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To eat or not to eat: Urbanization and the foraging behaviors of Michigan passerines

Abstract

Urbanization creates novel problems for wildlife, potentially altering the foraging behavior of passerine birds. Foraging is driven by factors like food preference and food accessibility; the foraging of urban birds may be more innovative due to frequent exposure to unfamiliar items. I hypothesized that high novelty exposure in urban birds would promote faster discovery and longer visits to novel feeders compared to rural conspecifics. Additionally, I hypothesized that birds would prioritize food quality over access regardless of habitat, but when faced with barriers, urban birds would be better at accessing food compared to rural birds because of frequent exposure to novel obstacles. Recording bird visitations to paired bird feeders of differing food quality, I found that feeder discovery was not significantly different between the seed types or habitats. Rural birds spent half as much time at low access feeders compared to urban birds; when feeders were caged, rural birds discovered both seed types more quickly than the urban counterparts. Additionally, higher-quality food had greater consumption in both environments regardless of accessibility, although rural birds removed more low-quality food than urban birds when the more nutritional option was obstructed. This study reveals the importance of food preferences in driving avian feeding behaviors and how bird communities may be shaped by the food quality and degree of fragmentation of the habitat.

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TO EAT OR NOT TO EAT: URBANIZATION AND THE FORAGING BEHAVIORS OF
MICHIGAN PASSERINES

by

Victoria T. Vo

A Senior Thesis Submitted to the
Eastern Michigan University
Honors College

in Partial Fulfillment of the Requirements for Graduation
with Honors in Biology

Approved at Ypsilanti, Michigan, on this date April 17, 2020

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Urbanization creates novel problems for wildlife, potentially altering the foraging behavior of passerine birds. Foraging is driven by factors like food preference and food accessibility; the foraging of urban birds may be more innovative due to frequent exposure to unfamiliar items. I hypothesized that high novelty exposure in urban birds would promote faster discovery and longer visits to novel feeders compared to rural conspecifics. Additionally, I hypothesized that birds would prioritize food quality over access regardless of habitat, but when faced with barriers, urban birds would be better at accessing food compared to rural birds because of frequent exposure to novel obstacles. Recording bird visitations to paired bird feeders of differing food quality, I found that feeder discovery was not significantly different between the seed types or habitats. Rural birds spent half as much time at low access feeders compared to urban birds; when feeders were caged, rural birds discovered both seed types more quickly than the urban counterparts. Additionally, higher-quality food had greater consumption in both environments regardless of accessibility, although rural birds removed more low-quality food than urban birds when the more nutritional option was obstructed. This study reveals the importance of food preferences in driving avian feeding behaviors and how bird communities may be shaped by the food quality and degree of fragmentation of the habitat.

INTRODUCTION

Habitat alterations such as urbanization cause the fragmentation of natural habitats and are problematic to ecosystem structure and function. The area, quality, and productivity of natural lands within these fragments are often reduced (Lepczyk et al., 2017; Palmeirim et al., 2019). Populations within fragmented areas are at risk of biotic homogenization and low

biodiversity due to functional replacement, poor dispersal ability, and the lack of gene flow (Devictor et al., 2008; Lepczyk et al., 2017; Shahan et al., 2017). Previously widely spread populations are concentrated within smaller ranges due to urban developments, leading to increased strain on resource consumption, genetic isolation, and local extinctions. These events could produce unprecedented effects for species interactions (e.g., food webs, trophic levels, speciation events) and the relationships with the surrounding habitat (e.g., nutrient cycling).

Passerine birds are an example of a taxa affected by habitat fragmentation due to urbanization. Passerines, common in many landscapes, provide important ecological services, like maintaining species diversity through seed-predation, and pest control (Heleno et al., 2010, Whelan et al., 2015). Although passerines can be abundant in urban environments and have significant ecological and economic value, these populations may still be harmed by urban activities. Some of the negative impacts of urbanization on passerine populations are noise pollution, the construction of impermeable surfaces, new predators, and the introduction of novel dangers like cars and pedestrian foot traffic (Thomas et al., 2003; Silva et al., 2017). These urban features have individual-level effects on passerines, such as increased stress levels and reduced reproductive success, but there are also large scale impacts like modified community structure and species interactions through the overlapping of niches and increased interspecific competition (Shochat et al., 2003; Francis et al., 2009; Møller and Díaz, 2017).

Changed wildlife behavior, especially of birds, is one large-scale influence of urbanization (Jokimaki et al., 2016, Marzluff., 2016). Neophobia, or the fear of the new or unfamiliar, is often lower in urban populations likely due to greater exposure to novelty (Sol et al., 2011). Habituation to novel features (i.e. reduced neophobia) and increased exploration for resources may be favored by natural selection in urban habitats (Schochat et al., 2013). As a

result, urban bird populations may exhibit increased foraging efficiency and develop unique foraging tactics, perhaps even replacing traditional feeding behaviors (Schochat et al., 2003; Marzluff., 2016).

One factor that influences feeding behavior is palatability, which indirectly measures food quality (Abdulwahab et al., 2019). Palatability is determined by characteristics such as nutritional content, mass, and structure (e.g., seed coat thickness) of the food item (Sundaram et al., 2017; Camin et al., 2016). The quality of food material (i.e., the caloric and macronutrient content) is critical to the survival of birds. Birds must consume food that counteracts energy lost through foraging effort, while also satisfying biological demands (e.g. thermoregulation, growth, and reproduction) (Molokwu et al., 2011; Coogan et al. 2018). Despite needing to balance food intake with energy output, the diets of birds in modified habitats may have to conform to the limiting macronutrient (Coogan et al., 2018). Over time, this shift can cause differences in food preference between urban populations and rural conspecifics and influence the willingness to exploit novel resources (Coogan et al., 2018).

Birds may adjust their feeding tactics in urban environments to meet metabolic demands through the exploration of novel objects, trial and error experiences, and parental or social observation (Mikolasch et al., 2011; Slagsvold & Wiebe., 2011; Aplin et al., 2014). Accessibility, however, can be hindered by biotic obstacles such as competition with other species and predation risk, or physical barriers like vegetative cover and heavily protected seeds (i.e. ability to digest food items). Urban habitats present novel versions of these natural obstacles, including trash receptacles and the packaging of food litter, which may require innovative methods of handling and processing (Thomas et al., 2003; Ducatez et al., 2013; Silva et al., 2017).

Innovative feeding behaviors are commonly developed by individuals but can be spread by social learning within and across populations (Ducatez et al., 2013). Individual birds are likely to modify their feeding strategies if they observe others succeeding in accessing a food item if they are capable of social learning. This can improve foraging efficiency, especially in areas of limited or highly variable resources (Aplin et al., 2014; van den Bosch et al., 2019). The exploration of opportunistic resources is higher in urban avian communities due to more frequent exposure to new objects and situations (Tryjanowski et al., 2016; Van Donselaar et al., 2018). Urban habitats provide new sources of food, such as garden bird feeders, thus, urban birds may differ in their ability to identify these features and successfully access them compared to their rural counterparts (Shochat et al., 2003; Tryjanowski et al., 2016). Unfamiliar objects and presumed predation-risk may deter rural birds from investigating novel food sources, whereas urban birds, accustomed to a variety of novelty, may be better at exploiting these sources. Some studies manipulating seed trays to examine the effects of urbanization on avian foraging behavior have produced contradictory results, as the works are species and context dependent (Shochat et al., 2003; Tryjanowski et al., 2016; Van Donselaar et al., 2018). For example, the results of a study by Shochat et al. (2003) on Arizona desert bird behavior found reduced foraging associated with greater perceived predation risk in a non-urban environment, whereas the results of Van Donselaar et al. (2008) found that black-capped chickadees, *Poecile atricapillus*, tolerated high predation risk in urban environments.

