Examining the effect of urbanization on personality, plasticity, and spatial cognition in scatter hoarders

Megan Joy Thompson

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
in partial fulfillment of the requirements
for the MSc degree in Biology

Department of Biology
Faulty of Science
University of Ottawa

Abstract

Anthropogenic environmental changes are occurring globally and are having dramatic effects on wildlife. Successful urban animals can alter behaviours to adjust to these conditions, but it is not well understood how these modifications arise. In particular, exploratory personality and behavioural plasticity are predicted to facilitate colonization in urban areas. The link between exploratory personality, cognition, and plasticity has received little attention, and has never been examined in urban animals. The first objective of this thesis was to examine the relationship between exploratory personality and habituation in a novel environment, and determine whether variation at the individual-level is predicted by urbanization. The second objective was to explore the association between exploratory personality and spatial cognition within scatter hoarders, and assess spatial memory along an urban gradient. At the individual-level, I report significant inter-individual differences in exploratory personality and habituation. I found evidence that fast initial explorers tend to habituate in a novel environment over time while slow explorers do not. There was no significant relationship between exploratory personality and spatial cognition within individuals. At the population level, urbanization did not significantly predict habituation or spatial cognition. I do report a significant positive relationship between urbanization and exploration. Overall, I conclude that urban individuals are significantly faster explorers, but are not more behaviourally plastic and do not show differences in spatial memory. Further work examining personality, cognition, and plasticity within individuals is needed to determine whether these traits have implications for populations under different environmental conditions.

Résumé

Des changements environnementaux anthropiques se produisent globalement et ont des effets importants sur la faune. Les animaux urbains peuvent modifier leurs comportements pour s'adapter à ces conditions, mais on ne comprend pas très bien comment ces modifications se produisent. En particulier, la personnalité exploratoire et la plasticité comportementale devraient faciliter la colonisation des zones urbaines. Le lien entre la personnalité exploratoire, la cognition et la plasticité a reçu peu d'attention et n'a jamais été examiné chez les animaux urbains. Le premier objectif de cette thèse était d'examiner la relation entre la personnalité exploratoire et l'habituation dans un environnement nouveau et de déterminer si la variation au niveau individuel est prédite par l'urbanisation. Le deuxième objectif était d'explorer l'association entre la personnalité exploratoire et la cognition spatiale chez les animaux qui cachent des ressources de façon dispersée, ainsi que de mesurer leur mémoire spatiale le long d'un gradient urbain. Au niveau individuel, je reporte des différences interpersonnelles significatives dans la personnalité exploratoire et l'habituation. Mes résultats montrent que les explorateurs rapides ont tendance à s'habituer dans un nouvel environnement au fil du temps alors que les explorateurs lents ne démontrent pas d'habituation. Il n'y a pas de relation significative entre la personnalité exploratoire et la mémoire spatiale chez les individus. Au niveau de la population, l'urbanisation ne prédit pas significativement l'habituation ou la mémoire spatiale, mais il y a une relation positive significative entre l'urbanisation et l'exploration. Je conclus que les individus urbains sont des explorateurs plus rapides, mais ne sont pas plus plastiques ni dotés d'une mémoire spatiale inférieure à celle des individus plus ruraux. D'autres travaux examinant la personnalité, la cognition et la plasticité sont nécessaires pour déterminer si ces traits ont des implications pour les populations exposées à d'autres conditions environnementales.

Acknowledgements

I would first like to thank my supervisor, Julie Morand-Ferron, for working so closely with me on this project and giving me countless opportunities throughout my degree. Her guidance, constant support, and immense knowledge have made me feel lucky to have her as a mentor. I would also like to thank my committee members: Sue Bertram, Jessica Forrest, Vincent Careau, and Catherine Plowright. Their praise, constructive feedback, and interest in encouraging me as a young researcher is greatly appreciated.

I am grateful to the Human Frontier Science Program, NSERC, the Ontario Graduate Scholarship, and the University of Ottawa for funding this work and myself. For access to my field sites, I would like to thank the City of Ottawa and the Nature Conservancy of Canada. I could not have done this work without our field techs, Celia Bodnar and Nicolas Bernier, who helped me catch chickadees.

My JMF lab family has supported me so much over the last years. I am grateful for Teri Jones (“lab mom”) who showed me the ropes and always gave the best advice. I would like to thank Shannon Whelan for her friendship and being one of my favourite humans ever - Shagen - enough said. I would like to thank my 6-pack buddy, Julian Evans, for being so R savvy and for initiating adventures. I would like to acknowledge Ethan Hermer, whose constant bugging made him a best bro. I am grateful to Isabel Rojas-Ferrer for being so compassionate and always being able to make me laugh. I of course can’t forget Sanjay Prasher, my #2 BFF, thanks for the sass and sorry you couldn’t be my #1 (see Shagen reference above). To all the other biograds who I have become so close to, thank you for tackling the ups and downs of grad school with me. Friday drinks, weekend adventures, DnD, coffee club, and office visits made my life in Ottawa feel full. Finally, I am grateful for my family. I would not have made it here without them!

Statement of Contributions

The second and third chapters of this thesis have been prepared as manuscripts and content overlaps between them. The pronoun "we" is used within manuscripts for inclusion of additional authors, however the writing of this thesis was accomplished by myself.

Chapter 2: Remote sensing via satellite imagery for the quantification of urbanization was conducted with assistance from postdoctoral fellow Dr. Julian Evans. Sheena Parsons assisted with field work and initiated interest in this topic by completing an honours thesis on the subject.

Chapter 3: Honours students Sofia Karabatsos and Kayla Humphreys assisted with data collection for the multi-trial spatial task in captivity.

NB: Work in this thesis was completed in accordance with the regulations of the University of Ottawa Animal Care Committee (protocols 1758-59), and under scientific (SC-42) and banding permits (10854) from Environment Canada, Canadian Wildlife Service.

Table of Contents

List of Tables

Chapter 2

Chapter3

List of Figures

Chapter 2

Chapter 3

Chapter 1

General Introduction

Behavioural adjustments to urbanization

Urbanization is a process that leads to changes in natural environments by consequence of human settlement and has been recognized as one of the most important drivers of species extinction (Marzluff 2001). The introduction of anthropogenic noise and light, novel competitors or pests, as well as degradation of natural habitat may deter animals from establishing in urban areas. However, the creation of novel habitats, biotic interactions, and ecological opportunities may also facilitate the persistence of some animals in these areas (reviewed in McDonnell & Hahs 2015). As a result, some species are declining in response to human-induced environmental changes, while other closely-related species are thriving in these novel habitats (Sih *et al.* 2011). It is puzzling that closely-related species have dramatically different responses to anthropogenic stressors and it will be important to determine what mechanisms are responsible for successful adjustment to urbanization moving forward (Sih *et al.* 2011; Lowry *et al.* 2013; Miranda 2017).

Modification of behaviour has been proposed as an important mechanism allowing individuals to occupy urban areas (Lowry *et al.* 2013; Sol *et al.* 2013). Behavioural adjustments have been shown to help animals deal with novel challenges in urban areas in relation to reproduction, foraging, anthropogenic stressors, and novel resources or habitats (reviewed in Sih *et al.* 2011; Lowry *et al.* 2013). There is growing evidence that behavioural differences exist between populations in urban and non-urban areas, but is not well understood how these behavioural differences arise (Sol *et al.* 2013; Lowry *et al.* 2013; Miranda 2017). Animal personality and behavioural plasticity are two traits that are expected to facilitate or restrict arrival, colonization, and persistence of individuals, and thus populations, in urban environments (Sol *et al.* 2013; Lowry *et al.* 2013).

Personality and urbanization

There has been an explosion of research in the biological sciences in the last decade that has examined consistent between-individual differences in behavioural tendencies. These individual differences in behaviour are now known as animal personalities (Réale *et al.* 2007). Animal personality traits are expected to influence and modify ecological and evolutionary processes, and thus personality is suggested to be an important dimension within these fields (Dall *et al.* 2004; Wolf & Weissing 2012). Certain personality traits are expected to be favoured in urban environments and intrinsic differences in personality may develop along an urban gradient via microevolution. Particular personalities may facilitate colonization of urban areas (precolonization adaptation) or may be selected for as the fitness optimum shifts in these new environments (post-colonization adaptation; Miranda *et al.* 2013). Individuals that are faster explorers, more aggressive, and bolder are predicted to adopt novel ecological opportunities more readily and thus are expected to have higher fitness in urban areas (Lowry *et al.* 2013; Sol *et al.* 2013). A number of studies report differences in personality between urban and non-urban individuals, where urban animals are generally faster explorers, more neophilic, more aggressive, and have reduced escape behaviours in comparison to non-urban conspecifics (reviewed in Miranda 2017). Consistent behavioural tendencies provide fitness benefits under the conditions that they have been selected for, but when environmental conditions change, it may be more advantageous to be behaviourally flexible (Sol *et al.* 2013).

Behavioural plasticity and urbanization

Behavioural plasticity is predicted to be an important trait possessed by urban wildlife. Urban individuals may need to avoid or cope with stimuli that is initially perceived as dangerous and the ability to alter behaviours quickly in response to non-threatening stimuli would be advantageous for urban animals (Lowry *et al.* 2013; Sol *et al.* 2013). The ability to be behaviourally plastic may therefore be more beneficial both before and after colonization in urban areas. Behavioural plasticity can cause immediate behavioural modifications in comparison to adjustements that are evolved over generations (Miranda 2017). Work examining behavioural plasticity of urban wildlife has mainly focused on the ability to habituate and adjust behaviours to novel and potentially risky stimuli (Lowry *et al.* 2013). The process of habituation requires cognitive processes since individuals over time or exposures learn and remember information about a novel stimulus (Groves & Thompson 1970; Shettleworth 1998), and therefore it may also be important to examine cognition within urban animals when examining habituation or plasticity.

Cognition influences most, if not all behaviours, but only recently have individual differences in cognition been attempted to be explained by individual traits like personality (Griffin *et al.* 2015). As well, individual differences in behavioural plasticity have been shown to be associated with individual differences in personality in a number of studies (e.g. Verbeek *et al.* 1994; Guillette *et al.* 2010; Gibelli & Dubois 2016). Both personality and behavioural plasticity are expected to be important traits in successful urban animals, but the relationship between these traits in general, and especially in urban wildlife, remains unknown. In particular, the link between exploratory personality (tendency to seek out novel information) and cognition has been predicted to explain the degree of behavioural plasticity demonstrated by individuals under different environmental conditions (Guillette *et al.* 2010; Mathot *et al.* 2012).

Cognition, exploratory personality, and plasticity

It has been suggested that between-individual differences in cognitive abilities may cause variation in behavioural traits (personality) or vice versa, and therefore personality and cognitive differences together may be affecting the responsiveness of individuals to environmental change (i.e. plasticity; Griffin *et al*. 2015). Although animal personality has received considerable attention in the literature, we still know little concerning the relationship between personality and cognition, and how these traits affect behavioural plasticity (Gibelli & Dubois 2016). Verbeek *et al.* (1994) were the first to point out a potential link between exploratory personality, cognition, and plasticity. These authors found that slow exploring great tits (*Parus major*) adjusted more quickly to a new spatial distribution of food compared to faster explorers. It was hypothesized that slow exploratory tendencies allowed the collection of higher quality spatial information via thorough searching of the environment, and slow explorers were thus more likely to adjust their behaviours accordingly when experiencing changes in food distribution. This work has inspired others to determine whether slow explorers are more behaviourally plastic, and whether these individuals would outcompete fast explorers in variable environments where information is constantly changing (Guillette *et al.* 2010; Mathot *et al.* 2012). There is evidence that fast exploring individuals learn more quickly (Guillette *et al.* 2009, 2014; Cole & Quinn 2011), but take longer to learn reversal tasks suggesting behavioural rigidity (Guillette *et al*. 2010). It is hypothesized that fast explorers may perform better in stable environments where they can form behavioural routines, in comparison to slow explorers who may be more sensitive to environmental changes (Guillette *et al*. 2010).

As mentioned previously, individuals in urban environments are expected to be more exploratory and behaviourally plastic. This prediction contradicts the slow-but-thorough hypothesis predicting that slow explorers are more behaviourally plastic (Arvidsson & Mathyssen 2016). The interplay between cognition, exploration, and plasticity has yet to be examined within urban individuals, and determining the nature of this relationship along an urban gradient may shed light on important behavioural processes for colonizing urban habitats. As well, following initial work by Verbeek *et al.* (1994), there has been limited work on the relationship between exploration and spatial cognition (but see Bousquet *et al.* 2015; Schuster *et al.* 2017). More plastic individuals, associated with slower exploration rates, are expected to store higher quality spatial information to long-term memory due to more thorough and accurate exploration strategies, which may cause differences in spatial and temporal cognition between-individuals (Sih & Del Giudice 2012). This hypothesis has not yet been examined in individual scatter hoarders, despite the fact that these traits are assumed to be important for fitness and survival in these individuals.

Spatial memory in scatter hoarders

Food caching, also referred to as food storing or food hoarding, is a foraging strategy that allows animals to store food items in their external environment that can be retrieved and consumed hours or months later (Krebs 1990). Caching food items creates stores of extra reserves, which may be critical for an animal's survival through periods of food scarcity (McNamara *et al.* 1990). Scatter hoarding is a type of food hoarding that involves placing single food items in dispersed cache sites throughout a home range or territory. This type of food hoarding decreases the incidence of cache pilferage by making caches more difficult to find, but puts a greater pressure on the hoarder to recall their previous cache sites in the future (Andersson & Krebs 1978; Sherry 1985). In order for food storing strategies to be adaptive when cache pilferage is a possible cost, hoarders should develop a mechanism that allows them to locate their previous caches better than competitors (Odum 1942; Andersson & Krebs 1978). Developing specialized spatial abilities to remember locations of previous caches would be an obvious mechanism allowing hoarders to relocate cache sites better than competitors (Andersson & Krebs 1978).

Studies with captive scatter hoarding birds have found overwhelming evidence supporting spatial memory as the mechanism used for recalling the locations of previously stored food (reviewed in Brodin 2010; Pravosudov & Roth 2013). In these studies, random searching, cache site or route preferences, and marking of caches were not used as strategies to remember cache sites (Hoshooley 2007). For example, black-capped chickadees (*Poecile atricapillus*) were shown to remember previous cache sites in captive experiments by visiting their cache sites significantly more than expected by chance. Birds avoided revisiting sites where they had already consumed the contents or once discovering caches had been removed by an observer, indicating that birds were able to update their spatial information concerning caches (Sherry 1984). Literature in this area provides evidence that food storing birds have specialized spatial memory, and as a result, underlying brain features in these birds (i.e. the hippocampus), appear to have become specialized as well (Krebs *et al.* 1989; Sherry & Vaccarino 1989).

Spatial memory across environmental gradients

For scatter hoarding species, the adaptive specialization hypothesis (ASH) was put forward to determine whether superior spatial cognition evolved to support scatter hoarding behaviours and the associated demand for spatial memory (Krebs 1990). As previously mentioned, storing extra reserves is expected to be crucial for survival through periods with variable food sources (Sherry 1985). Therefore, climatic or environmental harshness has been hypothesized as a factor that may contribute to increased food storing intensity in environments with variable food sources (Pravosudov & Clayton 2002; Roth *et al*. 2012). ASH predicts that hoarders living in more food scarce or harsher environments should develop superior spatial cognition and corresponding neurological features to support a higher reliance on caches in their environment (Pravosudov & Clayton 2002).

Numerous comparative studies support that superior spatial abilities have evolved in birds that live under harsher conditions. Hampton *et al*. (1995) were first to demonstrate a relationship between food caching intensity and the relative hippocampal size in parids. In this study, black-capped chickadees cached more frequently and had larger relative hippocampal volumes than Mexican chickadees (*Poecile sclateri*) or bridled titmice (*Baeolophus wollweberi*). Black-capped chickadees occupy more climatically harsh and food-restricted environments, and therefore these results were concluded to be a consequence of these species' climatic ranges. A common-garden experiment by Roth *et al*. (2012) compared black-capped chickadees from harsh environments in Alaska to chickadees from less harsh environments in Kansas. Alaskan chickadees were found to cache more, retrieve caches with fewer inspections, and learned an associative spatial task faster than chickadees from Kansas, confirming previous observations along a latitudinal gradient (Pravosudov & Clayton 2002). Since chickadees were raised in captivity from ten days of age, this study was able to conclude that differences in spatial ability were likely a result of microevolution. Alaskan chickadees had larger absolute hippocampal volumes and more neurogenesis supporting these behavioural findings. Overall, it was concluded that superior spatial abilities and corresponding brain features in Alaskan chickadees are likely a result of local adaptations (Roth *et al*. 2012).

Food caching and spatial abilities of mountain chickadees (*Poecile gambeli*) were compared on a smaller spatial scale (Freas *et al*. 2012). This study compared chickadees from environments at different altitudes along the same mountain range within ten kilometers. Chickadees from higher altitudes endure harsher environments, and consistent with previous literature, these chickadees had significantly higher spatial accuracy than lower altitude chickadees. This work provides further support that enhanced spatial ability is related to environmental harshness and also shows that differences can exist on small spatial scales (Freas *et al*. 2012). Studies in this area have compared birds from different latitudes or altitudes. Further gradients of environmental harshness should be explored to determine whether ASH is supported in other contexts.

