

University of Nevada, Reno

**Behavioral Responses to Urban Environments of Food-caching Mountain
Chickadees**

A thesis submitted in partial fulfillment of the
requirements for the degree of
Bachelor of Science in Biology and the Honors Program

by

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May, 2016

**UNIVERSITY
OF NEVADA
RENO**

THE HONORS PROGRAM

We recommend that the thesis
prepared under our supervision by

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entitled

**Behavioral Responses to Urban Environments of Food-caching Mountain
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be accepted in partial fulfillment of the
requirements for the degree of

BACHELOR OF SCIENCE, BIOLOGY

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May, 2016

ABSTRACT

As anthropogenic centers continue to expand, it becomes increasingly important to understand the traits associated with successful urban invading species. Previous research has focused on exploratory behavior, neophobia, and problem solving abilities as traits that are associated with urban invaders. Here, I focused on the mountain chickadee, *Poecile gambeli*, a resident species that relies on cached food to survive the winter. Chickadees have populated the Reno, NV area from surrounding forest populations and therefore provide an opportunity to study what traits are associated with a specialized caching species successfully inhabiting urban environments. I compared forest and urban chickadees in exploratory behavior, neophobia in a feeding context, problem solving ability, food-caching rates, short-term spatial memory and long-term spatial memory. Urban chickadees explored more substrates in a novel environment and were more active overall than forest birds. Response to novelty was similar between urban and forest chickadees, while urban chickadees solved a novel problem faster than their forest counterparts. Urban and forest chickadees cached similar amounts, performed similarly on a one-trial associative spatial learning task and on a repeated trials associative spatial learning task, but urban chickadees were able to recall cache locations better after a long term retention interval pointing toward better memory retention. These results suggest that there are differences that may be associated with urban and forest populations of chickadees, though it remains unclear what suite of traits makes an ideal invader and whether these traits are adaptive for life in urban conditions.

TABLE OF CONTENTS

ABSTRACT	i
INTRODUCTION	1
MATERIALS AND METHODS	6
RESULTS	15
DISCUSSION	18
REFERENCES	24
FIGURES	28

INTRODUCTION

Human activity drastically changes landscapes, and anthropogenic activity is continuously expanding these landscapes. As anthropogenic centers continue to grow, understanding what behaviors are associated with the successful colonization of nonhuman animals in urban environments becomes increasingly important (Alig & Healy, 1987). Due to differences in urbanized environments compared to native environments, there may be corresponding differences in the traits between populations that live in urban and rural environments (Greenberg, 1990; Sol & Lefebvre, 2000; Sol et al., 2001; Martin & Fitzgerald, 2005). Research on traits associated with successful invasions of urban environments have focused on neophobic tendencies, exploration, and problem solving abilities (Greenberg, 1990; Sol & Lefebvre, 2000; Sol et al., 2001; Martin & Fitzgerald, 2005), though it remains unclear which traits or suite of traits are ideal for the success of a species in urban environments, or are favored by urban environments.

Species that rapidly explore unfamiliar environments may tend to be exposed to urban centers more than their less exploratory counterparts. This is because urban environments are novel, and increased exploration may allow species to find urban environments (Sol et al., 2011). In addition to being more prone to finding urban environments, more exploratory behavior allows for a more thorough examination of unfamiliar environments, allowing for the discovery of novel foraging opportunities and nesting locations. Due to both the increased tendency to find novel environments, and success at locating resources in unfamiliar environments, it is expected that species that exhibit rapid exploration may be more successful in urban centers.

Animals may avoid unfamiliar stimuli in novel situations, a characteristic referred to as neophobia (Greenberg, 1990). Since reduced neophobia allows individuals to approach unfamiliar stimuli more rapidly, this characteristic may also be associated with populations in urban environments (Greenberg, 1990). Increased willingness to approach unfamiliar stimuli in novel environments allows invaders to quickly identify and utilize new resources (Webster & Lefebvre, 2001; Greenberg, 1990; Martin & Fitzgerald, 2005; Sol et al., 2002). Sol et al. (2011) found that in highly urbanized common mynas (*Acridotheres tristis*), reduced neophobia was associated with increased ability to solve a novel problem (Sol et al., 2011). These individuals with reduced neophobia may be better able to acquire food and shelter in novel environments than their neophobic counterparts that tend to avoid novel objects (Greenberg, 1990). Urban environments are characterized as novel to invading species, so it is expected that species residing in urban environments will have reduced neophobic responses. Populations that reside in urban environments may also exhibit reduced neophobia as they habituate to their urban environment. Though it is expected that reduced neophobia would be associated with urban environments, there have been equivocal results in the literature. For instance, house sparrows (*Passer domesticus*) and shiny cowbirds (*Molothrus bonariensis*) have been shown to have a strong neophobic response to novel objects in a feeding context, despite being successful urban invaders (Echeverria et al., 2006).

It has also been suggested that problem solving ability may differ between urban and rural populations. Species with increased forebrain size and greater problem solving abilities have been suggested to be more successful invaders than those with smaller brains and reduced ability to innovate in unfamiliar situations (Sol & Lefebvre, 2000; Sol

et al., 2005; Sol et al., 2008). Animals with a greater ability to innovate tend to be more flexible and able to adapt to novel environments (Griffin et al., 2013). Urban environments are expected to be associated with increased problem solving ability, since those better problem solving individuals may have access to resources that would otherwise be inaccessible; the classic example of tits that open milk bottles (Fisher & Hinde, 1949; Hinde & Fisher, 1951) demonstrates that those individuals that have learned to solve a problem gain access to resources that other do not have.