My study examined the decision-making process of passerine feeding behavior in relation to novelty exposure associated with urbanization, food quality, and food accessibility, on a local scale. I hypothesized that if a modified environment encourages greater exposure to and reduced fear of unfamiliar objects (i.e., reduced neophobia), then urban birds will be faster at discovering

and more likely to remove seeds from novel feeders compared to rural birds. Additionally, I hypothesized that if birds must balance meeting metabolic needs and energy expenditure, birds of both environments will prioritize food quality to food access, but urban birds will remove more seed from both caged feeders due to reduced neophobia. To test my hypotheses, I conducted field experiments using two food types and caged bird feeders, in urban and rural environments within the Southeast Michigan area.

MATERIALS AND METHODS

Study site determination and feeder installation

To determine whether urbanization reduces neophobia among birds and increases the likelihood of seed removal from novel feeders, I conducted this study over a fourteen-week period from June through the first week of September 2019, using urban and rural habitats, each with two site locations. All site locations were within a 25km² area, spanning the cities of Ann Arbor, Chelsea, and Ypsilanti Michigan. Urban sites were located on the campus of Eastern Michigan University in Ypsilanti, MI, and on a residential lot in Ann Arbor, MI. Rural sites were located on two residential lots, one in Ypsilanti, MI, and the other in Chelsea, MI (Figure 1). Using the watershed-mapping app, *Model My Watershed*, sites were ranked based on the percent area of anthropogenic development (i.e., open space, low, medium, and high-intensity development) within 1km² of each site (Table 1). Sites with greater than 60% anthropogenic development were considered to be urban. Although the sites at W Clark Rd and Arborview Neighborhood had similar percentages of medium intensity development (50%-79% impervious surface), the site at W Clark Rd had the greatest percent area of natural landscape (i.e., deciduous

forest, grassland/herbaceous, woody and emergent herbaceous wetlands), ideal habitat for passerine species, of all four sites (Table 1).

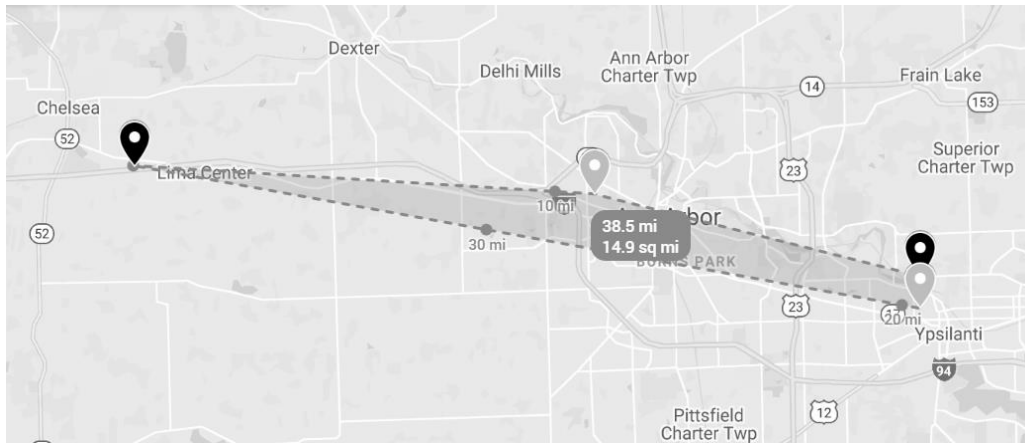


Figure 1. Map of the distance between urban (light) and rural (dark) sites in Southeast MI.

Table 1. Location of sites organized by city, habitat type (urban or rural), percentage of natural cover and anthropogenic development within a 1km square of each site. Development is categorized by % impervious surface: Open space (<20%), Low Intensity (20%-49%), Medium Intensity (50%-79%), and High Intensity (80%-100%).

Site	City	Habitat Type	Natural Cover (%)	Open Space (%)	Low Intensity (%)	Medium Intensity (%)	High Intensity (%)	Total Development (%)
Eastern Michigan University	Ypsilanti	Urban	0	6.4	30.4	45.4	17.4	99.6
Arborview Neighborhood (residential)	Ann Arbor	Urban	0	21.0	54.8	17.7	6.5	100
W Clark Rd (residential)	Ypsilanti	Rural	27.3	21.8	14.8	15.3	2.3	54.2
Luick Dr (residential)	Chelsea	Rural	11.3	26.1	19.9	5.2	0.3	51.5

Food material in this study consisted of high-quality shelled sunflower seeds and low-quality thistle seeds. Sunflower seeds have a high lipid content and caloric value compared to thistle seeds, which are smaller in size and lower in caloric value per seed. Seeds were weighed to 83 ± 0.2 g and stored in plastic zip-top bags. The seeds were contained in a tube feeder with a

catching dish to minimize spillage and mammal interference. I constructed the feeders to the dimensions of 17cm x 8cm, using ¼” and ⅛” hardware cloth for sunflower seeds and thistles seeds respectively (Figure 2a, b). Feeders were elevated 91cm off the ground on a rebar rod; 27cm wide plates acted as baffles to deter squirrels and raccoons. Wooden stakes reinforced the rebars as necessary. One feeder of each seed type created a matched pair and each site had a replicate pair (total of 4 feeders per site). Feeders within a pair were placed 5m apart (Figure 2c); the replicate pair was placed at least 10m away. I placed the feeders 1 to 2m away from vegetative cover or refuge in all study sites.

Feeder visitation rates at urban and rural locations

To test the hypothesis that urban birds will be faster at discovering and more likely to visit the feeders compared to rural birds because a modified environment provides greater exposure to novel features and reduces neophobia, I conducted a visitation test the first week of each month, over fourteen weeks, to determine the adequate amount of time for birds to recognize and approach the feeders. I positioned trail cameras to face the feeder pairs to document all visitations throughout the fourteen-week period. Time-stamped photographs were taken in intervals of 6s when triggered by motion. Although I took preventative measures to inhibit or reduce mammal interference (i.e., feeder baffles, reinforced rebar, distancing from overhanging branches), some mammal consumption did occur. If time permitted, I conducted additional trials to replace the data tampered by mammal activity. After I conducted the additional trials, 22 of 276 data points were replaced and excluded from analysis due to mammal interference.

Feeders were left in the field for one week before I retrieved the photographs and reset the cameras. I reviewed all photographs, recording the timestamps, bird species ID, number of individuals, and if determinable from plumage characteristics, the sex of all visiting birds. ‘Visits’ were defined as instances of removing seeds from either the tube feeder or the catching dish. Timestamps were used to record the arrival and departure of each bird and were converted into seconds to determine the latency before the first visit (i.e. after initial set up and for each day throughout the trial) and the duration of each visit. Individual birds were not identifiable thus revisits are not detectable in this data set.

Seed mass removal between caged and uncaged feeders

To examine how balancing food quality and accessibility affects decision-making processes during foraging in urban and rural habitats, I conducted a repeated-measures test with caged and uncaged thistle and sunflower seed feeders, to determine if birds would still prioritize food quality despite having reduced access to the food source. The cages surrounding the feeder were intended to obstruct access to the seeds and potentially discourage feeding attempts since the enclosed space could inhibit quick escapes (e.g. fleeing for cover). Cages were made from ½” hardware cloth, approximately 30cm x 50cm x 30 cm, with two opposite facing entry points of 5cm x 5cm x 5cm. To avoid prolonged entrapment, each cage has an additional 5cm x 5cm opening in its ceiling (Figure 2d). To access the food, a prospective bird had to reach one of the two entry points on the cage, where it could then fly to the feeder at the center of the cage. Centering the feeder inside the cage allowed the feeder to be utilized by all angles and by multiple birds inside the cage. To leave the cage, the bird returned through either entry points or through the additional opening at the top of the cage.

