interact with hummingbirds. These observers were a self-selected group, presumably with an active interest in wildlife, who volunteered to participate in a wildlife monitoring program. We expect that the higher rate of wildlife interactions enjoyed by participants in hummingbird-favorable environments could spill over to neighbors, who might not otherwise seek wildlife interactions. The potential to increase human-wildlife interactions is a fundamental motivation for wildlife-gardening programs. Increased human-wildlife interactions have been shown to have positive effects on residents' perceptions of relaxation and happiness (Belaire, Westphal, Whelan, & Minor, 2015; Cox & Gaston, 2016; Curtin & Fox, 2014; Jones, 2011; Soulsbury & White, 2016), with logical implications for physical health (Schneider et al., 2005; Sirois & Burg, 2003; Veenhoven, 2008). Further, it is often suggested that people with connections to wildlife are more likely to value, provide for, and vote for wildlife conservation, creating a positive feedback loop that accelerates wildlife conservation activities more broadly (Cox & Gaston, 2018; Dunn et al., 2006; Shaw, Miller, & Wescott, 2013).

CRediT authorship contribution statement

Timothy D. Meehan: Methodology, Formal analysis, Visualization, Writing - original draft. **Kathy Dale:** Investigation, Data curation, Writing - review & editing, Project administration. **Geoffrey S. Lebaron:** Investigation, Data curation, Writing - review & editing. **John Rowden:** Writing - review & editing, Project administration. **Nicole L. Michel:** Formal analysis, Writing - review & editing, Supervision. **Chad B. Wilsey:** Writing - review & editing, Project administration. **Gary M. Langham:** Project administration, Funding acquisition.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2020.103774>.

References

- Altman, N., & Krzywinski, M. (2015). Association, correlation and causation. *Nature Methods*, 12, 899–900.
- Arnold, C. L., Jr, & Gibbons, C. J. (1996). Impervious surface coverage: The emergence of a key environmental indicator. *Journal of the American Planning Association*, 62(2), 243–258.
- Belaire, J. A., Westphal, L. M., Whelan, C. J., & Minor, E. S. (2015). Urban residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices. *Condor*, 117(2), 192–202.
- Belaire, J. A., Whelan, C. J., & Minor, E. S. (2014). Having our yards and sharing them too: The collective effects of yards on native bird species in an urban landscape. *Ecological Applications*, 24(8), 2132–2143.
- Bezemer, T. M., Harvey, J. A., & Cronin, J. T. (2014). Response of native insect communities to invasive plants. *Annual Review of Entomology*, 59, 119–141.
- Biermann, F., Bai, X., Bondre, N., Broadgate, W., Arthur Chen, C.-T., Dube, O. P., ... Seto, K. C. (2016). Down to Earth: Contextualizing the Anthropocene. *Global Environmental Change*, 39, 341–350.
- Blangiardo, M., & Cameletti, M. (2015). *Spatial and spatio-temporal Bayesian models with R-INLA*. John Wiley & Sons.
- Burghardt, K. T., Tallamy, D. W., & Gregory Shriver, W. (2009). Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology*, 23(1), 219–224.
- Cannon, A. (1999). The significance of private gardens for bird conservation. *Bird Conservation International*, 9(4), 287–297.
- Cotton, P. A. (2007). Seasonal resource tracking by Amazonian hummingbirds. *Ibis*, 149(1), 135–142.
- Cox, D. T., & Gaston, K. J. (2016). Urban bird feeding: Connecting people with nature. *PLoS One*, 11(7), e0158717.
- Cox, D. T., & Gaston, K. J. (2018). Human–nature interactions and the consequences and drivers of provisioning wildlife. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1745), 20170092.
- Curtin, S., & Fox, D. (2014). Human dimensions of wildlife gardening: Its development, controversies and psychological benefits. *Horticulture: Plants for People and Places* (pp. 1025–1046). Springer.
- Daniels, G. D., & Kirkpatrick, J. B. (2006). Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation*, 133(3), 326–335.
- Derraik, J. G., Early, J. W., Closs, G. P., & Dickinson, K. J. (2010). Morphospecies and taxonomic species comparison for Hymenoptera. *Journal of Insect Science*, 10(108), 1–6.
- Dickinson, J. L., Zuckerman, B., & Bonter, D. N. (2010). Citizen science as an ecological research tool: Challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics*, 41, 149–172.
- Dunn, R. R., Gavin, M. C., Sanchez, M. C., & Solomon, J. N. (2006). The pigeon paradox: Dependence of global conservation on urban nature. *Conservation Biology*, 20(6), 1814–1816.
- Evans, K. L., Newson, S. E., & Gaston, K. J. (2009). Habitat influences on urban avian assemblages. *Ibis*, 151(1), 19–39.
- Fuller, R. A., Warren, P. H., Armsworth, P. R., Barbosa, O., & Gaston, K. J. (2008). Garden bird feeding predicts the structure of urban avian assemblages. *Diversity and Distributions*, 14(1), 131–137.
- Gaston, K. J., Smith, R. M., Thompson, K., & Warren, P. H. (2005). Urban domestic gardens (II): Experimental tests of methods for increasing biodiversity. *Biodiversity and Conservation*, 14(2), 395–413.
- Goddard, M. A., Dougill, A. J., & Benton, T. G. (2010). Scaling up from gardens: Biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, 25(2), 90–98.
- Goddard, M. A., Dougill, A. J., & Benton, T. G. (2013). Why garden for wildlife? Social and ecological drivers, motivations and barriers for biodiversity management in residential landscapes. *Ecological Economics*, 86, 258–273.
- Goddard, M. A., Ikin, K., & Lerman, S. B. (2017). Ecological and social factors determining the diversity of birds in residential yards and gardens. *Ecology and Conservation of Birds in Urban Environments* (pp. 371–397). Springer.