Animals may have access to more food sources in urban environments, especially when food availability is low during variable or seasonal periods, compared to rural environments (Lepczyk *et al.* 2004; Lowry *et al*. 2013; Tryjanowski *et al*. 2015). A recent study found that urban areas contain significantly more supplementary food sources and bird feeders than rural areas, and consequently urban areas were reported to support twice as many wintering birds (Tryjanowski *et al*. 2015; see also Clergeau *et al.* 1998; Marzluff *et al.* 2001). In response to year-round food availability in urban areas, animals may alter their foraging behaviours (Lowry *et al.* 2013). When considering food caching behaviours, access to year-round food sources in urban environments may decrease the demand for this foraging strategy since food availability, especially during winter months, is not as variable. Food storing behaviours have been observed in urban animals like squirrels (Thompson & Thompson 1980; van de Merwe *et al*. 2007) and kestrels (Rejt *et al*. 2000). However, to my knowledge, food caching intensity or spatial cognition of urban scatter hoarders have not been compared to rural counterparts. It is widely unknown how different feeding rates in urban environments affect foraging strategies in animals and research in this area would make an interesting contribution to the urban ecology literature (Lowry *et al*. 2013).

Research goals

My research aimed to examine differences in personality, plasticity, and cognition at the individual level, as well as the population level with respect to urbanization. In the second chapter of this thesis I examine the link between exploratory personality and habituation (plasticity) to a novel environment, within and between individual variation of these traits, and explore whether this variation can be explained by urbanization at the population-level. As expected, I found significant between-individual differences in exploration and habituation. Fast explorers tended to habituate during the assay while slow explorers did not. Urbanization was not found to predict habituation responses in the assay, but was found to predict exploratory personality. I therefore conclude that individuals occupying urban areas are not more behaviourally plastic but do possess faster exploratory personalities.

Significant differences have been reported between-individuals along our urban gradient, both in terms of social information use (Jones *et al.* 2017) and exploratory personality (chapter 2). I therefore aimed to further explore differences along this gradient by examining the relationship between exploratory personality and spatial cognition within individuals and, at the population-level, I explored how this relationship may change with increasing urbanization. These aims were designed to determine the association between spatial cognition and exploratory personality in a scatter hoarding model, as well as further test ASH along an urban gradient. Since urban individuals were found to be more exploratory (chapter 2), I expected these individuals to show inferior spatial accuracy in comparison to rural individuals. Thus, since urban individuals were predicted to have inferior spatial cognition compared to rural conspecifics, I predicted to find support for ASH along this gradient. I report no significant relationship between spatial cognition and exploratory personality within-individual scatter hoarders, and report no significant effect of urbanization on spatial accuracy. To address my research questions in chapters two and three, I used the black-capped chickadee, a scatter-hoarding, winter-resident, passerine bird that occupies both urban and rural habitats (Smith 1991; Foote *et al.* 2010). In the final chapter, I summarize the major results of this thesis, discuss all findings together, and illustrate how this work contributes to the cognitive and urban ecology fields.

Chapter 2

The effect of urbanization on individual differences in exploratory personality and habituation

Abstract

Urban environments impose novel challenges on animals and, as a result, the behaviors of urban wildlife are changing. Both personality traits and behavioral plasticity have been suggested to be major behavioral drivers allowing animals to colonize urban areas. In particular, high exploratory tendencies and an ability to habituate to novelty may facilitate adoption of novel ecological opportunities and adjustment to anthropogenic stressors. However, as of yet, there are no studies examining the effect of urbanization on plasticity in exploration behaviours. To explore the relationship between exploratory personality and behavioral plasticity in urban wildlife, we used black-capped chickadees (*Poecile atricapillus*; N=168 individuals from 14 sites) caught along an urban gradient to examine individual differences in exploration and changes in exploration over time under a reaction-norm framework. We predicted that urban birds would be significantly faster explorers and habituate more quickly to a novel environment compared to rural conspecifics. Individual chickadees significantly differed in initial exploration behavior as well as rate of habituation to the novel environment over time. Faster explorers tended to decrease exploration behaviours over time while slower explorers did not, as indicated by a significant negative intercept-slope correlation. Rate of habituation was not predicted by urbanization. However, we found that urban birds were overall significantly faster explorers in comparison to rural birds. We therefore conclude that urbanization significantly affects individual variation in exploratory personality but not behavioral plasticity.

Introduction

Human-induced environmental changes have created novel challenges that urban wildlife must overcome in order to colonize and persist in these areas. These challenges include adjusting to anthropogenic stressors (urban noise, artificial light) and novel biotic interactions (competitors, predators, parasites), as well as adopting novel resources (foods or habitats, reviewed in McDonnell & Hahs 2015). As a result, the behaviours of urban animals are shifting to better accommodate life in the city (Sol *et al.* 2013; Lowry *et al.* 2013). Recent comparative studies have begun to explore how consistent individual differences in behavioral tendencies, or personality (Réale *et al.* 2007), are changing in populations occupying urban areas. Individuals living in urban areas have been reported to be more aggressive, neophilic, and exploratory compared to those living in rural areas (Miranda 2017). Higher exploratory tendencies are expected to aid colonization in urban areas by facilitating adoption of novel ecological opportunities via faster environmental sampling (Sol *et al.* 2013).

Exploration behaviour has been shown to be a repeatable and heritable trait (Dingemanse *et al*. 2002; Quinn *et al.* 2009) that affects fitness-related behaviours, including discovery of novel food patches (van Overveld & Matthysen 2010; Herborn *et al*. 2010), competitive ability (Cole & Quinn 2011), and dispersal (Dingemanse *et al.* 2003; Quinn *et al*. 2011). Exploratory personality is commonly quantified using a novel environment assay (open-field test) by recording the movements of individuals through a novel space, where fast explorers contact more features and move more than slow explorers (Verbeek *et al*. 2004; Réale *et al.* 2007). Although exploration has been examined in urban animals using object or food neophobia/neophilia assays (Sol *et al*. 2011; Bókony *et al*. 2012; Miranda *et al.* 2013), only a few studies have compared exploratory tendencies within a novel environment (Atwell *et al*. 2012; Devost *et al.* 2016;

Moule *et al.* 2016). Atwell *et al.* (2012) found that urban dark-eyed juncos (*Junco hyemalis*) were significantly faster explorers than rural juncos and, since a common garden approach was used, it was concluded that these population differences were likely a result of microevolution, and not simply plasticity. Alternatively, some studies report no differences in exploratory personality between urban and rural individuals (Devost *et al.* 2016; Moule *et al.* 2016). Additional work is needed to determine whether urban environments select for faster explorers and to identify the mechanism(s) behind personality differences along this gradient. The rate of phenotypic change is reported to be higher in urban environments, and it has been suggested that most of these changes are likely a result of plasticity rather than microevolutionary effects (Hendry *et al.* 2008).

Like certain personality types, plastic behaviours also facilitate adjustment to novel anthropogenic stressors, and thus behavioural plasticity has been suggested as one of the most important mechanisms allowing colonization and persistence in urban areas (Lowry *et al.* 2013; Sol *et al.* 2013). For example, urban animals may learn over time that novel anthropogenic stressors or humans do not pose a serious threat, so they will then adjust behaviours in their presence (Evans *et al.* 2010). Flight initiation distances (FID) are reported to be significantly shorter for individuals in urban areas, meaning that these individuals tolerate the approach of an observer at closer distances before retreat than do rural conspecifics (Møller 2010; Evans *et al.* 2010; Atwell *et al.* 2012; Vincze *et al.* 2016). Urban individuals were also found to resume activity more quickly when approached by an observer on repeated occasions in a captive environment (Vincze *et al.* 2016), further demonstrating that urban animals alter behaviours to novel stimuli more readily. Individuals may regularly need to adjust their behaviours to novel stimuli, especially in urban environments, but the degree to which behavioural responses change may vary between individuals (Dingemanse *et al.* 2012).

It is not well understood how behavioural plasticity differs between individuals over time and, in cases where variation is present, it is unknown whether this variation is associated with individual-level traits such as personality (Ensminger & Westneat 2012; Finger *et al.* 2016). One study reports a link between exploratory personality and inter-individual differences in plasticity for FID to a predator within lizards, where individuals that explored a novel environment more quickly were also found to decrease their FID more rapidly in response to a predator over time (Rodriguez-Prieto *et al.* 2011). Other studies have found a similar link between personality and plasticity (Mathot *et al.* 2012). However, it is not well understood how potential differences in personality affect inter-individual variation in plasticity along an urban gradient, and work in this area could give insight into how animal personality is selected for in different environments (Réale *et al*. 2010). As well, demonstrating plasticity in exploration behaviours may be beneficial for urban animals and, as of yet, the effect of urbanization on this plasticity has not been explored.

Demonstrating personality, or consistent individual differences in behavioural tendencies, does not imply a lack of behavioural plasticity, or the ability to change behaviours in response to the environment (Sih *et al.* 2004; Dingemanse *et al.* 2012). Both personality and plasticity traits affect how individuals respond to environmental change and thus both may be subjected to selective pressures (Sih *et al.* 2004). Exploratory personality has commonly been found to differ between-individuals in different environments and has been suggested to affect the amount of sampling or information collected by an individual (Mathot *et al.* 2012). Fast explorers move more quickly through their environment and have been hypothesized to have more superficial sampling of environmental information in comparison to slow explorers (Verbeek *et al.* 1994; Sih & Del Guidice 2012). Since slow explorers are expected to have more thorough searching strategies, they are also expected to be more sensitive to environmental changes and be more behaviourally plastic (Guillette *et al.* 2010; Mathot *et al.* 2012). This hypothesis is supported in great tits (*Parus major*) where slow explorers adjusted to novel food patches more quickly (Verbeek *et al.* 1994), and in black-capped chickadees (*Poecile atricapillus*) where slow explorers reversed a learned vocal association more quickly than fast explorers (Guillette *et al.* 2010). Alternatively, fast explorers have been shown to learn more quickly (Guillette *et al.* 2009, 2014), and thus may be better at assessing risk and be more behaviourally plastic in response to novelty (Rodriguez-Prieto *et al.* 2011). The direction of the association between exploratory personality and plasticity may depend on the stimulus to which an individual is responding, and plasticity may then be expected to vary between contexts (Bell & Peeke 2012).

Habituation is one of the most elementary forms of behavioral plasticity and is useful for understanding more complex forms of plasticity and learning (Groves & Thompson 1970; Shettleworth 1998). Habituation is defined as a decrease in responsiveness over repeated stimulation and sensitization, a process independent of habituation, is defined as an increase in responsiveness. Together, the dual-processes of habituation and sensitization produce the net behavioural response of an individual to repeated stimulation (Groves & Thompson 1970; Rankin *et al.* 2009). Habituation during novel environment exploration is considered behavioral plasticity since an individual may adjust behaviors as its perception of novelty and risk in an environment change over time (Dingemanse *et al.* 2012). Studies examining habituation in response to a novel environment commonly report that individuals habituate with successive exposures, resulting in a decrease in exploratory behavior (e.g. Martin & Réale 2008; Finger *et* *al.* 2016). However, great tits were found to increase exploration with novel environment trials (Dingemanse *et al.* 2012), showing sensitization rather than habituation over time. The authors suggest that the observed increase in exploration with assays likely involves more complex mechanisms such as overcoming an initial fear response, as well cognitive traits such as learning and memory. There are also studies that demonstrate inter-individual differences in habituation responses, with some individuals habituating, some sensitizing, and others showing no change under the same conditions (Montiglio *et al.* 2010; Bell & Peeke 2012; Dingemanse *et al.* 2012). Mixed results concerning the direction of habituation to novelty, as well as the presence or absence of between-individual differences in habituation, suggests that this process may not be as well understood as previously thought.

Habituation rates are commonly explored over multiple assays and, outside of the rodent literature, it is not well understood how habituation/sensitization occurs over time within the first assay when the environment is still truly novel (within-session habituation; Brennan *et al.* 1984; Poucet *et al.* 1988; Montiglio *et al.* 2010). Short-term responses to novelty may have several ecological and fitness-related consequences (Montiglio *et al*. 2010), and may be relevant for urban dwellers who are exposed to novel stimuli that require quick assessment (i.e. novel foods or predators, vehicle traffic, urban noise, etc.). Additionally, examining habituation over time within the first session may help explain mixed results reported by studies evaluating between-session habituation in relation to the direction of responsiveness and the presence or absence of individual variation.

In this study, we focus on how exploratory personality affects habituation in response to a novel environment. To examine inter-individual differences in habituation rate (plasticity) to a novel environment over time we take a reaction norm approach (Via *et al.* 1995) via random regression (Nussey *et al.* 2007; Réale *et al.* 2010). A reaction norm visualizes individual regression lines, each with an elevation or intercept representing the behaviour of an individual, and slope as a measure of plasticity or change in behaviour across an environmental gradient or across time (Dingemanse *et al.* 2010). Intercept and slope values in a reaction norm may evolve independently and are considered independent traits, but when used together in this framework, can help visualize behavioural processes and facilitate ecological and evolutionary analyses (Dingemanse *et al.* 2010). Using this approach, we hope to determine whether: 1) differences in exploration (intercept) exist between-individuals, 2) individuals differ in their rate of habituation or sensitization over time (slope) in the novel environment, 3) a significant covariation between exploratory behavior and habituation exists (intercept × slope correlation), and 4) urbanization predicts exploratory personality and/or habituation to novelty. We predict that individuals will significantly differ in both exploratory personality and the rate at which they habituate to a novel environment. Due to lack of theoretical attention and mixed results concerning the relationship between exploratory personality and habituation at the individual-level (positive covariation, Dingemanse *et al.* 2012; negative covariation, Montiglio *et al.* 2010; Rodriguez-Prieto *et al.* 2011; Finger *et al.* 2016), we make no a priori predictions concerning the relationship between these variables within the current study. Individuals occupying more urban environments are predicted to have faster exploratory personalities and habituate more quickly to the novel environment assay compared to rural individuals. To explore these hypotheses, we use the black-capped chickadee, a passerine bird found in habitats along an urban gradient, which is a relative of the great tit, a species at the center of research on exploratory personality.

Methods

Sites and capture

Wild black-capped chickadees were captured at 14 sites in and around the city of Ottawa, Canada (45°45’ N, 75°69’ W; Figure 2.1) between September 22 and December 07, of 2015 and 2016. Chickadees (N = 168) were captured using mist nets between the hours of 8:00-13:00. Individuals were measured, weighed, and then aged as either hatch-year (HY) or after-hatch-year (AHY) birds by shape and wear of the outermost rectrices (Pyle 1997).

At least 2 km of distance separated each site to ensure that the home ranges of study subjects from different sites were not overlapping (8.8 - 22.6 ha; Smith 1991). A baited feeder was established at each site and was present no more than two weeks prior to capture. Urban sites (N = 7) were selected close to downtown Ottawa (< 10 km) and were partially forested city parks. Rural sites (N = 7) were selected further away from the downtown area (> 25 km) and were completely forested areas (at least 500 x 500 m) with feeders set-up > 300 m away from the nearest residence.

Quantifying urbanization

Remote sensing via satellite imagery (NASA Landsat Program 2016a&b) was used in QGIS v2.18.2 (QGIS Development Team 2017) in conjunction with the Semi-Automatic Classification Plugin (Congedo 2016) to quantify the amount of urbanization at each site. The number of pixels associated with land cover types of forest, bare earth, building, and tarmac within a 1 km radius of the established feeder were used in a principal component analysis (PCA) to generate a single urbanization score for each site (similar to Liker *et al*. 2008; Bókony *et al.* 2012). A 1 km radius area may be over-representing the home range of chickadees, so we also generated PCA scores for each of our sites using a smaller 200 m scale for comparison. See Figure 2.2 for site map with remote sensing land cover classification overlay.

Housing conditions

Following capture, individuals were transported to indoor aviaries at the University of Ottawa. Urban and rural sites alternated weeks in captivity so individuals from different locations were not housed together. Birds were maintained on a 10D:14N light cycle at 20±1°C and were housed independently in cages (40x60x40 cm) that separated them both physically and visually, but allowed auditory contact. Birds had access to water and food (mixture of husked and de-husked sunflower seeds) ad libitum outside of testing periods, and were supplemented with mealworms at the end of each day. Subjects were housed in a room adjacent to an indoor flight room, which they could access directly from their home cages through a sliding opaque door, which avoided unnecessary handling prior to tests. Movement of individuals between the aviary and their home cages was controlled using light manipulation (Pravosudov & Clayton 2002). Prior to releasing birds back at their point of capture, we extracted blood samples from the brachial vein of all individuals to determine sex and baseline corticosterone levels (stress; Pravosudov *et al.* 2004).

Novel environment exploration

Exploration of a novel environment (Verbeek *et al*. 1994) took place on the third day in captivity between 7:30 - 11:00. Individuals were introduced to a novel flight room which contained four artificial wooden trees, each with 15 wooden perches (Figure 2.3-A). Birds were able to enter the novel environment at their discretion for up to 5 minutes to avoid altering behaviours via forcing entry to the room (Carter *et al.* 2013). After entry to the room, behaviours were live coded for 10 minutes by the same observer (M.J.T.) behind a one-way plexiglass window using J-Watcher software (v.1.0; Blumstein & Daniel 2007). Similar to Quinn *et al*. (2009), the duration of flights, duration of hops (number of hops*0.5 sec), number of visits to each tree (1 - 4), and number of visits to other features in the room (ceiling, floor, walls) were recorded and used in a principal component analysis (PCA) to generate a composite variable or score to represent an individual's exploration behaviour over the entire trial, termed cumulative exploration score. In 2016, exploration behaviour was assessed again the following morning in an altered environment (Herborn *et al.* 2010) to assess repeatability. The aviary environment was altered by using artificial trees that differed in shape, colour, and placement within the flight room (Figure 2.3-B). Assays in the altered environment followed the same procedure as the first novel environment exploration, and cumulative exploration scores were again generated with a PCA using the same variables.

To explore changes in exploration behaviours over time within the novel assay, we programmed the JWatcher software to also record behaviours separately in five two-minute bins throughout the trial. We again conducted a principal component analysis (PCA) for each two-minute bin to generate exploration scores that explained an individual's exploration behaviour during each bin of the assay (each individual = 5 exploration scores over the trial).