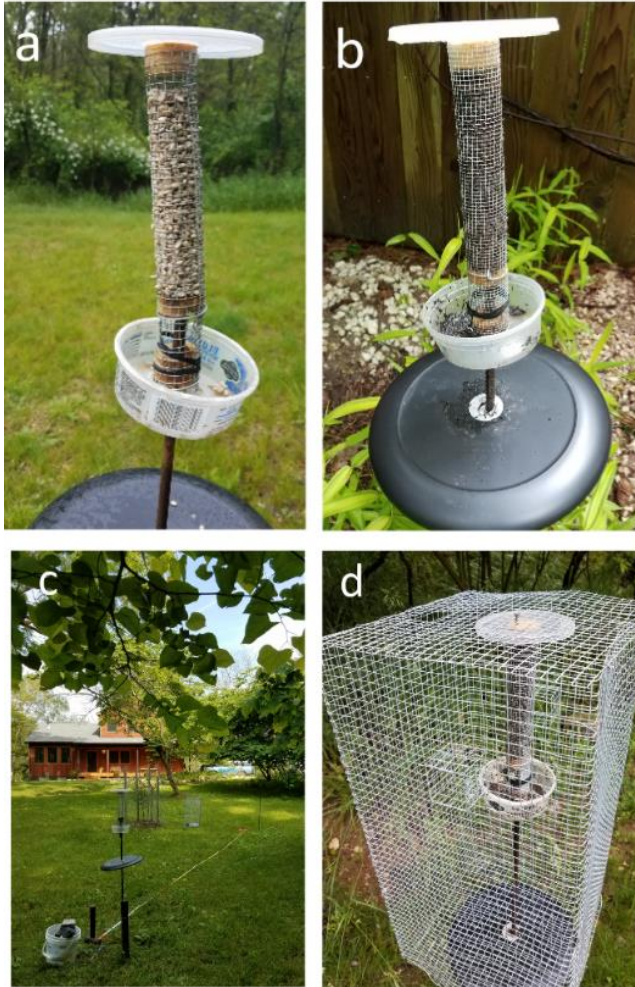


Figure 2. Feeders and cages used to acquire bird visitation and access data. **a** Sunflower seed feeder. **b** Thistle seed feeder. **c** Placement of paired feeders from the perspective of the trail camera; sunflower seed feeder (bottom left) reinforced with a wooden stake. **d** Caged thistle seed feeder with opposite-facing entrance points (center) and an additional escape point (top left).

Feeder pairs scored during the visitation tests (i.e. uncaged feeders) were the controls, as the cages, not the feeders, were intended as the novel object. On the days photographs from the visitation test were retrieved (i.e. seven days after feeder filling), the remaining seeds were collected in their respective bags. Seeds contained in the catching dishes also contributed to the final mass, as spillage and unintentional jostling of the feeder could have occurred. Seeds were sun-dried on plates with protective screens to remove excess moisture, as necessary. Starting the second week of each month, I placed a cage around the sunflower feeder, continuing to collect

seed mass removal in addition to visitation and access rate using the trail cameras. The following week, I switched the cage onto the thistle feeder, collecting the same data to document whether food preferences or feeding specialization (e.g., beak size) was an influential factor in the choosing of feeders.

Data Analysis

I conducted a two-way ANOVA to determine the effect of seed type and habitat type on the time before the first visit (TBF), and the duration of each feeder visit (seed type x TBF and duration; habitat type x TBF and duration; seed type x habitat type x TBF and duration). To determine whether there were significant differences in seed mass removal and the presence of cages (i.e. accessibility), I ran a two-way ANOVA (seed type x habitat type) on seed mass removal for caged and uncaged feeders. I conducted all statistical analyses in Vassarstats.

RESULTS

Visiting bird species and feeder visitation rates

Urban sites had a combined species richness of 5 bird species present, whereas rural sites had a combined species richness of 8 bird species. Urban sites had the shared presence of 1/5 species, whereas rural sites had a shared presence of 5/8 species. Urban sites had 2 species not present in rural sites, and rural sites had 3 species not present at urban sites (Table 2). House sparrows (*Passer domesticus*) and house finches (*Haemorhous mexicanus*), observed in both urban and rural environments, were the only two non-native species.

Table 2. Bird species observed at each study site, * denote unshared species, ** denote non-native species.

Site	Habitat type	Present species
Eastern Michigan	Urban	American goldfinch (<i>Spinus tristis</i>)

University		House sparrow (<i>Passer domesticus</i>)** Northern cardinal (<i>Cardinalis cardinalis</i>) Red-winged blackbird (<i>Agelaius phoeniceus</i>)*
Arborview neighborhood (residential)	Urban	Black-capped chickadee (<i>Poecile atricapillus</i>) House wren (<i>Troglodytes aedon</i>)* Northern cardinal (<i>C. cardinalis</i>)
W Clark Rd (residential)	Rural	American goldfinch (<i>S. tristis</i>) Black-capped chickadee (<i>P. atricapillus</i>) Blue jay (<i>Cyanocitta cristata</i>)* Northern cardinal (<i>C. cardinalis</i>) Downy woodpecker (<i>Picoides pubescens</i>)* House finch (<i>Haemorhous mexicanus</i>)** House sparrow (<i>P. domesticus</i>)** Red-bellied woodpecker (<i>Melanerpes carolinus</i>)*
Luick Dr (residential)	Rural	American goldfinch (<i>S. tristis</i>) Black-capped chickadee (<i>P. atricapillus</i>) House finch (<i>H. mexicanus</i>)** House sparrow (<i>P. domesticus</i>)** Northern cardinal (<i>C. cardinalis</i>)

In the absence of cages, there was no significant effect of habitat type or seed type on time before the first visit (TBF) ($p > 0.05$; Fig. 3).

In the presence of cages on the sunflower feeders, there was a significant effect of habitat type on TBF, but not seed type on TBF. Birds from rural sites took a quarter less time finding the feeders of both seed types compared to urban birds when the sunflower feeders were caged ($p = 0.0322$; $p_{\text{seed type} \times \text{environment}} = 0.9211$; Figure 4)

In the presence of cages on thistle seeds, there was no significant effect of habitat type or seed type on TBF ($p > 0.05$; Figure 5).