Food-caching animals are typically resident individuals that cope with fluctuating food availability by storing food in times of abundance for later use in times of food scarcity (Roberts, 1979). Food-caching animals that rely on scatter-hoarding may cache thousands of food items and must recover their stores in order to be successful (Sherry et al., 1989). North American food-caching birds include corvids, nuthatches, and chickadees (Sherry et al., 1989). Caching is especially important for individuals that reside in harsh climates and experience reduced seasonal food availability (Roth, 2010; Freas et al., 2012). Caching animals have distinct characteristics, such as recall of the location of cached stores of food (Andersson & Krebs, 1978) and greater spatial memory abilities than non-caching counterparts (Krebs, 1990). Caching animals' traits may interact with urban environments in unique ways, making them an interesting case for the study of urban invaders. Food caching species that have invaded urban environments provide an opportunity to explore how such environments affect food-caching behavior and thus allow individuals to be successful invaders.

Urban centers provide supplemental food to populations (Robb et al., 2008) and are more sheltered from inclement weather conditions than their rural counterparts

(Courtney & Fenton, 1976). Supplemental food, in the form of bird feeding, is quite extensive in urban centers and may contribute to increased rates of overwinter survival and increased reproductive success (Robb et al., 2008). It has been shown that supplemental feeding can contribute to earlier onset of the breeding season, associated with increased brood survivorship, increased quantity or quality of eggs in broods, and increased juvenile survival (Robb et al., 2008). In order to be successful, caching species must be able to recover their caches (Vander Wall & Jenkins, 2003). However, since supplemental food is provided to populations residing in urban centers, it may be that these populations do not rely as heavily on stored food caches and associated spatial memory ability for recovering caches as their forest dwelling counterparts. This may be expected to manifest as a reduction in both caching and spatial memory abilities in urban birds. Conversely, these urban populations may rely more heavily on long-term spatial memory ability to navigate to relatively consistent, but remote locations of supplemental food, especially because their preferred native food may not be available in urban areas. Caching animals may experience pilferage or removal of their caches by conspecifics or other species in both urban and rural environments. Some species exhibit re-caching behaviors (removing a cache and replacing it elsewhere) as a pilferage preventative measure (Emery & Clayton, 2001). In rural areas, birds may be found in larger flocks, increasing the chance that their caches will be recovered by conspecifics. Urban centers host novel pilferers that species may not have encountered in their rural environments, therefore, it is likely that both urban and rural species will retain characteristics aimed at reducing pilfering.

This study aims to explore differences in behavioral characteristics of urban and forest populations of mountain chickadee, *Poecile gambeli*, a food-caching species native to montane regions of western North America (Mccallum et al., 1999). Chickadees provide a unique opportunity to study how food-caching species react to urbanization, as they populated the Reno area from surrounding nearby forest populations. I predicted that urban chickadees would explore a novel environment faster, display less neophobia to novel stimuli in a feeding context, and solve a problem faster than their forest counterparts. On the other hand, I predicted that forest chickadees would exhibit higher caching rates and have more accurate spatial memory on both the one trial task and repeated associative learning tasks than their urban counterparts. Both urban and forest chickadees were expected to maintain caching traits that would reduce pilferage by conspecifics or unfamiliar pilferers, and display similar spatial memory recall in long term situations.

MATERIALS AND METHODS

Bird Capture and Bird Enclosures

Chickadees were captured in Reno (urban) and Sagehen Experimental Forest (forest) outside of Truckee, CA. Trapping was conducted from October 2014 to November 2014. At Sagehen, chickadees were captured using mist nets at established feeders maintained by the Pravosudov lab group. In Reno, chickadees were captured using mist nets and potter traps in various residential areas where chickadees were being fed with supplemental food. Relatively equal numbers of birds were captured from Southwest Reno, Rancho San Rafael Park, West University, and South Reno. A total of 25 chickadees were brought into the lab: 13 chickadees were captured at Sagehen Experimental Forest and 12 chickadees were captured from various locations in Reno. Upon arrival to the lab, wing length and mass were measured and each chickadee was fitted with unique color band combinations. The sex of each bird was determined using wing length (males: >71mm, females: <69mm).

Chickadees were housed individually in 42" x 60" x 60" enclosures. Enclosures were arranged so that urban and forest chickadees alternated and were not in adjacent enclosures (vertically or horizontally). Chickadees were separated from their neighbors with metal cage separators allowing for acoustic, but not visual interaction. Chickadees habituated to their enclosures for three weeks: during the first two weeks enclosures were covered with a white sheet and for the last week the sheet was removed. During this time chickadees were fed and cages were cleaned regularly.

Chickadees were fed a diet of sunflower seeds, pine nuts, insect pate, mealworms, and crushed peanuts. Food was provided and refreshed once a day. Unless deprived for

testing purposes, chickadees were fed *ad libitum*. Fresh water was provided daily *ad libitum* and supplemented with vitamins three times a week. Chickadees were kept on a 9x15 light-dark schedule (9 hours light, and 15 hours dark) following the shortest photoperiod of the year.

At the end of experimentation, chickadees were euthanized, sexed, and brains were removed for future analyses.

Testing Room

Except for novelty response testing and problem solving tasks (which were conducted in chickadee's home enclosures), all tasks were conducted in a testing room adjacent to the bird enclosure rooms. The testing room was equipped with macro substrates including four artificial perch trees and twelve perches with cache sites arranged on opposing walls (Figure 1). Each perch tree was furnished with 20 micro substrates: individually labeled cache sites consisting of a perch, drilled holes, and a string and knot apparatus available to cover cache sites. Food and water dishes were available during testing. All bird enclosures connected to the testing room through a trapdoor that allowed a single chickadee into the testing room. Lights in the testing room could be controlled from the outside, allowing birds to be moved from their enclosures into the testing room using light manipulation. This method has been shown to reduce handling and stress that could affect testing results (following Pravosudov & Clayton, 2002). All observations were conducted through one of two one-way mirrors outside the testing room.

Experiment 1 – Novel Environment Exploration

The novel environment exploration test was conducted to measure differences between exploration of urban and forest chickadees. Birds had no exposure to the testing room prior to the novel environment exploration test. Only one trial of this experiment was conducted, as after the chickadees were exposed to the testing room it was no longer a novel environment. Each test lasted for thirty minutes. Each movement (whether it was a flight or hop), return flight activity, and number of micro and macro substrates were recorded cumulatively over the 20 mins. Variables of interest were binned into two minute intervals for analysis.

