Effect of urbanization on neophobia in black-capped chickadees (*Poecile atricapillus*)

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Abstract

As human populations increase and city borders grow, many animals have to modify their foraging behaviours to exploit evolutionarily novel urban food sources that could aid their survival. Neophobia, the fear of novelty, can lead to missed opportunities in these cases. Novelty is therefore expected to elicit different responses in urban and rural populations, a difference that has been frequently studied, but with mixed results. The main objective of my thesis was to study the novelty response of wild black-capped chickadees (*Poecile atricapillus*) in ecologically relevant conditions while controlling for individual characteristics and potential differences in foraging group size. I predicted that urban black-capped chickadees would be more likely to initially contact novelty than rural chickadees, and that subordinates and juveniles would be more likely to first contact novelty than dominants and adults, respectively. I ran replicated experiments using three novelty types (object, colour, or food) on six sites, during which I registered feeder choice of 71 tagged individuals. I found that urban chickadees showed less neophobia than their rural counterparts, the latter initially contacting the familiar feeder before approaching the novel feeder, while the former were equally likely to contact any feeder. There was no significant effect of an individual's dominance, age or sex on its first choice of feeder, nor was there an effect of novelty type. Overall, my results suggest that urban chickadees exhibit less neophobia than their rural counterparts, because they have generally learned to tolerate novelty in their habitat and/or they have adapted to live in an environment that rewards low neophobia.

Résumé

L’augmentation de la population humaine et l’agrandissement des villes forcent de nombreux animaux à modifier leur comportement afin d'exploiter de nouvelles sources de nourriture urbaines. La néophobie, la peur de la nouveauté, peut alors nuire à la survie. La nouveauté devrait susciter des réactions différentes chez les populations urbaines et rurales. Ces deux groupes et leur néophobie sont fréquemment comparés, mais avec des résultats mitigés. L'objectif principal de ma thèse était d'étudier la réponse à la nouveauté des mésanges à tête noire (*Poecile atricapillus)* sauvages dans des conditions écologiquement pertinentes, tout en contrôlant pour les caractéristiques individuelles et les différences potentielles de la taille du groupe. J'ai prédit que les mésanges à tête noire urbaines seraient plus susceptibles de contacter la nouveauté que les mésanges rurales, et que les subordonnés et les juvéniles seraient plus susceptibles de contacter la nouveauté que les dominants et les adultes respectivement. J'ai mené des expériences répliquées en utilisant trois types de nouveauté (objet, couleur ou nourriture) sur six sites au cours desquelles j'ai enregistré le choix de la mangeoire de 71 individus bagués. J’ai trouvé que les mésanges urbaines présentaient moins de néophobie que celles des zones rurales, ces dernières ayant d’abord contacté la mangeoire familière avant de s’approcher de la nouvelle mangeoire, alors que les mésanges urbaines ne montraient pas de préférences entre les mangeoires. La dominance, l’âge ou le sexe d’un individu n’a pas eu d’effet significatif sur le premier choix de mangeoire. Il n’y avait pas non plus d’effet du type de nouveauté. Globalement, mes résultats suggèrent que les mésanges urbaines expriment moins de néophobie que leurs homologues rurales, car elles ont généralement appris à tolérer la nouveauté dans leur habitat et/ou se sont adaptées pour vivre dans un environnement qui récompense une faible néophobie.

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Statement of Contributions

Chapter 2 of this thesis is adapted from a manuscript submitted as a research article to the journal *Behavioral Ecology*. All supplementary materials appear in the appendix. The pronoun "we" is used within the manuscript to include additional authors, however this thesis was produced by myself.

Fall chickadee banding in the field was done by myself, Laetitia Desbordes and Celia Bodnar, with help at capturing from Dr. Julian Evans and Mélanie Routh. The algorithms used to determine the sex and dominance rank of individual chickadees were created and applied to chickadees in this study by Dr. Julian Evans. As well as assisting with data collection, Mélanie Routh completed an honours thesis on the topic. Site selection, experimental design and data analysis were done by myself in collaboration with Dr. Julie Morand-Ferron.

NB: Work on this thesis was conducted under scientific and banding permits from Environment Canada's Canadian Wildlife Service (10854) and approved by the Animal Care committee of the University of Ottawa (1759).

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Chapter 1

General Introduction

Urbanization is the process whereby a natural area undergoes human development. This procedure involves the construction of human settlements and an increase in the resident population. More than half of all humans now live in cities (United Nations 2014), and that number constantly rises. Unfortunately, as urbanization increases so too does the urbanized areas' loss of biodiversity and species richness (Aronson et al. 2014; McDonald et al. 2008). Most species evolved in natural areas and some are unable to survive in urban landscapes, disappearing from them without establishing urban populations (McCleery 2009; Møller 2009). These unsuccessful urban colonizers show different characteristics to those that do succeed, which generally have, among other traits, a higher foraging innovation rate, higher dispersal propensity (from natal to novel environments), and show higher risk-taking (Lowry et al. 2013; Møller 2009; Sol et al. 2013), such as birds' decreased flight initiation distance when approached by potential predators (Møller 2009).

While some species do appear to have natural characteristics that may advantage them for urban colonization, not all individuals of these species inhabit cities, meaning that they may exist in the environment as both urban and rural populations. These two groups can differ from each other in several ways, one being by their morphology. For example, urban house finches (*Haemorhous mexicanus*) were found to have longer and narrower bills than rural, which may allow easier access and handling of seeds in feeders, or alter their song characteristics so as to be heard over anthropogenic noise (Giraudeau et al. 2014). Urbanized Anole lizards (*Anolis cristatellus*) possess longer legs relative to their body size than their rural counterparts, proposed to improve locomotion on urban areas' broader substrates (Winchell et al. 2016). Physiological differences occur between urban and rural individuals too, as was found in the crustacean *Daphnia magna*, whose urban-dwelling members stored higher fat, sugar and protein concentrations than rural members, overall increasing their energy reserves and stress resistance (Brans et al. 2018). The stress physiology of European blackbirds (*Turdus merula*) was similarly affected by urbanization, with urban individuals consequently showing a reduced stress response when compared to rural (Partecke et al. 2006). Behaviour is yet another way that urban and rural groups can differ. These changes are particularly important for biologists to understand, as they may affect how urbanized species interact with humans, with possible negative or positive repercussions for both parties. For example, species such as raccoons are found at higher densities in urban than in rural areas, allowing for increased spread of disease and parasites among them, and an increased risk of contact with humans (Riley et al. 1998). Meanwhile, some large urban predators such as coyotes (*Canis latrans*) alter their time budget to minimize human contact (McClennen et al. 2001; Riley et al. 2003; Tigas et al. 2002), while other urbanized species, like Eurasian red squirrels (*Sciurus vulgaris*), alter their anti-predator response, allowing a closer approach by humans before fleeing (Uchida et al. 2016).

Neophobia and urbanization

Behaviours such as reactions to new items or situations can also be altered due to urbanization. Neophobia is the fear of anything that is new or unfamiliar to an individual (Greenberg and Mettke-Hofmann 2001). This behavioural response has been studied in multiple species across multiple contexts along an urban-rural gradient, with urban individuals generally predicted to be less neophobic than rural. Reduced neophobia is an expected characteristic of the urban-colonizing species that would most benefit from novel human-based food sources (Audet et al. 2016; Candler and Bernal 2015; Sol et al. 2011), from rapid exploration of novel environments (Kozlovsky et al. 2017), or from the reduced predation risk of urban areas (De Meester et al. 2018; Griffin et al. 2017). Studies often find inconsistent results however (Table

1). Interpretation of the various studies' findings can be complicated by different testing conditions (e.g. wild or captive individuals), different variables being controlled for (e.g. age, sex, dominance and foraging group size) and different kinds of novelties tested, such as foods and objects (Greggor et al. 2015). These different categories of novelty and the neophobic reactions to them may not be directly comparable, as each may be the result of different underlying mechanisms, through either a learned or evolved response (though these two mechanisms are not mutually exclusive; Miranda 2017). Neophobic reactions to only one category of novelty could indicate a learned response, rather than a selected behaviour that should lead to a neophobic response to many novelty types.

Table 1. Some studies comparing neophobia between urban and non-urban individuals of the same species. Wild = tested on wild individuals in their natural habitat; Captive = wild individuals temporarily brought into captivity for testing; Common garden = hand-raised individuals tested in captivity; > more neophobic than; < less neophobic than; NS no significant difference in neophobia between the two groups; R = rural, suburban or forest; U = urban. There is a bias in the literature towards testing avian species' neophobia between urban and rural environments, as can be seen in Miranda et al. (2013), whose literature review found double the number of avian-based studies to non-avian.

Species	**Source**	**Novelty Type**	**Variables**	**Result**	**Reference**
Great tit (*Parus major*)	Wild	Object	Group size	U < R	Tryjanowski et al. 2016
Eastern gray squirrel (*Sciurus carolinensis*)	Wild	Object	NA	U < R	Bowers and Breland 1996
Common myna (*Acridotheres tristis*)	Captive	Object	Age, sex	U < R	Sol et al. 2011
Various species (9)	Wild	Object	NA	U < R	Ducatez et al. 2017
Various species (12)	Wild	Object	Group size	NS	Greggor et al. 2016
Mountain chickadees (*Poecile gambeli*)	Captive	Object	Sex	NS	Kozlovsky et al. 2017
Cane toad *(Rhinella marina*)	Captive	Food, object	Age	NS	Candler and Bernal 2015
Dalmation wall lizard (*Podarcis melisellensis*)	Wild	Object	NA	NS	De Meester et al. 2017
House sparrow (*Passer domesticus*)	Captive	Food, object	Sex	NS	Bókony et al. 2012
House sparrow (*Passer domesticus*)	Captive	Object	Sex, group size	NS	Liker and Bókony 2009
European blackbirds (*Turdus merula*)	Common garden	Object	Age, sex	U > R	Miranda et al. 2013
Bullfinch (*Loxigilla barbadensis*)	Captive	Object	Sex	U > R	Audet et al. 2016
Shiny cowbird (*Molothrus bonariensis*)	Wild	Object	Group size	U > R	Echeverria et al. 2006, 2008

Neophobia, dominance and age

Urbanization is not the only factor that can influence an animal's neophobia. It can also vary with dominance rank and age. Young individuals may appear more risk-prone and less neophobic than adults as they are still gaining information about their environment and must spend more time exploring novelties than older individuals (Greenberg and Mettke-Hofmann 2001; Mata et al. 2013). For example, young baboons (*Papio ursinus*) approach novel objects more readily than older conspecifics (Bergman and Kitchen 2009). Similarly, juvenile chimango caracara (*Milvago chimango*) return to feed faster than adults when a novel object is placed near a familiar food source (Biondi et al. 2010). There are cases, however, where similar methods reveal neophobia to be independent of the subject's age, as with an experiment on common mynas (*Acridotheres tristis)* that found no difference between adults' and juveniles' latency to approach food near a novel object (Lermite et al. 2017).