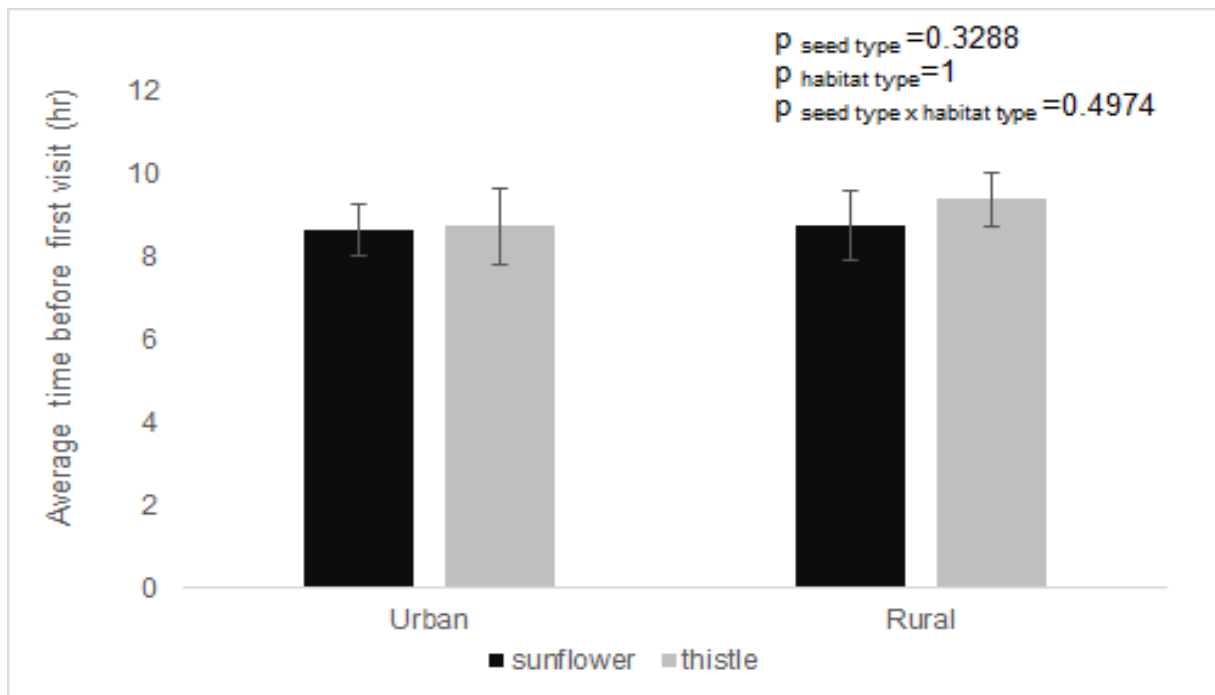


Figure 3. Average time(s) before the first visit (TBF; \pm standard error) to a feeder by urban and rural birds when neither seed type is caged.

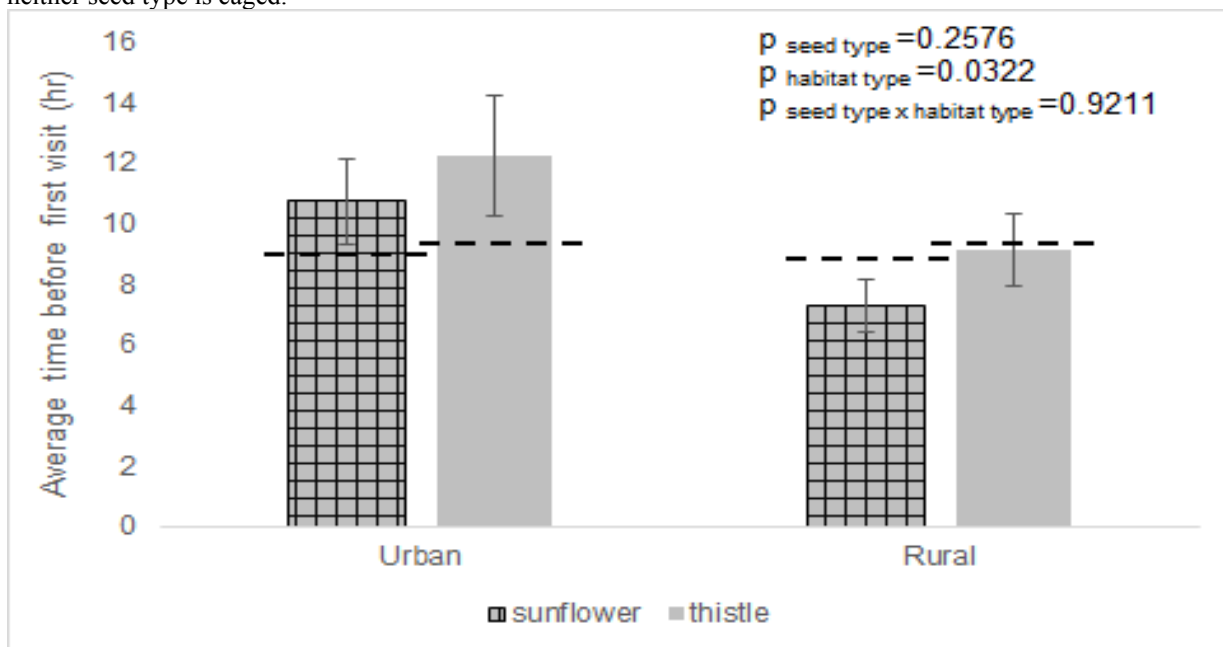


Figure 4. Average time(s) before the first visit (TBF; \pm standard error) to a feeder by urban and rural birds when sunflower feeders are caged. Dashed lines indicate TBF of uncaged feeders.

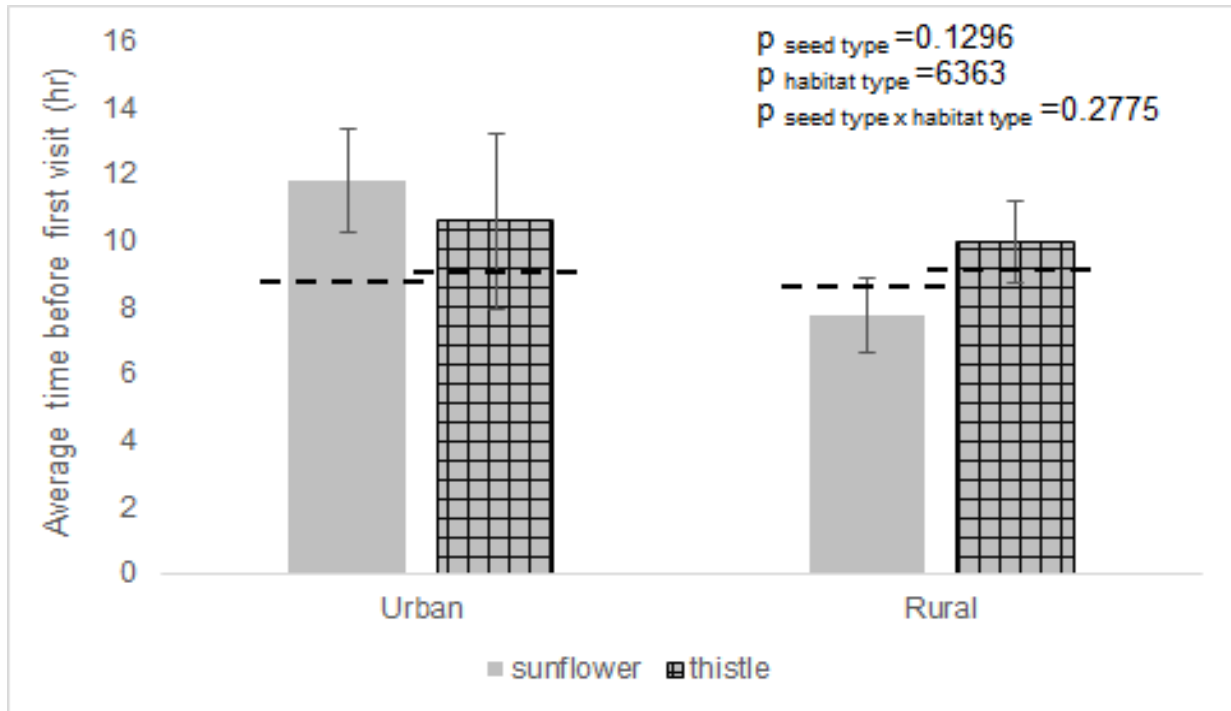


Figure 5. Average time(s) before the first visit (TBF; \pm standard error) to a feeder by urban and rural birds when thistle feeders are caged. Dashed lines indicate TBF of uncaged feeders.

In the absence of cages, habitat type had a significant effect on visit duration. Rural birds spent half as much time at feeders of each seed type than urban birds ($p = 0.0126$; Figure 6). In the presence of cages on sunflower feeders, habitat type and seed type had no significant effect on visit duration ($p > 0.05$; Figure 7). In the presence of cages on thistle feeders, habitat type and seed type had no significant effect on visit duration ($p > 0.05$; Figure 8).

