

Fall 11-26-2019

Songbird use of problem-solving feeders in urban and rural areas

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Songbird use of problem-solving feeders in urban and rural areas

A Thesis

Presented in

Partial Fulfillment of the
Requirements for the Degree of
Master of Science

November 2019

BY

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Acknowledgements

Thank you to Jalene LaMontagne, who has given me plenty of feedback on my research and whatnot, but for what I most appreciate is her encouragement to keep a good balance and to enjoy life rather than overwork. Her advising could not have been more ideal for me, and I will take with me her kind words and encouragement.

Thank you to my committee members. Dennis Meritt always gave interesting and useful information on any bird I could ask about and was always extremely kind. Seth Magle for helpful advice and keeping me on track with urbanization. And a special thanks to Lydia Hopper who helped me keep my love of psychology alive while in a biology department, and always appreciated an on-theme outfit.

Thank you to the many people who helped me with my thesis. Many undergraduates volunteered their time to help sort videos, but a special thanks to Jessica Harris who helped me build feeders and Bre Connolly who sorted an ungodly number of videos and had the most positive attitude. Thanks to all the volunteers who had my feeder in their backyard for 9 weeks and dealt with all the madness. A very large thanks to Kim Boyle, who helped me recruit all my study volunteers and went with me to set up my feeders (and prevented me from having a full on meltdown in the process).

Thank you to Abby Leeper, Jill Sterman, Jessica Barton, and Jazmin Rios. Y'all are undoubtedly the best labmates I could have asked for and gave me so much support and encouragement. The shared love of cats and birds and all the cute and weird things made my time at DePaul so much fun. I am grateful for your friendship and will remember our lab shenanigans.

Thank you to Austin Plymill, my partner and biggest supporter. I apologize for the number of meltdowns I've had during this thesis, but I would have had many more if it wasn't for your encouragement and belief in me.

Abstract

Behavioral flexibility is important for animals to adapt to novel situations in their environment. It has been suggested that birds living in complex environments (e.g., urban areas) should be more flexible than conspecifics in less complex environments. Birds are a particularly well studied group, where novel foraging problems are used to assess flexibility and problem-solving performance of urban and rural animals of the same species; however, this is most frequently done in a lab setting with wild-caught birds originating from different habitats. Using a field-based method to test problem-solving performance should give additional insight into other factors influencing birds' flexibility. For my thesis research, to test birds' neophobia of a novel feeder and to assess problem-solving performance of songbirds in the wild, I conducted a four-phase field-based study in urban and rural areas, including both backyard and forest habitats. The phases included i) habituation, ii) initial problem-solving task, iii) color association task, and iv) reversal task. Birds' use of the feeder largely varied across time and habitats. Backyard birds used the feeder during the habituation phase in most sites (urban and rural) but stopped visiting the feeder once problem-solving was required to access food, suggesting that motivation plays a role in problem-solving and that birds' motivation differs across sites. Use of feeders by urban birds was low and may be due to the high presence of mammalian competitors (e.g., squirrels and raccoons). Only birds in rural forests used the feeder throughout the study, and generally solved the puzzle more quickly over time. Factors influencing feeder use, such as neophobia or competition, creates challenges for testing cognition in the wild, and opens opportunities to study other factors influencing urbanizations' effects on problem-solving.

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Chapter 1. Introduction

Cognition is defined as all the ways (i.e. perception, learning, memory, and decision making) animals take in information through their senses and process it in order to retain information and act on it (Shettleworth 2001). Cognition helps in tasks such as problem-solving, foraging, mate choice, and reproductive success. For instance, grasshoppers (*Schistocerca americana*) that were able to use associative learning to associate a visual cue with a nutritious food had higher growth rates than grasshoppers that were unable to learn the association (Dukas and Bernays 2000), while female threespine sticklebacks (*Gasterosteus aculeatus*) preferred males with higher inhibitory control (ability to ignore irrelevant stimuli) (Minter et al. 2017). Cognitive ability has also been linked to fitness (Dukas 2004): nesting pairs in great tit (*Parus major*) that were able to solve a barrier removal problem had higher nestling success than non-solvers (Cauchard et al. 2013), and females that problem-solved had a higher clutch size than non-solvers (Cole et al. 2012). Learning more efficient ways to forage, foraging flexibility, can also decrease time spent looking for food and thus decrease the amount of time that an individual may be at risk to predation (Dukas and Bernays 2000).

Urbanization and Behavior

Urbanization is categorized as a shift from a natural environment to one with habitat loss, fragmentation, high human and animal population densities, and an addition of noise and light pollution (Sol et al. 2013). Urbanization is rapidly increasing across the globe and it has been predicted that by 2030, over 60% of the world's population will live in cities (United Nations 2014). With rapidly increasing urbanization, animals are more likely to be affected by human disturbances (e.g., human-induced stressors such as noise and light pollution, litter, cars)

(Ditchkoff et al. 2006). Additionally, urban environments are highly complex and have an abundance of novel stimuli (e.g., litter, humans, pets, noise) (Echeverría and Vassallo 2008) and animals living in these environments may need to be more behaviorally flexible than animals living in less complex environments to survive these altered conditions (Griffin et al. 2017). Some urban-dwelling species have successfully shifted their behavior to accommodate living in human-dominated environments. For instance, great tits (*Parus major*) living in cities have a higher minimum frequency of their song compared to non-urban conspecifics, thought to help them avoid competing with the noise associated with urbanization (Slabbekoorn and Peet 2003). Bobcats (*Felis rufus*) and coyotes (*Canis latrans*) display less daytime activity in highly fragmented areas compared to conspecifics in less fragmented areas (Tigas et al. 2002), and marmosets (*Callithrix penicillata*) adjust their home range size and activity behaviors throughout the week based on human activity levels to avoid humans (Duarte et al. 2011). While urban landscapes present challenges for animals inhabiting them, they also provide opportunities.

Urban environments provide many opportunities for new sources of food, and it is predicted that individuals that use novel foraging innovations are better suited to urban environments (Griffin et al. 2017). Birds are a common group of organisms in cities and thus many species of birds appear to be well suited to living in urban environments (Griffin et al. 2017). Additionally, birds are the most extensively studied taxonomic group when it comes to urban wildlife (Griffin et al. 2017). Birds, mostly passeriformes, have been the subject of many cognitive studies, with a focus on innovation, neophobia, and behavioral flexibility (Griffin and Guez 2014). To test behavioral flexibility, investigations of problem-solving performance have

shown that birds can successfully complete novel problem-solving tasks to acquire food rewards (Boogert et al. 2008; Liker and Bokony 2009; Auersperg et al. 2011; Quinn 2011; Sol et al. 2011; Aplin et al. 2013; Bokony et al. 2013; Griffin and Guez 2014; Papp et al. 2014; Griffin and Diquelou 2015; Audet et al. 2016; Preiszner et al. 2017; Prasher et al. 2019). More recently, there has been an interest in the effects of urbanization on bird behavior and cognitive flexibility (Griffin et al. 2017), and there have been a variety of findings (Liker and Bokony 2009; Sol et al. 2011; Papp et al. 2014; Audet et al. 2016; Preiszner et al. 2017; Prasher et al. 2019). For example, wild-caught lab-tested urban bullfinches (*Loxigilla barbadensis*) solved food acquisition problems faster than non-urban conspecifics (Audet et al. 2016) and field-tested urban great tits problem-solved faster and more often than non-urban conspecifics (Preiszner et al. 2017). However, urban birds are not always better problem-solvers than non-urban birds and factors outside of urbanization have also been shown to affect birds' problem-solving success (Papp et al. 2014; Prasher et al. 2019). For example, in black-capped chickadees, rank was the only factor affecting problem-solving success (Prasher et al. 2019); and in house sparrows, body mass was the only factor that affected problem-solving success, with urban birds with more mass being the best problem-solvers (Papp et al. 2014).