Age is often used as a proxy for dominance, with young individuals subordinate to older ones. Older and dominant individuals may use their higher rank to gain priority access to food over their younger subordinates (Ekman 1989; Reader and Laland 2001). Younger individuals could therefore be led to be less averse to novelty (i.e. be less neophobic) by being forced to forage in less safe environments, risking encounters with potential predators or toxic food sources (Crane and Ferrari 2017; Domjan and Gillan 1976). On the other hand, there always exists the possibility that a novelty will turn out to be useful, for example if it can become a reliable food source, and so some dominants may take more risks by approaching novelty before subordinates. For example, in an experiment with hand-raised common ravens (*Corvus corax*), dominants were first to initially contact novel food items over their subordinates (Heinrich et al. 1995). It has previously been found that this species' dominants tend to initiate contact with unfamiliar food items, with subordinates only approaching afterwards (Gwinner 1964; Heinrich 1989). In contrast, a study on hand-raised individuals of a related species, rooks (*Corvus frugilegus*), found no difference in neophobia between dominant and subordinate individuals towards novel objects (Greggor et al. 2016b). Birds raised in captivity however are not likely to experience the same costs and benefits as wild individuals, as they have a reduced perceived predation risk and abundantly available food sources. Research on wild carrion crows (*Corvus corone*) had novel foods presented to the birds in their natural habitat, while a hidden camera recorded their behaviour (Chiarati et al. 2012). In this case, dominant individuals contacted novelties first, and subordinates after (Chiarati et al. 2012). These mixed findings regarding the relationship between neophobia and the dominance and age of individuals may also indicate influence from other untested variables.

Research goals

In this thesis, I aim to examine the effect of urbanization on neophobia of a common bird species, the black-capped chickadee (*Poecile atricapillus*). Previous mixed findings across multiple species could be the result of different underlying mechanisms, and my study aims to examine chickadees' approach to different novelty types (colour, object and food), in order to allow us to better determine the causes for habitat-related differences in neophobia. Running this study on wild individuals in their natural habitat also allows us to explore the results from an ecologically relevant perspective. In the next chapter, I describe my research performed in the fall and winter of the 2017-2018 season, when I presented wild flocks of chickadees with novelty near a familiar food source, in order to determine 1) the effect of urbanization on neophobia and 2) what individual characteristics (dominance rank and age) may also affect their neophobia. I predicted decreased neophobia among urban-dwelling individuals. I control for potential confounding variables, including sex of individuals (tied into dominance rank in this species; Smith 1991) and foraging group size (Stöwe et al. 2006). In the third and final chapter, I discuss the possible mechanisms for my findings of Chapter 2, and how these may change through time.

Chapter 2

Urbanization affects neophobia in black-capped chickadees (*Poecile atricapillus*)

Introduction

Most animals display a natural aversion to novelty known as neophobia (Ferrari et al. 2015; Villalba et al. 2009; Visalberghi et al. 2003; Walsh et al. 2018). Fear of new or unfamiliar items can be beneficial or detrimental to survival, depending on the context in which the novelty is encountered (Greenberg and Mettke-Hofmann 2001). Neophobia is advantageous when an individual's caution helps them avoid a novel threat, such as a new predator or a new but toxic food source (Crane and Ferrari 2017; Ferrari et al. 2015; Greenberg and Mettke-Hofmann 2001; Salo et al. 2007). However, when novelty is not dangerous, an individual could waste time or miss foraging opportunities by responding fearfully. For example, wild rats (*Rattus* spp) in captivity do not immediately eat food from a new container or new location, some choosing to go hungry for several days (Barnett 1958; Cowan 1977; Modlinska et al. 2015). Neophobia level and its plasticity are thus expected to be adjusted by natural selection, depending on costs and benefits associated with novelty in various environments (Greenberg 1990).

Neophobia has been found to vary between species and populations. Closely related species that have evolved different foraging methods show varying levels of neophobia (Greenberg 1983). For example, the specialized lesser Antillean bullfinch (*Loxigilla noctis*) was shown to be more neophobic than the generalist bananaquit (*Coereba flaveola*; Webster and Lefebvre 2001). Neophobia levels can also vary between individuals of the same species who develop in different habitats. For instance, Trinidadian guppies (*Poecilia reticulata*) from high-predation-risk streams presented higher spatial and foraging neophobia than those raised in low-risk streams (Elvidge et al. 2016). Results from common garden experiments, where individuals from different habitats develop in a common environment, suggested a genetic basis for some of these differences, but could not always completely rule out early-life learning (Greenberg 1992; Miranda et al. 2013; Roth et al. 2010).

It is frequently hypothesized that urbanization can lead to changes in neophobia through learning and/or selection. A common prediction is that urban animals should be less neophobic, because this trait would enable them to approach and thus exploit new resources (Sol et al. 2011; Tryjanowski et al. 2016) and increase their colonization success in urbanized areas (Liebl and Martin 2012; Sol et al. 2013). Few empirical studies have found support for this prediction, however (summarized in Griffin et al. 2017). Some find the opposite trend (Audet et al. 2016; EcheverrÌa and Vassallo 2008; Miranda et al. 2013), while even more find non-significant differences in neophobia level between urban and less urbanized habitats (Bókony et al. 2012; Candler and Bernal 2015; De Meester et al. 2018; Kozlovsky et al. 2017; Liker and Bókony 2009; Van Donselaar et al. 2018). These mixed findings are likely due to the possibility of there being both advantages and disadvantages to being more neophobic in cities. Urbanized animals could exhibit more neophobic behavior because they may encounter new predators, toxins or poisoned urban food sources (Bókony et al. 2012; Greggor et al. 2016a). Moreover, urban animals can have access to stable food sources, reducing the need to take risks and sample novelty (Miranda et al. 2013). There is therefore a need to understand the generality of these differences, preferably with experiments that examine the impact of various types of novel stimuli as suggested by Greggor et al. (2015). Using different novelty types could allow us to differentiate between the effect of natural selection on neophobia, i.e. as supported by a general habitat difference across several novelty types, or a learned reduction in fear response specific to certain object types (e.g. Greggor et al. 2016a), though these effects may not be mutually exclusive.

While population-level variation in neophobia is common, individual variation within a population also exists. Dominant individuals often have priority access to food and lower-risk environments than subordinates (Ekman 1989; Reader and Laland 2001). They therefore should not need to risk exploring potentially dangerous novelties while foraging. In line with this, a previous study on wild-caught black-capped chickadees (*Poecile atricapillus*) found dominants to be more neophobic than their subordinates (Seok An et al. 2011). By contrast, dominant carrion crows (*Corvus corone*) in the wild approached novel food sources before their subordinates (Chiarati et al. 2012), and captive-raised dominant common ravens (*Corvus corax*) and coyotes (*Canis latrans*) were also found to be less neophobic (Heinrich et al. 1995; Mettler and Shivik 2007). More work is needed to clarify the relationship between neophobic behavior and an individual's dominance rank.

Younger individuals must often spend more time foraging due to lack of experience (Crane and Ferrari 2017), or explore new areas and risk encounters with potentially dangerous situations. A possible reason that young appear more risk-prone could be that they are still gaining information about their environment, and so explore more than adults (Bergman and Kitchen 2009; Mata et al. 2013). Benefits to exploration are thought to decrease over time, as ageing individuals will have already learned as much as they need to survive, and exploring novelty further could be unnecessarily risky given the drop in the future value of information with age (Mata et al. 2013; Sherratt and Morand-Ferron 2018). While studies examining the effect of individual characteristics (such as dominance, age and sex) on neophobia exist, few have explored how these might influence the neophobia of individuals in free-ranging groups.

In this study, we examine the tendency of wild individuals to approach novelty in both urban and more pristine (rural forests) habitats. We performed replicated experiments where we presented a choice between familiar bird feeders and similar feeders with three different types of novelty (novel colors, objects and foods). Our experimental set-up allowed behavior of individuals to be studied under ecologically relevant conditions while controlling for potential differences in foraging group size that could co-vary with habitat type (Coleman and Mellgren 1994; Soma and Hasegawa 2004) and thus potentially bias neophobia comparisons. Our study species, black-capped chickadees, inhabit both urban and rural habitat, and their stable small winter groups demonstrate a linear dominance hierarchy where older male birds are dominant to younger birds and females (Devost et al. 2016, reviewed in Smith 1991). We predicted that: (1) urban chickadees would be more likely to initially contact novelty over familiar feeders than rural chickadees, and (2) young and subordinate chickadees would be more likely to first visit novel feeders than older and more dominant individuals, respectively.