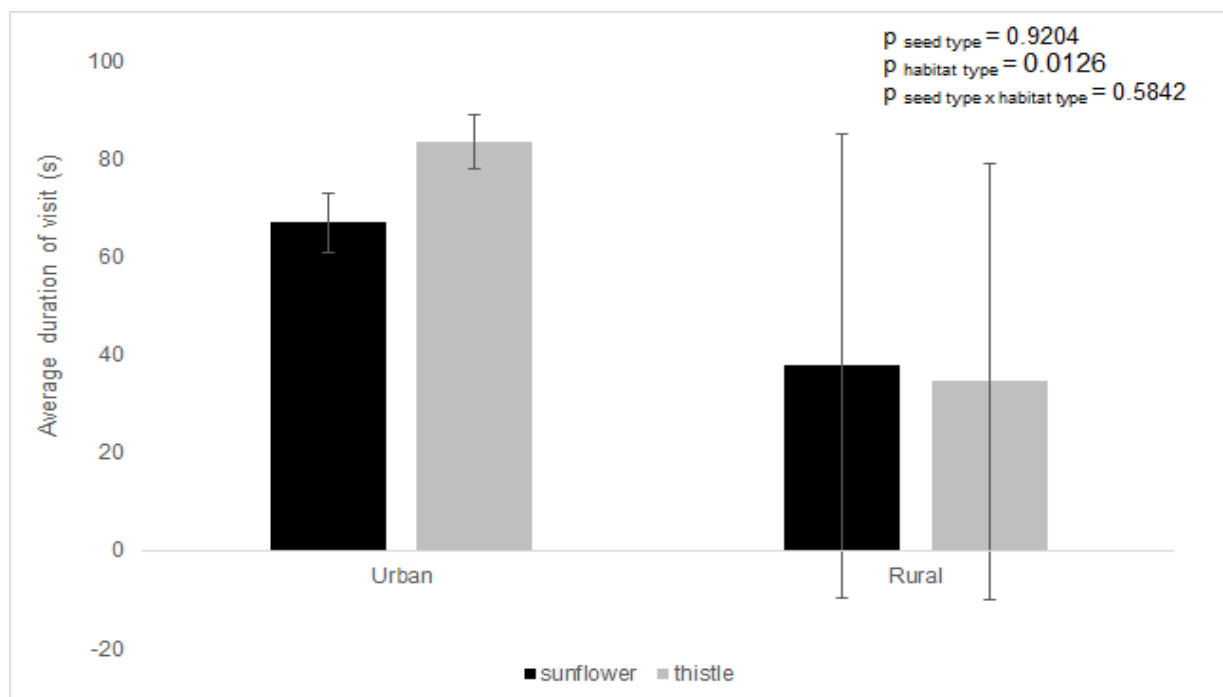


Figure 6. Average time(s) (\pm standard error) of visitation by urban and rural birds to feeders when neither seed type is caged.

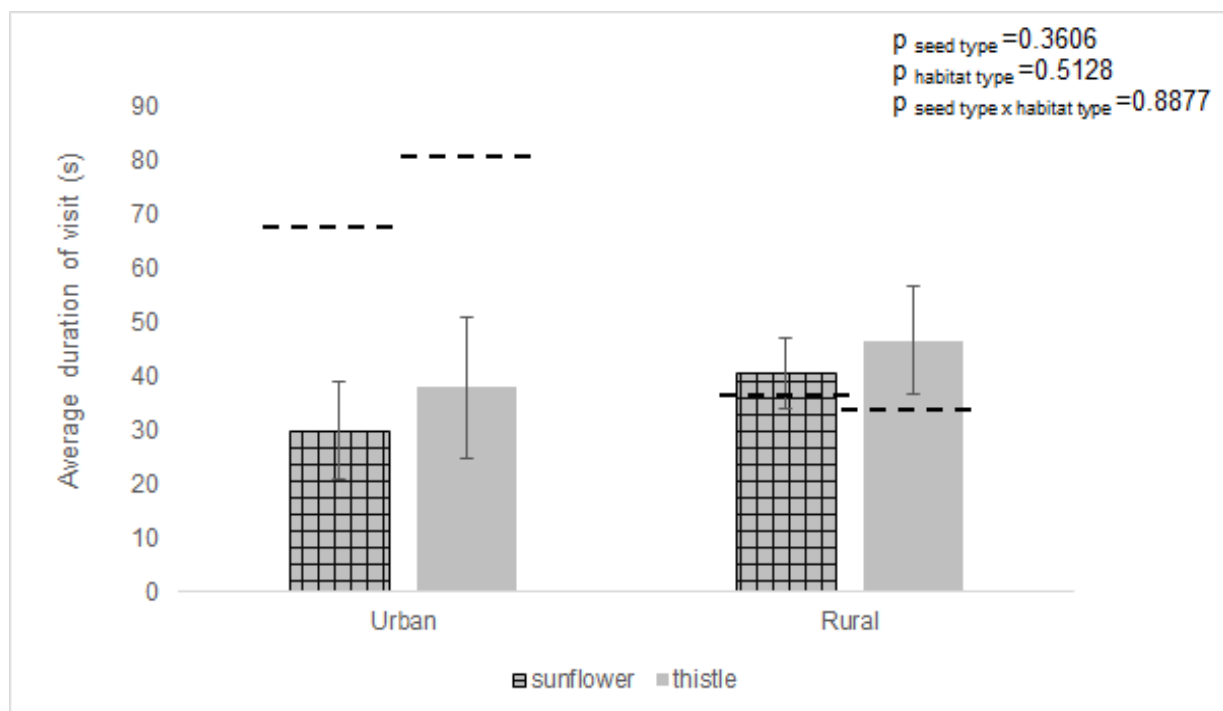


Figure 7. Average time(s) (\pm standard error) of visitation by urban and rural birds to feeders when sunflower seeds are caged. Dashed lines indicate average times at uncaged feeders.

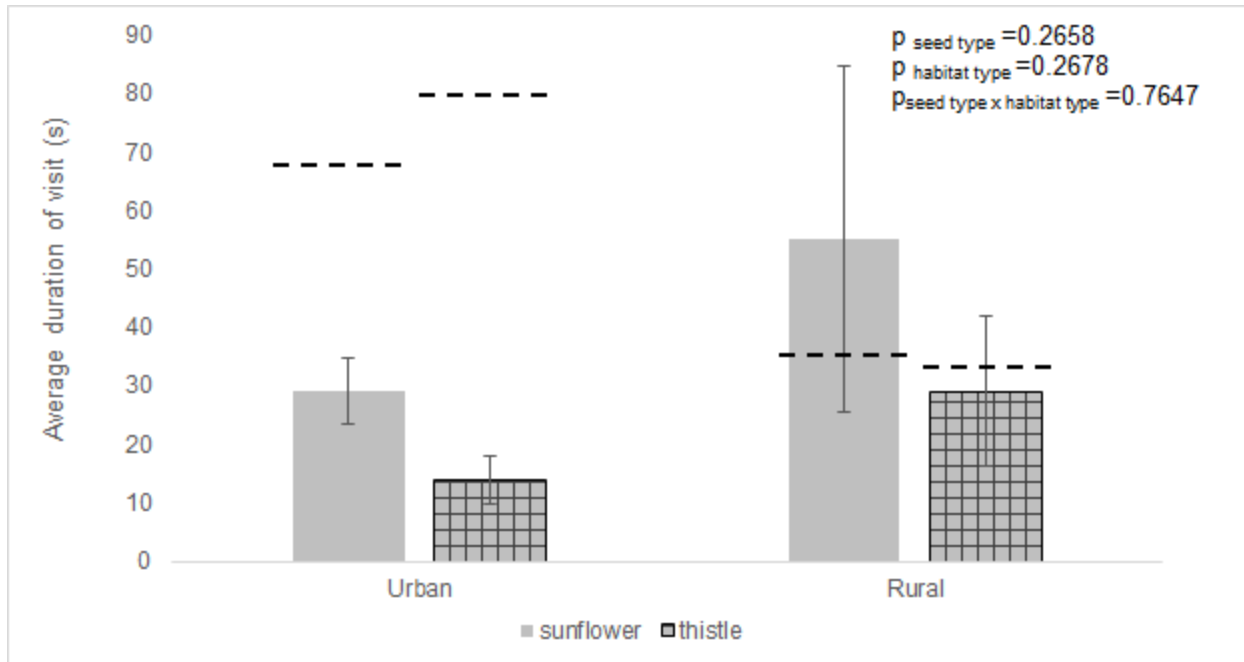


Figure 8. Average time(s) (\pm standard error) of visitation by urban and rural birds to feeders when thistle seeds are caged. Dashed lines indicate average times at uncaged feeders.