Lab and Field Studies

Most studies testing the effects of urbanization on problem-solving performance in songbirds are done in the lab with wild-caught birds from different habitats (Liker and Bokony 2009; Sol et al. 2011; Papp et al. 2014; Audet et al. 2016; Kozlovsky et al. 2017; Prasher et al. 2019). In reviewing the literature, there appears to be only one study to test the effects of urbanization on problem-solving performance in the field (Preiszner et al. 2017). While lab-based tests have

the advantage of being a more controlled setting, it is extremely difficult to determine if birds would problem solve the same way in the lab as they would in their natural environment. In the wild there are potentially different factors affecting problem-solving performance (e.g., motivation, competition, risk of predation, environmental factors) that a lab-based studies cannot assess. Additionally, many studies on the effects of urbanization on problem-solving performance of songbirds take a binary view of urbanization and capture birds from only two types of sites for comparison (Liker and Bokony 2009; Sol et al. 2011; Papp et al. 2014; Audet et al. 2016; Kozlovsky et al. 2017; Prasher et al. 2019); however, it is likely that different levels of environmental use and anthropogenic influence affect problem-solving in different ways. Despite the loss of some control, testing the effects of urbanization of birds' cognitive flexibility in the field can potentially reveal other factors influencing problem-solving performance, such as motivation or competition. To gain a better understanding of the effects of urbanization on problem-solving performance of songbirds, I conducted a field-based study across four habitat types that included aspects of urbanization and land use, in which participation by birds was voluntary.

Thesis Research

For my thesis research, I tested problem-solving performance of songbirds in the wild, using two levels of urbanization (urban and rural) with two land-use types for each (backyards and forests). My thesis research had two goals: (1) To test the neophobia of birds in the wild in relation to a novel feeder, and (2) to assess problem-solving performance and flexibility of songbirds in four differently-urbanized habitats in the wild. I conducted my thesis research in Cook County, IL, which includes the city of Chicago, the third most populous city in the United

States (United States Census Bureau 2010) and surrounding rural counties. The city of Chicago is a highly urbanized environment with both backyard and forest land-use types found within; additionally, the rural surrounding areas allow for a comparison of similar species in the area. I designed and built novel bird feeders to test neophobia (bird-feeder use), problem-solving performance (latency to solve and number of correct solves), and behavioral flexibility (association and reversal learning) of songbirds in four habitats (rural forests, rural backyards, urban forests, urban backyards).

I hypothesized that habitat would affect birds' neophobia towards a novel feeder. I predicted that urban birds would be less neophobic towards a novel problem-solving feeder as they live in a complex environment with a high level of novel stimuli, and the ability to approach a novel object that could be a source of food is valuable for these birds. Additionally, I predicted that urban backyard birds would have the lowest level of neophobia towards a novel feeder, as backyard birds readily use feeders and should associated them as an important source of food. Second, I hypothesized that habitat would affect problem-solving performance (time to solve and number of solves) and behavioral flexibility (measured via a color association and reversal task). I predicted that urban backyard birds would be the best problem-solvers (fastest and most solves) of the four bird groups I studied as they live in the most complex environment, and many previous studies have found that urban birds are better problem-solvers than rural birds (Liker and Bokony 2009; Sol et al. 2011; Audet et al. 2016; Kozlovsky et al. 2017; Preiszner et al. 2017). Additionally, I predicted that urban backyard birds would be the most behaviorally flexible, as this is also important for successful city living.

The following chapter presents my thesis research, conducted in collaboration with Lincoln Park Zoo's Urban Wildlife Institute and Lester E. Fischer Center for the Study and Conservation of Apes. In the Appendix is a short article I prepared for WingTips, the Illinois Ornithological Society newsletter, describing the study.

Chapter 2. Songbird use of problem-solving feeders in urban and rural forests and backyards

Introduction

Behavioral flexibility is the ability of animals to change their behavior to adapt to variability in environmental conditions (Audet and Lefebvre 2017). There is inter- (Sol et al. 2005) and intra- (Boogert et al. 2010) species variation in flexibility, and animals with more behavioral flexibility are better able to adapt to new conditions in their environment and do so more rapidly than behaviorally-inflexible animals (Reader 2003), resulting in enhanced fitness outcomes (Dukas 2004). Foraging flexibility is an aspect of behavioral flexibility, where animals with flexible foraging strategies tend to be less neophobic and better able to exploit new foraging opportunities (Martin and Fitzgerald 2005). Thus, behavioral/foraging flexibility is likely beneficial for animals living in environments with greater levels of distinct, novel stimuli, such as urban areas (Sol et al. 2013).

Cities are human-dominated landscapes that have been highly modified from their natural state to one filled with buildings, roads, cars, light and sound pollution, increased human population density, and non-native animals and plants etc. (Sol et al. 2013). In addition, urban environments are highly complex and unpredictable with an abundance of novel anthropogenic stimuli (Echeverría and Vassallo 2008). These novel stimuli within a complex environment may require animals to adopt new foraging innovations, which make individuals better able to attain food (Griffin et al. 2017). Some problem-solving research on urban and non-urban birds supports this theory. Urban house sparrows (*Passer domesticus*), great tits (*Parus major*), barbados bullfinches (*Loxigilla barbadensis*), common mynas (*Acridotheres tristis*), and mountain chickadees (*Poecile gambeli*) were all better problem-solvers than their

non-urban conspecifics (Liker and Bokony 2009; Sol et al. 2011; Audet et al. 2016; Kozlovsky et al. 2017; Preiszner et al. 2017). However, other studies report better problem-solving performance by non-urban, compared to urban, members of a species (e.g., (Prasher et al. 2019), while other studies find no effect of birds' local environment on their problem-solving success (e.g., Papp et al. 2014). Furthermore, there are likely interaction effects between the local environment and the current state of birds, such as hunger, rank, and age. For example, while black-capped chickadees (*Poecile atricapillus*) were found to be more successful at problem solving in non-urban, compared to urban areas, this effect was more pronounced for dominant than subordinate birds (Prasher et al. 2019).

Most studies testing the effects of urbanization on problem-solving performance in songbirds are done in the lab with wild-caught birds from different habitats (Liker and Bokony 2009; Sol et al. 2011; Papp et al. 2014; Audet et al. 2016; Kozlovsky et al. 2017; Prasher et al. 2019). While lab-based tests have the advantage of being a more controlled setting, it is extremely difficult to determine if birds would problem solve the same way in the lab as they would in their natural environment. Despite the loss of some control, testing the effects of urbanization of birds' cognitive flexibility in the field can potentially reveal other factors influencing problem-solving performance, such as motivation or competition. In reviewing the literature, there appears to be only one study to test the effects of urbanization on problem-solving performance in the field. This field study, on great tit (*Parus major*) nesting pairs, tested the performance of urban and forest birds on two problem-solving tasks, a barrier-removal task and a peg-removal task (Preiszner et al. 2017). They studied 55 pairs of birds living in two urban and two forested habitats in Hungary and found that urban birds solved the tasks faster and

more often than forest birds, an effect that was driven by the performance of the females (Preisner et al. 2017). Given the success of this previous field-based study exploring urbanization on bird cognition, we conducted a field-based study of the links between urbanization and problem solving across four habitats (20 sites) that differed in the degree of human disturbance.