- Greig, E. I., Wood, E. M., & Bonter, D. N. (2017). Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. *Proceedings of the Royal Society B: Biological Sciences*, 284(1852), 20170256.
- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, 319, 756–760.
- Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, 85(1), 3–28.
- Hostetler, M., & Holling, C. S. (2000). Detecting the scales at which birds respond to structure in urban landscapes. *Urban Ecosystems*, 4(1), 25–54.
- Hülsmann, M., Von Wehrden, H., Klein, A.-M., & Leonhardt, S. D. (2015). Plant diversity and composition compensate for negative effects of urbanization on foraging bumble bees. *Apidologie*, 46(6), 760–770.
- Jones, D. (2011). *An appetite for connection: Why we need to understand the effect and value of feeding wild birds*. Taylor & Francis.
- Kery, M., & Schaub, M. (2011). *Bayesian population analysis using Winbugs: A hierarchical perspective*. Academic Press.
- Krainski, E. T., Gómez-Rubio, V., Bakka, H., Lenzi, A., Castro-Camilo, D., Simpson, D., ... Rue, H. (2018). *Advanced spatial modeling with stochastic partial differential equations using R and INLA*. CRC Press.
- Lerman, S. B., & Warren, P. S. (2011). The conservation value of residential yards: Linking birds and people. *Ecological Applications*, 21(4), 1327–1339.
- McDonald, R. I., Kareiva, P., & Forman, R. T. (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141(6), 1695–1703.
- McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11(2), 161–176.
- Miller, J. R. (2005). Biodiversity conservation and the extinction of experience. *Trends in Ecology and Evolution*, 20(8), 430–434.
- Narango, D. L., Tallamy, D. W., & Marra, P. P. (2017). Native plants improve breeding and foraging habitat for an insectivorous bird. *Biological Conservation*, 213, 42–50.
- Oliver, L., & Beattie, A. J. (1996). Invertebrate morphospecies as surrogates for species: A case study. *Conservation Biology*, 10(1), 99–109.
- Paker, Y., Yom-Tov, Y., Alon-Mozes, T., & Barnea, A. (2014). The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. *Landscape and Urban Planning*, 122, 186–195.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Retrieved from <http://www.R-project.org>.
- Remsen, J. V., Stiles, F. G., & Scott, P. E. (1986). Frequency of arthropods in stomachs of tropical hummingbirds. *The Auk*, 103(2), 436–441.
- Rue, H., Riebler, A., Sørbye, S. H., Illian, J. B., Simpson, D. P., & Lindgren, F. K. (2017). Bayesian computing with INLA: A review. *Annual Review of Statistics and Its Application*, 4(1), 395–421.
- Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M., & Thompson, K. (2015). Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): Should we plant native or exotic species? *Journal of Applied Ecology*, 52(5), 1156–1164.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113.
- Schneider, R. H., Alexander, C. N., Staggers, F., Rainforth, M., Salerno, J. W., Hartz, A., ... Nidich, S. I. (2005). Long-term effects of stress reduction on mortality in persons \geq 55 years of age with systemic hypertension. *The American Journal of Cardiology*, 95(9), 1060–1064.
- Shaw, A., Miller, K., & Wescott, G. (2013). Wildlife gardening and connectedness to nature: Engaging the unengaged. *Environmental Values*, 22(4), 483–502.
- Simpson, D., Rue, H., Riebler, A., Martins, T. G., & Sørbye, S. H. (2017). Penalising model component complexity: A principled, practical approach to constructing priors. *Statistical Science*, 32(1), 1–28.
- Sirois, B. C., & Burg, M. M. (2003). Negative emotion and coronary heart disease: A review. *Behavior Modification*, 27(1), 83–102.
- Soga, M., & Gaston, K. J. (2016). Extinction of experience: The loss of human–nature interactions. *Frontiers in Ecology and the Environment*, 14(2), 94–101.
- Soulsbury, C. D., & White, P. C. L. (2016). Human–wildlife interactions in urban areas: A review of conflicts, benefits and opportunities. *Wildlife Research*, 42(7), 541–553.
- Veenhoven, R. (2008). Healthy happiness: Effects of happiness on physical health and the consequences for preventive health care. *Journal of Happiness Studies*, 9(3), 449–469.
- Wang, X., Ryan, Y. Y., & Faraway, J. J. (2018). *Bayesian regression modeling with INLA*. Chapman and Hall/CRC.
- Zuefle, M. E., Brown, W. P., & Tallamy, D. W. (2008). Effects of non-native plants on the native insect community of Delaware. *Biological Invasions*, 10(7), 1159–1169.