Seed mass removal between caged and uncaged feeders

When neither seed type was obstructed, both urban and rural birds removed more sunflower seed mass than thistle seed mass ($F=61.06$, $p<0.0001$). Urban and rural birds removed similar amounts of sunflower seed; however, rural birds removed more than twice as much thistle seed mass than urban birds ($F=5.84$, $p=0.020$). Combined, seed type and habitat type had a significant effect on seed mass removal ($F=7.05$, $p=0.0112$; Figure 9).

The caging of sunflower feeders (i.e., the second week of each month) did not change food preference, as both urban and rural birds still consumed more sunflower seeds than thistle seeds ($F=14.72$, $p=0.0005$). Again, urban birds did not significantly differ from rural birds in the amount of sunflower seed removal, and rural birds removed more thistle seed mass than urban birds ($F=7.8$, $p=0.0081$). The effect of seed type did not, however, rely on the habitat type categorization (urban/rural) ($F=1.39$, $p=0.2457$; Figure 10).

The caging of thistle feeders (i.e., the third week of each month) reduced thistle consumption, as both urban and rural birds, consumed more sunflower seeds than thistle seeds when thistle feeders were obstructed ($F=115.36$, $p<0.0001$). Urban birds did not significantly differ from rural birds in the amount of sunflower seed removal and rural birds did not consume more thistle seed than urban birds ($F=0.41$, $p=0.526$). Across both environments and seed types, urban and rural birds did not differ significantly in seed mass removal ($F=2.53$, $p=0.1204$; Figure 11).

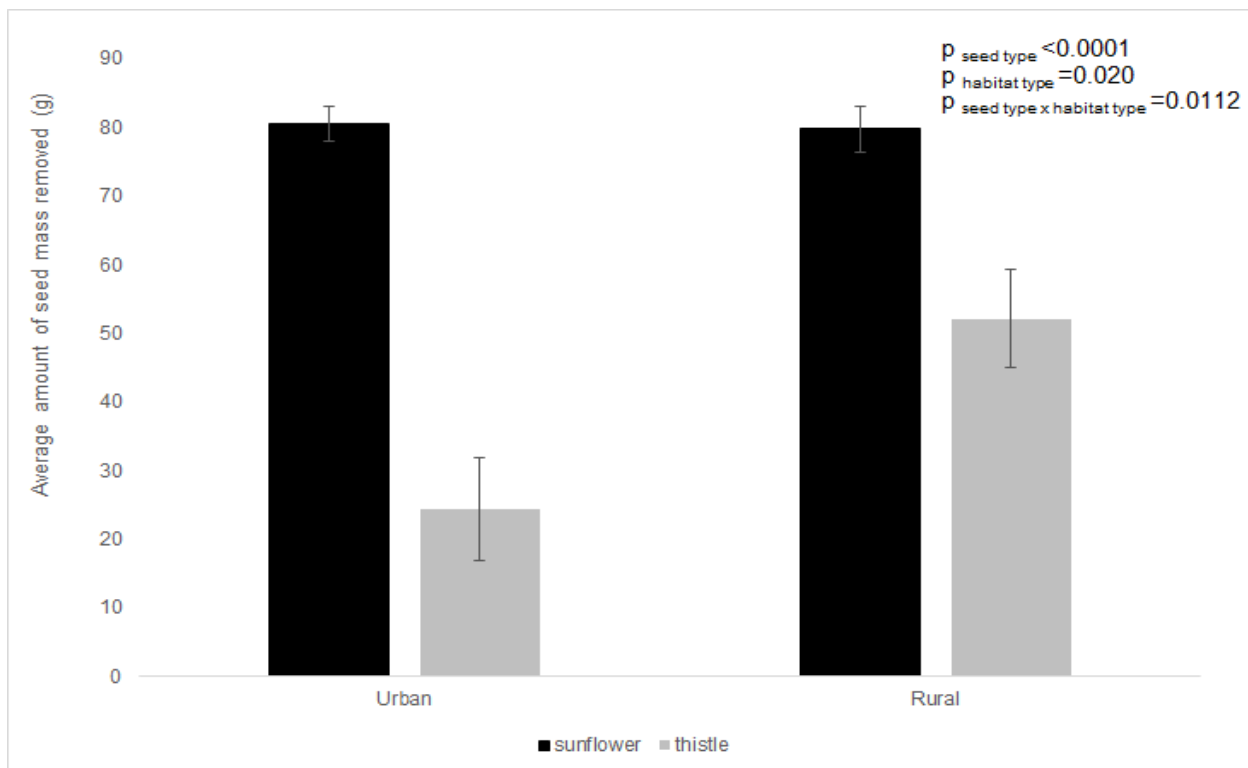


Figure 9. The effect of habitat type on the average amount of seed mass removed by seed type (\pm standard error) when neither seed type is obstructed.