While most previous studies evaluating the impact of local ecology on bird cognition have tested birds across two conditions (e.g., urban or non-urban), we wished to gain a more nuanced perspective on how human land use influences birds' problem solving and foraging success. Therefore, we studied birds across four different habitats representing a 2x2 design with surrounding urbanization (rural and urban) by human-impact (forests and backyards) as our modifiers and with five sites per habitat type. Forests were used to represent a relatively lower level of human impact and backyards as a relatively higher degree of human impact as there are higher anthropogenic influences in backyards. We had two main objectives with this experiment. First, we assessed birds' neophobia towards a novel bird feeder across the four habitats. Second, we assessed birds' problem-solving performance and flexibility across these four habitats. We hypothesized there would be variation in the birds' use of urban and rural bird feeders, and we predicted that birds in urban sites would use the feeders more often as birds in urban areas may be more accustomed to novel stimuli being present than would birds in rural habitats (Echeverría and Vassallo 2008). We also predicted that birds in peoples' backyards would visit the feeders more than birds in forests as backyard birds readily use feeders provisioned by homeowners (Bonnington et al. 2014; Hanmer et al. 2018). Thus, overall, we predicted that urban backyard feeders would have the most activity of the four

habitats. We also hypothesized that the birds' problem-solving performance (latency to solve the novel task and the number of solves) and flexibility (associative learning and reversal learning success) would vary by habitat. We predicted that birds' problem-solving performance and flexibility would be higher at urban than rural sites, and highest in urban backyard, due to these birds living in a highly complex environment. This study will work to provide further insight into factors affecting problem-solving success of birds in the wild.

Methods

Study area

Our study was conducted in northeastern Illinois, USA from mid-August to mid-October 2018. Our urban area included locations in Cook County, which covers 2,450 km², with a mean population density of 2,129 people·km⁻², and includes Chicago, the third most populous city (2.7 million) in the United States (United States Census Bureau 2010) (Fig 1). Our rural area consisted of locations in surrounding counties including Lake County (1,150 km², 612 people·km⁻²), McHenry County (1,560 km², 198 people·km⁻²), and Will County (2,170 km², 310 people·km⁻²) (United States Census Bureau 2010). The mean distance of the urban and rural feeding stations from Chicago's city center was 18.9 ± 6.4 km and 74.0 ± 17.9 km, respectively.

We set up a total of 20 sites, with a single novel bird feeding station at each. Sites were qualified as 'rural' if the city/town had a population density of <1000 people·km⁻², and as 'urban' if >2,700 people·km⁻² (United States Census Bureau 2013). Ten feeding stations were located in urban and ten in rural areas. Across the two habitat types, we further divided the feeding stations across two land-use types: residential backyards and forest preserves with five

feeding stations per habitat/land-use category (Fig 1). Using ArcGIS, mean human population density (\pm SD, range) within a 1.5km diameter area around each feeding station for each habitat was estimated using 2010 census data. Rural forests had 92 people·km⁻² (\pm 66, 11 – 173 people·km⁻²), rural backyards had 1,063 people·km⁻² (\pm 855, 119 – 2031 people·km⁻²), urban forests had 2,155 people·km⁻² (\pm 1100, 608 – 3,685 people·km⁻²), and urban backyards had 6,600 people·km⁻² (\pm 2,718, 3,743 – 11,000 people·km⁻²).

Backyard sites were selected based on eligibility of volunteers that met urban/rural requirements and could commit to the duration of the study. To recruit volunteers, we used local contacts and social media. Areas surrounding backyards included buildings, some grassy space, and roads nearby. All backyard sites included grass with trees scattered throughout the yard, and differences between urban and rural backyards included that the overall size of yards was larger in rural areas with lower building densities (Fig. 2). If the participants had any bird feeders in their yard prior to our study, we asked them to remove or empty their feeders for the duration of the study. All forest sites were located in County Forest Preserves, and included grassy areas and trees and a path nearby with feeders placed on forest edges, which were used because songbirds prefer edges (McCollin 1998). To avoid birds visiting multiple feeding stations, we set up all feeding stations a minimum of 1.5 km apart, which is outside of the average home range for target songbird species: black-capped chickadees (*Poecile atricapillus*) (Odum 1942), house sparrows (*Passer domesticus*) (Vangestel et al. 2010), and northern cardinals (*Cardinalis cardinalis*) (Dow 1969).

Feeding Station Design

Lid lifting tasks have been used to test songbird problem-solving performance and are a good test of ability without being overly difficult (Boogert et al. 2010; Aplin et al. 2013; Bokony et al. 2013; Griffin and Guez 2014; Papp et al. 2014). We adapted this common problem-solving task by creating a lid-lifting task placed on a platform feeder. A previous study in our lab had a feeder low to the ground that did not attract many birds, so we used a raised feeder (1.25 m post, 5cm x 10cm) to try to attract songbirds. A flat platform (30cm x 40cm) was affixed on top, with 8 individual plastic bowls (5cm wide by 2cm deep) each with a lid that the birds needed to lift to obtain food inside (for phases 2-4 of the study). The bowl lids (6cm diameter) were made from duct tape and affixed using hot glue. Lids could be lifted open by birds using their head. To reduce tampering by squirrels, raccoons, larger birds, etc. we constructed and affixed a chicken wire box (40cm x 28cm x 23cm) around the feeding platform with three openings (6.5cm diameter) on one side large enough for small songbirds to enter. We attached bowls to the feeding platform with hook-and-loop tape to allow for changing the bowls between study phases (see below).

Experimental Phases

We ran the study for 61 days with four distinct phases: habituation (days 1-14), problem-solving task (days 15 - 35), association-learning task (days 36 - 49) and reversal-learning task (days 50 – 61; Fig. 3). To attract birds to the feeding station and assess feeder neophobia, we ran an initial habituation phase in which we put out the bird feeder with food and used bowls with no lids. To attract songbirds, we used shelled sunflower seeds as the food reward, which have the benefit of being a work-free meal because the shells are already removed (Project Feederwatch 2019). We placed 30g of food in the bowls weekly, split

between two refill days per week. A pilot study demonstrated that this quantity of food was a surplus for feeders with bird activity (Miller, personal observation) so we continued with this approach throughout the study. After habituation, for the initial problem-solving task (phase 2), we used bowls with gray lids, which required birds to learn to open the lids in order to receive food. Gray was used as a neutral color in between the black and white colors used in the next two phases. Next, we implemented association- and reversal-learning tasks to test the birds' behavioral flexibility (Boogert et al. 2010). To test the birds' association-learning ability, in phase 3 we used the same feeder but replaced half the grey lids with black lids and four with white lids and we randomly assigned the location of the black and white lidded bowls on the feeder. For this third phase of the study, we only baited the bowls with white lids. Then, to test behavioral flexibility of birds, to determine if they could change their problem-solving focus, for the fourth and final phase of the study, and to test the birds' reversal-learning ability, we now only baited the bowls with black lids.

Video Monitoring and Coding

At each site, we attached a motion-activated trail camera with night vision (Bushnell Trophy Cam HD) to a tree adjacent to the feeder (1m away) (with one exception, in one urban yard a wooden post was used instead of a tree) to monitor feeding stations and record any animal activity on or near the feeder. The feeder was positioned such that the three openings into the mesh cage were on the same side as the camera. In forests, we also chained the feeding station to the tree to keep from tampering. Cameras recorded 60 seconds of video when motion triggered, with a minimum of a 3 second delay in recording between activations.