Statistical analyses

We assessed individual repeatability of exploration behaviour by calculating adjusted repeatability (Nakagawa & Schielzeth 2010) using a linear mixed-effects model (LMM). Cumulative exploration scores within a novel and altered environment were used as the response variable, and underwent a square-root transformation to improve normality. We controlled for date, order of testing, age class, baseline corticosterone, and trial type (novel vs. altered), and used individuals nested within sites as random-intercept effects. Confidence intervals around the repeatability estimate were generated using 1000 parametric bootstrap iterations (Nakagawa & Schielzeth 2010).

We evaluated inter-individual differences in habituation, and the effect of urbanization on habituation rate and exploration tendency using a LMM with a random intercept and slope for individuals across bins, as well as controlling for site as a random intercept effect. Exploration score for each bin was used as the response variable and was square-root transformed to improve normality prior to analysis. We tested pair-wise interactions between bin number and the fixed-effects of urban score, baseline corticosterone, sex, and age class to determine if any of these factors explained habituation rate. We also controlled for the fixed effects of date and order tested in the model. We used likelihood ratio tests (LRT) under a chi-square distribution to evaluate the significance of between-individual variation in both initial exploration (individual effect) and habituation across bins (I×E effect; Dingemanse *et al.* 2010) by comparing against a model without individual-level random intercepts and random slopes respectively (Pinheiro & Bates 2000). We allowed the model to calculate a correlation estimate between individual slope (habituation) and intercept (personality), and evaluated the significance of this correlation via LRT by comparing to a model where this correlation was set to zero. We additionally examined the relationship between an individual's initial exploration (score within the first 2 min bin) and their cumulative exploration score using a Spearman's rank correlation test.

All analyses were conducted using R statistical software (v.3.4.0; R Core Team 2017). Significance of pair-wise interactions between bin and predictors were evaluated using F tests with type III ANOVA, and non-interacting terms were evaluated using F tests with type II ANOVA. Degrees of freedom for F tests were generated using the Kenward-Roger approximation (Bolker *et al.* 2009). LMMs were fitted via restricted maximum likelihood using the *lmer* function in conjunction with the lme4 (Bates *et al*. 2015) and lmerTest (Kuznetsova *et* al. 2015) packages. All PCAs were generated using the *prcomp* function with correlation matrices of the untransformed variables.

Ethical note

All procedures were conducted under scientific (SC-42) and banding permits (10854) from Environment Canada, Canadian Wildlife Service and were approved by the Animal Care Committee at the University of Ottawa (protocols 1758-59).

Results

Urbanization PCA

The urban PCA returned the first principal component (PC1) as the only component with an eigenvalue > 1 (Kaiser 1960), which explained 81.82% of the variation. All variable loadings on PC1 were considered significant (> 0.4; Huang *et al.* 2016), and land cover associated with urban (tarmac/buildings) and rural (forest/earth) pixels loaded strongly in opposite directions (Table 2.1). PC1 was inferred to explain variation pertaining to the degree of urbanization and was used to extract an urban score for each site (Figure 2.4).

Exploration PCA and repeatability

The PCA for cumulative novel environment exploration (2015 & 2016; N = 168) returned PC1 as the only component with an eigenvalue > 1, which explained 67.84% of the variation (Table 2.2). All variable loadings on PC1 were positive and > 0.4, and we inferred that PC1 explained variation pertaining to both movement and exploration within a novel environment. Therefore, PC1 was used to generate a composite score for each individual as a measure of exploration behaviour for subsequent analyses. To assess within-individual repeatability of exploration behaviour, we also generated an altered environment score for birds in 2016 (N =

70). This PCA analysis returned PC1 as the only component with an eigenvalue > 1, and all variable loadings on PC1 were positive and > 0.4 (Table 2.2). When examining repeatability of exploration scores, the model was not returning a variance value for site when computing confidence intervals and, since inclusion of random intercepts for sites was not significant via LRT (df = 1, $\chi^2 = 1.53$, $P = 0.22$), we only included random intercepts for individuals in the final model. The confounds of date, age, corticosterone, and trial had non-significant effects on exploration ($P < 0.16$), but order tested was found to be marginally significant (estimate±SE = 0.32±0.16, $F_{1,115} = 4.02$, $P = 0.047$). Cumulative exploration behavior was found to be significantly repeatable between novel and altered environment assays (adjusted repeatability LMM: N = 127 indiv, 58 indiv both assays, R = 0.43, CI = 0.43 – 0.50, $\chi^2 = 11.21$, $P < 0.001$; unadjusted repeatability LMM: N = 168 indiv, 70 indiv both assays, R = 0.45, CI = 0.44 – 0.49, $\chi^2 = 17.90$, $P < 0.001$), and fell within the reported range for exploration behaviors (Bell *et al.* 2009).

When conducting the exploration PCAs for each bin, the "other features" variable was consistently found to show weaker loadings. There was little variation in this measure when bins were considered separately and we therefore removed this variable from the analyses. The remaining variables loaded strongly in a positive direction on the first principal component (PC1) for all bins. All variable loadings were >0.4, with exception of flight duration in bin 1 (loading = 0.37; Table 2.3). This loading is just below our 0.4 significance level and so we retained this variable to remain consistent. PC1 explained a large proportion of variation for each bin and each bin's PC1 was the only component to return an eigenvalue > 1 (Table 2.3). Exploration scores were generated using PC1 from the analyses and were used to describe exploration behaviour of individuals within each bin of the assay. Separate plots showing the relationship between exploration scores over time bins for each individual are provided in the appendix, and are sorted by habitat category (urban vs. rural) and exploration score category (slow < 0, fast > 0).

Exploration, habituation, and urbanization

The pair-wise interactions between bin and urban score, baseline corticosterone, sex, and age class were all non-significant in the full random slope model (Table 2.4-A), and therefore these interactions were dropped. When evaluating separately, baseline corticosterone, sex, age class, date, and order tested all had non-significant effects on exploration (Table 2.4-B), and were therefore excluded in subsequent analyses to allow use of the full dataset. Individuals significantly differed in their initial exploration (intercept: df = 1, $\chi^2 = 395.02$, $P < 0.001$; Figure 2.5) and their rate of habituation over time bins (slope: df = 2, $\chi^2 = 59.11$, $P < 0.001$; Figure 2.5). The model returned a significant negative correlation estimate between individual-level intercepts and slopes (correlation = -0.59, df = 2, $\chi^2 = 193.25$, $P < 0.001$; Figure 2.6) suggesting that fast initial explorers (high intercept) tended to habituate over bins (negative slope) and slow initial explorers (low intercept) tended to sensitize or showed no change over bins (positive/neutral slope). Similar results were found when moving bin 1 exploration to the intercept (correlation = -0.42, df = 2, $\chi^2 = 284.78$, $P < 0.001$). When removing the non-significant interaction between urban score and bin from the model, urban score was found to be a significant predictor of exploration scores (estimate±SE = 0.083±0.03, $F_{1,11} = 7.48$, $P = 0.020$; Table 2.4-C; Figure 2.7), with urban birds having higher exploration scores in comparison to rural birds (Figure 2.8). The effect of urban score remained significant when evaluating urbanization at a smaller 200 m scale around capture sites (estimate±SE = 0.11±0.034, $F_{1,9} = 9.82$, $P = 0.012$) and as a dichotomous predictor (estimate±SE = 0.35±0.088, $F_{1,11} = 15.70$, $P =$

0.0023). We also found a significant positive correlation between an individual's initial exploration scores and their cumulative exploration scores (Spearman rank correlation: N = 168, rho = 0.73, $P < 0.001$; Figure 2.9).

Discussion

The link between personality and plasticity in urban animals is not well understood and examining the relationship between these traits along an urban gradient may improve our understanding of the characters that allow animals to successfully colonize urban areas. We set out to determine whether between-individual differences in habituation and exploratory personality existed in the first session of a novel environment assay, and whether these differences could be explained by urbanization. Cumulative exploration scores of individuals were found to be significantly repeatable and therefore we conclude that exploration behaviours measured within our novel environment assay are indicative of exploratory personality. Individuals significantly differed in both initial exploration behaviour (intercept) and their habituation response through time (slope) in the novel environment, but habituation was not significantly predicted by urban scores. We report a significant negative intercept-slope correlation suggesting that fast initial explorers tended to habituate while slow did not in the environment over time. Finally, there was a significant positive relationship between exploration and urbanization, showing that more urban birds were significantly faster explorers.

Inter-individual variation in habituation to novelty is suggested to be a target of natural selection and may be biologically meaningful (Bell & Peeke 2012). As predicted, individuals were significantly different in both initial exploration of the novel environment (intercept) and the change in exploration behaviours over time (slope). Individual differences in habituation have only recently been reported in wild animals in the context of open field tests (between sessions, Bell & Peeke 2012; Dingemanse *et al.* 2012; within a session, Montiglio *et al.* 2010). Differences in habituation responses between individuals have previously been explained by the effects of age (Brennan *et al.* 1984; Montiglio *et al.* 2010), and sex (Ellenberg *et al.* 2009; Ensminger & Westneat 2012). However, these effects were not found to explain individual changes in exploration over time in the current study. An individual's previous experiences have also been found to contribute to between-individual differences in habituation (Ellenberg *et al.* 2009), although it is unknown how previous experiences may have affected habituation responses of wild-caught individuals in this study. Variation in habituation at the individual level may also arise if individuals differ in the way they perceive a stimulus' strength (Groves & Thompson 1970; Rankin *et al.* 2009), or if they differ in their ability to overcome initial fear of the novel stimulus (Russel 1973; Brennan *et al.* 1984). In terms of our findings, individuals that sensitized, rather than habituated, may have perceived the environment as a stronger novel stimulus and may have taken longer to overcome an initial fear response. These between-individual differences in habituation may be due to a combination of mechanisms including an individual's previous experiences, cognitive attributes, and perhaps other facets of personality.

At the population level, we hypothesized that habituation to a novel environment would be predicted by urbanization, where urban birds were predicted to habituate more quickly than rural birds. Urban birds likely habituate to novelty in the environment more frequently than rural birds, and as a result are expected to be more behaviourally plastic (Sol *et al.* 2013). Despite finding significantly different habituation responses at the individual-level, the direction of habituation in the novel environment was not explained by urban scores. Therefore, we report no evidence that urban birds habituate more quickly to spatial novelty, or show more plasticity, compared to rural birds. Other than work on flight initiation distances, there is a lack of comparative research in urban ecology on habituation to novelty. House sparrows (*Passer domesticus*) showed significant between-individual differences in rate of habituation to a novel object (Ensminger & Westneat 2012), and although house sparrows are common urban dwellers, urbanization effects were not explored. Our study is the first to examine individual differences in habituation responses to novelty while exploring the effect of urbanization on this variation. Research in this area is still in the early stages and more work will be needed to determine whether individual differences in plasticity or habituation can be explained by environmental factors such as human-induced changes.

Our model returned a significant negative correlation between initial exploration behaviour (intercept) and change in exploration or habituation response over time (slope). Initially fast exploring birds tended to decrease exploration with time and habituate, compared to initially slow exploring birds who tended to either increase exploration over time and sensitize or show no change in exploration. We join other similar studies who have reported this trend (Montiglio *et al.* 2010; Rodriguez-Prieto *et al.* 2011; Finger *et al.* 2016). Fast explorers initially moved through the environment more quickly, and perhaps through rapid learning and risk assessment, decreased their exploration behaviours as the environment became less novel (Rodgriguez-Prieto *et al.* 2011). Alternatively, slow explorers may have increased exploration behaviors over time possibly as their motivation to explore was initially insufficient to overcome their fear or inclination to avoid novelty (Russel 1973; Brennan *et al.* 1984). A negative correlation between exploration and habituation may provide evidence that individuals with different exploratory personalities collect information in different ways (Montiglio *et al.* 2011). Fast explorers move more quickly and are expected to sample environmental information superficially as a result, while slow explorers move more slowly and would thus have more thorough searching (Verbeek *et al.* 1994; Sih & Del Guidice 2012). Fast explorers may habituate since they collect information quickly, as opposed to slow explorers who may sample more thoroughly at first and show sensitization, and then potentially habituate after a longer time period. It could therefore be possible that we may have missed the habituation period of slower explorers in our assay. It would be interesting to determine at what point slow explorers habituate, if ever, in the novel environment by examining non-linear changes in exploration over a longer time period. Individuals that did not explore initially (low intercept) theoretically are unable to decrease exploration further (negative slope), and therefore it is important to note that a negative intercept-slope correlation may be an artifact of numerical constraints. Cumulative exploration scores were highly correlated with initial exploration behaviour, suggesting that fast initial explorers were overall fast explorers throughout the assay and vice versa for slow explorers (Montiglio *et al.* 2010), but this result may be sensitive to assay duration. We provide evidence that individuals with different exploratory personalities show different temporal patterns of exploration over time within a novel environment assay.

Although urban and rural animals are known to differ in several personality traits, we are among the first (see also Atwell *et al.* 2012) in reporting that urban individuals were significantly faster explorers in a novel environment assay. Exploratory personality has previously been linked with dispersal, where fast explorers disperse further and are more likely to immigrate than slow explorers (Dingemanse *et al.* 2003; Quinn *et al*. 2011). Individuals may need to first arrive in urban areas from native habitats before colonization in these environments (Sol *et al.* 2013), and thus fast explorers may be more likely to arrive in urban areas in the first place. After arrival, faster exploration behaviours may promote rapid collection of information concerning novel foods, predators, competitors, or dangers in urban environments. Collecting information regarding the benefits and risks of novel ecological stimuli more quickly is expected to increase fitness and aid colonization within urban habitats (Lowry *et al.* 2013; Sol *et al.* 2013). As of yet, we are unable to determine if the observed differences in exploratory personality along our gradient are due to local adaptation or behavioral plasticity, or perhaps a result of both. Our results seem to support the predicted importance of fast exploration behaviours for urban animals (Sol *et al.* 2013), but we are unable to determine whether exploratory tendencies are important during initial colonization. Exploratory personality has previously been found to be correlated with other personality traits, forming a behavioural syndrome (Sih *et al.* 2004). Since exploratory personality has been found to differ along an urban gradient, it would be interesting to determine whether behavioural syndrome structure also differs between individuals along this gradient.

We join other recent studies in demonstrating that individual differences in habituation to novelty exist, and we are the first to test whether these differences were explained by urbanization. Although urbanization was not found to predict differences in habituation, it significantly predicted exploratory personality between-individuals, where urban birds were faster explorers. Further work is needed to assess habituation responses of urban wildlife in a comparative manner to confirm that behavioral plasticity is an important trait involved in colonization of urban areas. A better understanding of habituation and sensitization, and the underlying mechanisms moderating these responses, would help promote better methods for conservation and wildlife management programs. For example, protocols designed to facilitate rapid habituation may encourage colonization of sensitive species in urban areas, and protocols designed to prohibit habituation could deter unwanted behaviors of existing urban wildlife (Blumstein 2016). By evaluating personality differences alongside inter-individual variation in plasticity in urban and rural individuals, it may be possible to predict how selection acts on variation within populations. An ability to predict, and potentially promote or divert, phenotypic shifts would be especially beneficial for populations adjusting to challenging novel conditions, such as in urban landscapes.

Table 2.1 Urbanization variables associated with the number of pixels for land cover types of forest, bare earth, tarmac, and buildings and their first component correlation loadings from a principal component analysis (PCA). The first component (PC1) explained 81.82% of the variation and had an eigenvalue > 1.

Pixel number	PC1 Loadings
Forest	-0.94
Open Earth	-0.81
Tarmac	0.94
Buildings	0.91
% variation explained	81.82%
Eigenvalue	1.81

Table 2.2 Exploration variables and their component correlation loadings from principal component analyses (PCAs) for cumulative novel environment exploration in both 2015 & 2016 (N = 168) and altered environment exploration in 2016 (N = 70). All PCA analyses returned the first principal component (PC1) as the only component with an eigenvalue > 1 and all variable loadings were positive with values > 0.4.

	PC1 Loadings	
Variables	Novel (2015 & 2016)	Altered (2016)
Visits to tree 1	0.92	0.86
Visits to tree 2	0.91	0.88
Visits to tree 3	0.94	0.85
Visits to tree 4	0.92	0.85
Other features	0.50	0.52
Flight duration	0.52	0.92
Hop duration	0.90	0.69
% variation explained	67.84%	65.21%
Eigenvalue	2.18	2.14

Table 2.3 Exploration variables and their component loadings from principal component analyses (PCAs) for novel environment exploration assays separated by five two-minute bins. All PCA analyses returned the first principal component (PC1) as the only component with an eigenvalue > 1 and all variables had strong positive loadings.

	PC1 Loadings				
Variables	Bin 1	Bin 2	Bin 3	Bin 4	Bin 5
Visits to tree 1	0.79	0.90	0.90	0.83	0.88
Visits to tree 2	0.77	0.89	0.90	0.88	0.91
Visits to tree 3	0.82	0.93	0.94	0.95	0.89
Visits to tree 4	0.65	0.89	0.88	0.89	0.85
Flight duration	0.37	0.89	0.86	0.84	0.88
Hop duration	0.76	0.87	0.83	0.87	0.86
% variation explained	50.61%	80.47%	78.42%	76.92%	77.44%
Eigenvalue	1.74	2.20	2.17	2.15	2.16

Table 2.4 Evaluation of fixed-effects on exploration scores within the (A) full hypothesized model, (B) model evaluating predictors once dropping pair-wise interactions, and (C) final model. All models are linear mixed-effects models with random intercepts and slopes for individuals across bins, as well as random intercepts for sites.