Methods

Study population, sites and feeders

Our six study sites were located in and around the city of Ottawa, Ontario. Sites were located at least 2 km away from each other to ensure no overlap of winter flock ranges (maximum size 38.9 ha (0.4km^2); reviewed in Smith 1991). Birds caught in one location were never observed or caught in another. Urban sites (N=3) were partially forested urban parks in close proximity to human residences, and within 7.0 km of downtown Ottawa (see Figure 1). Rural sites (N=3) were forested areas situated at least 0.7 km away from the nearest human residence and at least 25.0 km outside of downtown Ottawa. All sites were baited in early October with black oil sunflower seed-filled feeders to attract chickadees for banding. Birds were caught using standardized mist-netting techniques, and were fitted with a Canadian Wildlife Service-issued band, as well as a unique color combination of plastic band and passive integrated transponder (PIT; Eccel Technologies, UK) tag. This band allowed them to be detected automatically by radio frequency identification (RFID) antennae (Priority 1 Design, Australia). An antenna, built into the single perch of every custom feeder, recorded the arrival and departure of each chickadee with a PIT. We combined detections of multiple visits by the same individual within three seconds into a single visit, as such a pattern is likely to represent a single, uninterrupted visit by a given bird (Evans et al. 2018b). We defined foraging group size as the number of different individuals registered on the feeders of a site up to 5 min prior to each focal visit (Morand-Ferron and Quinn 2011). This is a measure of the size of the foraging group at a given moment, which is assumed to relate to perceived predation risk (Pulliam 1973), and not the total number of birds living at each site.

Age, sex and dominance rank

We aged birds in hand by rectrices' shape in the fall (Meigs et al. 1983; Pyle 1997), and released them on site, ensuring that the experiment was conducted in their regular environment. A black-capped chickadee hatched the year of capture was classified as a juvenile bird, while a chickadee one year old or greater was classified as an adult. Any bird we were unable to adequately age (due to ambiguous characteristics) was marked as being of unknown age. Chickadees are not strongly sexually dimorphic, and thus cannot be sexed in hand. To determine sex, we used the R package 'caret' to train a general logistic regression, carried out in R package 'glmnet' (Friedman et al. 2010; Kuhn 2008). We built an algorithm from morphometric traits of the species (predictors included tarsus, tail, wing length and residuals of body mass regressed against time of day caught). This model was trained using repeated k-fold cross validation on a random 80% subset of 170 blood samples taken for molecular sexing in the context of another study in our population (Thompson et al. 2018; protocol from Griffiths et al. 1998). Twenty percent were retained to test the algorithm's applicability: the model had an accuracy of 0.78, compared to the 0.52 accuracy of the discriminant function previously used in chickadee studies when applied to our population (Desrochers 1988; Desrochers et al. 1988). We then used this algorithm to sex chickadees for the current study.

We determined an individual's dominance rank by evaluating dyadic interactions (displacements) registered when a single feeder was on each site. A displacement occurred when a bird arrived on the feeder one second after the previous individual departed, and then remained on the feeder for five seconds (these times were determined to provide the most accurate results when compared with video data; Evans et al. 2018a). The results of all displacements between individuals were used to calculate each bird's dominance score. As winter flocks of chickadees follow a linear dominance hierarchy, we evaluated the transitivity of triads (i.e. the linearity of relationships between multiple sets of three interacting individuals). We calculated transitivity instead of direct linearity as some pairs of individuals did not interact together, likely because subordinates of established dominant-subordinate pairs would avoid agonistic interactions with dominants on the feeder (de Vries et al. 2006; Devost et al. 2016). The transitivity of triads was evaluated using the following measurements from Shizuka and McDonald (2012, 2014): proportion of transitive triads relative to all triads (P_t) and the triangle transitivity metric (t_{tri}). We found all triads were transitive at one site ($P_t = 1.00$, $t_{tri} = 1.00$), three sites had significantly more transitive triads than expected by chance (mean $P_t = 0.97$, mean $t_{tri} = 0.90$, $P < 0.05$), while another site was borderline ($P_t = 0.91$, $t_{tri} = 0.66$, $P = 0.051$). The 6th site had the lowest number of visits to the feeders (3,698 compared to 10,547 visits of the next least visited site) and consequently did not generate enough interactions to properly evaluate dominance relationships. Data from this site were excluded in models including dominance score.

Experimental design

We placed an RFID-enabled feeder at each site three days prior to introducing novelty, allowing as many chickadees as possible to have enough time to locate, use and become familiar with the feeder. Three days appeared to be an appropriate amount of time, as we only had to remove five instances where an individual visited a feeder for the first time during an experiment, and could thus not be included in analyses for neophobia. This feeder, named the "Familiar feeder", remained on the site throughout the entire study period. Each of the six experiments lasted 9 days at each site and began with the Familiar feeder recording the three day period of baseline activity, i.e. bird usage of the feeder without novelty present. For the fourth, fifth and sixth days, two more feeders (named the "Novelty Feeder" and the "Control Feeder") were added to the site, placed an average of 4.3 meters away from the Familiar feeder and from each other. The "Novelty feeder" included some novel aspect that the birds had not been exposed to before: a novel color, object or food, each chosen based on Greggor et al. 2015's suggestions (see below). The "Control feeder" was identical to the Familiar feeder, and was added to control for the fact that any new object in the environment might elicit a neophobia response, regardless of the type of novelty it represented. In this case the control feeder could be considered to be spatially novel, being identical to the familiar feeder, but in a new location. The Novelty and Control feeders were removed after three days, allowing the chickadees to resume normal feeding at the Familiar feeder for a three day period. Sites were paired so that an experiment ran simultaneously at both an urban and a rural location to control for potential effects of different weather conditions on different days. We replicated each novel stimulus type twice, with the second replicates presented in the reverse order of the first. The positions of the Novelty and Control feeders were alternated between the two replicates to change where the main novelty was located, while the Familiar feeder remained stationary.

Novelty tests

For experiments where the novelty was placed externally on the feeder (colours, objects), the Familiar feeder had an opaque white cover (Figure 2a), so as not to let the quantity of seed in each feeder influence the birds' behaviour. For experiments where the contents of the feeder (i.e. the food) was the novelty, we used a transparent version of the same feeder (Figure 2b). Colors and objects were chosen so as to be novel for birds of both habitats, and not to mimic stimuli evoking evolved fear responses, such as aposematic coloring or predators (Crane and Ferrari 2017; Greggor et al. 2015). Components of the Familiar feeders were black, white, silver, grey and green; novel colors chosen for the two replicates were blue and pink. We covered the feeders with blue paper including a silver snowflake pattern, and pink striped with white, to accentuate the novelty (Figure 2c, 2d). For novel objects, we used objects of familiar colors black and white: dice glued in an upside-down 't' pattern, and white plastic atoms from an organic chemistry kit on a black cord (Figure 2e, 2f). These objects were built to be of similar height, and were installed directly above the feeding hole. For food tests, black oil sunflower seeds (fat 24%, fiber 30%, protein 15%) were replaced in the Novelty feeder by dried mealworms (fat 28%, fiber 6%, protein 53%) and hulled sunflower seeds (fat 35%, fiber 17%, protein 18%; Figure 2g, 2h).

Statistical analyses

We performed all statistical analyses with R version 3.4.4 (R Core Team 2018). We first used general linear mixed models (GLMM; function 'glmer') in statistical package 'lme4' (Bates et al. 2015) to determine whether there was a difference in an individual's first choice of feeder after the Novelty and Control feeders were added (model 1). The first feeder to register a bird's PIT (i.e. the first feeder a bird made contact with after all three feeders were deployed) was considered the bird's first choice. For each individual, initial choice of feeder was encoded as a binomial response where 1 was the first feeder visited, with feeder type (Familiar, Novelty or Control), habitat, date and a habitat*feeder type interaction term as explanatory variables, and individual as a random intercept. The results of this model indicated that chickadees behaved similarly towards both the Novelty and Control feeders, so we do not consider them as separate entities in the following analyses, but as both being novelty. For our subsequent main analyses, we ran three further GLMM (models 2, 3 and 4) to determine which variables affected the first choice of feeder. Each of these models had key predictor variables that would differ, which were dominance rank (model 2), age and sex (model 3), and group size (model 4). Separating these three sets of variables across models allowed us to avoid co-variance issues between dominance and age and sex (Devost et al. 2016, Thompson 1983), and avoid convergence issues caused by inclusion of foraging group size in models 2 and 3. It also allowed us to maintain a maximum sample size for each, as not all individuals could have their rank or age determined due to uncertainty in the ageing process. Based on findings of model 1, models 2, 3 and 4 used a binomial response variable that described a first visit as either a visit to a novel (1), or familiar feeder (0). Predictor variables examined were an individual's habitat (urban or rural), treatment (novel color, food or object), date and time of the visit (both rescaled and grand mean centered), and one of dominance rank (model 2), age and sex (model 3) or group size (model 4). Date and time were included to account for the possibility that birds registering their first visit later during a given experiment would be more likely to select the novel feeders, for instance due to social facilitation or observation of conspecifics. As we ran a total of six experiments at each site, we included individuals as random intercepts in the three models. The random intercept of capture site was excluded due to convergence issues (see Supplementary Tables 1 and 2 and supplementary Figure 1 for analyses showing this variable's non-significance within each habitat class). An interaction term between treatment type and habitat was included to examine whether the reaction to novelty types differed based on whether an individual was from an urban or rural area. This interaction was only included in the model with dominance rank (model 2), where the larger sample size allowed its inclusion without convergence issues.

For models 2-4, we used Akaike's information criterion corrected for small sample size (AICc) for model selection (package MuMIn; Bartoń 2018). When there were competing models within delta AICc < 2 of the top model, we performed model averaging using said models (Burnham and Anderson 2002; Grueber et al. 2011; Symonds and Moussalli 2011). Five data points were removed from analyses because the individuals were not previously registered on the site before the start of the experiments (i.e. all feeders may have been novel to them). Four of the thirty-six experiments (6 experiments x 6 sites) were removed from analyses due to a technical failure that occurred at the start of an experimental session. These four sites were comprised of two urban and two rural, and no single site had more than one experiment fail. To further ensure the robustness of our conclusions, we performed the same analyses with the paired site of failed experiments also removed, to restore a balanced design: our conclusions were qualitatively unchanged, i.e. each variable's statistical significance remained respectively above or below the threshold for significance (see Supplementary Tables 3, 4, 5 and 6).

Ethical note

This study was conducted under scientific and banding permits from Environment Canada Canadian Wildlife Service (10854) and approved by the Animal Care committee of the University of Ottawa (1759).