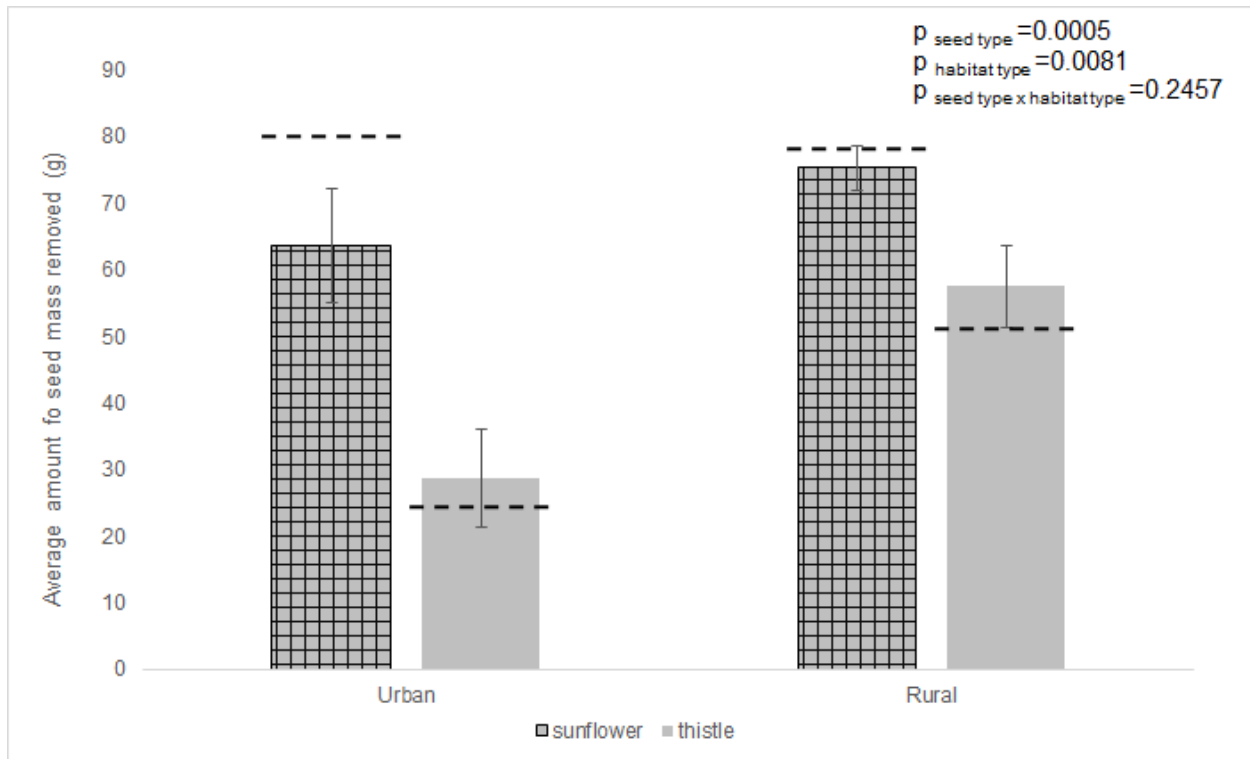


Figure 10. The effect of habitat type on the average amount of seed mass removed by seed type (\pm standard error) when sunflower seeds are obstructed. Dashed lines indicate seed mass removal from uncaged feeders.

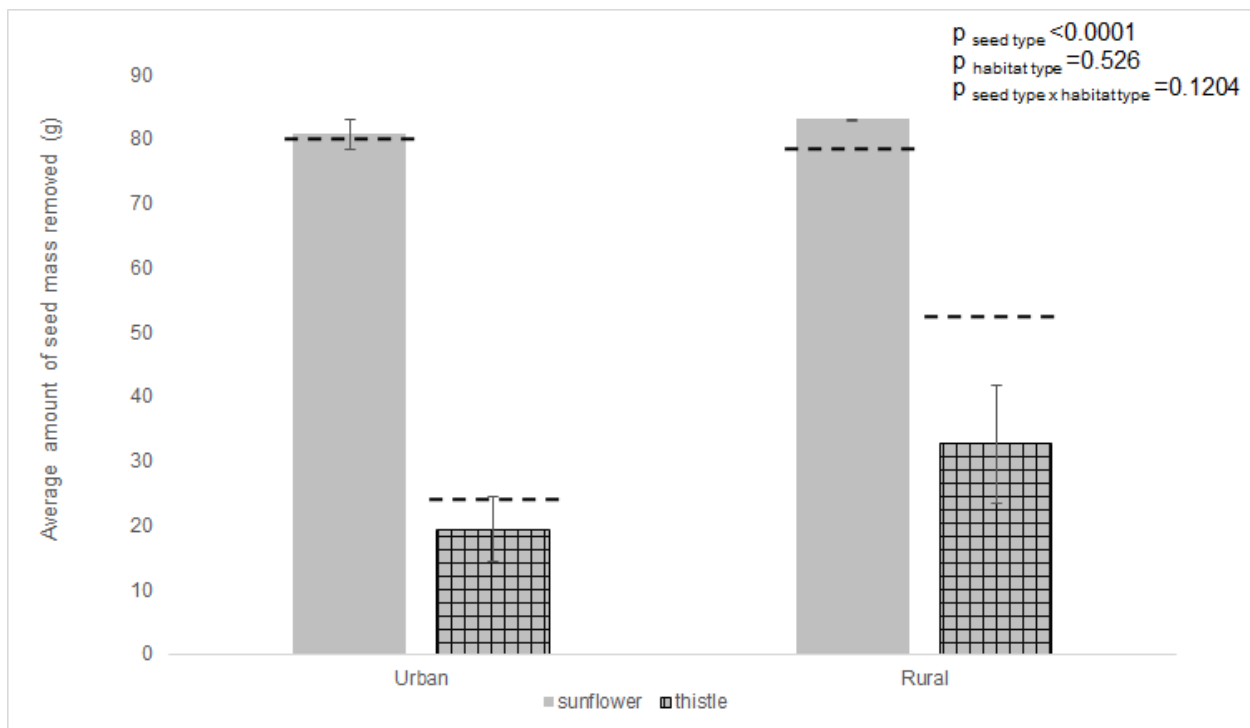


Figure 11. The effect of habitat type on the average amount of seed mass removed by seed type (\pm standard error) when thistle seeds are obstructed. Dashed lines indicate seed mass removal from uncaged feeders.

DISCUSSION

My results show that habitat type only occasionally influenced the time it took birds to first visit a feeder (TBF) and how long birds stayed at caged and uncaged feeders.

Additionally, food preferences and bird species diversity may be more important in driving the foraging behavior of passerine populations than habitat type and food accessibility. The consistent preference for highly nutritious food (i.e. sunflower seeds) in both urban and rural environments, despite the presence of barriers, supports the hypothesis that in order to balance meeting metabolic needs and energy expenditure, individual birds of both environments will prioritize food quality to food access.

The greater thistle seed removal by rural birds when no barriers were present did not support the hypothesis that urban birds would remove more seeds, regardless of type, due to lower neophobia. This result may be attributed to the difference in species richness and the relative abundance of observed bird species across all sites (Table 2). Though the urban and rural feeders were both visited by some species like the American goldfinch (*Spinus tristis*) and black-capped chickadee (*Poecile atricapillus*), there was variation between sites for other species. Species richness and abundance, especially of specialist bird species, may have influenced the results by selectively feeding on seeds their diets have adapted to rather than the more nutritional option. For example, both rural site visitations were dominated by goldfinches and house finches (*Haemorhous mexicanus*), both of which specialize in consuming small seeds like those produced by plants in the daisy family. Although seed-eating species like goldfinches, chickadees, and northern cardinals (*Cardinalis cardinalis*) were present at urban feeders, they were either few in number or preferentially consumed the more nutritional option. It is possible, however, that the species observations may not accurately reflect the true diversity of the bird

communities since my sampling method was solely based on the willingness of individual birds to visit the feeders. Differences in urban passerine community composition may be the result of ecological filtering or directional selection for more well-adapted, or phenotypically plastic species (Pape Møller and Díaz, 2017). Generalist bird species tend to survive and thrive in urban, highly disturbed, or fragmented habitats compared to specialists because of the ability to utilize a variety of habitats and resources (Devictor et al., 2008). The increased establishment of these well-adapted, urban generalists promotes anthropogenic association and the potential of producing successful invading species (Pape Møller and Díaz, 2017).

The lack of significant effect of habitat type on seed consumption when food barriers were present did not support the hypothesis that frequent exposure to unfamiliar objects reduces neophobia and increases foraging (seed mass removal) among urban birds compared to rural birds. Studies assessing the effect of novelty associated with urbanization on avian foraging behavior have noted that although urban birds may be more tolerant to human presence and better novel problem solvers, neophobia in urban populations may actually be the same, if not greater than rural conspecifics due to the higher severity of risk associated with approach (Sol et al. 2011; Audet et al., 2015; Pape Møller and Díaz, 2017). A limiting factor in this study was that I was not able to determine if the observed birds were new or repeat visitors. The inability to distinguish new from returning birds was most evident in the rural environments where there was the greatest abundance of finches. Although I am unable to confidently confirm the identity of individuals, it seemed that the same pair of cardinals were observed repeatedly visiting the feeders in the Arborview urban site. Additionally, I noted that as my study progressed, a family of house wrens (*Troglodytes aedon*) began nesting near the feeders. Although it often takes some time for individual birds to discover feeders, over time, the use of feeders will likely increase for

nearby breeding birds since many passerine species are central-place foragers with relatively small home ranges during their breeding seasons. Repeat visitors could have become habituated to the feeder experiment and likely access the caged feeders more quickly than new visitors, skewing my results. Banding the birds as they entered the feeder cages would allow me to distinguish the visiting birds and record the frequency and duration of each bird more precisely.