For coding, we used only videos containing birds that landed on the feeding station; if a bird triggered the camera but did not land on the feeder, it was not used. In each video, a bird was given a unique identifier based on the video identification number. If a video had more than one bird, each bird was given an individual ID; if a bird was on screen and then left visibility followed by a bird appearing in the video after the first bird appearance, it was given a separate bird ID. Observations were not blind, however, to prevent bias in data entry as videos were watched over time, we watched and cataloged behaviors in 10 videos from one site before switching to another. From each video coded, we identified the species of all birds that landed on the feeding station (anywhere on the feeder, including the outside of the wire enclosure) and recorded the time of day. For phase 1, habituation, we coded for each bird whether they entered the feeder or remained on the outside of the enclosure. For phases 2 – 4 (initial problem-solving task, associative-learning task, reversal-learning task), we coded whether the bird entered the wire enclosure, and if so, the bird's attempts to manipulate lids (and whether successful or not). To assess latency to enter and problem-solve we also recorded the time stamp for each behavior coded (Table 1).

Lastly, we used videos with animals other than birds and humans to collect information on broad species richness of each habitat, by randomly selecting 30 videos from each site. We watched and recorded the number of each non-bird, non-human species present in the video which we then used to calculate species richness.

Statistical Analysis

Using Shannon's Diversity Index, we calculated species richness and diversity of birds for each site, using all birds that landed on the feeder throughout the study. We calculated weighted means and standard deviations using the *radiant* package in R. We used a weighted linear model to determine if there was a difference in richness and diversity with urbanization (rural = 0, urban = 1) and land-use (forest = 0, backyard = 1) as main effects and their interaction, with sites weighted based on bird abundance. To test whether the number of visits to the feeder differed in each of the four habitats among each phase, we used a G-test of independence (using *DescTools* in R); we pooled all visits to the feeder by habitat and separated by phase. We used a weighted linear model to determine if there was variation in latency (date of first arrival on the feeder) for birds with urbanization (rural = 0, urban = 1) and land-use (forest = 0, backyard = 1) as main effects and an interaction, with each site weighted for bird abundance. To calculate weighted means and standard deviations, we used the *radiant* package in R. We used a generalized linear mixed effects model to determine if there was a difference in willingness to enter the feeder (as a binary variable: did not enter = 0, entered = 1) with main effects of bird species (black-capped chickadee as reference species), study phase (habitation as reference phase), urbanization (rural = 0, urban = 1), and land-use (forest = 0, backyard = 1) with site as a random location (*lmerTest* in R).

For these analyses on problem-solving performance, we used data from the three phases that required lid lifting, separated by phase. We used a linear mixed effects model with site as a random effect to test if there was a change in problem-solving time among the three problem-solving phases of the study (*nlme* in R). To determine if there was a change in problem-solving latency within each phase of the study, we used linear regressions. We

analyzed data for the initial problem-solving task from days 26 to 60 because videos from days 15 – 25 were not available due to technical issues (some cameras died or recorded one second videos instead of 60, some cameras shifted and angled so that feeder was not in view). We also tested if there was variation in efficiency (a decrease in failed attempts to problem-solve over time) and persistence (continued attempts to problem-solve in the presence of continued failures) in problem-solving over time. To assess efficiency, we did a linear regression on the number of failed attempts before a success to the day of the study, and to assess persistence we did a linear regression on the number of fails before attrition (giving up) to the day of the study.

We also calculated species richness for all animals at each site. Any animal that was on or in the feeder was used to determine overall animal species richness. We used a linear model to determine if there was a difference in overall species richness with urbanization (rural = 0, urban = 1) and land-use (forest = 0, backyard = 1) as main effects and an interaction.

We conducted all analyses in R version 3.5.2.

Results

We collected data on a total of 2,574 bird visits across the 20 sites throughout the course of the study. Bird visits to the feeders were higher in rural areas (1,585 in Rural Forest; range 0 - 942, comprising 62% of total observations; 862 in Rural Backyard; range 6 - 450, 33%) with less birds visiting feeders in urban areas (4 Urban Forest; range 0 - 3, 0.16%; 123 Urban Backyard; range 0 - 106, 5%). The most abundant bird species present at the feeder throughout the study were: black-capped chickadees (1,713; 67%), house finches (701; 27%), house sparrows (72; 3%), and

northern cardinals (57; 2%). Videos revealed a small number of other species visiting the feeders (fewer than 10 visits per species) for a total of 23 (0.9%) visits (e.g., warblers, woodpeckers, wrens)), as well as a small number of birds that were unidentifiable due to their position in the video ($n = 7$; 0.003%). Unidentifiable birds were not used in analysis, and the other 'rare' birds were only used for species diversity, species richness, and date of first appearance.

During the habituation phase (phase 1), birds were present at sites within all habitat (range: Rural Forest 0 – 459, Rural Backyard 0 – 439, Urban Forest 0 – 1, Urban Backyard 0 – 106), however birds were only recorded visiting the feeders in rural forests after the habituation phase (i.e. no visits to feeders were recorded at the urban backyards, urban forests or rural backyards in phases 2, 3, and 4). There was a significant difference in the number of visits (based on all bird species) by phase across habitats (Fig. 4; $G = 1221.4$, $df = 9$, $p < 0.001$). Mean species richness of birds on the feeder was 6.28 ± 1.14 in rural backyards (weighted mean \pm SD) and lower in the other habitats (rural forest = 1.82 ± 0.98 , urban forest = 2.5 ± 0.87 , urban backyard = 1.92 ± 0.27). There was an overall significant difference in richness ($F_{3,9} = 12.73$, $p = 0.001$), with backyard land-use having significantly greater species richness than forests ($p = 0.002$) but there was no effect of urbanization ($p = 0.94$) or an interaction between urbanization and land-use ($p = 0.58$). There was also a significant influence of habitat on Shannon's Diversity Index for birds ($F_{3,9} = 12.05$, $p = 0.002$, $r^2 = 0.80$) based on land-use type with backyards having a higher diversity ($p < 0.001$), but there was no significant effect of urbanization ($p = 0.44$) or the interaction between urbanization and land-use ($p = 0.52$). The diversity index for rural backyards (weighted mean \pm SD: $H = 0.48 \pm 0.18$) was only slightly lower than urban backyards

($H = 0.62 \pm 0.19$). Species diversity of birds was lowest in rural forests ($H = 0.02 \pm 0.02$), with black-capped chickadees the most dominant species and highest in urban forests as they had more evenness ($H = 0.83 \pm 0.48$), but visits to the urban forest feeders were very uncommon.

First Appearance

The earliest birds appeared at a feeder during the habituation phase was on day 2 of the study, and this was by a blue jay (*Cyanocitta cristata*) at a rural forest habitat. The weighted mean day of first appearance for feeders ('1' represents the first day of the study; rural forest = 3.17 ± 0.98 , rural backyard = 4.02 ± 3.87 , urban forest = 3.00 ± 0 , urban backyard = 8.61 ± 12.02) did not differ significantly based on land-use (backyard vs. forest), urbanization (urban vs. rural), or their interaction (weighted linear model, $F_{3,9} = 0.34$, $p=0.8$, $r^2 = 0.1$). Thirteen sites (including all habitats) had birds present at some point during the study, and eight sites had birds appear within the first week of the study, with the other five sites not having birds arrive until after the beginning of phase 2 (initial problem-solving task). Sites with birds that first appeared after the beginning of phase 2 all had fewer than 10 birds at the feeder throughout the entire study (with a range of 1-9 visits).