Results

We registered a total of 294 first visits from 71 chickadees across all six sites. Of these 71 birds, we identified the dominance rank of 59, and the age of 50 individuals. In only 2.7% of cases did a bird's first visit to a feeder coincide to the nearest second with another feeder already being occupied, and thus we do not consider further the possibility that a bird would be unable to land on their preferred feeder because it was already in use.

Rural birds had a nearly three times higher probability than urban birds of first visiting the Familiar feeder over the Novelty (represented as effect size ± standard error: -1.66 ± 0.26) or Control feeders (-1.60 ± 0.25), a difference that was statistically significant (see Table 1; Figure 3). The latter two feeders had a nearly equal probability to each other of being the rural birds' first visit (-0.06 ± 0.28). In contrast, urban birds showed a similar probability to initially contact any of the three feeders. As the Novelty and Control feeders had a similar probability of being first visited within the rural and urban environments, we considered a visit to either of these two feeders as a visit to novelty for subsequent analyses. Running similar analyses with only the

Novelty feeder considered a visit to novelty led to qualitatively unchanged results; see Supplementary Tables 7-9.

Habitat and date were variables with significant (positive) effects on first choice of feeder (Table 2 and Table 3), i.e. birds from urban habitats were significantly more likely to first visit novelty (Novelty or Control feeders) than those from rural areas (1.55 ± 0.38), and birds were significantly more likely to first visit the new feeders as the days increased from the start of the initial experiment (i.e. as more experiments were conducted; 1.23 ± 0.53). Dominance rank was a non-significant explanatory variable (Table 2; for visual representation see Figure 4), as were age and sex (Table 3). The interaction term between treatment type and habitat in the model with dominance was also non-significant.

While habitat influenced foraging group size (i.e. smaller groups were found in urban sites; see Supplementary Tables 12 and 13), foraging group size itself did not influence a bird's first choice of feeder. Model 4's results were qualitatively unchanged from those of models 2 and 3 (see supplementary Tables 14 and 15 for details).

Discussion

Our study is the first to our knowledge that examines the tendency of animals to approach different novelty types in their natural urban and rural habitats while controlling for variation in group size and individual differences in social status (age, sex and dominance rank). As predicted, urbanized chickadees were more likely to initially contact novelty than those from rural habitats, though it remains unclear whether this difference is due to learning and/or natural selection, as well as whether the effect was specific to novelty or the combination of new colours, objects or food with new spatial locations. An individual's dominance rank, age and sex did not affect its willingness to first approach the new feeders over the familiar one. The type of novelty –color, object, food- also had little effect. There was however a decrease in aversion for novelty over the course of the experiments, as birds possibly became habituated to the new feeders' appearances at the sites between replicates.

Urban birds were more likely to first visit feeders with added novelty than rural birds, as seen in all three main models (2, 3 and 4). This difference could occur because urbanized birds see more human-made objects throughout their development and adult life, some of which contain food provided by humans accidentally through litter or intentionally through bird feeders (Tryjanowski et al. 2015b). Urban chickadees have the opportunity to visit multiple styles of feeders, witnessing variations in size, color, shape and food, possibly leading them to become habituated to most added novelties and express low levels of neophobia. Our study did not reveal any significant interaction between habitat and novelty type, i.e. neophobia levels between rural and urban groups did not differ based on the category of novelty (colour, object, or food). This result contrasts with the Greggor et al. (2016a) study, which only found a faster approach to litter-type objects in urban than in rural areas, but no difference between habitats for natural or novel objects. They reasoned that such specific differentiation between novelty types most likely arose through urban and rural groups' different learning experiences relative to specific types of novelty. Learning through experience that feeders are important food resources in urban areas could also explain our urbanized individuals' relative willingness to approach novel feeders compared with their rural counterparts. However the lack of effect of novelty type in our study could also result from a more generalized difference in neophobia levels between the habitats, and thus local adaptation cannot be discounted in our population.

Microevolution was suggested as the underlying mechanism in a common garden experiment by Miranda et al. (2013) which showed that urban European blackbirds (*Turdus merula*) were more neophobic than rural, contrary to our results with chickadees. As that study could not completely discount early-life experience or maternal effects, it is still possible that both selection and learning mechanisms influenced neophobia in blackbirds. Individuals living in the urban environment may have recently adapted to live in an area that encourages exploration and risk-taking (Greenberg 1992; Miranda et al. 2013). The urban habitat could favour increased neophobia through its more stable resources and warmer temperatures, as individuals may not be as driven to approach novelty while foraging (Miranda et al. 2013). Overall, these mixed findings on the degree of neophobic behaviour in urban and rural environments could be due to the mechanisms behind them not being mutually exclusive, as it has recently been proposed that both learning and selection may play a role (Miranda et al. 2013; Sol et al. 2013). Future studies should attempt to disentangle further the effect of a reduced need to explore novelty in the urban environment (as a result of warmer temperatures and stable resources) against the facilitating effect of exposure to beneficial novelties.

Interestingly, in our study the spatial control feeder received similar visitation patterns to the novelty feeder in both habitats, with significantly less use than the familiar feeder in rural areas and similar use in urban (model 1). It is possible that rural chickadees exhibit neophobia towards any type of novelty in their environment, whether they have seen an identical item before or not, while urban individuals quickly treat novelty – novel color, object, food, or locations – as they do familiar ones, as they are also known to use novel food resources sooner than rural individuals (Tryjanowski et al. 2015a). To our knowledge, spatial novelty in the form of familiar objects encountered in a nearby location has not been explored before, as neophobia tests generally involve adding novelty to an already established feed station (e.g. Bókony et al. 2012; Herborn et al. 2010; Lermite et al. 2017; Webster and Lefebvre 2001). Similarities exist between our setup and spatial exploration tests that examine frequency of movement in novel rooms (open field tests), although these tests conducted with birds usually involve new objects in a new location, and do not involve food (e.g. Dingemanse et al. 2002; Quinn et al. 2011; Verbeek et al. 1994). The rural chickadees' reluctance to first visit the new feeders may have originated from their new/less familiar locations and not the novelty on its own. Our results suggest that this potential responses to spatial novelty could be an important future direction of study.

A potential explanation for our findings of greater neophobia in rural compared with urban chickadees is that group size could have differed between urban and rural sites. Fear of novelty could be reduced in urban habitats if individuals are part of larger groups, via effects such as shared vigilance and safety in numbers (Coleman and Mellgren 1994; Pulliam 1973; Soma and Hasegawa 2004). High population density could also increase intraspecific resource competition and social information transfer, leading to faster use of new bird feeders when foraging groups are larger (Tryjanowski et al. 2015a). Despite a general finding that bird abundance is higher in urban than in rural areas (possibly due to increased supplemental food sources; Tryjanowski et al. 2015b), in our study foraging group size was smaller among our urban sites, yet this variable did not affect our birds' first choice of feeder. Though it has been shown that individuals feel safer in larger groups (Pulliam 1973), greater group size does not automatically decrease neophobia. Captive-raised ravens were slower to approach novel objects in groups than when isolated, while captive-bred zebra finches (*Taeniopygia guttata*) had the opposite tendency, and wild house sparrows (*Passer domesticus*) tested in captivity showed no difference in object neophobia whether they were in a small or large group (Coleman and Mellgren 1994; Liker and Bókony 2009; Stöwe et al. 2006), the latter similar to our findings on free-ranging chickadees. The significant effect of date in our study may have been due to social facilitation or observation of conspecifics (Jones et al. 2017; Ogura and Matsushima 2011; Zentall and Hogan 1976), as initial visits to novelty increased over days. In any case, we wish to draw attention to the potential confounding effect of group size when assessing habitat differences in behavior of social animals in the wild, a variable that is rarely taken into account. Another explanation for our findings of habitat-related differences in neophobia consists of a greater ratio of more exploratory juveniles to less exploratory adults (Greenberg and Mettke-Hofmann 2001), which could be expected in urban flocks in our population (Kozlovsky et al. in rev.). However, we found no significant effect of age class in predicting neophobia, and therefore the observed habitat differences cannot be explained by differences in age structure of the wild groups. It is possible that juvenile chickadees are not forced into approaching novelties by more dominant adults in our studied groups. Finally, we cannot reject the possibility that increased rural neophobia was due to the added feeders being less noticeable in rural than in urban areas, but we find this explanation unlikely, as the experiment was performed in winter when there is little foliage present to mask the new feeders (example photos in supplementary Figure 2). Each feeder was placed an average of 4.3 meters away from the others to ensure that an individual would be able to see all three as it approached.

An individual's dominance, as well as its sex (a strong predictor of dominance in chickadees), did not influence willingness to first approach the new feeders over the familiar feeder. In contrast, dominant wild-caught chickadees were more neophobic than subordinates, the latter approaching novel objects and eating novel foods more rapidly (Seok An et al. 2011). These individuals were, however, tested in isolation, while our subjects freely associated with their conspecifics in the wild. The free association between individuals in our study could have encouraged dominant chickadees to be less neophobic (safety in numbers effect), or could have hindered some subordinates' willingness to first approach novelty as they instead followed the dominants' lead (for an example in carrion crows, see Chiarati et al. 2012), leading to no effect of dominance on neophobia. Interference is unlikely to have hampered the ability of individuals to express their preferences in our study, as in only 2.7% of the time did an individual's first visit coincide with another feeder being occupied. Other studies have found contrasting results on the effect of dominance (Greggor et al. 2016b; Heinrich et al. 1995); these may arise due to differing developmental (captive-raised or wild-caught) and test contexts (isolated or grouped) as well as novelty types. Our results seem to indicate that the dominance rank of wild chickadees does not heavily influence their feeding neophobia level in their natural environments, similar to the lack of age effect.