Experiment 2 – Response to Novelty

Chickadee's response to novelty was measured in their home enclosure. Chickadees were deprived of food (dishes were removed from enclosures, newspapers were changed and dropped food was disposed of, and cache sites in enclosures were cleared) the night before testing one hour before the lights turned off. Testing was conducted approximately two hours after lights on in the morning. Testing protocol was adapted from Roth et al. (2010) and Kozlovsky et al. (2015). Latency to touch and land on the feeding dish, and to take a wax worm was recorded using digital video recording. Recordings were taken for a pre- and a post-trial conducted with a control familiar feeding dish that was not designed to produce a neophobic response; and during the response to novelty trial with a feeder modified with colorful paint and spokes designed to evoke a neophobic response (Figure 2). Neophobia feeding dishes were different colors (red, orange, lime green, and pale pink), and colors were randomly assigned. The feeding dishes were provided to the birds and the birds were recorded via video

equipment so that their behavior was not affected by observer presence. Latency to touch the feeder and take the worm was recorded in seconds for both control trials and novel feeding dish trials.

Experiment 3 – Problem Solving

The problem solving trials were conducted to measure differences in birds' abilities to solve a novel problem. Birds were not deprived of food prior to the problem solving trials. Problem solving procedures were adapted from Kozlovsky et al. (2015). Clear test tubes were held upside down in the bird enclosure with a binder clip/wire and stoppered with cotton to keep a wax worm held securely in the tube, but visible (Figure 3). In order to obtain the wax worm, the cotton plug had to be removed from the test tube by the bird, causing the wax worm to fall to the cage floor, and was then available for the bird to eat. Regular food was available to the birds during testing. This task was designed to test the bird's ability to solve a problem for a highly desired food item (the wax worm), and so the presence of other food was not intended to influence the behavior during testing. The birds were allowed to habituate to the problem solving apparatus during a one-hour habituation period prior to testing, during which time latency to approach the problem solving apparatus was recorded. A trial was considered successful when birds took the wax worm in the one-hour testing time period. In order to check that the first successful completion of the test was not a fluke, and to measure differences in performance between first and subsequent trials, additional trials were given (until they solved the problem again or until they reached the twenty trial ceiling) and successful chickadees solved the task a second time. Two trials were conducted in a day with at least four hour periods separating them.

Experiment 4 – Caching Rates

Testing of food-caching rates was conducted to measure differences in caching rates between urban and forest chickadees. This experiment was adapted from Freas et al. (2012) methodology. Chickadees were deprived of food one hour before lights turned off the previous night and testing was conducted approximately two hours after lights on in the morning. Testing was only carried out once a day. The order of birds was counterbalanced so that all chickadees experienced early morning and late morning testing. Pine nuts, peanuts and sunflower seeds were provided in the testing room during caching testing. A bird was released into the testing room via trapdoor and light manipulation and allowed to eat and cache for twenty minutes before being returned to its enclosure. Cached food (type and location), eaten food, and false and re-caching was recorded via observation from the one-way mirrors. False caching was defined as placing the beak into a cache then removing it without depositing the food item, and re-caching was defined as removing a previous cache and replacing it in another cache location. Caches were cleared between testing. Individuals were tested three times and data was summed from the three trials.

Experiment 5 – One Trial Associative Learning Task

The one trial associative learning task was conducted to measure differences in ability to recall the location of a previously discovered cache after one exposure. This experiment was adapted from Freas et al. (2012) methodology. Chickadees were deprived of food using the same deprivation methodology as Experiment 2. Deprivation occurred one hour before lights turned off the previous night and testing was conducted approximately two hours after lights on in the morning. Each chickadee was assigned to a

random site, and a wax worm was visually accessible in the site (securely in the cache site to prevent falling, but hanging out so that it was readily visible to each bird). Individuals were allowed to find the food (defined as pecking at the food but not removing it from the cache site) but were removed from the room before they were allowed to eat the wax worm (ensured by turning off the lights at the bird's first peck). Individuals remained in their enclosure for twenty minutes, during which time all sites were closed with the string-knot apparatus and the wax worm was closed into the same site that the bird found it in. After twenty minutes, the chickadee was allowed back into the testing room, and incorrect sites opened and time until the wax worm was found was recorded. This experiment was conducted four times, with a new unique site for each new trial, so that sites were only the same for a chickadee's pre and post one trial associative learning trials.

Experiment 6 – Repeated Associative Learning Task

This experiment was conducted to measure differences in performance on recalling the location of a site after multiple exposures to the designated site containing food. This experiment was adapted from Freas et al. (2012) methodology. Chickadees were deprived of food one hour before lights turned off the previous night and testing was conducted approximately two hours after lights on in the morning. Each chickadee was assigned a random site to be used throughout the repeated testing (different from the previous experiment). Three pre-trials were conducted, during which the chickadee was allowed to eat the wax worm out of its assigned site (all sites were open) and remain in the testing room for five minutes after it had eaten. Pre-trials were conducted no more than once a day. When all pre-trials were finished the repeated associative learning task

was conducted by closing all sites (with the wax worm placed into the chickadee's assigned site) and the time and incorrect sites (location and number) was recorded until the wax worm was found. The repeated associative learning trials were only conducted once every three days. A long-term retention test was conducted nineteen days after the last of the trials had been completed to test the chickadee's long-term retention of their sites.

Statistical Analyses

A repeated measures general linear model (GLM) was used to analyze the number of new substrates visited for a measure of exploratory behavior. Five blocks were analyzed (for a total of ten minutes divided into two minute intervals). Data was analyzed as a summation of micro-substrates and macro-substrates. The predictor variable was the chickadee's site of origin. In addition, because the data did not meet the assumption of normality, a Mann Whitney U-test was used to analyze only the first block. It has been argued that the first interval is a sufficient measure of exploratory behavior (e.g. Dingemanse et al., 2002). Flight activity and return flight activity (leaving from a perch and returning to the same perch without landing on another substrate) were also analyzed using a repeated measures GLM. The entire thirty minutes were analyzed as fifteen intervals, using the cumulative number of flights as the response variable and the chickadee's site of collection as the predictor variable.