Including sites with a very low degree of anthropogenic development could be beneficial to this study, as these sites could capture a wider range of avian behavior. Habitats may not need to be highly urbanized (i.e., 80-100% impervious surface) to influence local bird populations, rather, the difference between 'rural' or 'natural' sites and Low/Medium Intensity Development could be more significant (Sochat et al., 2004; Audet et al., 2016). Although I took care in selecting my sites based on the degree of anthropogenic development, the rural sites could have exhibited some level of habitat fragmentation due to the presence of roads cutting through critical nesting habitat (Table 1; Figure 1). Another limiting factor of my study is that the sequence in which I installed the feeder cages may have impacted the willingness of birds to visit the thistle feeder. It is possible that since the cage installations were scheduled, that some birds could have learned that the cages were not a threat during the first week on the sunflower seeds, thus approaching the thistle feeders more quickly, independent of food preference.

In addition to individual survival, the quality of food items may influence urban bird population demographics. The maintenance of established populations may be reliant on the availability of quality food items to ensure optimal breeding and the survival of offspring (Chamberlin et al. 2009). However, urban environments tend to lack highly nutritious food items, resulting in urban bird populations producing smaller clutch sizes, low nestling weight, and low nesting productivity (Chamberlin et al. 2009; Sepp et al. 2017). Feeders and other

human food sources that are present in urban environments tend to contain particular food types (e.g., suet feeder, mesh-sock feeder, bird table feeder) that only support birds that are specialized to consume those foods, thus selectively filtering the local bird community (Tryjanowski et al. 2015).

Expanding urbanization steadily increases the trend of wildlife populations having to associate with humans or reducing natural ranges. Some urban areas are ‘sink habitats’, where the death rate of a population exceeds the birth rate. These sink habitats can become ‘ecological traps’ for populations fragmented or isolated by anthropogenic development (Sievers et al., 2018). Although urban environments may provide benefits like unclaimed nesting territories and novel food sources, it is often at the cost of new challenges including excessive predation, frequent disturbance, or increased foraging effort that causes urban environments to become sinks (Bonnington et al., 2015). In combination with these obstacles, the selection for generalist species or adaptive traits may reduce biodiversity and make urbanized fragments inhospitable for some species. The findings of this study may aid land managers, urban developers, and community stakeholders in better understanding the impacts of urbanization on songbird behavior. In addition, policies and conservation efforts can be developed to monitor the diversity, phenology, and behaviors of passerine populations within modified habitats. Steps to continue this work include the integration of bird-banding and vocalization capture in this camera-trap based field experiment, in hopes to better gauge the relative abundance of species within habitat fragments created by urbanization.

REFERENCES

- Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*. 518(7540):538–541. doi:10.1038/nature13998.
- Audet J-N, Ducatez S, Lefebvre L. 2016. The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*. 27(2):637–644. doi:10.1093/beheco/arv201.
- van den Bosch M, Baert JM, Müller W, Lens L, Stienen EWM. 2019. Specialization reduces foraging effort and improves breeding performance in a generalist bird. *Behav Ecol*. 30(3):792–800. doi:10.1093/beheco/arz016.
- Camín SR, Cueto VR, Casenave JL de, Marone L. 2015. Exploring food preferences and the limits of feeding flexibility of seed-eating desert birds. *Emu - Austral Ornithology*. 115(3):261–269. doi:10.1071/MU14090.
- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis*. 151(1):1–18. doi:10.1111/j.1474-919X.2008.00899.x.
- Coogan SCP, Raubenheimer D, Zantis SP, Machovsky-Capuska GE. 2018. Multidimensional nutritional ecology and urban birds. *Ecosphere*. 9(4):1-N.PAG. doi:10.1002/ecs2.2177.
- Devictor V, Julliard R, Jiguet F. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*. 117(4):507–514. doi:10.1111/j.0030-1299.2008.16215.x.
- Ducatez S, Audet JN, Lefebvre L. 2013. Independent appearance of an innovative feeding behaviour in Antillean bullfinches. *Anim Cogn*. 16(3):525–529. doi:10.1007/s10071-013-0612-4.
- Francis CD, Ortega CP, Cruz A. 2009. Noise pollution changes avian communities and species interactions. *Curr Biol*. 19(16):1415–1419. doi:10.1016/j.cub.2009.06.052.
- Jokimäki J, Suhonen J, Jokimäki-Kaisanlahti M-L, Carbó-Ramírez P. 2016. Effects of urbanization on breeding birds in European towns: Impacts of species traits. *Urban Ecosyst*. 19(4):1565–1577. doi:10.1007/s11252-014-0423-7.
- Mikolasch S, Kotrschal K, Schloegl C. 2011. African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food. *Biol Lett*. 7(6):875–877. doi:10.1098/rsbl.2011.0500.

- Molokwu MN, Nilsson J-Å, Olsson O. 2011. Diet selection in birds: trade-off between energetic content and digestibility of seeds. *Behav Ecol.* 22(3):639–647. doi:10.1093/beheco/arr025.
- Pape Moller A, Diaz M. 2018. Niche segregation, competition, and urbanization. *Curr Zool.* 64(2):145–152. doi:10.1093/cz/zox025.
- Sepp T, McGraw KJ, Kaasik A, Giraudeau M. 2018. A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? *Glob Change Biol.* 24(4):1452–1469. doi:10.1111/gcb.13969.
- Shochat E, Lerman SB, Katti M, Lewis DB. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *Am Nat.* 164(2):232–243. doi:10.1086/422222.
- Silva AD, Diez-Méndez D, Kempnaers B. 2017. Effects of experimental night lighting on the daily timing of winter foraging in common European songbirds. *Journal of Avian Biology.* 48(6):862–871. doi:10.1111/jav.01232.
- Slagsvold T, Wiebe KL. 2011. Social learning in birds and its role in shaping a foraging niche. *Philos Trans R Soc Lond B Biol Sci.* 366(1567):969–977. doi:10.1098/rstb.2010.0343.
- Sol D, Griffin AS, Bartomeus I, Boyce H. 2011. Exploring or Avoiding Novel Food Resources? The Novelty Conflict in an Invasive Bird. *PLOS ONE.* 6(5):e19535. doi:10.1371/journal.pone.0019535.
- Stofberg M, Cunningham SJ, Sumasgutner P, Amar A. 2019. Juggling a “junk-food” diet: responses of an urban bird to fluctuating anthropogenic-food availability. *Urban Ecosyst.* 22(6):1019–1026. doi:10.1007/s11252-019-00885-3.
- Sundaram M, Lichti NI, Widmar NJO, Swihart RK. 2018. Eastern gray squirrels are consistent shoppers of seed traits: insights from discrete choice experiments. *Integrative Zoology.* 13(3):280–296. doi:10.1111/1749-4877.12294.
- Thomas K, Kvitek RG, Bretz C. 2003. Effects of human activity on the foraging behavior of sanderlings *Calidris alba*. *Biological Conservation.* 109(1):67–71. doi:10.1016/S0006-3207(02)00137-4.
- Tryjanowski P, Møller AP, Morelli F, Biaduń W, Brauze T, Ciach M, Czechowski P, Czyż S, Dulisz B, Goławski A, et al. 2016. Urbanization affects neophilia and risk-taking at bird-feeders. *Sci Rep.* 6:28575. doi:10.1038/srep28575.

Van Donselaar JL, Atma JL, Kruyf ZA, LaCroix HN, Proppe DS. 2018. Urbanization alters fear behavior in black-capped chickadees. *Urban Ecosystems*. 21(6):1043–1051. doi:10.1007/s11252-018-0783-5.