Fixed Effects	Estimate	±SE	DF	F	*P*
(A) Full hypothesized model (N = 126)					
Bin	-0.036	±0.050	1,121	0.53	0.47
Urban Score	0.08	±0.037	1,16	4.31	0.054
Baseline corticosterone	-0.0003	±0.0028	1,174	0.011	0.92
Sex	-0.06	±0.13	1,175	0.22	0.48
Age class	0.09	±0.12	1,173	0.51	0.48
Date	-0.0031	±0.0028	1,13	1.17	0.30
Order tested	0.026	±0.014	1,117	3.25	0.074
Bin*Baseline corticosterone	-0.00012	±0.00062	1,121	0.035	0.85
Bin*Sex	0.0093	±0.029	1,121	0.11	0.74
Bin*Age	0.051	±0.028	1,121	3.30	0.072
Bin*Urban score	-0.0022	±0.0080	1,121	0.075	0.79
(B) Dropped interaction terms (N = 126)					
Bin	-0.004	±0.014	1,125	0.084	0.77
Urban score	0.073	±0.014	1,5	6.05	0.053
Baseline corticosterone	-0.00065	±0.002	1,116	0.098	0.75
Sex	-0.032	±0.091	1,119	0.12	0.73
Age class	0.065	±0.089	1,117	0.53	0.48
Date	-0.0038	±0.0028	1,13	1.17	0.30
Order tested	0.026	±0.014	1,117	3.25	0.074
(C) Final Model (N = 168)					
Bin	0.0048	±0.012	1,168	0.16	0.69
Urban score	0.083	±0.03	1,11	7.48	0.020

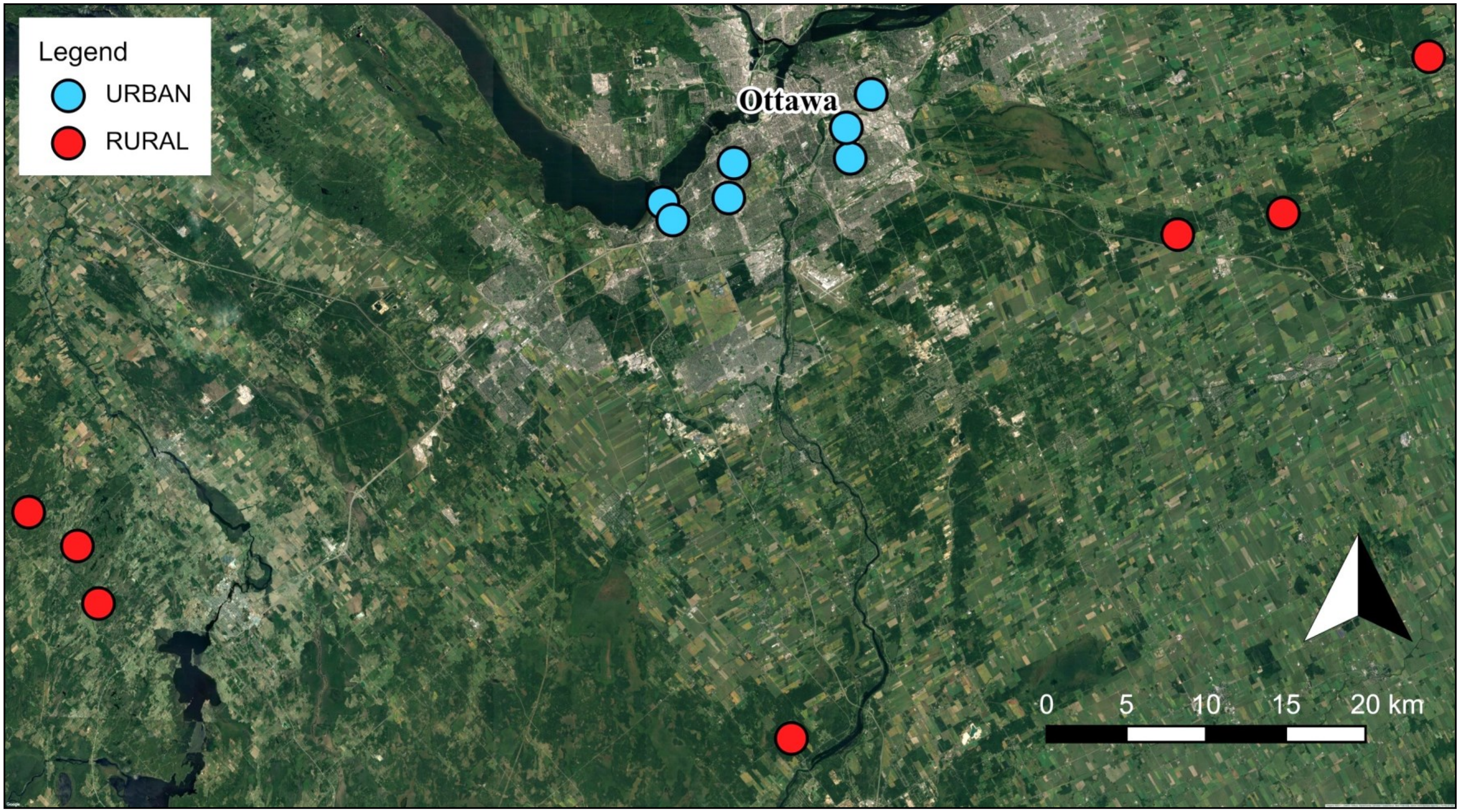


Figure 2.1 Satellite image of field sites surrounding Ottawa, Canada (45°45’ N, 75°69’ W). Urban sites (N = 7; blue circles) were located < 10 km of the downtown area and rural sites (N = 7; red circles) were located > 25 km from downtown.

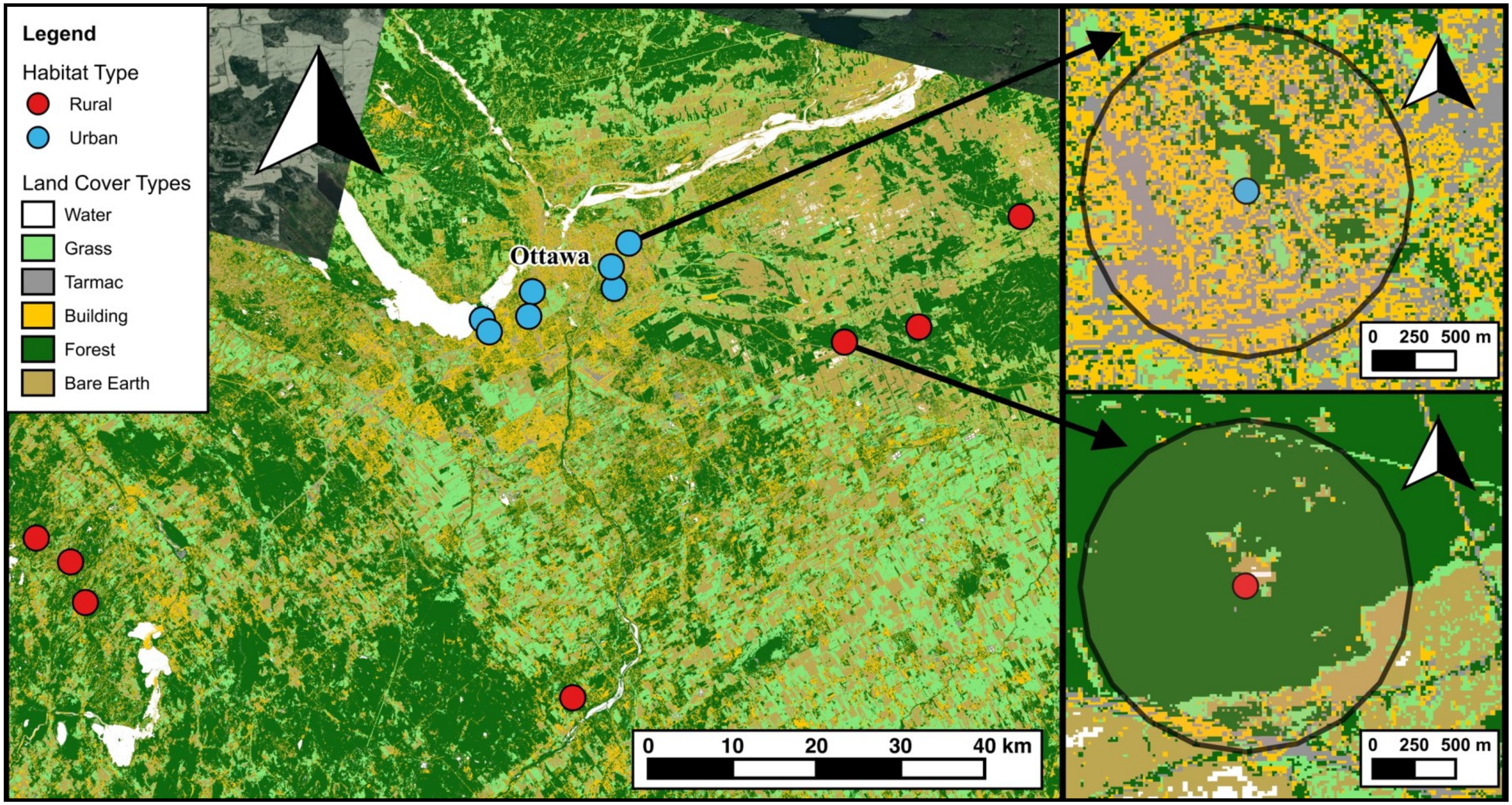


Figure 2.2 Map of field sites with land-cover classification overlay, and an example of an urban and rural site showing land cover pixels used for the quantification of urbanization.

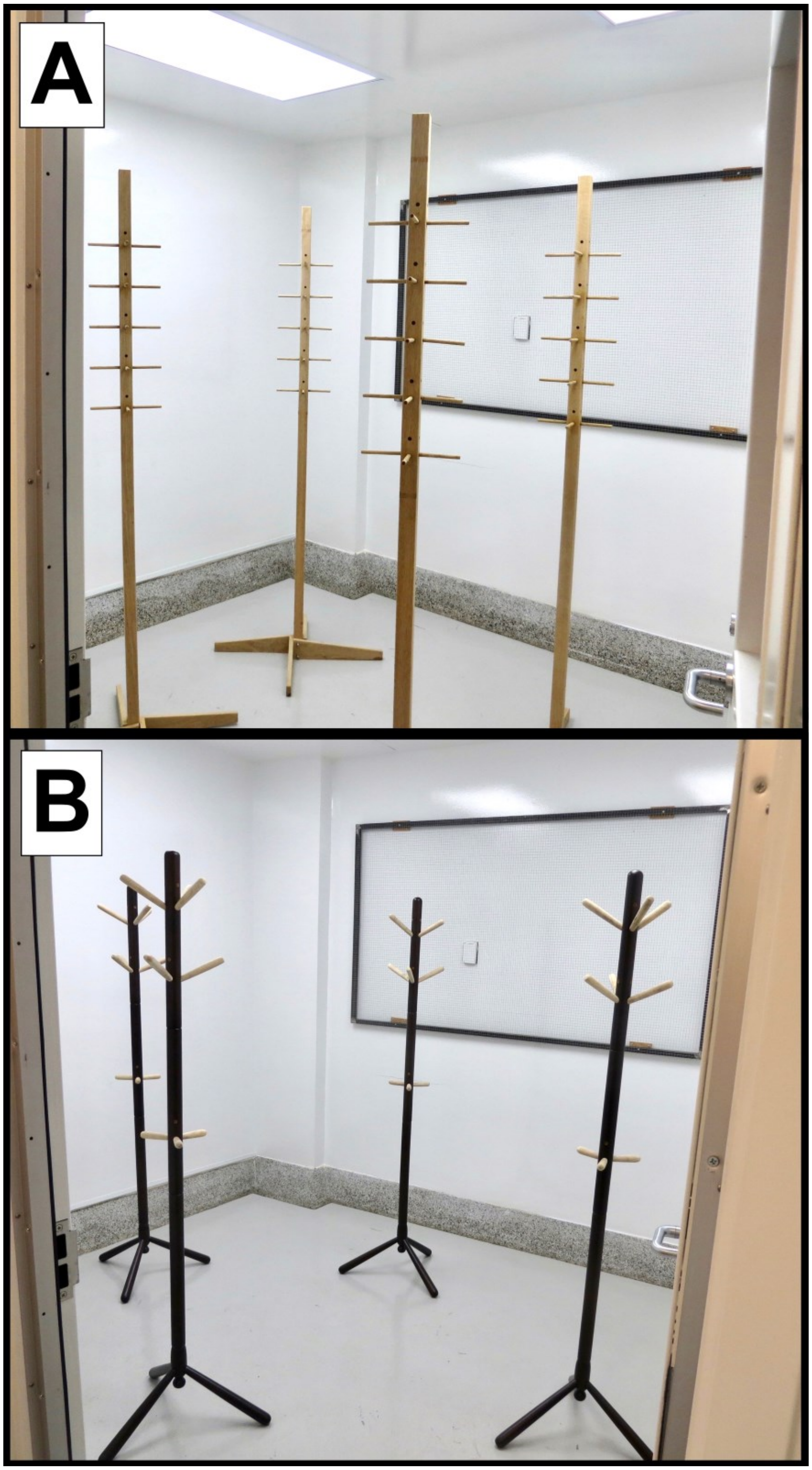


Figure 2.3 Flight room used to assess exploration behaviour of individuals in a A) novel environment and B) altered environment.

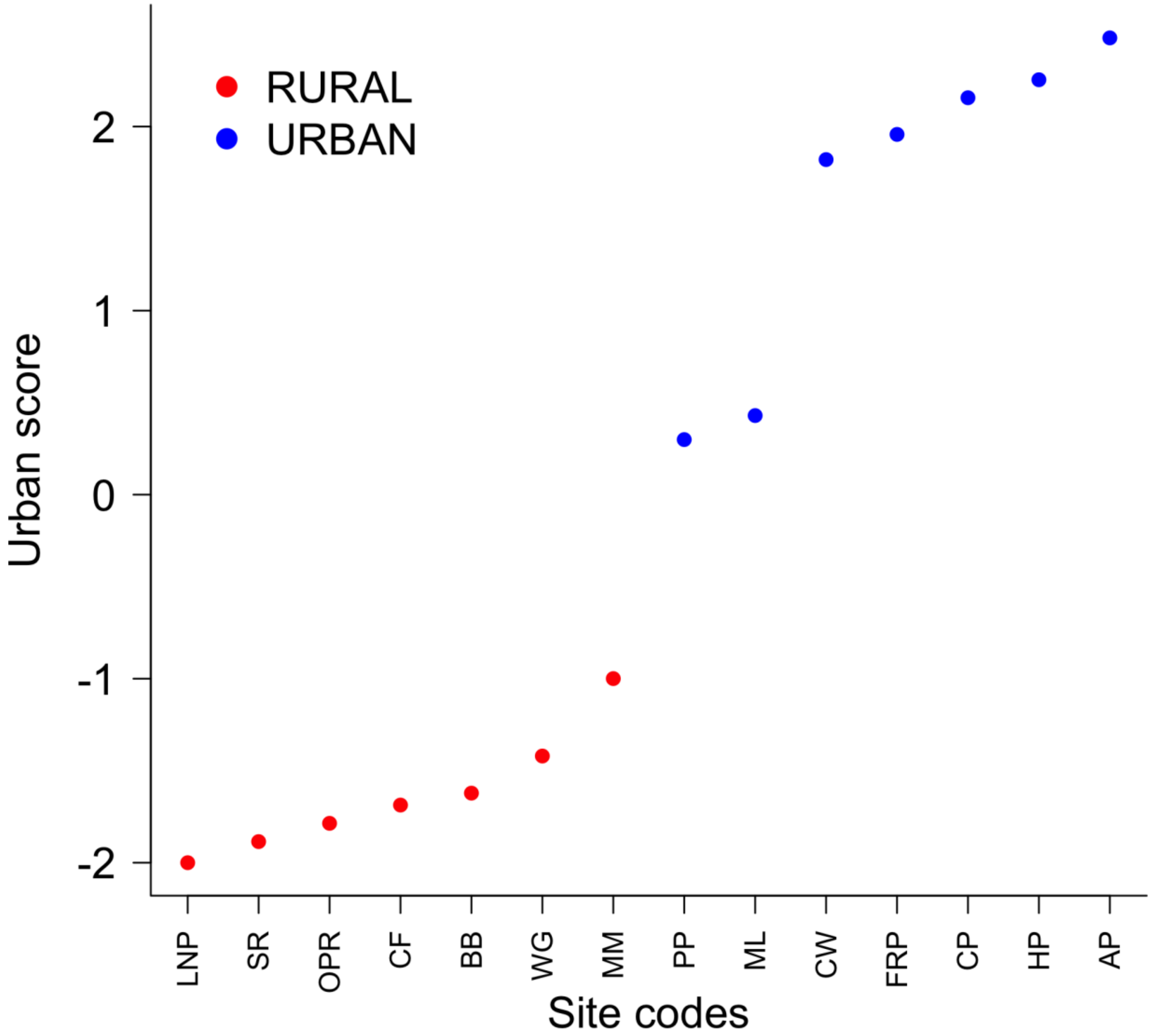


Figure 2.4 Urban PCA scores generated for each site (N = 14, represented by site codes along x-axis) to visualize the quantified urban gradient (red circles = rural sites, blue circles = urban sites).