In this study, we found that urban chickadees had a higher probability than rural ones of initially contacting the familiar feeder before approaching novel feeders. This difference could be due to urban birds having experienced increased encounters with novelty throughout their lives and having thus learned to approach various colors or shape of feeders, as well as novel food types and feeder locations. While developmental differences, learning and generalisation could play a key role in determining feeding neophobia in our population, there is also the non-mutually exclusive possibility of natural selection influencing neophobia and its plasticity. The learning mechanism would be supported by evidence of an age effect, as older individuals would become more tolerant to novelty as they aged and experienced more novelties throughout their lifetimes. As no such effect of age was seen, evolutionary mechanisms could be favoured, however we cannot rule out early life learning since our chickadees were tested several months after fledging. In order to distinguish between these two mechanisms (learning vs. local adaptation), studies of wild individuals in their natural habitat such as the current one should be complemented by laboratory-based common garden experiments. Moreover, using various novelty types, either in the wild or in the lab, informs us on whether habitat-related neophobia differences are generalized or specific to the type of novelty. Next steps could include testing further forms of novelty, such as novel predators or sounds, as well as investigating the adaptive significance of reluctance to feed in novel locations highlighted in the rural birds of our study. While our work includes the benefits of exploring effects of novelty type, individual characteristics and foraging group size, there still remains much work to do to understand how wild populations will react to evolutionary novel environments and adapt as human populations and cities continue to grow.

Figure 1. Map showing positions of rural sites (N=3; blue circles) and urban sites (N=3; red circles) in and around Ottawa, Canada (45˚45’ N, 75˚69’ W). Landsat 8 OLI satellite image provided courtesy of U.S. Geological Survey.

Figure 2. Familiar feeders for a) novel color and object trials and b) novel food trials. Control feeders were identical to Familiar feeders. Novelty Feeders with: novel colors c) blue and d) pink; novel objects e) dice and f) chemistry model pieces; and novel food g) mealworms and h) hulled sunflower seeds.

Figure 3. Model 1 predictions. Probability with 95% confidence intervals of a chickadee first contacting any of the three feeders, as predicted by habitat (rural, urban) and feeder type (Familiar, Novelty, Control).

Figure 4. Percentage of individuals that made a first visit to novelty after the addition of Novelty and Control feeders to the site. Both additional feeders were considered to be novelty based on previous analyses. Individuals were ranked within each site and binned based on dominance rank. The dashed line (y = 66) shows the proportion of individuals that would be expected to visit the two additional feeders by chance if all else was equal. All sites where rank could be established are included (N=5).

Table 2. **Model 1.** Results of GLMMs modeling the feeder an individual first visits after Novelty and Control feeders were added. Feeder visited is fitted as a binomial response variable (where 1 is the first feeder visited by an individual), with feeder type (Familiar, Novelty, Control), habitat (rural, urban), feeder type x habitat, and date as explanatory variables. Individual ID is fitted as a random intercept. Significant p-values are in bold.

	Estimate	SE	Df	χ^2	z-value	p-value
Intercept	0.35	0.16			2.16	0.031
Feeder (ref. cat. Familiar)			2	25.49		
Feeder (Novelty)	-1.66	0.26			-6.39	**<0.001**
Feeder (Control)	-1.60	0.25			-6.32	**<0.001**
Feeder (ref. cat. Control)				25.49		
Feeder (Novelty)	-0.06	0.28			-0.21	0.837
Habitat (Urban)	-0.99	0.25	1	0.97	-3.95	**<0.001**
Date	-0.03	0.25	1	0.02	-0.14	0.891
Habitat : Feeder (ref. cat. Familiar)			2	33.24		
Habitat (Urban) : Feeder (Novelty)	1.92	0.37			5.23	**<0.001**
Habitat (Urban) : Feeder (Control)	1.67	0.36			4.58	**<0.001**
Habitat : Feeder (ref. cat. Control)				33.24		
Habitat (Urban) : Feeder (Novelty)	0.26	0.38			0.68	0.498

Table 2. **Model 2.** Model averaged estimates of variables (with dominance rank) affecting an individual's first choice of feeder (1: novelty, 0: familiar; for candidate models, see Supplementary Table 10). Estimates are from full average of six models < 2 ΔAICc of the top model. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-0.65	0.35	(-1.35, 0.04)		0.066
Habitat (Urban)	1.55	0.38	(0.81, 2.29)	1.00	**<0.001**
Dominance	0.24	0.45	(-0.64, 1.13)	0.35	0.592
Treatment (ref. cat. Color)				0.56	
Treatment (Food)	0.35	0.41	(-0.46, 1.15)		0.400
Treatment (Object)	-0.03	0.27	(-0.57, 0.50)		0.908
Treatment (ref. cat. Food)				0.56	
Treatment (Object)	-0.38	0.43	(-1.21, 0.46)		0.377
Date	1.23	0.53	(0.18, 2.27)	1.00	**0.022**
Time	0.12	0.39	(-0.66, 0.89)	0.21	0.768

Table 3. **Model 3.** Model averaged estimates of variables (with age and sex) affecting an individual's first choice of feeder (1: novelty, 0: familiar; for candidate models, see Supplementary Table 11). Estimates are from full average of four models < 2 ΔAICc from top model. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-0.44	0.27	(-0.96, 0.08)		0.099
Habitat (Urban)	1.46	0.37	(0.72, 2.19)	1.00	**<0.001**
Age (Juvenile)	0.03	0.15	(-0.28, 0.33)	0.16	0.868
Sex (Male)	0.07	0.21	(-0.34, 0.48)	0.24	0.728
Date	1.15	0.53	(0.11, 2.20)	1.00	**0.031**
Time	0.06	0.33	(-0.60, 0.71)	0.16	0.869

Figure 1.

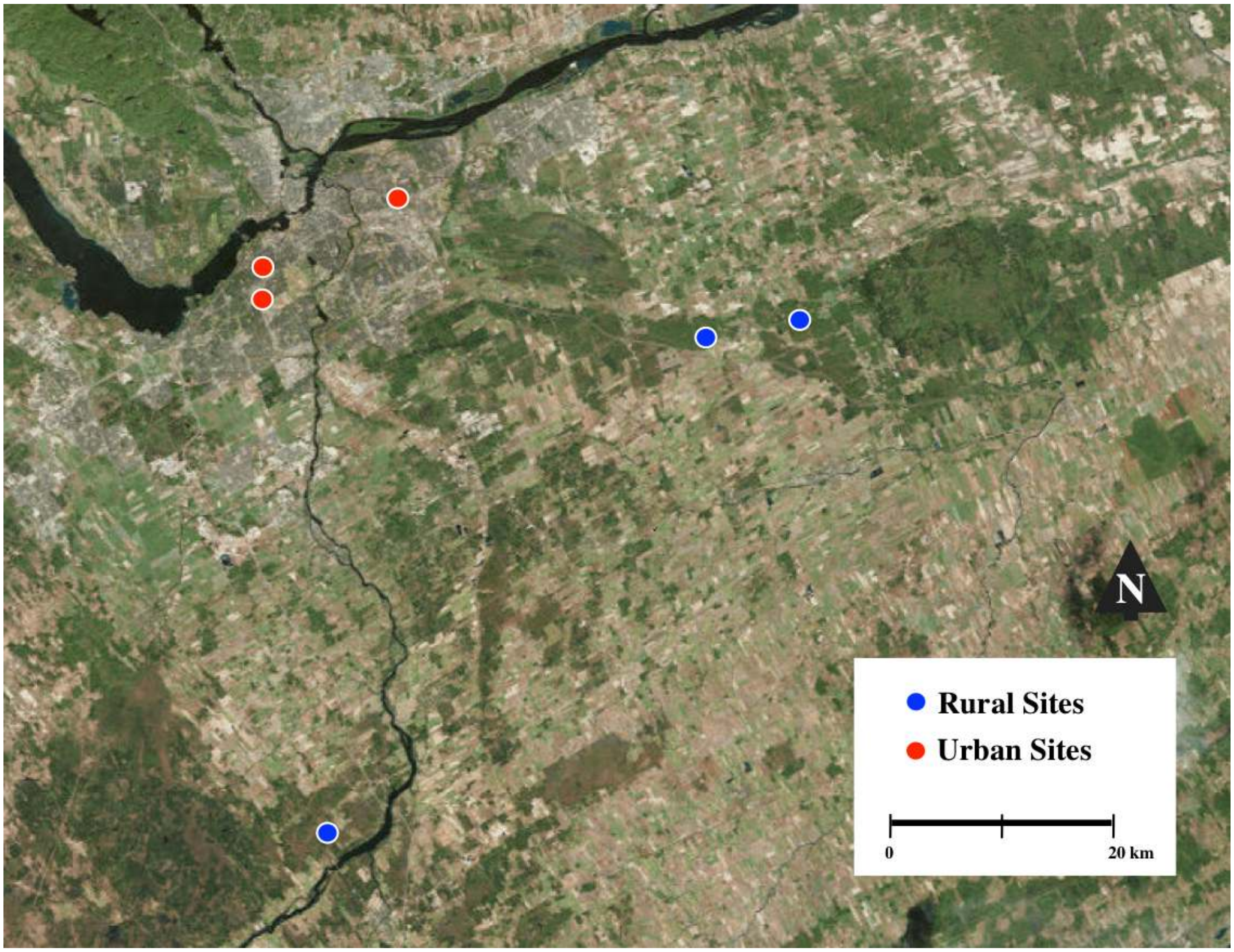


Figure 2.