A repeated measures GLM was used to analyze differences in latency to touch, land on, and take the wax worm from the control and novel feeder as the response variable. The pre-trial, novelty trial, and post-trial were used as the repeated measure and the chickadee's collection site as the predictor variable.

A t-test was used to analyze latency to interact with the problem solving apparatus. Chickadee's origin was the predictor variable. A t-test was used to analyze differences in the number of trials taken to solve problems using the chickadee's origin as the predictor variable and latency to touch the apparatus was the response variable. A repeated measures GLM was conducted to analyze latency to solve the problem using the first and second problem solving trials as repeated measures and the chickadee's origin as the predictor variable.

Caching, false caching, and re-caching rates were analyzed using three separate t-tests with mean number of caches, false caches, and re-caches (the mean was calculated from the individual's three trials) as the response variable and the chickadee's origin as the predictor variable.

The mean number of incorrect inspected sites from the one trial associative learning task of the individual's multiple trials were analyzed using a t-test with the number of incorrect inspected sites as the response variable and the chickadee's origin as the predictor variable.

A repeated measures GLM was used to analyze the number of incorrect inspected sites from the repeated associative learning task, using the trials as the repeated measure. Only the first four trials were analyzed because it is assumed that the number of errors for all chickadees should converge during later trials. The chickadee's origin was the between subject variable. The long-term retention trial was analyzed using a repeated measure GLM with trial 9 (the last of the repeated associative learning task) and the long-term retention trial. The number of incorrect sites inspected was the response variable and

the chickadee's origin as the predictor variable. The Fisher Least Significant Difference (LSD) was used as a post hoc analysis when significant results were obtained.

RESULTS

Experiment 1 – Novel Environment Exploration

There were no significant differences between forest and urban chickadees in the number of substrates visited during the first ten minutes of testing ($F_{1,25} = 1.19$, $p=0.29$; Fig. 4). However, urban chickadees tended to explore novel environments more rapidly than their forest counterparts during the initial two-minute interval of testing (Mann-Whitney $U = 51.5$, $n_s = 14$, $n_c = 13$, $p = 0.06$; Fig. 4). Urban chickadees flew significantly more throughout the entire thirty minute trial for each of the two minute measurement blocks, measured as flights ($F_{1,25} = 13.02$, $p = 0.001$; Fig. 5) and flight returns ($F_{1,25} = 7.07$, $p = 0.01$). There was a significant interaction between time interval and the number of flights and flight returns ($F_{14,350} = 9.59$, $p < 0.001$ and $F_{14,350} = 5.13$, $p < 0.001$; respectively).

Experiment 2 – Response to Novelty

There were significant differences between latency to feed at the novel feeder and the control feeders ($F_{8,184} = 20.19$, $p < 0.0001$; Fig. 6). There were no significant differences in latency between urban and forest chickadees in approaching or taking the wax worm from the neophobic feeder ($F_{1,23} = 0.004$, $p = 0.9$, Fig. 6), with no significant interaction between control and novel feeder trials ($F_{8,184} = 0.04$, $p = 0.99$). There were significant differences between the latency to approach and take the wax worm from the neophobic feeder and from the control feeders during the pre and post-trials ($F_{8,184} = 20.19$, $p < 0.001$).

Experiment 3 – Problem Solving

City chickadees solved the novel problem in fewer trials than forest chickadees ($t_{23} = 2.3$, $p = 0.03$; Fig. 7). There were no significant differences in latency to interact with the testing apparatus ($t_{23} = 0.12$, $p = 0.9$) and all chickadees approached it within the first two minutes of testing. The chickadees solved the problems faster during the second trial ($F_{1,14} = 6.5$, $p = 0.02$), with no significant differences between city and forest chickadees ($F_{1,14} = 0.054$, $p = 0.8$), and no significant interaction between the site and trial ($F_{1,14} = 0.08$, $p = 0.8$).

Experiment 4 – Caching Rates

There were no significant differences in mean food-caching rates between city and urban chickadees ($t_{25} = 1.19$, $p = 0.24$; Fig. 8). City chickadees false cached significantly more, defined as placing a food item into a cache then removing the food item from the cache ($t_{25} = 3.01$, $p = 0.006$; Fig. 9), and city chickadees tended to re-cache more than the forest chickadees ($t_{25} = 1.96$, $p = 0.06$; Fig. 10).

Experiment 5 – One Trial Associative Learning Task

There were no significant differences in the one-trial spatial memory task performance in terms of the number of incorrect sites inspected ($t_{19} = 1.32$, $p = 0.2$; Fig. 11).

Experiment 6 – Repeated Associative Learning Task

There were no significant differences in spatial memory acquisition; the number of incorrect inspected sites was not significantly different between urban and forest chickadees ($F_{1,23} = 0.18$, $p = 0.7$; Fig. 12). All chickadees significantly improved between trials ($F_{4,92} = 3.70$, $p = 0.008$), with no significant interaction between trial and site ($F_{4,92}$

= 1.11, $p = 0.3$). There were significant differences between the number of incorrectly inspected sites in trial 9 and the number of incorrect sites inspected during the long term retention trial ($F_{1,21} = 10.14$, $p = 0.004$; Fig. 12), with a significant interaction between trial and site ($F_{1,21} = 4.88$, $p = 0.04$). Post hoc analysis revealed no significant differences in city chickadees performance between trial 9 and the long term trial ($p=0.5$) but the number of errors for forest chickadees significantly increased between trial 9 and the long term trial ($p=0.001$). Although there were no significant differences between forest and city chickadees in performance on trial 9, forest chickadees inspected significantly more cache sites during trial 9 ($p=0.01$) and the long term retention trial ($p=0.04$).