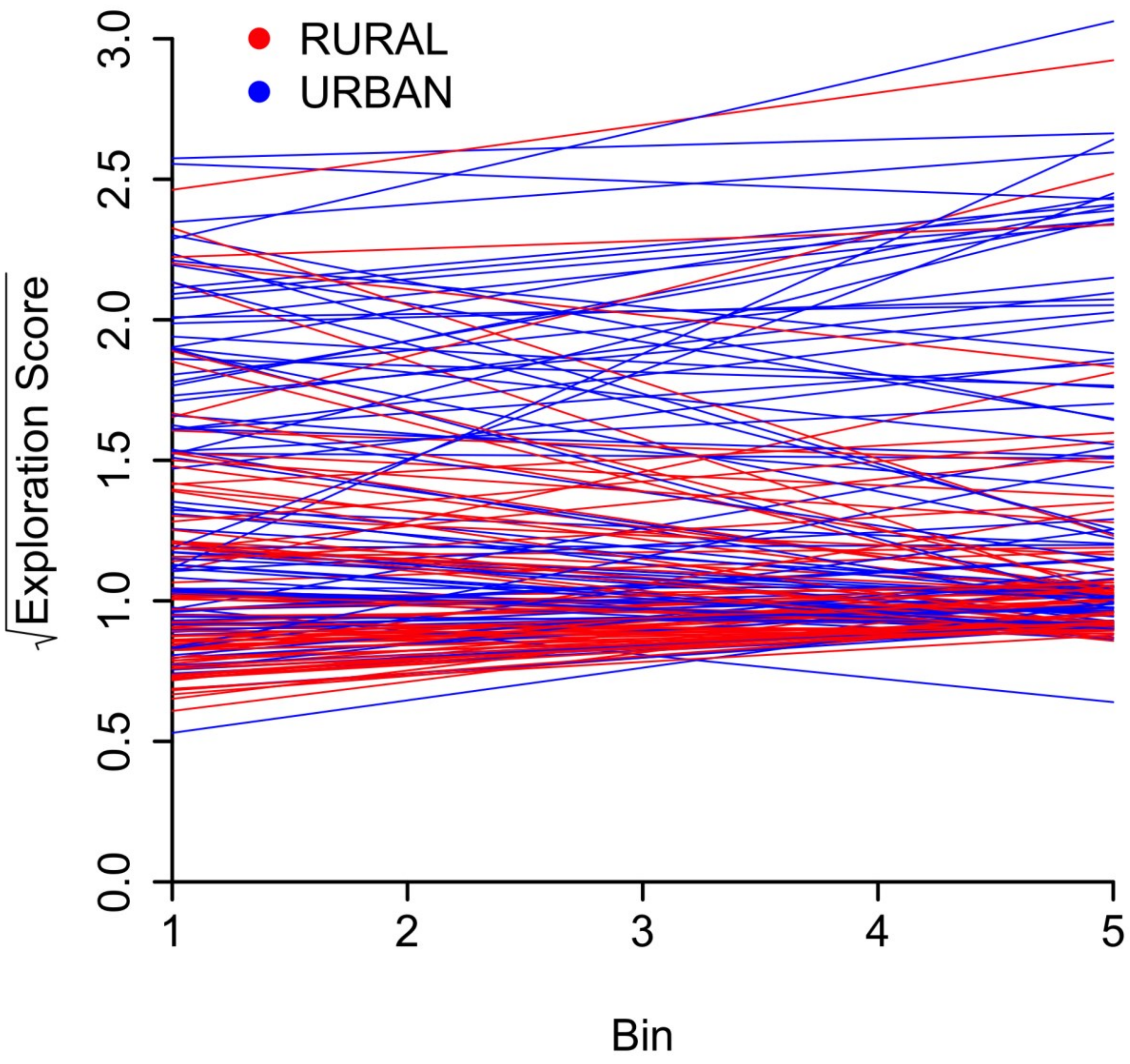


Figure 2.5 Inter-individual variation (N = 168) in exploration score (square-root transformed) over 5 time bins in the novel environment assay. Shows between-individual variation in habituation response as well as the effect of urbanization score. Lines indicate an individual's change in exploration over time during the assay using a LMM fitted with an individual-level random intercept (initial exploration) and slope (habituation). Red lines represent individuals from rural habitats and blue lines represent individuals from urban habitats.

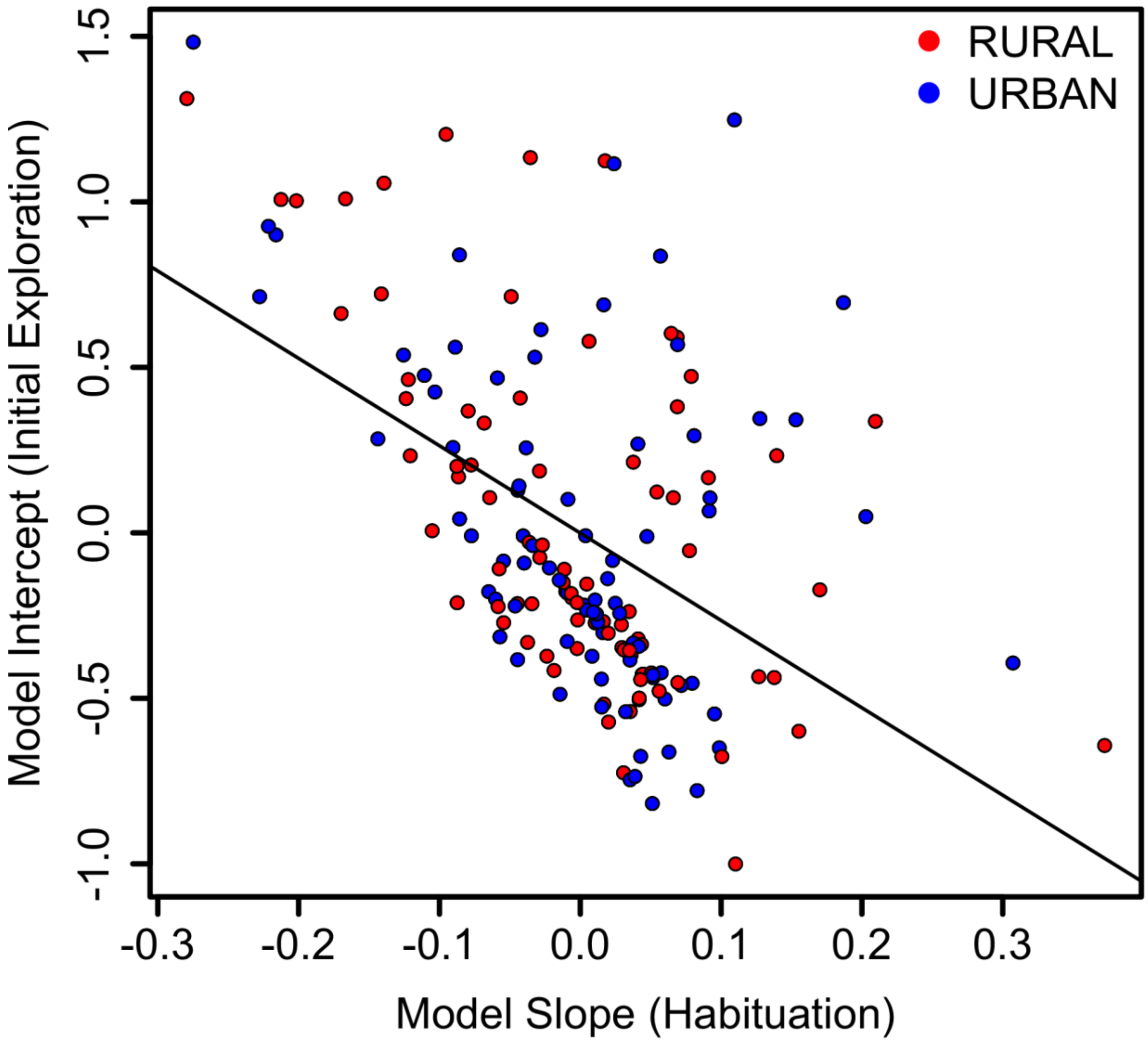


Figure 2.6 Relationship between model-generated estimates for individual random intercepts (initial exploration behaviour) and slopes (change in exploration over time bins, i.e. habituation). Exploration score was modeled as the response variable in a linear mixed-effects model with both an individual-level random intercept and a random slope for individuals (N = 168, rural = red, urban = blue) across bins while evaluating urban score and bin number as fixed-effects.

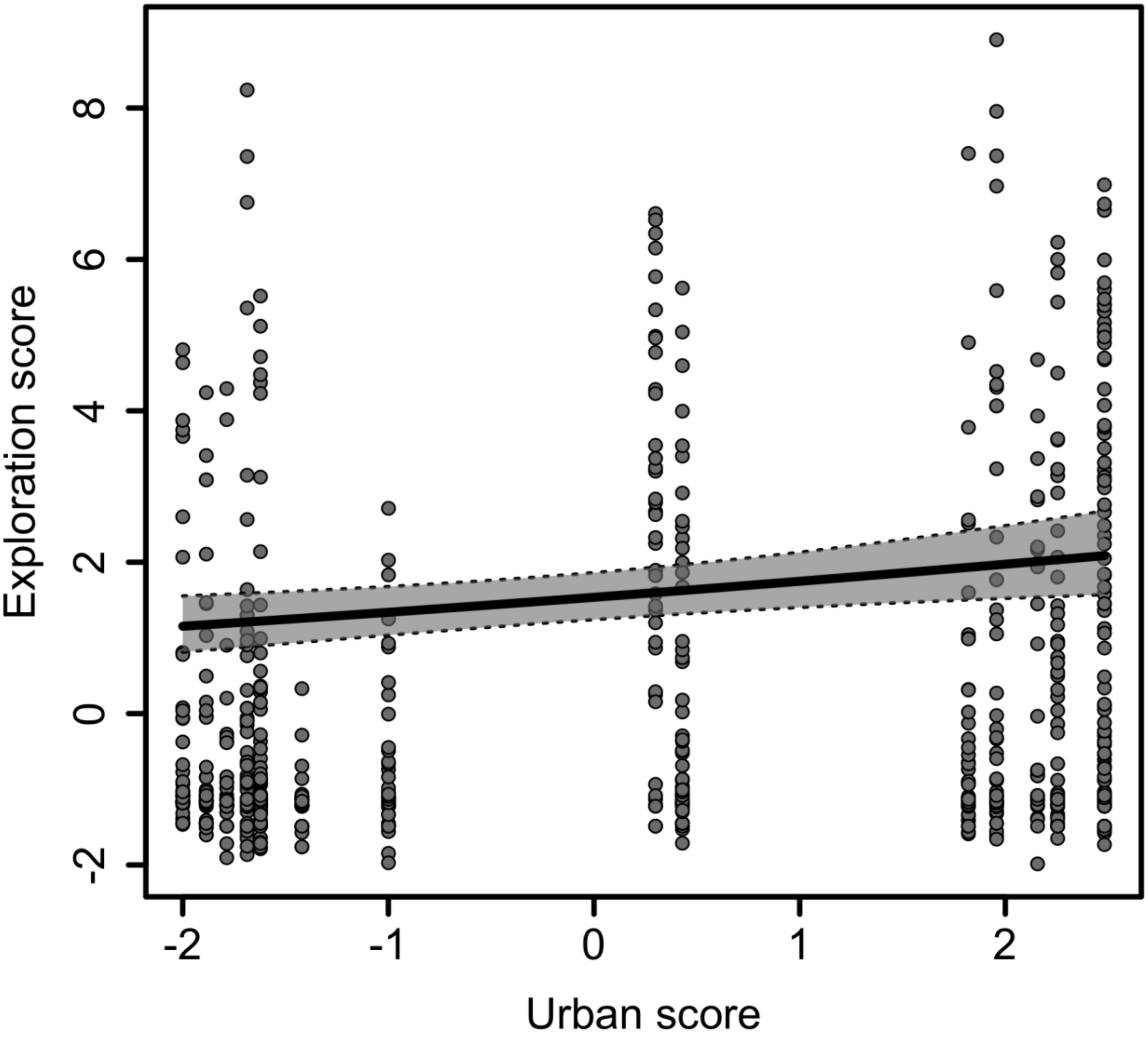


Figure 2.7 Effect of urbanization score (larger values indicate more urbanization) on an individual's cumulative exploration score (larger values indicate faster explorers) within the novel environment assay (N = 168). The significant effect (solid line) and 95% confidence intervals (dashed lines) are shown.

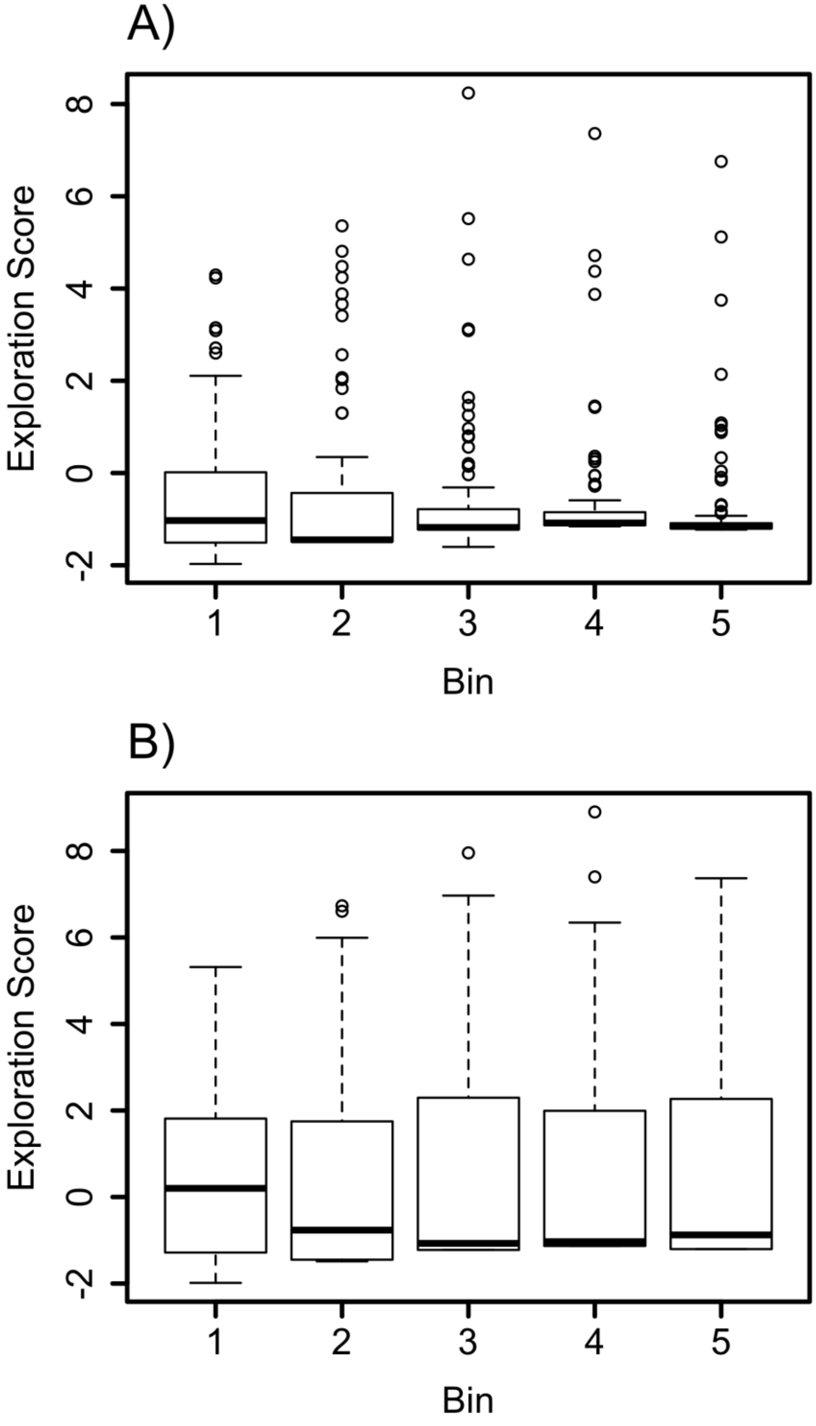


Figure 2.8 Exploration score over time bins in the novel environment assay for individuals from A) rural environments (N = 84) and B) urban environments (N = 84).