Willingness to Enter

There was no significant main effect of urbanization (OR = 0.0000008, 95% C.I. = 0.00 – Inf, $p = 0.98$) or land-use (OR = 0.523, 95% C.I. = 0.19 – 1.46, $p = 0.22$) on birds' willingness to enter the feeder throughout the study. Compared to habituation phase there was no significant difference compared to the initial problem-solving phase (OR = 1.69, 95% C.I. = 0.99 – 2.88, $p = 0.06$, however, there was a significant difference in the association phase (OR = 2.05, 95% C.I. =

1.42 – 2.95, $p < 0.001$) and the reversal phase (OR = 1.73, 95% C.I. = 1.02 – 2.94, $p = 0.04$). There was also a significant effect of species, where relative to black-capped chickadees, both house finches and house sparrows were significantly less likely to enter the feeder (House Finch: OR = 0.097, 95% C.I. = 0.04 – 0.25, $p < 0.001$; House Sparrow: OR = 0.01, 95% C.I. = 0.003 – 0.05, $p < 0.001$; Table 1). Birds that did not enter the feeder during the habituation phase of the study were able to reach through the wire enclosure to retrieve food without entering, which was what 47% of birds during this phase did.

Problem-solving latency

Black-capped chickadees were the only species to visit the feeders during all four phases of the study, and only in rural forest sites, therefore, the remainder of our results focus on this species at these sites. Additionally, only eight birds ever attempted to open a lid of the wrong color, thus we were unable to test behavioral flexibility; however, we did use data from the color association and reversal task phases to test problem-solving latency, efficiency, and persistence. Per visit, the weighted mean time (\pm SD) for black-capped chickadees to solve the task within the initial problem-solving phase (phase 2, days 25 – 35) was 7.02 sec (\pm 6.24), for associative learning task in phase 3 (days 36 – 49) it was 3.97 sec (\pm 0.09), and for the reversal learning task in phase 4 (days 50 – 61) it was 4.70 sec (\pm 1.60) (Fig. 5). There was a significant difference in the solve time among phases with birds faster in the color association and reversal tasks than in the initial problem-solving task (linear mixed effects, $F = 8.92$, $df = 1$, $p = 0.003$). Within phases, over days, the time to successfully problem-solve decreased significantly for black-capped chickadees in rural forest sites during phase 2 ($F_{1,43} = 10.23$, $p = 0.002$). However,

the solve-time did not change significantly within phase in phase 3 ($F_{1,117} = 1.21$, $p = 0.27$) or phase 4 ($F_{1,147} = 0.36$, $p = 0.55$).

Problem-solving efficiency and persistence

Out of 1224 total attempts to solve throughout all four phases of the study there were 800 total successful solves (65%), and 149 of these solves (19%) were preceded by a failed attempt in the same visit (Fig. 6). A solve was counted as successful if a bird was able to lift the lid enough to get their head in enough to retrieve food, regardless of whether the bowl had food in it or not. There was a significant decrease in the number of fails preceding a success (i.e. an increase in efficiency) across phase 2 when the birds were first presented with the problem-solving task (linear regression, $F_{1,41} = 6.88$, $p = 0.01$, $r^2 = 0.14$), but not in the association-learning task (phase 3) ($F_{1,45} = 0.48$, $p = 0.49$, $r^2 = 0.01$) nor the reversal-learning task (phase 4) ($F_{1,38} = 2.90$, $p = 0.10$, $r^2 = 0.07$). Sixty-eight birds with failed attempts ended in attrition (5%). The number of fails before attrition (persistence) did not differ over time during the initial problem-solving task ($F_{1,21} = 0.27$, $p = 0.61$, $r^2 = 0.01$), the association-learning task ($F_{1,25} = 0.44$, $p = 0.51$, $r^2 = 0.02$), nor the reversal-learning task ($F_{1,7} = 0.02$, $p = 0.90$, $r^2 = 0.002$).

Species Richness and Diversity – Birds and mammals

To examine potential interspecific interactions that could affect bird use and behavior at feeders, we calculated richness of all species using the feeders. There was a significant effect on species richness of all animals related to habitat ($F_{3,15} = 3.56$, $p = 0.04$, $r^2 = 0.42$) based on land-use ($p = 0.028$), but no significant effect of urbanization ($p = 0.88$) or the interaction ($p = 0.14$). Mean species richness of all animals was highest in rural backyards (4.20 ± 2.17) then urban

backyards (2.00 ± 0.71), and lowest in forest sites (rural forest = 1.75 ± 0.96 , urban forest = 1.60 ± 1.34). Mammals at the feeding stations included squirrels, raccoons, chipmunks, and mice. Raccoons (*Procyon lotor*) were present almost exclusively in urban forests (but also at one rural forest feeder), gray squirrels (*Sciurus carolinensis*) were present exclusively in urban backyards, eastern chipmunks (*Tamias striatus*) and field mice (*Apodemus sylvaticus*) were present at forest feeders.

Discussion

The goal of our field-based study was to determine if birds' levels of neophobia and behavioral flexibility differed across four habitats that represented different levels of urbanization and land-use types. Birds were observed to visit our feeding station in three out of four of our habitats (rural forests, rural backyards, urban backyards) during phase 1 (habituation), with extremely low use in urban forest feeders. Birds used the feeder most during the habituation phase, when food was freely available, but visitation stopped in most habitats when the cost to obtain the food was increased and problem-solving was required. Our prediction that urban and backyard birds would use feeders more readily than rural and forest birds was not supported as we found that rural birds used the feeder most frequently (rural forest = 62%, rural backyard = 33% of all observations) with little urban activity (urban forest = 0.16%, urban backyard = 5% of all observations). Contrary to our predictions, rural forest birds were the only birds to attempt to problem solve. For these sites, the latency to solve decreased over the course of the initial problem-solving task. We suggest that species interactions and environment explain many of the patterns we observed.

Black-capped chickadees in rural forests were the only birds to attempt to problem-solve and the latency to solve at these sites decreased over time from the initial problem-solving task to the other solving tasks. We showed increased problem-solving performance despite that we were unable to test behavioral flexibility (as only a handful of birds ever attempted to open wrong colored lids $n=8$). While we were unable to compare performance of rural black-capped chickadees to that of urban chickadees, our results do somewhat agree with a recent finding on black-capped chickadees. In this study, they found that dominant rural black-capped chickadees were the best problem-solvers and that problem-solving performance was more dependent on dominance status than location with dominant birds outperforming subordinates (Prasher et al. 2019). It's possible that urban birds have plenty of easier to access resources nearby that they could use, so they did not need to attempt to use a novel feeder (Papp et al. 2014; Preiszner et al. 2017). Additionally, since food was not visible during the last three phases (initial problem-solving task, color association and reversal tasks) of the study, it is possible that birds that are not used to looking for hidden food (e.g., urban birds because of abundant resources) may not have been motivated to search for food in our feeders if there was other food available in the area (Prasher et al. 2019).