DISCUSSION

Forest and city chickadees did not differ in the number of substrates visited during exploration of the novel environment, but city chickadees flew more, and tended to explore more rapidly during the first two minutes of testing. All chickadees tended to increase exploration as the trial proceeded. City and forest chickadees did not differ in food-caching rates, but city chickadees false cached more and tended to re-cache more. Forest and city chickadees did not differ in the number of incorrect inspected sites during the one trial associative learning task or the repetitive associative learning task. During the repetitive learning task, all chickadees improved in trials, and city chickadees performed better on the long-term retention trial. There were no significant differences in neophobia, though there were significant differences between latencies to touch, land on and take food from the novel food dish and control food dish. Finally, city chickadees completed the problem-solving task in fewer trials than forest chickadees.

As expected, city chickadees tended to explore more rapidly in the first two minutes and had more overall flights than their forest counterparts. It is likely that the chickadees that colonized urban areas, and thus were captured in urban environments, tended to exhibit characteristics of rapid exploration. Rapid exploration is an important factor determining success in invasion of new environments, because rapid exploration should allow for quicker discovery and utilization of resources (Sol et al., 2011). Birds that are adapted to living in forest conditions may tend to be shyer (Greenberg, 1989; e.g. Cole & Quinn, 2014), which may be manifested as less exploration by forest chickadees. It has also been suggested that individuals that are more suited to forest conditions show strong avoidance of being in open environments (Greenberg, 1989). Compared to the

forest chickadees, the city chickadees may have been those that tended to exhibit stronger willingness to explore in the open and utilize unfamiliar resources and were therefore the individuals that were successful in obtaining resources from unfamiliar sources found in urban environments. There was a significant interaction between time block and the number of flights and return flights, which may have been a result of the chickadees habituating to the testing room and increasing their comfort within the novel environment.

Both urban and forest chickadees had greater latencies to approach the novel feeding dish than the control feeding dish. Avoidance of novel stimuli is thought to be adaptive for species to lower their risk of predation during feeding (Brown, 1988). Though it was expected that city chickadees would have lower latency to approach the novel feeder than forest chickadees, there were no detectable differences. Urban environments are filled with novel objects, including previously unknown food sources and shelters, so it is thought that species with reduced response to neophobia may have some traits that are advantageous for colonization of urban environments (Martin & Fitzgerald, 2005). Echeverria et al. (2006) found that populations of highly urbanized house sparrows and shiny cowbirds exhibited a surprisingly strong neophobic response, which may have been the result of developmental influences. As such, responses to novelty in urban environments may be complicated by the type of urban environment and the species in question. Additionally, studies on neophobia along elevational gradients have found no significant difference in neophobia (Kozlovsky et al., 2014; Kozlovsky et al., 2015). Therefore, it may be that there are individual differences in neophobia, but as a

whole chickadee populations are fairly constant in neophobic responses to novel objects across environments and contexts.

As expected, city chickadees solved the novel problem faster than forest chickadees, although there were no significant differences in interacting with the problem solving apparatus. As aforementioned, there were no significant differences between city and forest chickadee neophobic response. Sol et al. (2011) found that in common mynas, reduced neophobia was associated with greater problem solving ability (Sol et al., 2011). Chickadees able to solve novel problems would have access to more resources in an unfamiliar environment than conspecifics that lacked the ability. Chickadees in urban environments were likely those that were able to gain access to novel sources of food, as urban environments require some innovation to gain access food that would otherwise be inaccessible and thus, they could more easily survive in urban environments compared to individuals that are slower to solve novel problems (e.g. Sol et al., 2011).

Though it was expected that forest chickadees would cache more than their urban counterparts, there were no significant differences in caching rates. Regardless of differences in food availability in urban and forest settings, chickadees from urban and forest environments may still rely relatively equally on food caches to survive. It is also possible that the populations of city and forest chickadees have not been separated for long enough to develop differences in caching rates. There were, however, differences in false caching rates, with city chickadees false caching significantly more and a tendency to re-cache more. It has been shown in previous studies that the environment in which caching takes place can have an effect on caching behavior (Dally et al., 2005; Emery et al., 2004; Emery & Clayton, 2001; Pravosudov, 2008). Dally et al. (2005) showed that

when in view of other birds, western scrub jays preferred to cache in more hidden locations, or re-cache multiple times (Dally et al., 2005). These strategies may be the result of scrub jays' modifications to food caching strategies to prevent pilferage of their caches (Emery & Clayton, 2001). Pravosudov (2008) showed that chickadees choose caching sites hidden from pilfering species, and in view of non-pilfering species – demonstrating that chickadees both utilize strategies to avoid pilferage and discriminate between pilfering and non-pilfering species (Pravosudov, 2008). There may be a higher density of pilferers living in urban conditions, since urban conditions may support survival of larger densities due to provisions of supplemental food and more shelter from harsh inclement weather (Robb et al., 2008; Courtney & Fenton, 1976). A higher density of potential pilferers living in urban environments may explain why city chickadees tended to false cache and re-cache more than forest chickadees. Additionally, it has been suggested that re-caching or frequently checking on the condition of the cached food may be adaptive, as it can reinforce longer term memory of the cache location, or may prevent pilferage of the cache if the contents are utilized before being discovered by others (Pravosudov & Grubb, 1994). If there are higher rates of pilferage in urban areas due to larger pilferer populations and more abundance of potentially novel pilferer species, it is possible that the city chickadees' tendencies to false cache are adaptive and have facilitated success in urban environments. There is not currently a large amount of research on differences in pilferage rates between urban and rural environments. Further research should be directed at uncovering differences in pilferage rates in urban and rural settings.