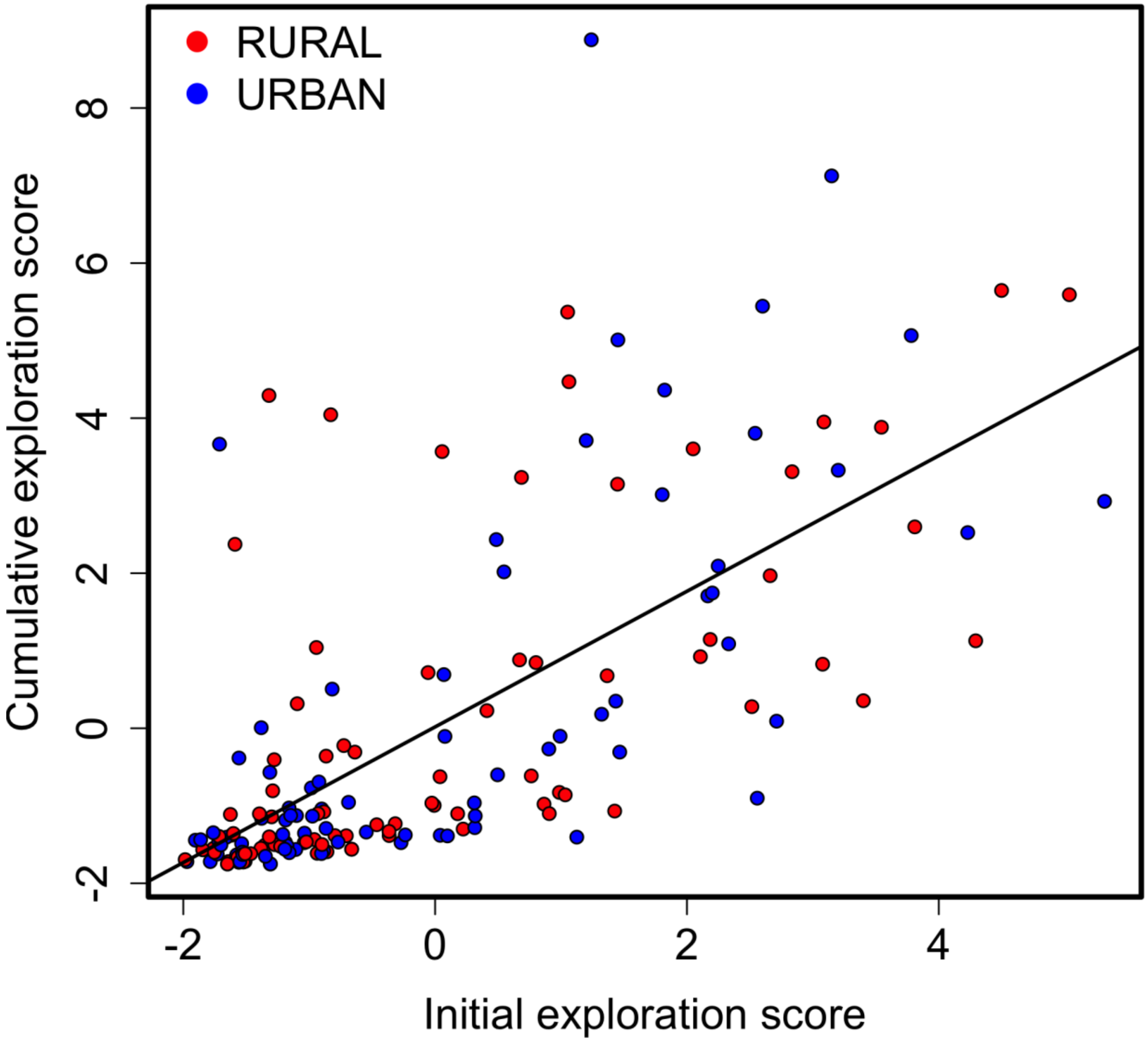


Figure 2.9 Relationship between individual (N = 168) initial exploration scores and cumulative exploration scores for the novel environment assay. Red circles indicate rural birds and blue circles indicate urban birds.

Chapter 3

Spatial cognition and exploration in scatter hoarders along an urban gradient

Abstract

Urbanization has been shown to affect a variety of traits in animals, including their physiology, morphology, and ecology. It is less clear how the behaviours of urban animals are modified, and even less is known about their cognitive traits. The adaptive specialization hypothesis (ASH) predicts that scatter hoarders in food-scarce environments possess superior spatial cognition due to a higher reliance on caches for survival. As of yet, it is not well understood how stable supplementary food sources in urban areas affects the caching behaviours and cognitive traits of scatter hoarders. In addition to population-level cognitive differences, variation may exist between individuals occupying the same environment. Within individuals, slow explorers are predicted to store higher quality spatial information to memory due to thorough searching of their environment. This hypothesis, and its applicability to scatter hoarding animals, has received little empirical attention. We examined whether ASH is supported along an urban gradient, as well as the within-individual covariation between spatial cognition and exploratory personality using a scatter hoarding model. We assessed spatial cognition of wild-caught black-capped chickadees (*Poecile atricapillus*; N=96) along an urban gradient using a spatial memory task, and exploratory personality was quantified using a novel environment assay. Rural individuals, and slower explorers, were predicted to perform more accurately on the spatial task. We find no evidence for ASH along an urban gradient, and find no significant relationship between spatial cognition and exploratory personality within individual scatter hoarders. Spatial cognition is known to be an important adaptation for scatter hoarders, and the absence of both spatial cognitive differences along an urban gradient and an individual-level covariation with exploratory personality in this study may reflect this.

Introduction

Urbanization is occurring globally at a dramatic rate, and in response some species are declining while others are thriving in urban environments (Sih *et al.* 2011; Lowry *et al.* 2013). Species that colonize urban environments may have access to more food sources, especially in variable or seasonal periods of low food availability, compared to rural environments (Lepczyk *et al.* 2004; Lowry *et al*. 2013; Tryjanowski *et al*. 2015). Large quantities of nutrients and energy are added into urban systems each year through commercial bird feeding activities (Galbraith *et al.* 2015) and, as a result, urban areas are reported to support significantly more over-wintering birds (Clergeau *et al.* 1998; Marzluff *et al.* 2001; Tryjanowski *et al*. 2015). Supplemental bird feeding has been shown to decrease over-winter mortality and thus has direct fitness consequences (Brittingham & Temple 1988; Desrochers *et al*. 1988). In response to predictable year-round food availability, ecological and behavioural traits of urban species are changing, especially those associated with foraging (Lowry *et al.* 2013; Galbraith *et al.* 2015).

Foraging requires cognitive processes, or in other words, mechanisms involving the acquisition, processing, storage, and utilization of environmental information (Shettleworth 1998). Certain cognitive traits have been defined as specialized adaptations shaped via natural selection, and thus are expected to vary under different selective pressures due to local environmental conditions (Healy *et al*. 2009). Innovativeness and learning abilities have been suggested as important traits that facilitate colonization of urban areas (Sol *et al*. 2013). However, it is not well understood how the cognitive traits of rural ancestors may be altered after establishment in urban environments. Studying cognitive processes that are directly associated with natural history and fitness is important for understanding the evolution of cognition in response to different environments (Morand-Ferron *et al.* 2016). In the cognitive ecology literature, scatter hoarders are a well-studied model used to explore how cognitive traits vary under different environmental conditions. Therefore, we use a scatter hoarding model to examine how spatial cognitive traits related with foraging may be altered in urban environments in response to differential food availability.

Scatter hoarders rely on spatial memory to recall locations of many previously stored food items, which may be critical for survival through periods of food scarcity (Krebs 1990; McNamara *et al*. 1990). Scatter hoarding birds have been empirically shown to possess enhanced spatial cognition, and specialized neurological features, which they use to recall and retrieve their stored caches (reviewed in Brodin 2010; Pravosudov & Roth 2013). Scatter hoarding strategies, and the underlying cognitive mechanisms, have previously been shown to vary in response to environmental conditions. In particular, variable food resources in harsh environments has been hypothesized as a factor that may contribute to increased food caching intensity (McNamara *et al*. 1990). This refers to the adaptive specialization hypothesis (ASH) for scatter hoarders, which predicts that hoarders living in harsher environments should develop superior spatial cognition and corresponding neurological features to support a higher reliance on caches in the environment (Krebs 1990). ASH has been supported at both latitudinal (Pravosudov & Clayton 2002; Roth *et al*. 2012) and elevational (Freas *et al*. 2012) gradients within species. These studies show that individuals occupying higher latitudes or elevations (harsher, food-scarce environments) cache more frequently and show superior spatial accuracy in comparison to conspecifics who occupy low latitudes or elevations. ASH has yet to be examined in scatter hoarders occupying environments that differ in the extent of urbanization, despite artificially increased food availability via the use of feeders in developed and urban areas. Scatter hoarding behaviours have been observed in urban squirrels (Thompson & Thompson 1980; van de Merwe *et al*. 2007) and urban kestrels (Rejt *et al*. 2000) but, to our knowledge, food caching intensity or spatial abilities of urban scatter hoarders have not yet been compared to rural conspecifics.

In addition to cognitive traits, personality or behavioural tendencies, have been suggested to be key traits allowing colonization of urban habitats (Miranda *et al*. 2013). Between-individual differences in cognitive abilities may cause variation in behavioural tendencies or vice versa, and therefore personality and cognitive differences may together be affecting the responsiveness of individuals to environmental change (Griffin *et al.* 2015). For example, individuals with fast exploratory personalities discover new foraging opportunities more readily (Herborn *et al*. 2010; van Overveld & Matthysen 2010), which may be important for inhabiting urban environments (Atwell *et al.* 2012; Sol *et al.* 2013). It has been hypothesized that a trade-off exists between exploratory personality and quality of spatial information acquired (Sih & Del Guidice 2012). Fast explorers are predicted to collect shallow spatial information due to rapid movement through their environment in comparison to slow explorers, who have more thorough searching strategies and collect higher quality spatial information. There is support for this hypothesis alongside ASH in high elevation mountain chickadees (*Poecile gambeli*). Chickadees at high elevations showed superior spatial accuracy (Freas *et al*. 2012), and different individuals from the same site were found to also be significantly slower explorers in comparison to low elevation chickadees (Kozlovsky *et al*. 2014). These findings suggest that selection for superior spatial cognition in harsh environments may be directly or indirectly linked to selection for slow exploratory personality (Kozlovsky *et al*. 2014). The hypothesized trade-off between personality and cognitive accuracy has received little empirical attention in relation to spatial cognition (but see Bousquet *et al.* 2015; Schuster *et al.* 2017), and has never been examined in individual scatter hoarders despite the ecological applicability of this hypothesis to caching behaviours.

This study aimed to examine whether ASH would be supported for scatter hoarders along an urban gradient, and explore the relationship between spatial cognition and exploratory personality within-individuals. We hypothesized that stable food sources in urban areas, especially over harsh winter months, would cause urban scatter hoarders to be less reliant on food caching behaviours, and therefore decrease selective pressures on enhanced spatial memory. We predicted that urban scatter hoarders would cache less, and show inferior spatial accuracy on both a multi-trial and one-trial spatial task in comparison to their rural conspecifics. We also expected to find evidence for within-individual covariation between exploratory personality and spatial accuracy, which would be indicative of a trade-off between exploration and quality of information collected. More specifically, we predicted that slow explorers would make fewer errors on spatial tasks and perform more accurately, while fast explorers were predicted to complete the task faster and perform more efficiently, despite making more errors. Urban individuals were found to be significantly faster explorers (chapter 2) and, following the predicted negative relationship between urbanization and spatial accuracy, urban birds were predicted to perform less accurately, but more efficiently than rural birds on the task.

Methods

Study species, sites, and captivity

To test our hypotheses, we use the black-capped chickadee (*Poecile atricapillus*), a scatter hoarding, non-migratory passerine bird that can be found in a variety of different habitats in North America, including both urban and rural environments (Smith 1991; Foote *et al.* 2010). We captured wild chickadees and transported them to the University of Ottawa to undergo a five-day captive schedule before release back at their point of capture. We used the same sites and same protocol as explained in chapter 2 for captures and maintenance of individuals in captivity. Individual cages provided 28 potential cache sites in which subjects could store food freely. Each individual's cage caches were counted and removed twice daily to quantify caching intensity. Urban scores and cumulative exploration scores in the novel environment assay used in this chapter were calculated as done previously in chapter 2.

Spatial tasks presented in captivity required individuals to be able to remove pompoms (1.5cm diameter white cotton balls) out of holes (cache sites; 1x1cm) in search of a hidden sunflower seed reward in different wooden apparatuses. Therefore, a gradual behavioural shaping procedure (visible seed, visible seed beside pompom, seed hidden behind pompom) was administered in individual cages during the morning of the second day to familiarize birds with the concept of hidden seed rewards and the motor movement required to remove pompoms. Birds were considered to have reached criterion when they removed a pompom from a cache site to retrieve a seed reward in three consecutive trials during initial training. Three individuals were close to completing training but did not reach criterion during the specified time. These individuals participated in tasks moving forward and we found that their inclusion did not affect results.

Multi-trial associative spatial learning task

Birds were tested on a multi-trial associative spatial learning task within their home cages (similar to Sanford & Clayton 2008; Roth *et al*. 2012) on their second day in captivity between 12:00-16:30. The task used two rectangular blocks (18x10 cm) that hung on the back wall of the subjects' home cages. Each block had 12 evenly spaced cache sites, giving a total of 24 sites. Task blocks were present in home cages at bird arrival to captivity and individuals had > 45 hours to habituate to and freely cache within the apparatus. Birds were deprived of food for 30 min prior to testing. The task began with a 5 min information trial, where birds retrieved a visible seed placed by the experimenter in one specific cache site of the task apparatus. Birds then attempted to relocate the location where they had previously found food in three repeated 15 min experimental searching trials, when all site contents were concealed using pompoms (Figure 3.1). This repeated twice more, for a total of 3 information trials and 9 searching trials. Repeated experimental trials provided subjects the opportunity to learn the location of the reward and information trials were presented at intervals to provide subjects with continuous information during the task. Birds were also familiarized with the concept of searching for a single food reward as not all site inspections were rewarded. During searching trials, latency to contact the hidden seed and the number of pompoms pulled (or errors) were recorded to evaluate task efficiency and spatial accuracy, respectively. We present results using data only from 2015 for this task (N = 67). However, this protocol was repeated in 2016 to maintain consistency in our captive protocol and familiarize birds with searching for a single food reward, but was shortened to 2 information trials and 6 searching trials.

One-trial associative spatial memory task

We again assessed spatial memory ability in a one-trial associative spatial memory task (Clayton & Krebs 1994), which was conducted on the third day in captivity between 12:00 - 13:00. This task also involved associative spatial memory, but did not involve repeated trials and therefore did not assess spatial learning. The task took place in the flight room using the four trees and 60 possible cache sites used for novel environment exploration, which birds had been familiarized to for 30 min prior to this test. This task included two phases. During phase one or the preliminary phase, birds entered the testing room and were given a maximum of five minutes to find and contact a specific site selected by the experimenter (same for all birds) containing visible sunflower seeds. Once a bird contacted a sunflower seed in the first phase, they were allowed 10 seconds to feed on the seed before the lights were turned off and they were returned to their home cage. The latency for individuals to find and contact the visible seed during the preliminary phase was recorded. Individuals then underwent a 30 min retention interval before re-entering the testing room for phase two or the experimental phase. At this time, the trees in the testing room were switched to ensure birds were not relying on visual cues from the trees and all cache site contents were concealed using pompoms. During the experimental phase, birds re-entered the testing room and attempted to find the location where they had found food in the previous phase (Figure 3.2). Birds were food deprived for 30 min prior to the preliminary phase and throughout the task for a total of 1 hr. How quickly the birds completed the task, or their efficiency, was measured as the latency to contact the hidden seed during the experimental phase. Additionally, an individual's spatial accuracy was inferred from the number of pompoms pulled (or errors) before contacting the hidden seed. In 2016, we assessed an individual's spatial performance again in a second session in an attempt to assess individual consistency of spatial performance. The second session occurred the next day at the same time and followed the same procedure as the first session, but the seed reward was placed in a different location.

Statistical analysis

We initially evaluated potential confounds associated with urban and rural environments by fitting a generalized linear model (GLM) to examine differences between urban and rural birds. We initially used a LM on square-root transformed urban scores; the results are qualitatively the same (Table 3.1) but the model returned poor diagnostics, we therefore present results from the GLM. We evaluated the fixed effects of sex, age class (HY/AHY), captive stress levels (baseline corticosterone), number of cage caches, and body condition. Body condition was estimated by extracting the residuals taken from a linear regression of body mass regressed onto tarsus length while controlling for time of capture (Schlute-Hostedde *et al.* 2005). The distribution for the number of cage caches was highly left-skewed and was causing patterning within residuals, therefore we separated this into three categories: 0 caches, 1-10 caches, and > 10 caches.

Latency to contact the hidden seed (efficiency) in the multi-trial spatial learning task was log-transformed to improve normality and fitted using a linear mixed-effects model (LMM). The number of errors (accuracy) within the spatial learning task was fitted using a generalized linear mixed-effects model (GLMM) with a negative binomial distribution, which accounted for overdispersion and aggregation within the count data (O'Hara & Kotze 2010; Harrison 2014). For both mixed-effects models, we tested an interaction between urbanization score and exploration score. We tested this interaction to explore the possibility that urbanization may differentially affect the link between exploratory personality and spatial cognition within-individuals. We also controlled for the effects of trial and baseline corticosterone (stress levels). Individuals nested within sites were used as random-level effects to account for repeated measures over trials.

In the one-trial spatial memory task, the log-transformed latency to contact the seed (efficiency) was fitted with a LMM and the number of errors (accuracy) was fitted with a GLMM (negative binomial distribution, again to account for overdispersion). In both models, we tested an interaction between urbanization and exploration score, controlled for order tested and stress, and included site as a random-level effect. No differences in spatial performance for this task were found between years so we pooled data over both years. The LMM evaluating latency returned a zero-variance for our random-effect of site, therefore we refitted using a linear model (LM). We excluded site as a fixed-effect in the LM since sites had non-significant effects and AIC indicated that excluding site was a more parsimonious fit. For this task, we wanted to assess whether differences in spatial memory existed only in those individuals that had already experienced caching requirements in their environment. We therefore also evaluated differences in spatial accuracy using only after-hatch year birds who had experienced at least a year within their environment.

In an additional analysis, we included the second session of the one-trial spatial task for individuals tested in 2016 to assess individual consistency of spatial performance. We evaluated the latency to the seed (LMM) and the number of errors (GLMM negative binomial) as done previously. An interaction between urbanization and exploration scores, as well as session (1 or 2) were included as fixed effects in the models. Individuals nested within sites were used as random-level effects to account for two observations per individual. We evaluated individual consistency of spatial accuracy by following the same procedure used to calculate adjusted repeatability (Nakagawa & Schielzeth 2010; Griffin *et al*. 2015).

Continuous fixed-effects in mixed models were standardized via grand mean-centering prior to analysis to improve convergence (Pinheiro & Bates 2000; Bolker *et al*. 2009). All tested interactions between urban and exploration scores were found to be non-significant (Table 3.2-A) and were therefore removed so that the main effect of predictors could be evaluated. Baseline corticosterone (stress) was found to be non-significant in all spatial task models (all $P > 0.4$) and we did not have data for all individuals, we therefore excluded this variable in order to include the full dataset in our final analyses. LMMs were fitted via restricted maximum likelihood approximations and GLMMs were fitted with a Laplace maximum likelihood approximation. We evaluated significance of fixed-effects using Type II ANOVA and interacting terms using Type III ANOVA. For LMMs we used F-tests with a Kenward-Roger approximation of degrees of freedom and Wald chi-square tests for GLMMs (Bolker *et* al. 2009). All statistical analyses were conducted using R v.3.4.0 (R Core Team 2017). Our mixed-effects models were generated using the *lmer* and *glmer.nb* commands in the lme4 (Bates *et al*. 2015), and lmerTest (Kuznetsova *et* al. 2015) packages.