Unexpectedly, there were very few uses of the feeder by urban forest birds for the duration of the study. In a review on the factors influencing behavioral flexibility, including neophobia, there are mixed findings on whether urban or non-urban birds tend to be more neophobic (Griffin et al. 2017). Some studies have found that urban birds are less neophobic than non-urban birds in both lab (Sol et al. 2011) and field (Tryjanowski et al. 2016) studies. Other research has found conflicting results, that urban birds are more neophobic than non-

urban birds, also in both lab (Audet et al. 2016) and field (Echeverría and Vassallo 2008) studies. These studies on the impacts of urbanization on neophobia collected birds from only two levels of urbanization, not considering different types of land-use within each urbanization type. With our study, we investigated forests and backyard land-use types and found different levels of feeder use between land-use within urbanization classification, which suggests there may be an effect of land-use rather than urbanization on neophobia. There is currently not a conclusive answer to whether urban or non-urban birds should be less neophobic. It has been proposed that birds that are less neophobic would initially do better in urban environments, but that this is only beneficial for invading populations (Sol et al. 2011). Another theory is the dangerous niche hypothesis which suggests that animals inhabiting a dangerous niche (e.g., highly urbanized/complex environments) should be more neophobic (Greenberg 2003). Birds living in Chicago, a well-established urban area, may be well past the colonization phase, and thus being more neophobic is more beneficial to these birds. Additionally, due to urban environments being complex, there is a high level of novel stimuli, so being neophobic might keep these birds safe. While backyards are likely more complex than forests due to human presence and an abundance of novel stimuli, the response of birds to supplementary feeders is generally well received (Robb et al. 2008a) and they may have a decreased neophobic response to feeders. This willingness to use supplementary feeders may explain why we had some activity at feeders by urban backyard birds, but not much by urban forest birds.

We found that birds in three out of our four habitats used a feeder when food was available freely but stopped using the feeder once lids were added. In most studies testing problem-solving performance of songbirds, birds were tested in a lab and either were deprived

of food beforehand or were in a test cage with no other food sources (Liker and Bokony 2009; Sol et al. 2011; Papp et al. 2014; Audet et al. 2016; Kozlovsky et al. 2017; Prasher et al. 2019). In our study, participation was voluntary, and birds had the ability to go elsewhere to search for food. With the decline in bird activity with the addition of lids in phase 2 onwards, our results suggest that an increased effort (problem-solving) to get food may be too high of an energy cost when food is freely available elsewhere. During the habituation phase, it was possible for birds to get food without entering the feeder (they could reach through the wire) and this is what 47% of birds did. However, to problem-solve it was necessary for birds to also enter the chicken wire enclosure which could have acted as an additional cognitive barrier (an extra problem) or additional effort of entry for birds. When given a problem-solving task with only one step, all Barbados bullfinches were able to successfully get food; however, when these bullfinches were given a two-step problem-solving task, only 26% of rural birds and 50% of urban birds were able to successfully solve (Audet et al. 2016). One study found that, when given the choice, birds preferred to use an uncaged rather than caged feeder (Hanmer et al. 2018), so a caged feeder may not be the best method to attract and keep birds, potentially because it is a larger risk to enter an enclosure. Also, it is possible that birds living in backyards or urban areas had access to other feeders (Tryjanowski et al. 2016) or food that was more easily accessible nearby, whereas birds living in rural forests did not have as many options and were more willing to work to get food.

Mammals were present at some feeders and may have impacted use by birds. Issues with squirrels using bird feeders is common with backyard feeders (Hanmer et al. 2018) and our attempts to deter them (the wire enclosure) were not entirely successful. Feeders that had

heavy mammal activity (particularly urban forest and urban backyards) also had very little or no bird activity, and the mammal presence may have deterred birds from using the feeders. Wild grey squirrels reduced bird use of feeders by 99% and this effect lasted beyond the duration of squirrel visit (Hanmer et al. 2018). Also, simulating use of a feeder with a stuffed squirrel found that birds used the feeder 98% less when the squirrel was present versus when there was no stuffed squirrel (Bonnington et al. 2014). According to the birding website eBird.org, there are birds consistently spotted at the locations we had feeders, so it is likely that there were birds in the area, but possible that they were deterred by mammals.

With this study, we also illustrate some of the challenges with testing problem-solving in the wild. We did not trap animals and therefore could not identify individuals. Birds reside within home ranges (Odum 1942; Dow 1969; Vangestel et al. 2010), and it is likely there were opportunities for reuse by individuals during the study. In field-based studies there is an unpredictable aspect not experienced in the lab. Participation in the field was voluntary, and we could not ensure participation by birds at all sites. Additionally, had we done this study in winter when food is more scarce, we may have been able to attract more birds, as winter supplementary feeders are an important source of food for overwintering birds (Robb et al. 2008b). Regardless of these challenges, setting up a field study of bird neophobia and problem solving, in the context of other food resources, competitors, and habitat complexity provides information on use in the context of broader motivations.

Almost all studies on the effect of urbanization on problem-solving performance of songbirds are done in the lab and find that urban birds tend to outperform non-urban conspecifics, however, we found that urban birds did not even attempt to problem-solve. This

suggests that urban birds may be better problem-solvers when they are forced to be, but in the 'real world' it might not be necessary to problem-solve and they can work 'smarter' not harder. Future work should look at the motivation (e.g., food availability in the area, seasonality, competition, neophobia) for problem-solving to determine if that plays a part in success. Additionally, with radio frequency identification technology, field-based studies can better track individuals and their behavior, making it possible to do a larger scale study to determine what factors influence problem-solving performance of songbirds in the wild.

Table 1 Ethogram with behaviors and their descriptions used for behavioral analysis

Behavior	Description
On feeder	Bird is on the feeder on the outside of the wire enclosure
In feeder	Bird is within the wire enclosure
Enter	Bird has gone into the wire enclosure
Manipulate lid	Bird is touching lid with beak
Success	Bird opens a lidded bowl enough to reach head inside
Fail	Bird that was manipulating lid does not open a lidded bowl
Wrong	Bird is manipulating lid of a bowl that does not have food in it (color association and reversal tasks)

Table 2 The total number of bird species that were seen on the feeding stations, the number of clips in which a bird entered the feeding station, and the percent of birds that entered the mesh cage to access the feeder. Note, these data are only for the common bird species at each habitat

Habitat	Species	Total	Entered	Percent entered
Rural Forest		1586	1258	79%
	Black-capped chickadee	1578	1255	80%
Rural Backyard		862	142	16%
	Black-capped chickadee	80	53	66%
	House Finch	701	86	12%
	House Sparrow	11	1	9%
	Northern Cardinal	50	0	0%
Urban Forest		4	0	0%
	Black-capped chickadee	1	0	0%
	Northern Cardinal	1	0	0%
Urban Backyard		123	45	37%
	Black-capped chickadee	54	43	80%
	House Sparrow	61	2	3%
	Northern Cardinal	6	0	0%



Figure 1. a) Map of the Chicago-land area designating feeding stations. Red icons indicate rural sites, blue icons indicate urban sites. Forest preserves and backyards are indicated by a rectangle and square, respectively. b) Camera box (attached to tree) and feeding station setup, c) and video still of a black-capped chickadee in the feeder during the color association phase.



Figure 2. Aerial view of the 20 feeding station sites. Images were taken using Google Earth with the top of the images facing north. Images show a 1 ha area centered on each feeder location.