Although it was expected that the forest chickadees would perform better on spatial learning tasks, there were no significant differences on performance on the one trial associative learning task or the repeated associative learning task between forest and urban chickadees. Although unexpected, the forest chickadees performed significantly worse on the long term retention trial than the urban chickadees, which contrasted the prediction that forest chickadees would perform better due to their heavy reliance on the recall of their cached food to survive the harsh winter. As aforementioned, there was no difference in caching rates between urban and forest chickadees. The similar performance on the spatial memory tasks by urban and forest chickadees may have resulted from relying equally on caches. With no difference in caching rates, chickadees from urban and forest environments would have the same need to recall locations of their caches. As with caching rates, it is also possible that the populations have not been separated long enough for selection to have acted on these behaviors. Additionally, in an urban environment, spatial memory could be used for navigating multiple supplemental feeders, which may also provide an explanation for the city chickadees' better performance on the long-term retention spatial memory tasks. Urban populations of chickadees may be exposed to regular supplementary feeding through bird feeders (Robb et al., 2008). Supplemental food may decrease the need for city chickadees to precisely remember the locations of their caches over long periods of time, conversely, it may be the case that these chickadees have a more accurate long term retention of potential food stores because these feeders are often maintained and remain constant throughout the year relative to the ephemeral resources associated with forest environments. These factors could make it adaptive for city chickadees to recall locations for longer in order to return to feeders,

while both city and forest chickadees acquire the same level of spatial memory about the location of their caches in the short term because both may need to recover similar number of caches.

Urban environments may be associated with the presence of certain traits or adaptations. Traits such as fast exploration may be associated with species' initial invasion into urban environments, while others such as neophobic response and problem solving may be associated with individuals' ability to obtain resources from a novel urban environment. Caching species that have invaded urban environments may have differences in their caching strategies (such as strategies to reduce pilferage from novel competitors in urban environments). Pilferage rates in urban and forest environments have not been compared, and further research in this area would provide insight into the pilferage avoidance strategies of urban chickadees. Additionally, future research will be directed towards understanding the mechanisms of the city chickadee's better problem solving abilities through analyses of the hippocampal regions of collected brains.

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FIGURES

Figure 1. The testing room, composed of four perch trees (macro-substrates) with 20 individual perch locations per tree (micro-substrates)



Figure 2. Neophobic food dishes



Figure 3. Novel problem solving apparatus



Figure 4. Exploratory behavior as cumulative number of substrates visited during each time block

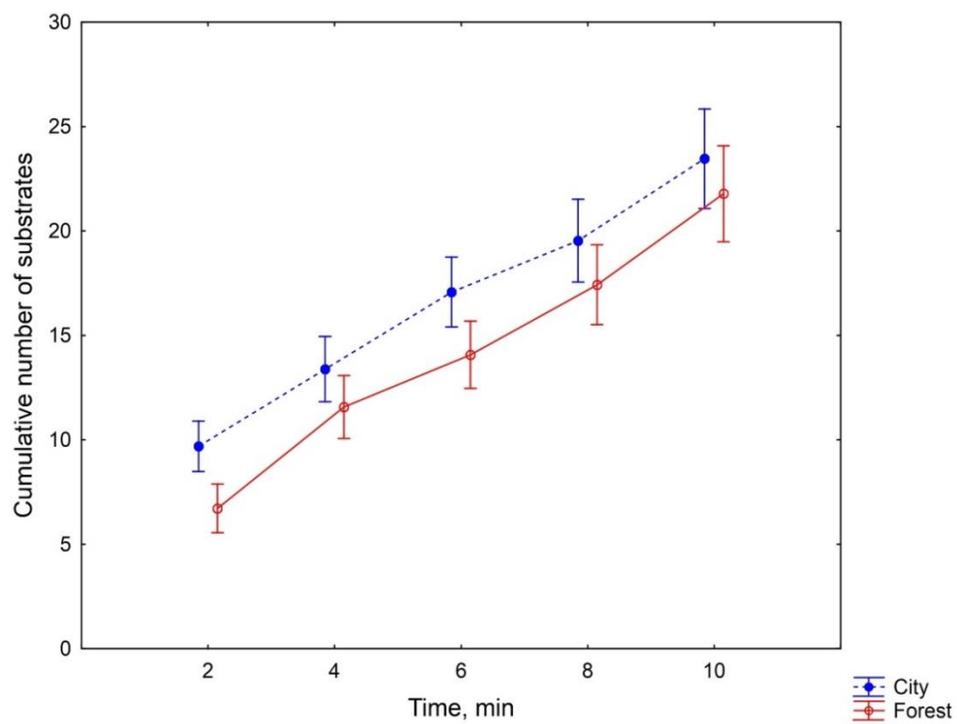


Figure 5. Exploratory behavior as cumulative number of flights during each time block

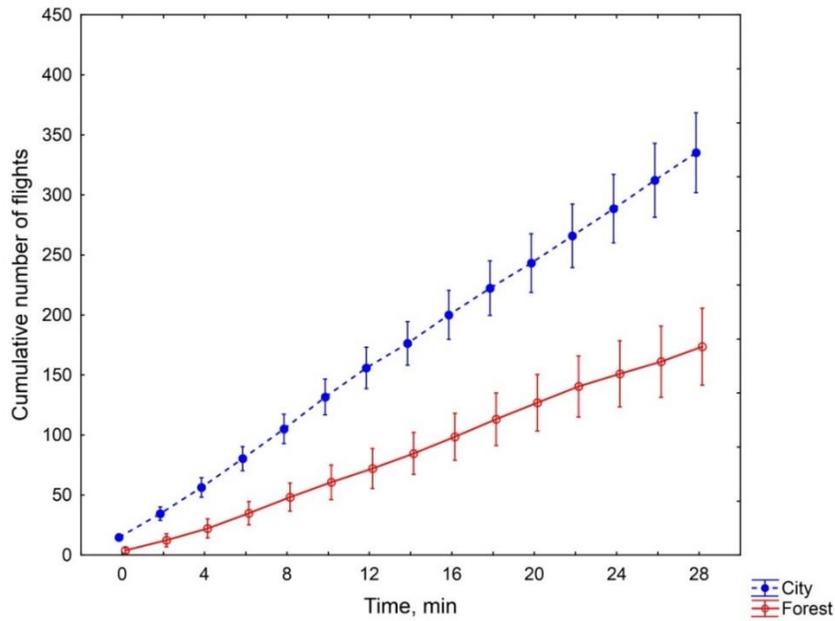


Figure 6. Response to neophobia measured as latency to approach feeding dishes during control and neophobia trials