Results

Urban vs. rural comparison

Caching intensity measured via cage caches did not significantly differ between individuals from urban and rural environments (Figure 3.3; Table 3.1). The effects of age class and body condition were also not significant (Table 3.1). However, individuals from rural environments had significantly higher baseline corticosterone (stress) levels after exposure in captivity than individuals from urban environments (GLM: estimate±SE = -0.019±0.009, $F_{1,121} = 4.99$, $P = 0.027$).

Spatial tasks

Multi-trial associative spatial learning task

The latency to contact the seed reward in the multi-trial spatial learning task significantly decreased with experimental trials (LMM: estimate±SE = -2.34±0.18, $F_{1,359} = 173.17$, $P < 0.001$; Figure 3.4-A), but the number of errors did not significantly decrease with trials (GLMM: estimate±SE = -0.20±0.15, $\chi^2 = 1.82$, $P = 0.18$; Figure 3.4-B). Since errors did not decrease with trials and we provide no evidence of learning, we do not report further results concerning this task.

One-trial associative spatial memory task

Birds found the seed reward in the experimental phase of the spatial task with significantly fewer errors than would be expected by random searching in both sessions (chance = 30.5 following the negative hypergeometric distribution; Tillé *et al.* 1996; Wilcoxon test: session 1, N = 96, median = 13, $P < 0.001$; session 2, N = 47, median = 21, $P = 0.001$). Urbanization and exploration scores were not significant predictors of the number of errors or the latency to contact the seed reward in the experimental phase of the one-trial spatial task (Table

3.2; Figure 3.5)**.** Results were qualitatively unchanged when running one-trial spatial accuracy models using only after-hatch year (AHY) birds, when urbanization was assessed on alternative scales (200 m scale or as binary predictor), when using the number of trees contacted instead of exploration scores, when removing individuals (N = 3) that were coaxed into the exploration assay after the 5 min had elapsed, and when removing individuals (N = 3) who had not reached training criterion (Table 3.3).

When including data from both sessions of the one-trial spatial memory task in 2016 (N = 47), urbanization and exploration scores still had no effect on the number of errors made (GLMM urban: estimate±SE = 0.20±0.23, χ^2 = 0.78, *P* = 0.38; exploration: estimate±SE = -0.53±0.38, χ^2 = 1.92, *P* = 0.17). Birds that underwent both sessions in 2016 made significantly more errors in the second session (GLMM: estimate±SE = 0.54±0.17, χ^2 = 10.25, *P* = 0.001; Figure 3.6-A), and were not found to be consistent in the number of errors they made during the one-trial spatial memory task (GLMM: R < 0.001, *P*=1; Figure 3.6-B).

Discussion

The adaptive specialization hypothesis (ASH) has been supported in scatter hoarders along elevational and latitudinal gradients (Pravosudov & Clayton 2002; Roth *et al.* 2012; Freas *et al.* 2012), but had not yet been examined along an urban gradient. As well, the relationship between exploratory personality and spatial cognition within-individuals has received little empirical attention and has never been explored within scatter hoarding animals. We report no differences in caching intensity or spatial accuracy between individuals along this gradient, suggesting that caching intensity and spatial memory are not affected by urbanization in our populations. We also report no significant association between exploratory personality and spatial cognition within a scatter hoarding animal.

We predicted that urbanization would be a significant predictor of spatial accuracy in the one-trial spatial task, and expected rural birds to perform more accurately than urban ones. However, we found no significant effect of urbanization on spatial accuracy or efficiency measures in the one-trial task. The potential confounds of body condition, sex, and age class were not found to differ between individuals along our gradient and therefore these were dismissed as potential confounds. Baseline corticosterone was found to be higher in rural individuals after exposure to captivity and we evaluated this potential effect in subsequent models, but this also had no effect on our results. Results remained unchanged when examining urbanization at a smaller scale (200 m vs. 1km) which more realistically represented the home range of our species. Due to the lack of an effect of urbanization using both age classes, we hypothesized that spatial abilities may only be affected by urbanization as a result of phenotypic plasticity. Scatter hoarders deprived of caching behaviours have been shown to develop relative hippocampal volumes similar to non-scatter hoarders, and may lose enhanced spatial memory due to lack of experience (Clayton & Krebs 1994). Therefore, we predicted that spatial abilities may decrease in urban individuals only once they had experienced decreased demands for caching in their environment. However, our analysis evaluating spatial accuracy using only after-hatch year birds yielded similar results. We report no differences in spatial memory abilities between individuals occupying areas that differ in the degree of urbanization, either as a result of unique selective pressures or phenotypic plasticity, and thus do not provide evidence for ASH along an urban gradient within the current study.

Urban environments have been considered to be more spatially complex than more natural environments (Griffin *et al.* 2017). The environmental complexity hypothesis proposes that enhanced cognitive mechanisms have evolved to allow individuals to collect, retain, and process more diverse information in heterogeneous environments (Godfrey-Smith 2002). For example, storm petrels living in a forest habitat were found to have larger relative hippocampi than their conspecifics living in an open meadow. The authors explain that these findings may be due to higher environmental complexity in forest habitats and speculate that individuals within the forest may have evolved enhanced spatial cognition for navigation purposes (Abbott *et al.* 1999). If caching behaviours and associated cognitive processes differ along an urban gradient, the spatial abilities of urban birds may remain comparable to rural conspecifics if urban birds require higher spatial cognitive processing for mapping a more complex environment. However, this explanation is unlikely since we did not observe differences in caching intensity along our gradient to begin with. Lack of differences in spatial cognition as a result of urbanization is more likely due to caching behaviours remaining similar between subpopulations, despite putative food availability differences (Lepczyk *et al.* 2004; Tryjanowski *et al.* 2015).

Degree of urbanization, or food stability, may not alter spatial abilities within scatter hoarders if there is sufficient gene flow occurring along this gradient. Work in this area initially compared distinct populations that were separated by large geographical distances and were likely genetically distinct (Pravosudov & Clayton 2002; Roth *et al.* 2012). However, further work along an elevational gradient showed differences in spatial abilities between subpopulations that were located only 10 km away (Freas *et al.* 2012). In this system, individuals at high and low elevations were later found to show differences in other behavioural traits which were thought to limit dispersal and gene transfer between sites (Kozlovsky *et al.* 2014), but these populations were not found to be genetically differentiated (Branch *et al.* 2017). In our system, we do not have information regarding genetic population structures, and thus gene flow may be acting as a buffer against divergent selection on spatial abilities, explaining why spatial traits were not found to differ within our system.

Past work on ASH in scatter hoarders have examined populations that differ in stability of food supply as a result of natural conditions. Our study is the first to compare spatial abilities of scatter hoarders along a gradient that differs in food availability due to anthropogenic effects. On an evolutionary time-scale, environmental change in relation to urbanization is still recent (McDonnell & Hahs 2015). Therefore, selective pressures in urban areas may be too novel for urbanization to have measurable effects on an important trait with direct fitness consequences, such as spatial memory in scatter hoarders. With the data at hand, we are unable to determine whether the lack of evidence for ASH in relation to urbanization is due to one of the above-mentioned explanations. Future work could examine whether potential differences in diet and food quality, or increased competition, along this gradient affect decisions concerning caching behaviours. Differences in exploratory personality (Chapter 2) and social information use (Jones *et al.* 2017) have previously been shown along this gradient in our study system. Examining how other ecological and behavioural traits vary with urbanization may further our understanding of how foraging-related behaviours in scatter hoarders are affected in urban areas.

Exploration behaviour within a novel and altered environment was significantly repeatable within individuals and this personality trait was found to differ between-individuals along this urban gradient (Chapter 2). To explore whether exploratory personality affects the quality of information collected by individuals (Sih & Del Guidice 2012), we predicted that slow explorers would perform more accurately while fast explorers would perform more efficiently on a spatial task. However, there was no significant interaction between exploratory personality and degree of urbanization on spatial performance during the one-trial task, and exploration remained non-significant when evaluated separately. Our study does not provide support for a trade-off between speed of exploration and spatial accuracy within a scatter hoarding model. These findings conflict with indirect evidence for an association between spatial accuracy and slow exploratory tendencies using different individual chickadees along an elevational gradient (Kozlovsky *et al.* 2014). As of yet, only a few studies have examined the relationship between spatial cognition and personality, and results are mixed (mallards *Anas platyrhynchos*, Bousquet *et al.* 2015; lizards *Eulamprus quoyii,* Carazo *et al.* 2014; mice *Micromys minutus*, Schuster *et al.* 2017). Spatial memory is an important adaptive mechanism used by scatter hoarders for survival, so perhaps this cognitive trait evolves independently of other traits, such as personality. This may explain why no significant relationship between spatial cognition and exploratory personality was found in the current study. Exploring whether a trade-off between these traits exists in a non-scatter hoarding relative, using the same experimental procedure, would be useful to understand whether our findings are scatter-hoarder specific.

In the multi-trial spatial learning task, latency to contact the seed reward significantly decreased with trials, but the number of errors did not significantly decrease over the task. These results suggest that individuals became more efficient during the task by learning to search for and retrieve the seed reward over consecutive trials, but were likely not using spatial memory to do this. We believe that chickadees in our study did not decrease the number of their errors since the cost of making errors was not high on this small spatial scale. Previous studies have used similar small-scale tasks to quantify spatial accuracy and have come to the same conclusions (Feeney *et al.* 2009; Shaw *et al.* 2015). These authors speculated that the small spatial grid of the multi-trial task may not have been appropriate to measure cognition utilized for behaviours at larger foraging scales (but see Roth *et al.* 2012). Since this task was likely not measuring spatial memory, we did not use these data for further analyses. In agreement with these authors, we suggest designing larger-scale spatial tasks to better represent natural behaviours related to scatter hoarding, which may better quantify spatial abilities used for caching (Feeney *et al.* 2009; Shaw *et al.* 2015).

In 2016, we conducted a second session of the one-trial task in an attempt to evaluate the consistency of spatial accuracy within individuals (Griffin *et al.* 2015). When moving the location of the rewarded site in the second session of the one-trial task, individuals still performed significantly more accurately than expected by random searching, but made significantly more errors than in the first session. Thus, individuals were not found to show consistency in spatial accuracy across sessions. We suspect that differences in performance between sessions was a result of memory interference (Hoshooley 2007), where spatial memory use in the first session impeded memory retention in the second session due to the short time interval between the successive tests. Individuals have been suggested to be more prone to interference when conducting spatial tasks where they themselves have not placed the food items, like is done when caching (Feeney *et al.* 2009). Studies using a one-trial task to quantify spatial memory often use three sessions with different food locations separated by a couple hours or days, and present the average of an individual's errors over trials to capture a more precise measure of spatial accuracy (e.g. Clayton & Krebs 1994); using an average from two trials however left our conclusions relative to the link with urbanization and exploration unchanged. It is to be noted that previous studies have not attempted to quantify consistency of spatial memory within individual scatter hoarders, and we know of only one published study reporting repeatability estimates for spatial cognition in mice (Schuster *et al.* 2017). In the future, having long-term intervals between tasks may help reduce potential memory interference or, ideally, consistency could be demonstrated using two unrelated tasks presented at larger scales which represent natural behaviours. Demonstrating a positive relationship between different tasks would suggest tasks are measuring the same trait and would thus also be important for establishing convergent validity (Carter *et al.* 2013).

In conclusion, ASH was not supported along an urban gradient since urban birds did not show inferior spatial accuracy in comparison to rural birds. The lack of support for ASH along this gradient may be due to one of the listed explanations above, or perhaps a combination of them. We report no significant relationship between spatial accuracy and exploratory personality, and thus are unable to provide evidence that slow explorers collect higher quality spatial information from their environment. An association between spatial cognition and personality traits may be unlikely within a scatter hoarding model since spatial cognition is an important adaptive trait that may be evolving independently. Nonetheless, identifying potential predictive relationships between behavioural and cognitive traits is an obvious direction for future research, which will help create a clearer picture for understanding adaptive individual variations in different environments.

Table 3.1 Evaluation of potential confounding effects that differ between individuals (A) within urban and rural habitat types (as a binary response), and (B) along an urban gradient (continuous response). Both analyses give qualitatively similar results.

Fixed Effects	Estimate	±SE	*F*	DF	*P*
(A) Urban vs Rural GLM					
Cage caches	-0.23	0.30	0.60	1,121	0.44
Body condition	-0.20	0.36	0.30	1,121	0.58
Age class	0.52	0.38	1.76	1,121	0.19
Sex	-0.33	0.44	0.53	1,121	0.47
Baseline corticosterone	-0.02	0.009	4.99	1,121	0.027
(B) Urban score LM					
Cage caches	-0.033	0.10	0.10	1,121	0.75
Body condition	-0.15	0.13	1.47	1,121	0.23
Age class	0.12	0.13	0.77	1,121	0.38
Sex	-0.15	0.15	0.96	1,121	0.33
Baseline corticosterone	-0.83	0.28	8.54	1,121	0.0041

Table 3.2 Predictors of the (1) number of errors (spatial accuracy) fitted using a generalized linear mixed-effects model with a random intercept for site levels, and (2) latency to contact the reward fitted with a linear model, in the one-trial spatial task. Shows evaluated effects in the (A) full model, (B) full model once dropping the interaction, and (C) final model using the full dataset.

	(1) Number of errors			(2) Latency to Reward			
Predictors	Estimate ±SE	χ^2	*P*	Estimate ±SE	*F*	DF	*P*
(A) Full model (N = 75)							
Urban score	0.35±0.21	2.69	0.10	0.078±0.057	1.86	1,69	0.18
Exploration score	-0.46±0.45	1.08	0.30	-0.055±0.052	1.11	1,69	0.30
Order tested	0.41±0.30	1.89	0.17	-0.0022±0.032	0.0047	1,69	0.95
Baseline corticosterone	-0.10±0.41	0.054	0.82	-0.00094±0.0054	0.030	1,69	0.86
Urban*Exploration	0.42±1.02	0.17	0.68	-0.013±0.026	0.25	1,69	0.62
(B) Dropped interaction (N = 75)							
Urban score	0.34±0.21	2.61	0.11	0.078±0.057	1.87	1,70	0.18
Exploration score	-0.43±0.44	0.93	0.33	-0.063±0.050	1.60	1,70	0.21
Order tested	0.40±0.30	1.80	0.18	-0.00092±0.032	0.00080	1,70	0.98
Baseline Corticosterone	-0.089±0.41	0.046	0.83	-0.0010±0.0054	0.030	1,70	0.85
(C) Final model (N = 96)							
Urban score	0.24±0.19	1.63	0.20	0.067±0.049	1.87	1,92	0.17
Exploration score	-0.32±0.38	0.75	0.39	-0.057±0.039	2.13	1,92	0.15
Order tested	0.27±0.26	1.10	0.29	-0.014±0.027	0.26	1,92	0.61

Table 3.3 Predictors of the number of errors (accuracy) in the one-trial spatial task from a negative binomial generalized linear mixed-effect model including a random intercept for sites and (A) using only after-hatch-years (AHY) birds, (B) examining the effect of urbanization at a smaller 200 m scale, (C) examining the effect of urbanization as a categorical predictor, (D) using the number of trees contacted during exploration instead of exploration scores, (E) excluding individuals (N = 3) who were coaxed into the novel environment assay, and (F) excluding individuals (N = 3) who did not reach criterion during pompom training. Despite using different variations of predictors, results remain qualitatively unchanged.

Fixed Effects	Estimate	±SE	χ^2	*P*
(A) After-hatch years only				
Urban score	0.16	±0.24	0.42	0.52
Exploration score	-0.42	±0.50	0.70	0.40
Order tested	0.23	±0.37	0.39	0.53
(B) Smaller urban scale				
Urban score (200m)	0.36	±0.22	2.74	0.10
Exploration score	-0.36	±0.37	0.98	0.32
Order tested	0.25	±0.25	0.98	0.32
(C) Urban vs. rural				
Intercept	2.41	±0.17		
Urban	0.25	±0.16	2.61	0.11
Exploration score	-0.35	±0.37	0.92	0.34
Order tested	0.26	±0.25	1.08	0.30
(D) Number of trees contacted				
Urban score	0.20	±0.19	1.20	0.27
Number trees contacted	-0.011	±0.23	0.0021	0.96
Order tested	0.27	±0.26	1.14	0.29
(E) Excluding forced-entry individuals				
Urban score	0.33	±0.20	0.10	0.10
Exploration score	-0.34	±0.37	0.37	0.37
Order tested	0.31	±0.27	0.27	0.26
(F) Excluding individuals not reaching criterion				
Urban score	0.23	±0.20	1.34	0.25
Exploration score	-0.40	±0.38	1.09	0.30
Order tested	0.33	±0.26	1.56	0.21

Figure 3.1 Photo of a subject that has retrieved the seed reward in the experimental phase of the multi-trial associative spatial learning task.