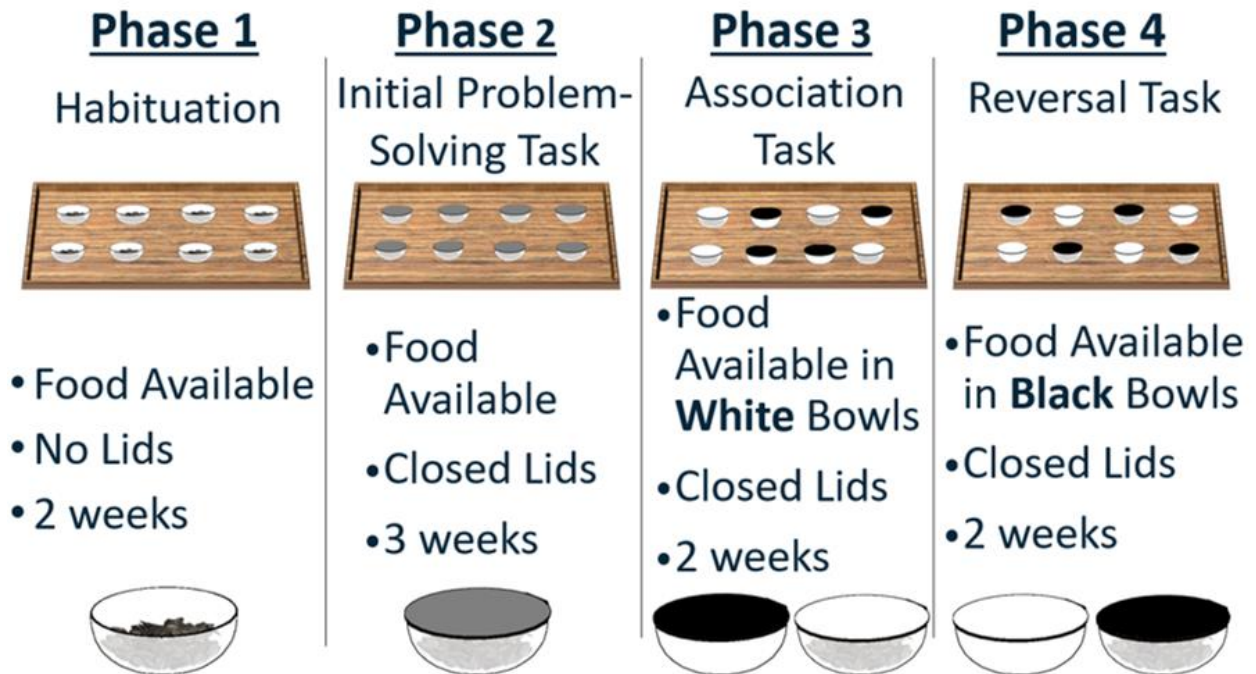


Figure 3. Phases of the study indicating the setup and duration of each phase of the study: habituation, initial problem-solving task, association task, and reversal task.

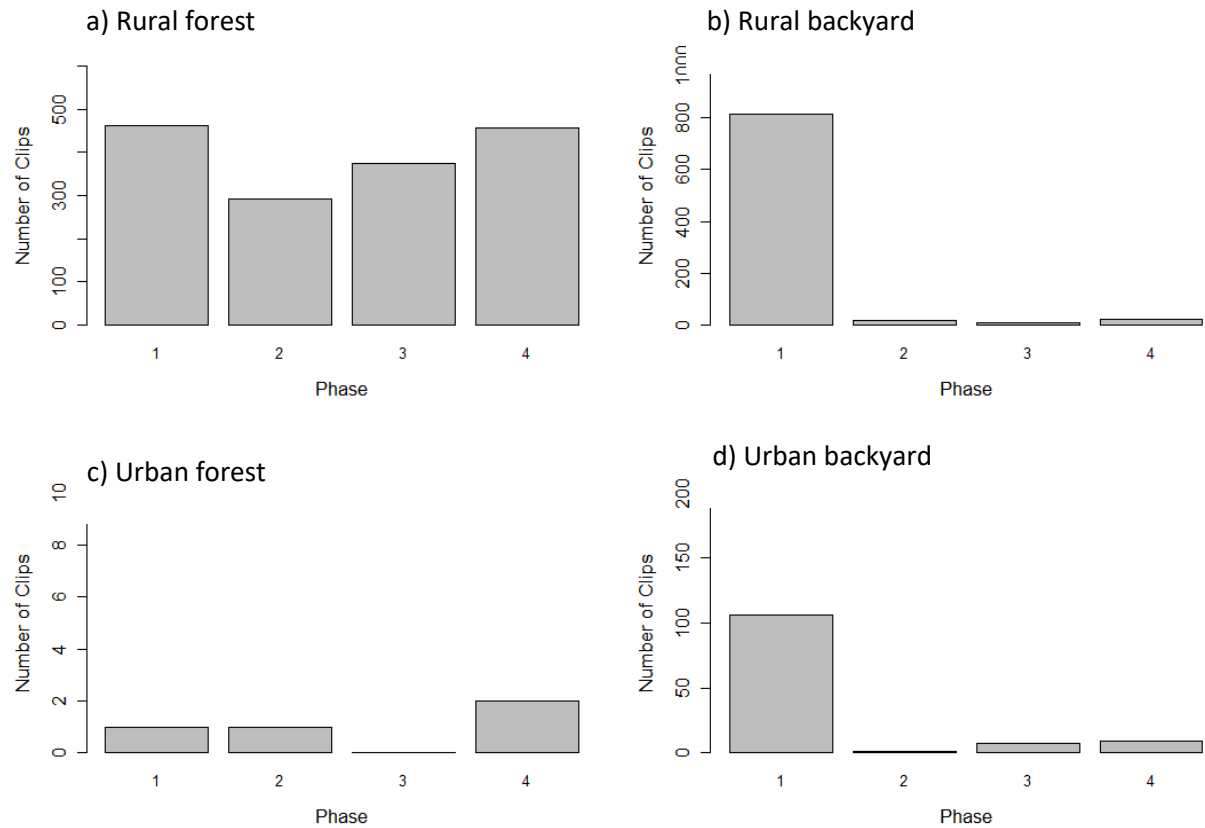


Figure 4. Visitation at each of the habitats based on the number of videos of birds for each phase for a) rural forests, b) rural backyards, c) urban forests, and d) urban backyards. Phase 1 (habituation) was days 1 – 14, Phase 2 (initial problem-solving task) was days 15 – 35, Phase 3 (color association-learning task) was days 36 – 49, and Phase 4 (reversal-learning task) was days 50 – 60. Note that y axes scales are not the same on all graphs.

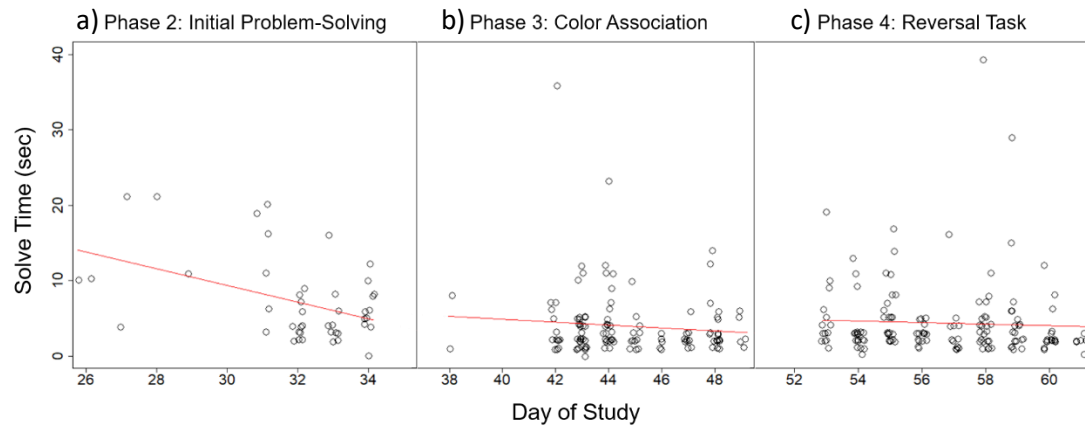


Figure 4. Latency from when the bird first entered the feeder until a successful solve for each day of study. a) Days 26 – 35 for phase 2 (initial problem-solving task), b) days 36 – 49 for phase 3 (color association-learning task), and c) days 50 – 61 for phase 4 (reversal-learning task). For each phase, a regression line was fit.