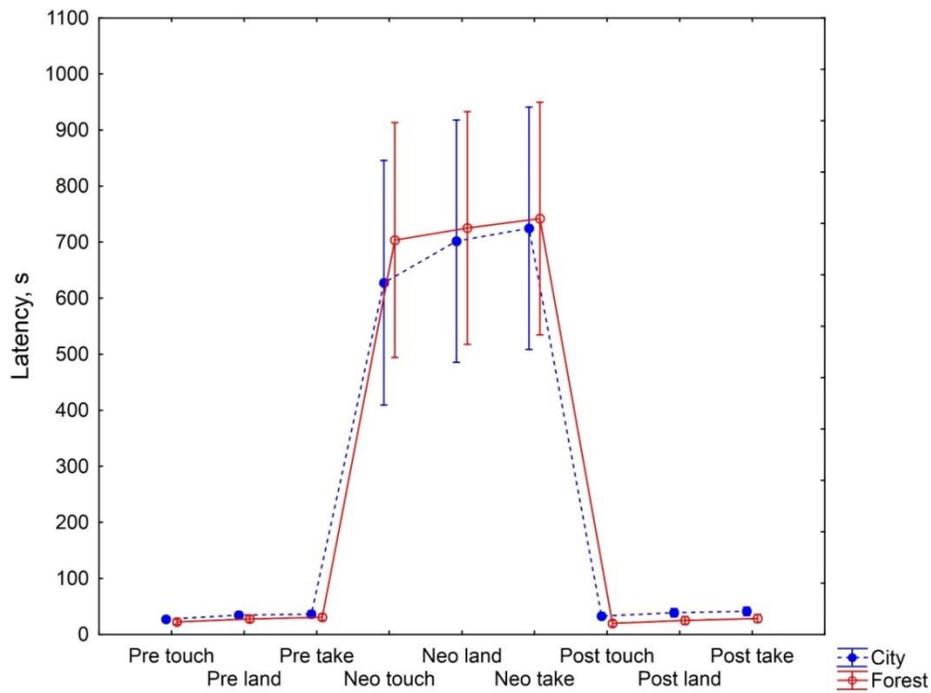


Figure 7. Number of trials to solve a novel problem

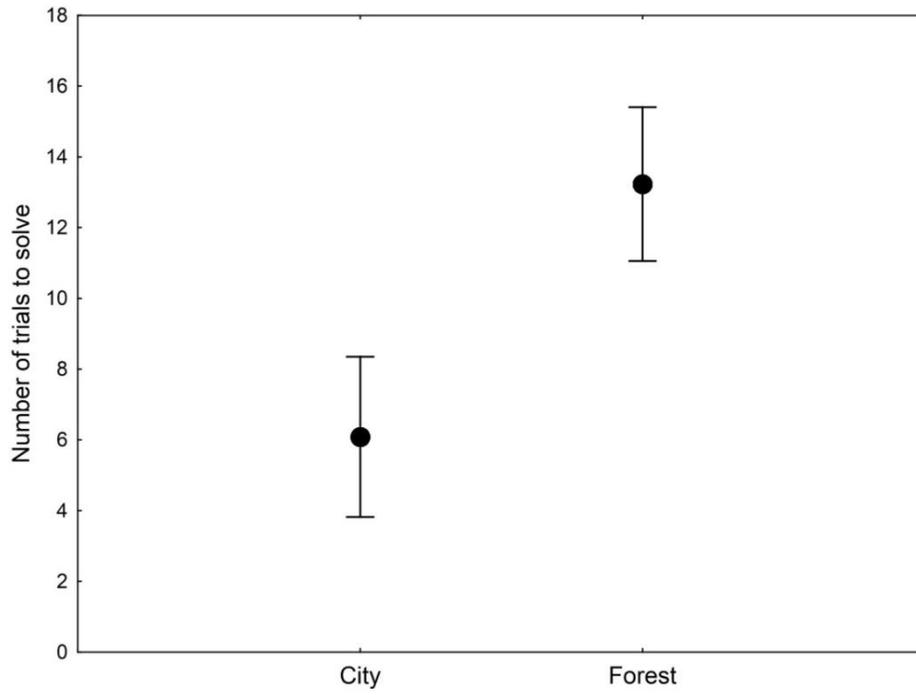


Figure 8. Caching rates as mean number of caches per trial

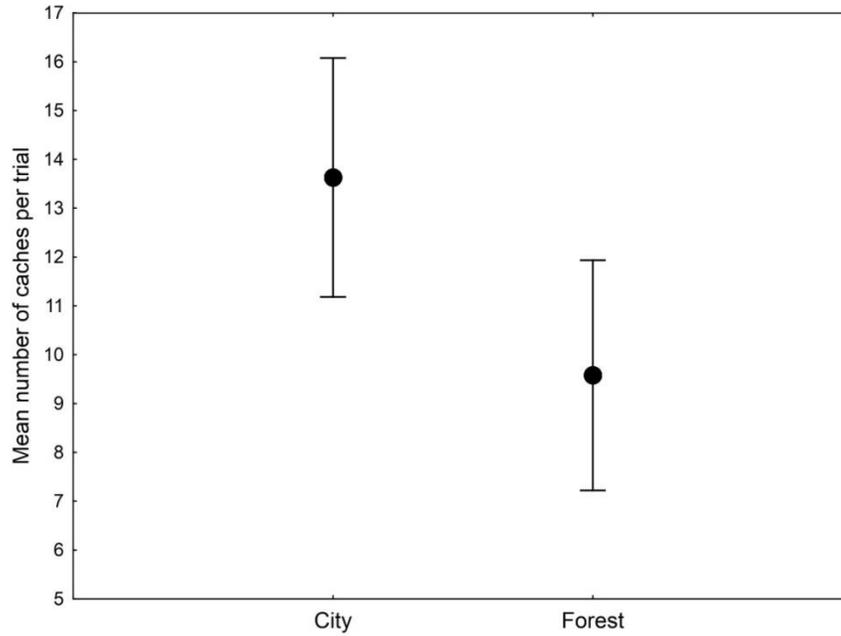


Figure 9. Mean number of false caches per trial

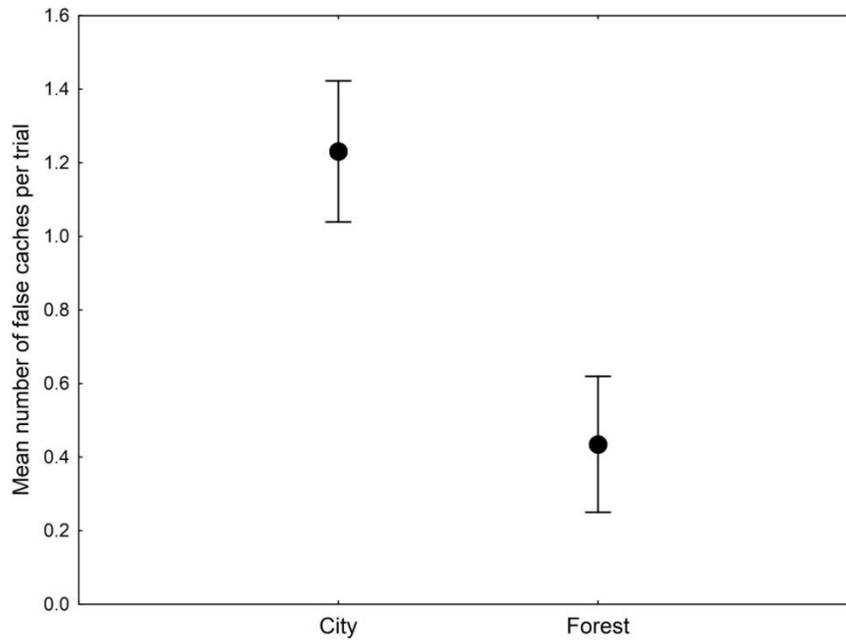