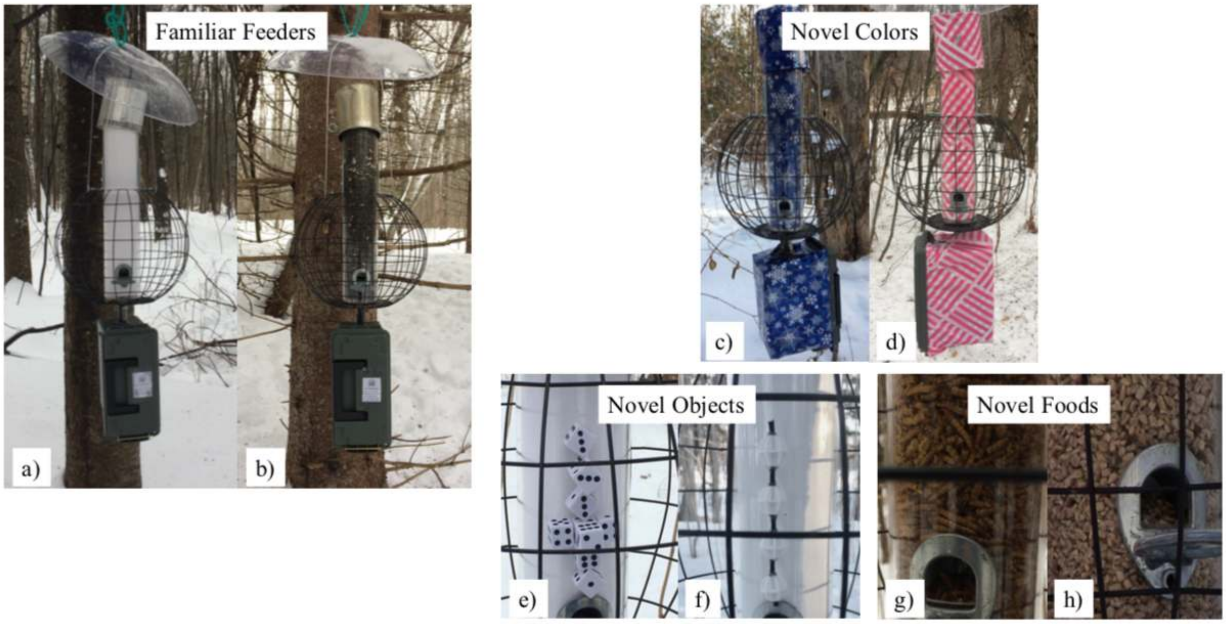

Familiar Feeders
a)
b)
Novel Colors
c)
d)
Novel Objects
e)
f)
Novel Foods
g)
h)

Figure 3.

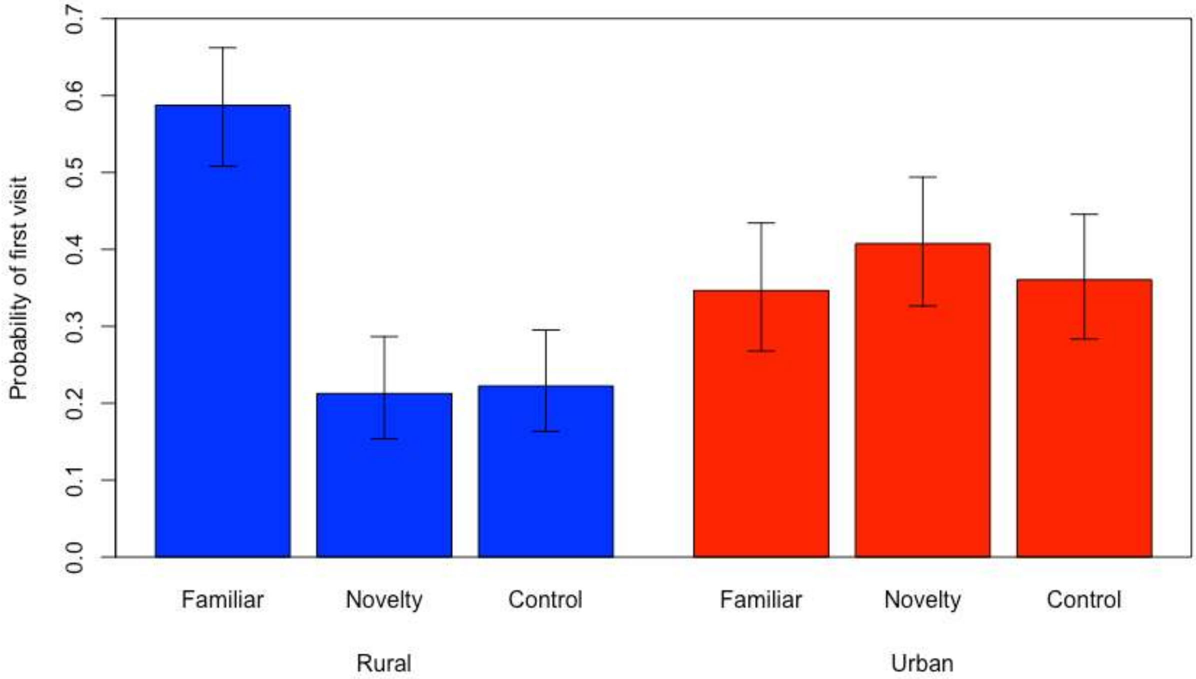
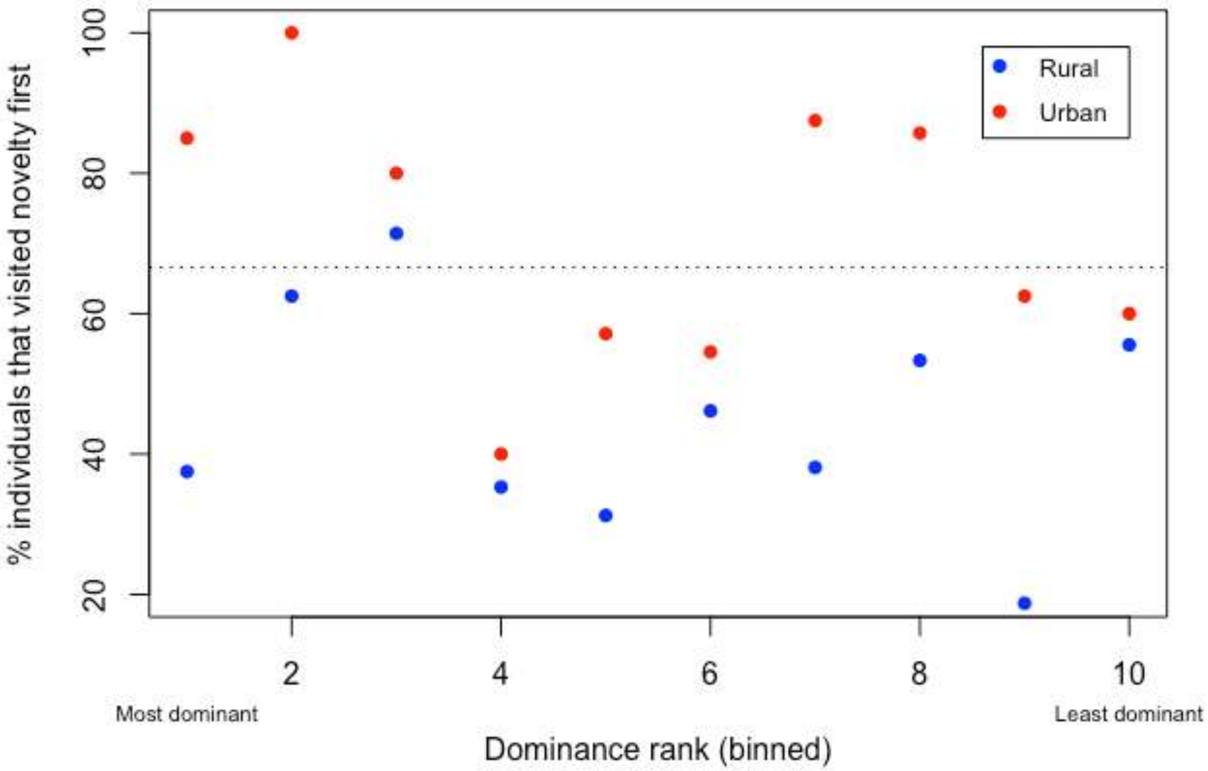

Probability of first visit
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Familiar
Novelty
Control
Familiar
Novelty
Control
Rural
Urban

Figure 4.


% individuals that visited novelty first
100
80
60
40
20
Rural
Urban
2
4
6
8
10
Most dominant
Least dominant
Dominance rank (binned)

Chapter 3

General Conclusion

Urbanization heavily alters the natural landscape, and its resultant habitat loss can lead to major repercussions on species richness and biodiversity (Aronson et al. 2014; McDonald et al. 2008). Despite this, some species persevere in the urban landscape, where evolutionarily novel threats and food sources can force them to modify or adapt their behaviour (Bókony et al. 2012; Lowry et al. 2013; Miranda et al. 2013). Multiple studies have explored the differences between urban and rural groups' neophobia, in an attempt to determine what makes some more likely to succeed in the novel city environment than others. As urbanization is still expected to increase worldwide (United Nations 2014), the importance of understanding how individuals survive in urban areas also increases. Mixed findings across and within species have so far made interpretation of the results difficult, but have led to a greater understanding of the complexity of the mechanisms causing these behavioural changes. My goal in this thesis was to examine the effect of urbanization on the neophobic response of black-capped chickadees, in an attempt to further our understanding of this behaviour. I predicted that urban chickadees would more likely initially contact novel feeders over familiar ones than rural, while young subordinate chickadees would more likely initially contact novel feeders over familiar ones than older dominants.

In chapter 2, I provide evidence that individuals inhabiting urban parks were less neophobic than those in rural forests, independent of any individual's age, sex or dominance rank. These latter three individual characteristics did not appear to significantly influence neophobia, nor did the time of day when individuals would visit the feeders. Date was a significant variable, implying a habituation effect, while foraging group size and the type of novelty did not significantly affect the initial approach to novelty. It was therefore not possible to determine whether avoidance of the novelties was due to a learned or selected response towards a specific type of novelty.

As discussed in chapter 1, previous research has found that significant differences in neophobia between urban and rural groups are not always existent (or possibly not evident using current study techniques). When trends appear however, they can be in either direction, with urban individuals either more or less neophobic than their rural counterparts (see Table 1). Behavioural changes such as these are thought to arise through two major mechanisms. First, through behavioural plasticity: individuals have the ability to modify their phenotype in order to suit the current environmental conditions (Thibert-Plante and Hendry 2011), allowing them to quickly change their behaviour. This plasticity is thought to greatly advantage individuals colonizing urban landscapes, as it allows them to adjust quickly to the new environment (Miranda 2017). The second major mechanism through which changes in neophobia of animals between urban and rural environments can occur is natural selection. Selective pressures from the urban environment can force species to adapt their behaviour over generations. In support of this, innate differences between groups have been discovered, though it is not always possible to completely discount the effect of early developmental differences (Atwell et al. 2012; Miranda et al. 2013). More support for microevolution can be found in genetic differences between urban and rural groups, though these studies are still rare (Mueller et al. 2013).