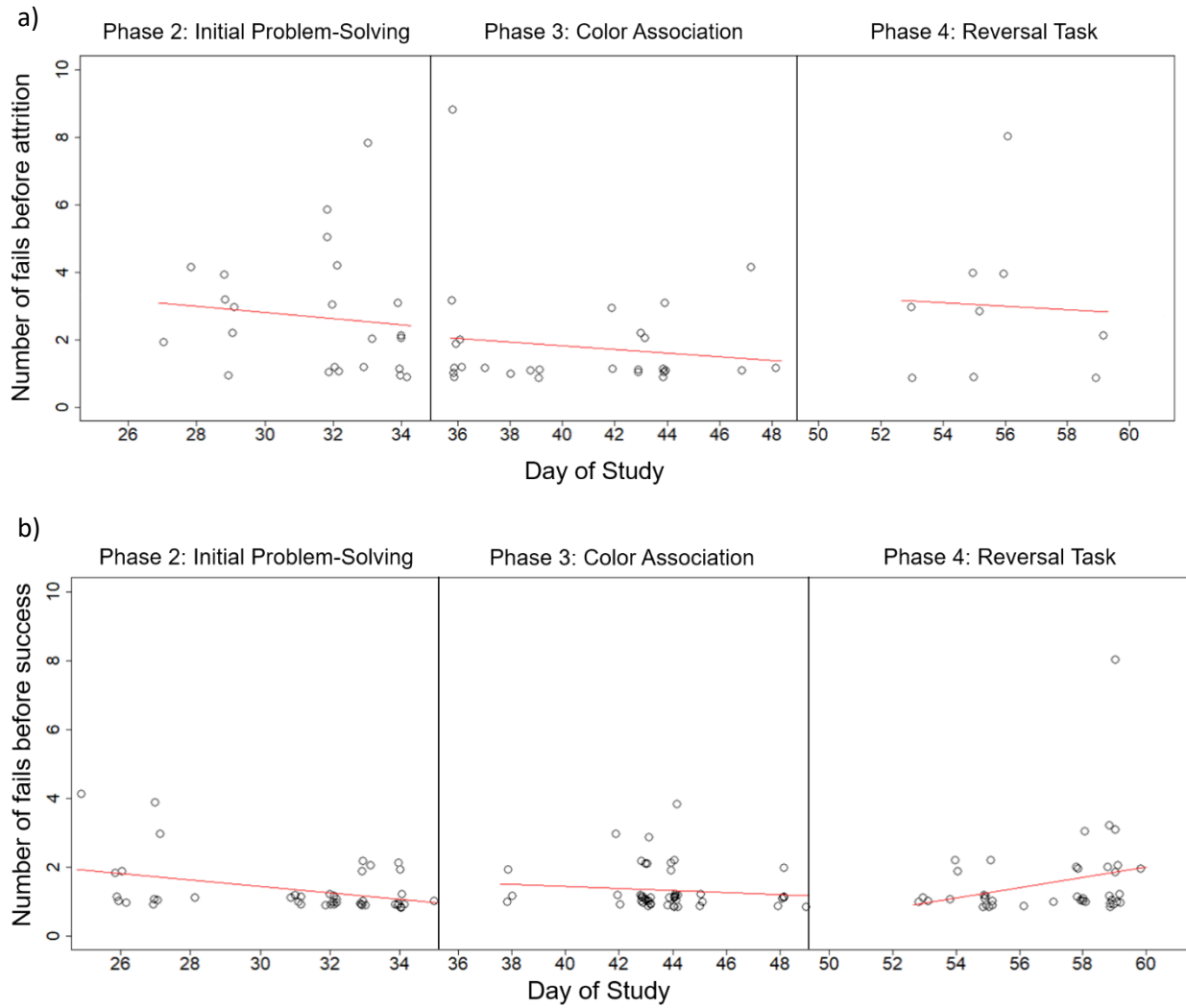


Figure 5. Scatterplot showing a) the number of fails per bird before attrition (giving up, leaving the feeder) on the top and b) showing the number of fails per bird before a success on the bottom for each phase of the study that required problem-solving. For each phase, a separate regression line was fit (shown in red).

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Appendix 1

Article in the Illinois Ornithological Society newsletter, WingTips, with a write-up of results of a study funded by members of the society.

WingTips

August 2019



Songbird Problem-Solving Abilities In Urban & Rural Environments



Researchers theorize that rapid urban expansion is changing the cognitive abilities of wildlife. Here De Paul University Master's student Kayce Miller, a Lake/Cook Chapter grant recipient, describes her work on urban versus rural songbird cognition.

Birds living in cities experience different challenges and opportunities than those living in less populated areas. City living can be difficult for birds because of less space for natural nesting sites, buildings that need to be avoided, and increased noise. However, there is also opportunity in city living because of new food sources that can be exploited such as birdfeeders, litter and garbage cans.

Researchers have been investigating whether birds living in urban areas may be smarter than their country counterparts. It is thought that birds that are better problem-solvers ("smarter") may be more likely to successfully find food, survive and reproduce. Since urban environments have a lot of change and unpredictability, problem-solving is especially important.

For my master's project, I am interested in finding out if there is a difference in the problem-solving ability in songbirds living in urban and rural environments. I am also curious if there is a difference in the problem-solving ability of birds living in forests (with fewer human interactions) and residential areas (with more human interactions).

For my experiment, I used 20 study locations. That included 10 in urban areas and 10 in rural areas, with 5 forest preserves and 5

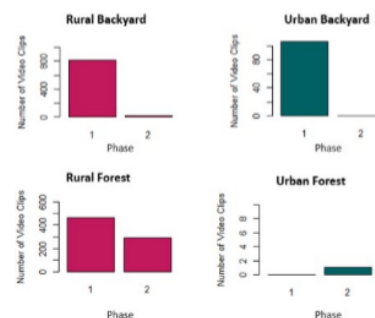
backyards in each. I built a platform bird feeder with 8 small cups. I then added a chicken wire enclosure with small openings to keep out squirrels, raccoons, large birds and other unwanted participants. For each study location, I put the feeder under a tree and attached a motion-activated camera on the tree to record the activities of visitors.



Each video recorded for 60 seconds.

My study ran for 9 weeks. The first 2 weeks were used to attract birds, so I used the feeder with no lids on the cups. The last 7 weeks of the study forced the birds to work for food by opening a lid, as shown in the preceding image of a black-capped chickadee.

Of 18,092 videos I collected during my study, 2,767 contained birds. Birds were active at feeders in rural locations but appeared at only one urban backyard feeder. One reason may be that, despite our best efforts to exclude non-bird intruders, many urban bird feeders were quickly occupied by raccoons at urban forests and squirrels at urban backyards.



Number of video clips of birds visiting the feeder at each location type during phase 1 (no lid) and phase 2 (lid)

The feeders in rural backyards attracted mostly house sparrows, house finches and northern cardinals, while those in rural forests drew black-capped chickadees almost exclusively. These birds were present in high abundance during the first two weeks (free food!). The backyard birds stopped coming to the feeder once they had to work for the food, perhaps because of easier-to-get food options such as those in neighboring yards.

In rural forests, black-capped chickadees continued to show up at the feeder for the duration of the study. They not only learned to open the lids in the feeder to get food but also became faster problem-solvers. In the first 2 weeks of problem-solving, the average amount of time it took for a chickadee to open a lid was 7 seconds. By the end of the study, average solve time was just 4 seconds.

It's possible that city birds may have the potential to be smarter than the country birds, or vice-versa. But in our study – one of the rare studies on bird problem-solving in the wild – we found that the country bird was the only one willing to participate and persist to work for food.