Figure 10. Mean number of recaches per trial

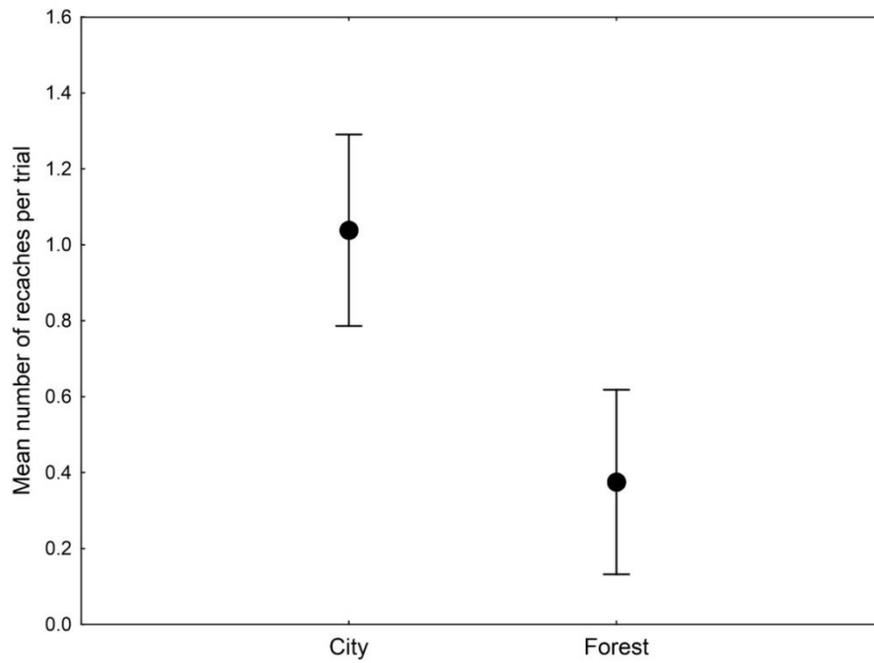


Figure 11. Mean number of inspected sites during one-trial associative learning task

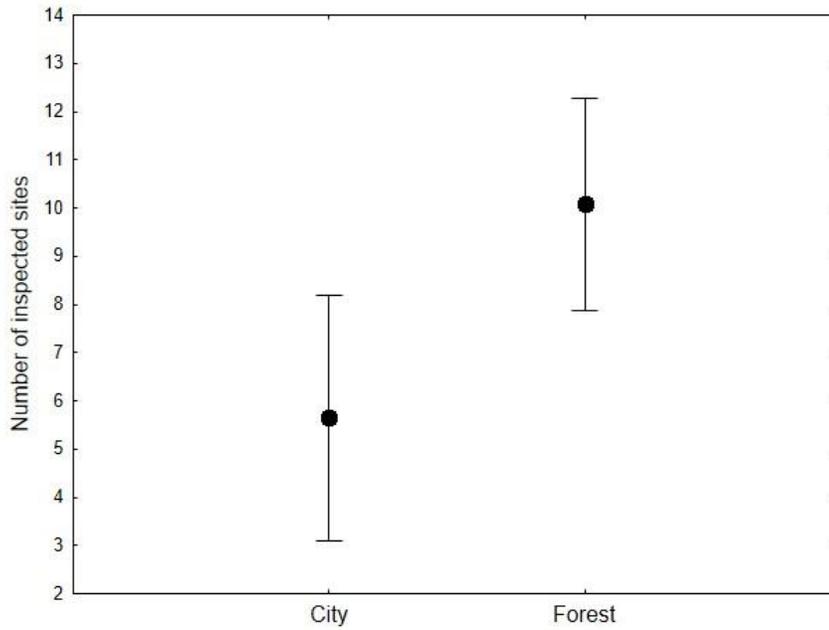


Figure 12. Mean number of inspected sites during repeated-trials associative learning task