While described separately above, these learning and selection mechanisms are not mutually exclusive. Recent research has proposed that both play a role in determining changes in species' neophobia in urban areas (Miranda et al. 2013; Sol et al. 2013). It has been shown that phenotypic plasticity greatly increases the chances of species successfully colonizing a new area (Martin and Fitzgerald 2005; Sol et al. 2002; Wang and Althoff 2019), but selection pressures may act upon these traits over time as well, causing a genetic divergence between groups from different environments (Mueller et al. 2013; Price et al. 2003). If this is true, we would expect both mechanisms to influence behaviours thought to improve urban survival in the same direction, as was the case with Eurasian Coots (*Fulica atra*), whose urban-associated behaviours (e.g. aggression, boldness) were more strongly expressed with increased time since urban colonization (Minias et al. 2018). This was not the case however for a study comparing neophobia of recently colonized and long established urban house sparrows (*Passer domesticus;* Martin and Fitzgerald 2005). The recently established urban house sparrows (28 years) showed less neophobia than long established ones (150 years). It is possible that traits thought to aid in initially colonizing urban landscapes (e.g. being less neophobic) are no longer necessary once the population has been firmly established, and eventually disappear (Liebl and Martin 2012). While black-capped chickadees have been recorded in urban Ottawa as early as 1951 (according to historic eBird records), it is unclear whether they had maintained a presence before then. I am therefore unable to comment on the neophobia of Ottawa chickadees in regard to time since urbanization.

Future work should aim to further explore the learning and selection mechanisms by evaluating neophobic behaviour using both an ecologically relevant (wild) and a common garden (captive) context. These two methods used concurrently may help better distinguish between the two mechanisms. More work is also necessary to better understand the effects of spatial novelty, i.e. whether the appearance of a familiar food source in a different but nearby location induces a neophobic response, or is the result of an individual preferring to remain with what is familiar (philopatry). Should more evidence be found to support the former, I would recommend including a spatial control in all neophobia experiments going forward. Overall, my work contributes to the literature regarding behavioural changes due to urbanization by suggesting the importance of testing multiple novelty types in various experimental contexts, while proposing a new method for evaluating neophobia in the wild using spatial control.

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Appendix

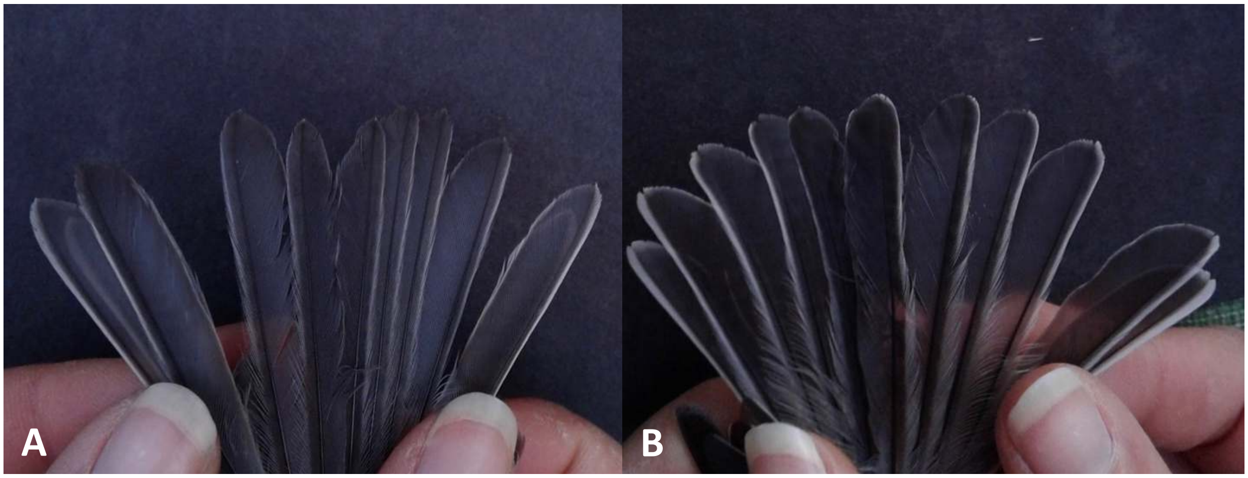
Individual characteristics per habitat

The total number of male, female, adult and juvenile chickadees studied within the rural and urban environments across all six sites.

	Rural	**Urban**
Male	14	15
Female	10	11
Adult	15	10
Juvenile	9	16

Ageing

Black-capped chickadees were aged via their tail feathers. A) A juvenile chickadee's outer tail feathers are pointed and worn, with no white on the inner vane's tip. B) An adult chickadee's outer tail feathers are rounded and show white edges on both sides of the tip. This ageing method yielded a 93.2% intra-seasonal success rate on our sites, i.e. 55 of 59 chickadees recaptured within the same season across several sites were re-placed in their initial age category.



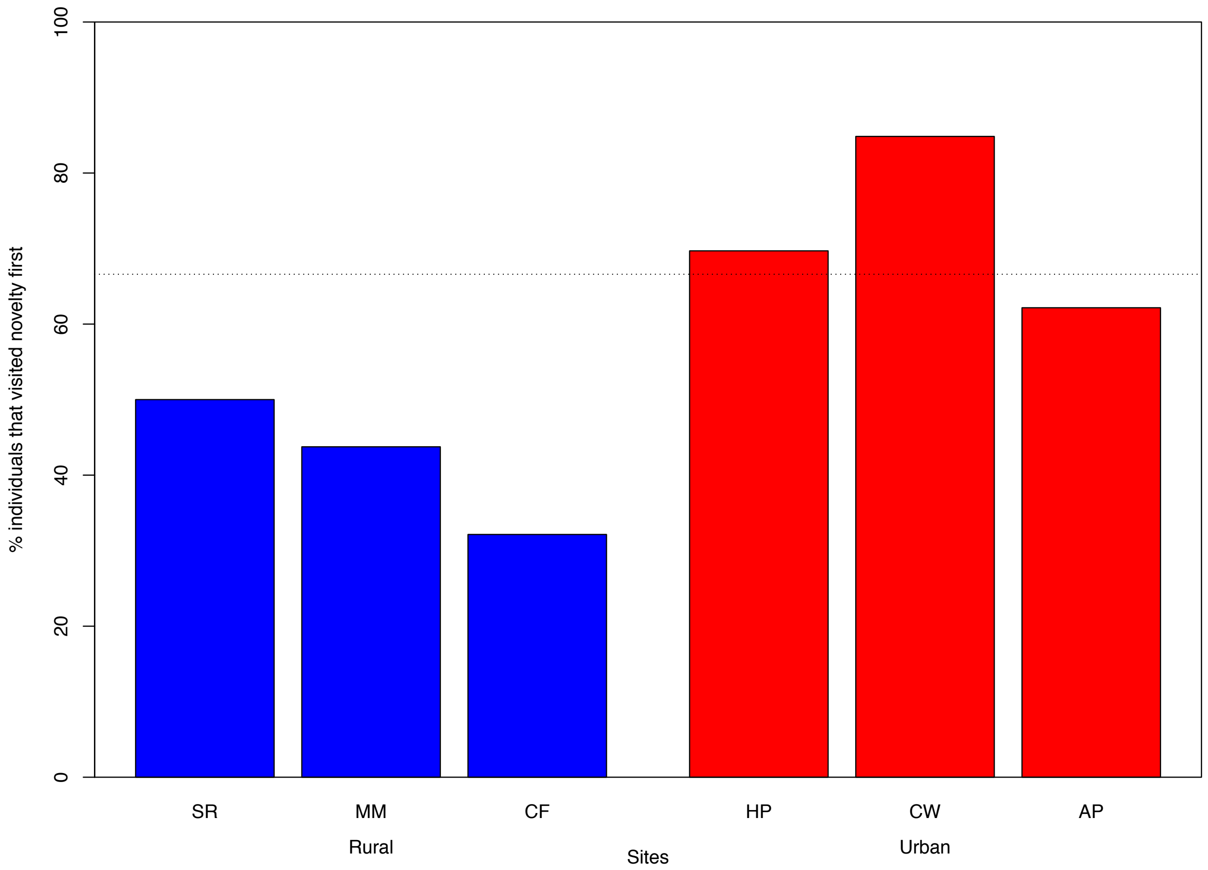
Novel Foods

Table comparing contents of the familiar food (black oil sunflower seeds) with the novel foods (dried mealworms and hulled sunflower seeds).

	Black Oil Sunflower Seeds	Dried Mealworms	Hulled Sunflower Seeds
			
Description	Seeds with shell from the common sunflower plant *Helianthus annuus*	Dried larva of a darkling beetle (genus *Tenebrio*), often fed to captive birds	Black oil sunflower seeds without the shell
Crude Protein	15%	53%	18%
Crude Fat	24%	28%	35%
Crude Fiber	30%	6%	17%

Chapter 2 Supplementary Material

Supplementary Figure 1. Percentage of individuals on each site across all experimental treatments that made a first visit to novelty after the addition of Novelty and Control feeders to the site. Both additional feeders were considered to be novelty based on previous analyses. The dashed line (y = 66) shows the proportion of individuals that would be expected to visit the two additional feeders by chance if all else was equal.



Supplementary Figure 2. Example photos of the positions of feeders on a) an urban site during novel food trial and b) a rural site during novel color trial.

Supplementary Table 1. Results of a general linear mixed model with first visit as a binomial response variable (1: novelty, 0: familiar), rural sites as fixed predictors and individual as a random intercept. Site was a non-significant variable. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**z value**	**p-value**
Intercept	-0.74	0.32	(-1.45, -0.14)	-2.30	0.02
Site (ref. cat. CF)					
Site (MM)	0.47	0.43	(-0.36, 1.38)	1.10	0.271
Site (SR)	0.66	0.43	(-0.16, 1.59)	1.55	0.120
Site (ref. cat. MM)					
Site (SR)	0.19	0.40	(-0.63, 1.04)	0.48	0.629

Supplementary Table 2. Results of a general linear mixed model with first visit as a binomial response variable (1: novelty, 0: familiar), urban sites as fixed predictors and individual as a random intercept. Site was a non-significant variable.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**z value**	**p-value**
Intercept	0.53	0.34	(-0.16, 1.27)	1.56	0.119
Site (ref. cat. AP)					
Site (CW)	0.99	0.54	(-0.03, 2.23)	1.81	0.070
Site (HP)	0.38	0.51	(-0.66, 1.49)	0.75	0.452
Site (ref. cat. CW)					
Site (HP)	-0.60	0.56	(-1.87, 0.48)	-1.08	0.282

Supplementary Table 3. Model averaged estimates of variables (with dominance) affecting an individual's first choice of feeder (1: novelty, 0: familiar; for candidate models, see Supplementary Table 4). Paired sites of treatments with technical failures are removed to restore balanced design. Estimates are from full average of four models < 2 ΔAICc from top model, each including individual as random intercept. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-0.90	0.42	(-1.72, -0.07)		0.033
Habitat (Urban)	1.36	0.39	(0.59, 2.12)	1.00	**<0.001**
Dominance	1.12	0.53	(0.07, 2.17)	1.00	**0.036**
Treatment (ref. cat. Color)				0.45	
Treatment (Food)	0.14	0.35	(-0.54, 0.82)		0.508
Treatment (Object)	-0.18	0.38	(-0.94, 0.57)		0.410
Treatment (ref. cat. Food)				0.45	
Treatment (Object)	-0.71	0.36	(-1.17, 0.52)		0.052
Date	1.56	0.68	(0.21, 2.90)	1.00	**0.023**
Time	0.32	0.63	(-0.91, 1.56)	0.39	0.279

Supplementary Table 4. Models within < 2 ΔAICc of the top model for novelty tests with dominance rank as a predictor variable. Paired sites of treatments with technical failures are removed to restore balanced design. Four candidate models with degrees of freedom, AICc, delta and Akaike weights. All include individual as random intercept.

Candidate Models	**df**	**AICc**	**Δ**	**w**
Habitat + Dominance + Date	5	267.8	0.00	0.343
Habitat + Dominance + Treatment + Date	7	268.2	0.49	0.269
Habitat + Dominance + Date + Time	6	268.8	1.05	0.203
Habitat + Dominance + Treatment + Date + Time	8	269.0	1.22	0.186

Supplementary Table 5. Model averaged estimates of variables (with age and sex) affecting an individual's first choice of feeder (1: novelty, 0: familiar; for candidate models, see Supplementary Table 6). Paired sites of treatments with technical failures are removed to restore balanced design. Estimates are from full average of four models < 2 ΔAICc from top model, each including individual as random intercept. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-0.50	0.34	(-1.16, 0.16)		0.141
Habitat (Urban)	1.25	0.37	(0.51, 1.98)	1.00	**<0.001**
Age (HY)	0.05	0.18	(-0.32, 0.41)	0.18	0.804
Sex (Male)	0.49	0.40	(-0.31, 1.28)	0.76	0.231
Date	1.43	0.58	(0.29, 2.58)	1.00	**0.014**
Time	0.09	0.39	(-0.68, 0.86)	0.17	0.815

Supplementary Table 6. Models within < 2 ΔAICc of the top model for novelty tests with age and sex as predictor variables. Paired sites of treatments with technical failures are removed to restore balanced design. Four candidate models with degrees of freedom, AICc, delta and Akaike weights. All include individual as random intercept.

Candidate Models	**Df**	**AICc**	**Δ**	**w**
Habitat + Sex + Date	5	240.4	0.00	0.410
Habitat + Date	4	241.5	1.11	0.236
Habitat + Age + Sex + Date	6	242.1	1.65	0.180
Habitat + Age + Sex + Date + Time	6	242.1	1.70	0.175

Supplementary Table 7. Model averaged estimates of variables (with dominance rank) affecting an individual's first choice of feeder (1: novelty, 0: familiar), with only visits to the Novelty feeder considered as a visit to novelty. The conclusions remain qualitatively unchanged from main text analyses (model 2) where visits to Novelty and Control feeders were both considered as visits to novelty. Estimates are from full average of three models < 2 ΔAICc of the top model. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-1.63	0.34	(-2.30, -0.97)		<0.001
Habitat (Urban)	0.93	0.32	(0.29, 1.57)	1.00	**0.004**
Dominance	0.25	0.45	(-0.64, 1.14)	0.37	0.580
Date	1.29	0.55	(0.19, 2.38)	1.00	**0.021**
Time	-0.07	0.35	(-0.76, 0.62)	0.18	0.839

Supplementary Table 8. Model averaged estimates of variables (with age and sex) affecting an individual's first choice of feeder (1: novelty, 0: familiar), with only visits to the Novelty feeder considered as a visit to novelty. The conclusions remain qualitatively unchanged from main text analyses (model 3) where visits to Novelty and Control feeders were both considered as visits to novelty. Estimates are from full average of three models < 2 ΔAICc of the top model. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-1.67	0.29	(-2.25, -1.10)		<0.001
Habitat (Urban)	1.16	1.16	(0.48, 1.84)	1.00	**<0.001**
Sex (Male)	0.05	0.18	(-0.31, 0.41)	0.23	0.778
Date	1.22	0.60	(0.04, 2.40)	1.00	**0.042**
Time	-0.14	0.48	(-1.10, 0.81)	0.24	0.768

Supplementary Table 9. Model averaged estimates of variables (with group size) affecting an individual's first choice of feeder (1: novelty, 0: familiar), with only visits to the Novelty feeder considered as a visit to novelty. The conclusions remain qualitatively unchanged from main text analyses (model 4) where visits to Novelty and Control feeders were both considered as visits to novelty. Estimates are from full average of two models < 2 ΔAICc of the top model. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**Importance**	**p-value**
Intercept	-1.45	0.31	(-2.05, -0.85)		<0.001
Habitat (Urban)	0.98	0.29	(0.40, 1.56)	1.00	**<0.001**
Group size	-0.06	0.07	(-0.12, 0.08)	0.34	0.676
Date	1.66	0.49	(0.69, 2.64)	1.00	**<0.001**

Supplementary Table 10. Models within < 2 ΔAICc of the top model for novelty tests including dominance rank as a predictor variable. Seven candidate models with degrees of freedom, AICc, delta and Akaike weights. All include individual as random intercept.

Candidate Models	**df**	**AICc**	**Δ**	**w**
Habitat + Treatment + Date	6	316.0	0.00	0.249
Habitat + Dominance rank + Treatment +Date	7	316.5	0.51	0.193
Habitat + Date	4	316.5	0.57	0.187
Habitat + Dominance rank + Date	5	316.8	0.87	0.161
Habitat + Treatment + Date + Time	7	317.5	1.55	0.115
Habitat + Date + Time	5	317.9	1.93	0.095

Supplementary Table 11. Models within < 2 ΔAICc of the top model for novelty tests with age and sex as predictor variables. Four candidate models with degrees of freedom, AICc, delta and Akaike weights. All include individual as random intercept.

Candidate Models	**df**	**AICc**	**Δ**	**w**
Habitat + Date	4	277.5	0.00	0.433
Habitat + Sex + Date	5	278.7	1.24	0.233
Habitat + Age + Date	5	279.4	1.90	0.167
Habitat + Date + Time	5	279.4	1.90	0.167

Supplementary Table 12. Model averaged estimates of variables affecting group size of chickadees (for candidate models, see Supplementary Table 13). Estimates are from full average of three models within < 2 ΔAICc of the top model. Group size included as a poisson-distributed response variable. Predictor variables included habitat, treatment type, date, time and individual nested in site as a random intercept. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**z value**	**p-value**
Intercept	1.45	0.10	(1.24, 1.65)	14.02	<0.001
Habitat (Urban)	-0.40	0.15	(-0.69, -0.11)	2.67	**0.008**
Date	-0.17	0.13	(-0.43, 0.00)	1.25	0.211
Time	-0.02	0.08	(-0.40, 0.20)	0.27	0.787

Supplementary Table 13. Models within < 2 ΔAICc of the top model for group size of chickadees. Three candidate models with degrees of freedom, AICc, delta and Akaike weights. All include individual nested in site as random intercept.

Candidate Models	**df**	**AICc**	**Δ**	**w**
Habitat + Date	5	1202.0	0.00	0.540
Habitat + Date + Time	6	1203.7	1.67	0.234
Habitat	4	1203.7	1.74	0.226

Supplementary Table 14. Model averaged estimates of variables (with group size) affecting an individual's first choice of feeder (1: novelty, 0: familiar; for candidate models, see Supplementary Table 15). Estimates are from full average of three models within < 2 ΔAICc of the top model. Predictor variables included habitat, treatment type, date, time and individual nested in site as a random intercept. Significant p-values are in bold.

Parameter	**Estimate**	**SE**	**CI (2.5%, 97.5%)**	**z value**	**p-value**
Intercept	-0.31	0.31	(-0.92, 0.29)	1.02	0.307
Habitat (Urban)	1.44	0.32	(0.81, 2.07)	4.49	**<0.001**
Group size	-0.03	0.05	(-0.14, 0.08)	0.54	0.590
Date	1.41	0.50	(0.51, 2.31)	3.06	**0.002**
Time	0.06	0.30	(-0.53, 0.66)	0.21	0.832

Supplementary Table 15. Models within < 2 ΔAICc of the top model for novelty tests with group size as a predictor variable. Three candidate models with degrees of freedom, AICc, delta and Akaike weights. All include individual as a random intercept.

Candidate Models	**df**	**AICc**	**Δ**	**w**
Habitat + Date	4	374.9	0.00	0.450
Habitat + Group size + Date	5	375.3	0.43	0.363
Habitat + Date + Time	5	376.7	1.76	0.186