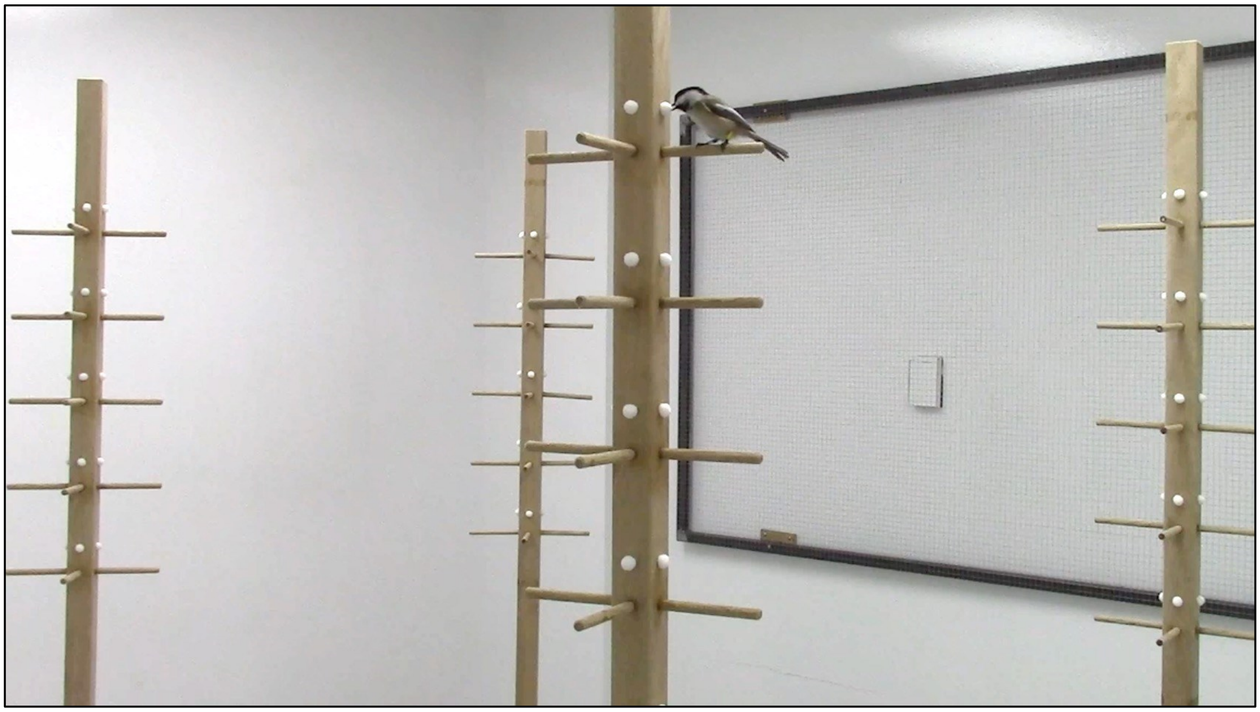


Figure 3.2 Photo of a subject pulling a pompom (an error) during the experimental phase of the one-trial associative spatial memory task.

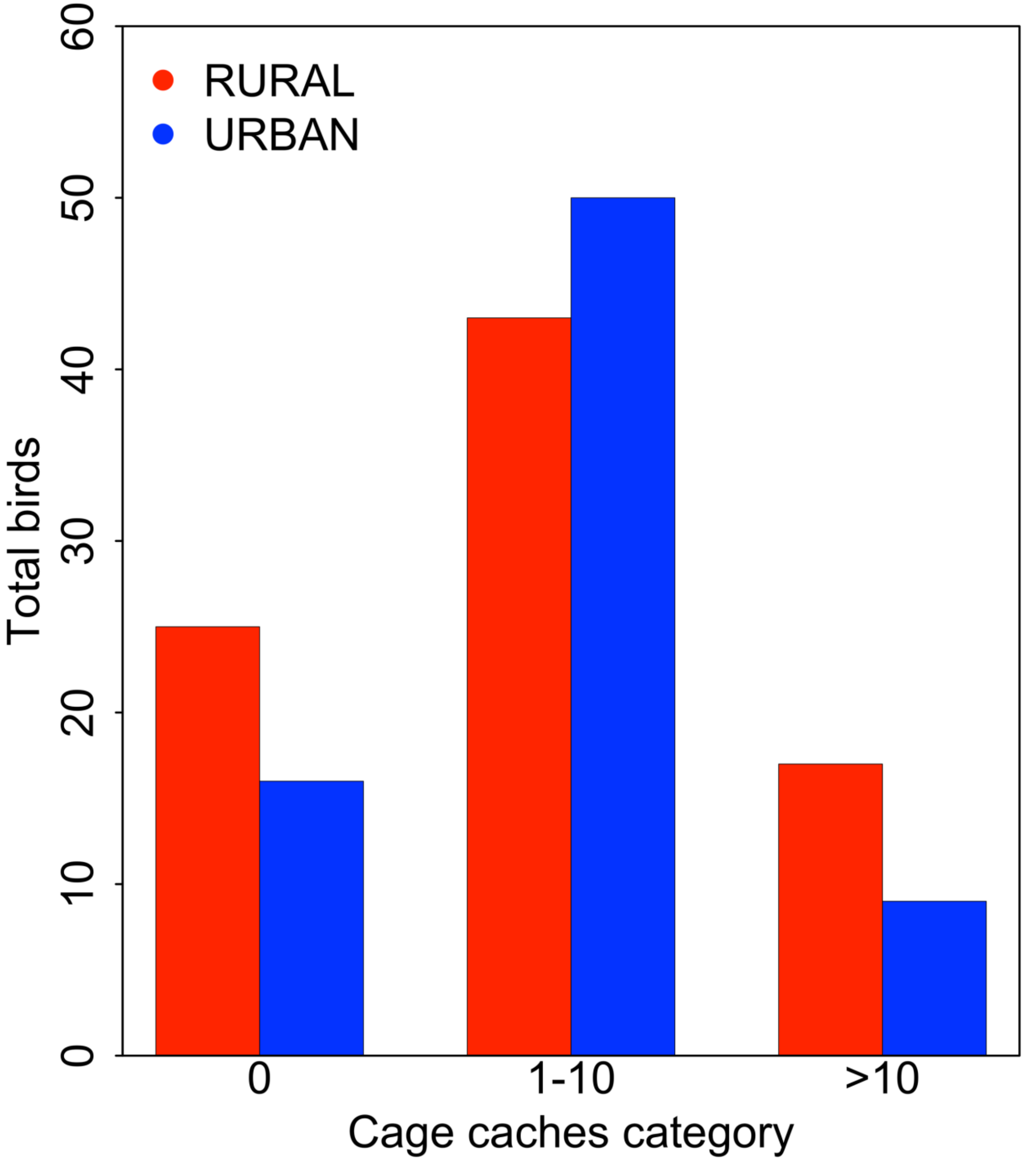


Figure 3.3 The number of cage caches separated by category (0 caches, 1-10 caches, or greater than 10 caches) made by birds (N = 168) from urban (blue) and rural (red) sites.

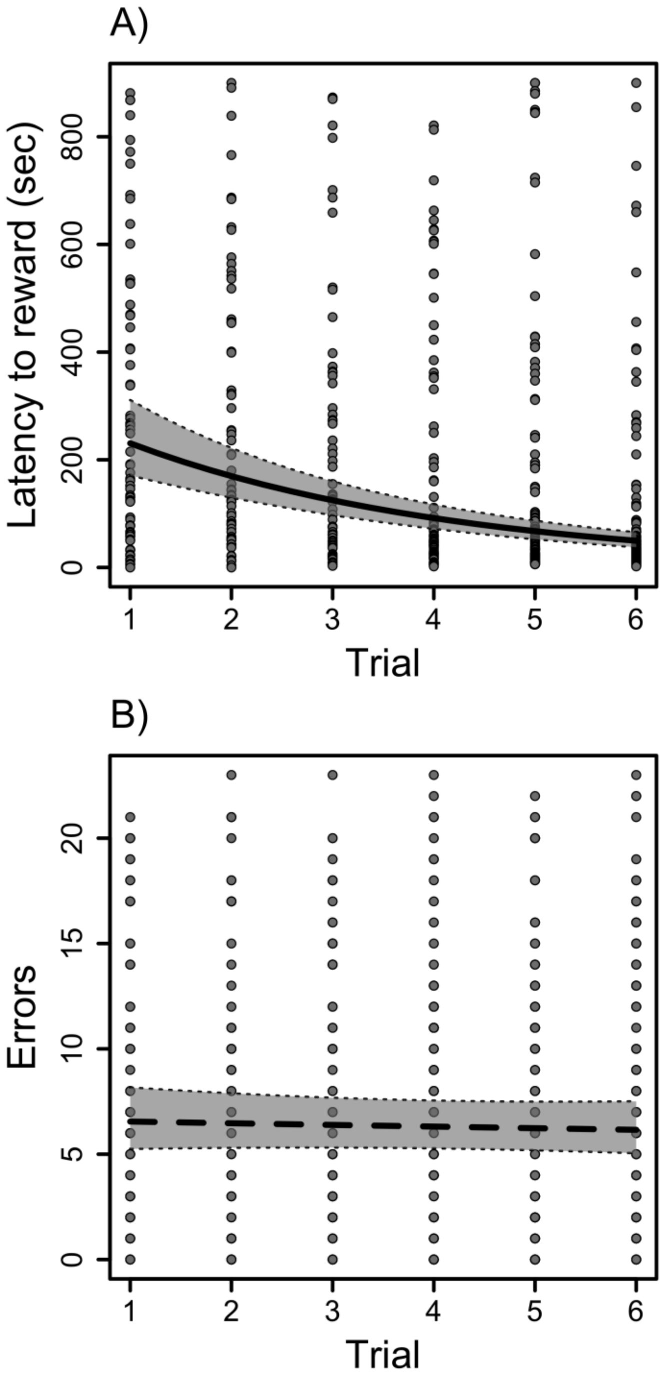


Figure 3.4 A) Latency to contact and B) the number of errors before contacting the hidden seed reward over experimental trials in the multi-trial associative spatial learning task. Significant (solid line, panel A) and non-significant (dashed line, panel B) estimated effects and corresponding 95% confidence intervals are shown.

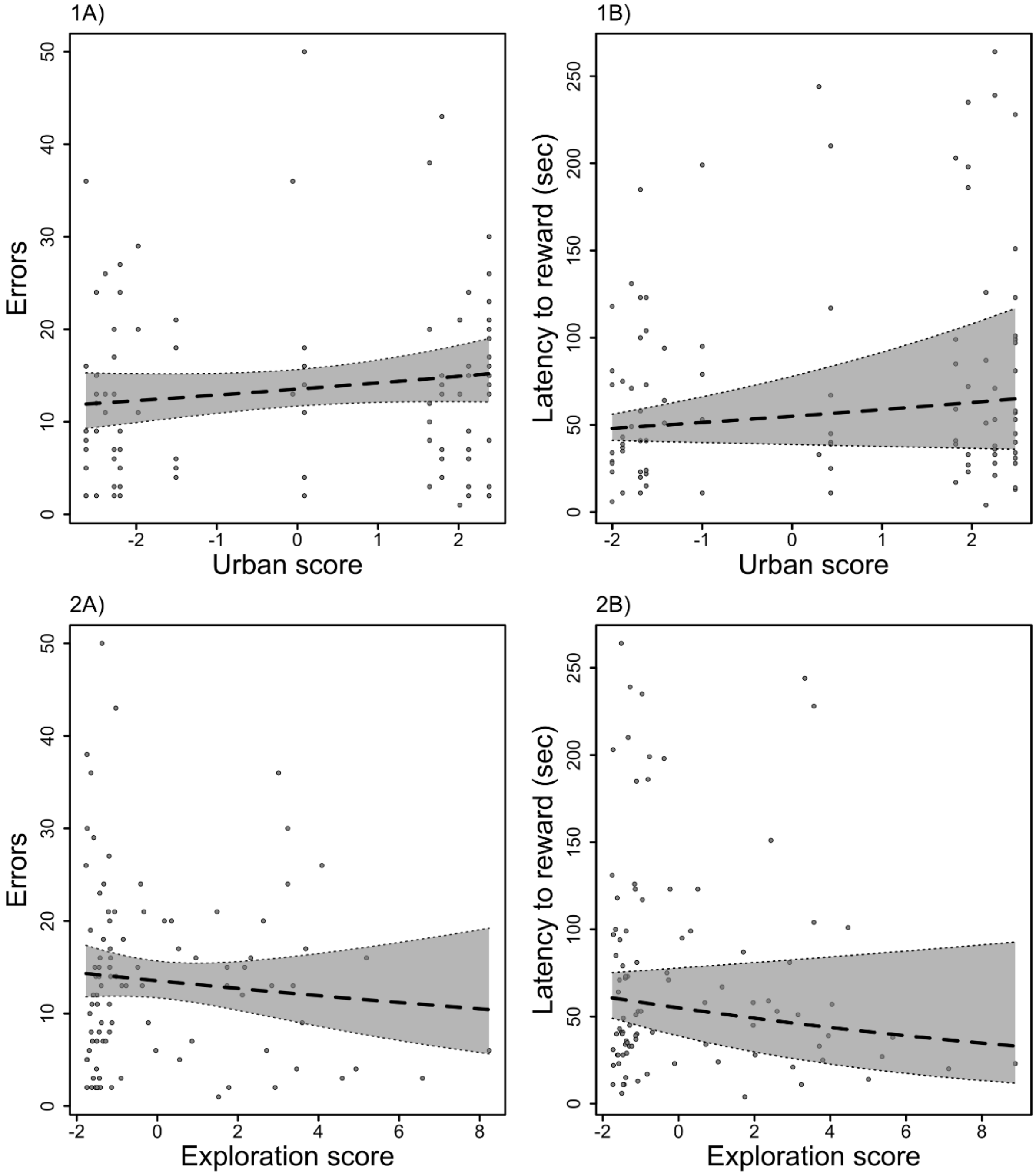


Figure 3.5 Final models showing the relationship between the effects of 1) urbanization and 2) individual exploration score, on the A) number of errors and B) latency to contact the hidden seed reward in the experimental phase of the one-trial associative spatial memory task. Non-significant estimated effects and corresponding 95% confidence intervals are shown.

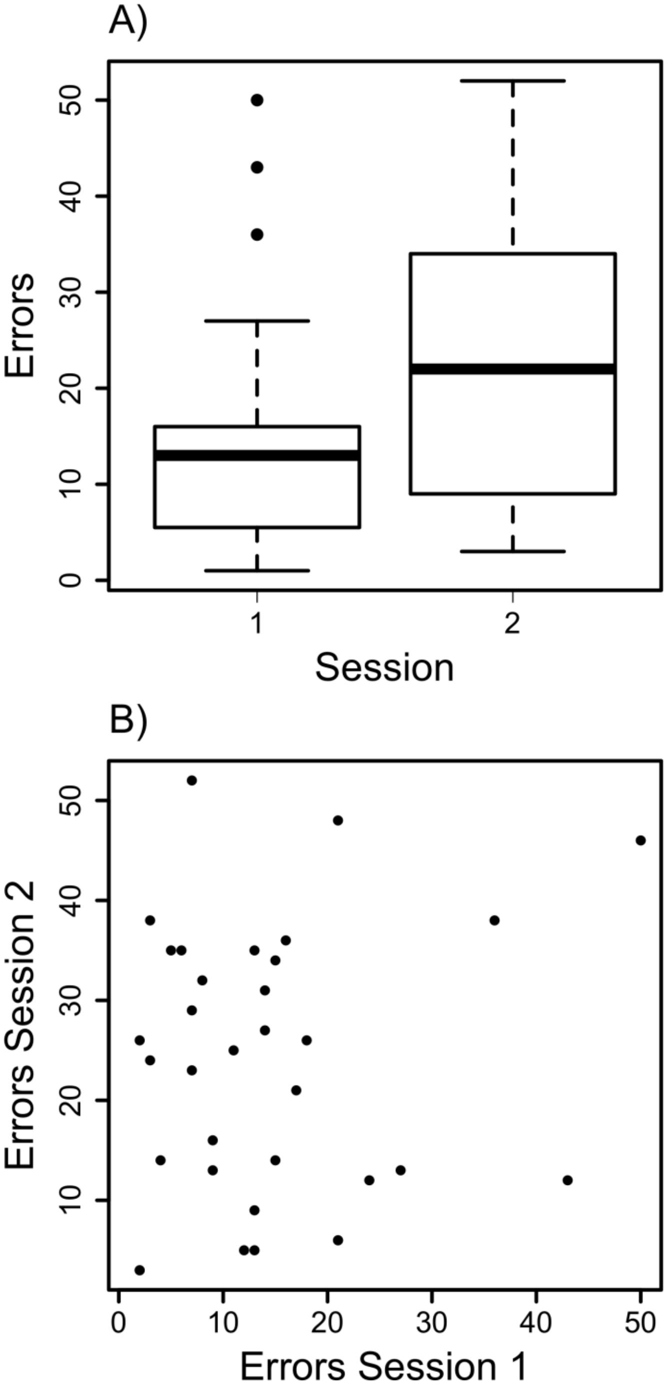


Figure 3.6 Number of errors made by individuals (N = 47) during the experimental phase for both sessions of the one-trial associative spatial memory task visualized to show A) the difference in errors between sessions and, B) the lack of consistency in the number of errors made by individuals between sessions.

Chapter 4

General Conclusion

Personality and plasticity are predicted to be major behavioural mechanisms that allow animals to successfully colonize urban areas (Lowry *et al.* 2013; Sol *et al.* 2013; Miranda 2017). Although work has begun to determine which personality traits facilitate colonization in urban areas (Miranda *et al.* 2013), little attention has been given to determine how these traits may be related to plasticity in urban animals. Additionally, there are a growing number of studies examining the relationship between personality and cognition (Griffin *et al.* 2015), but few studies have compared personality with spatial cognition, and of these few studies, none have utilized a scatter hoarding model. The work in this thesis aimed to examine the relationship between personality, plasticity, and spatial cognition between and within individual scatter hoarders. I also aimed to determine whether variation at the individual level could be explained by urbanization. Specifically, I hypothesized that exploratory personality would be significantly related with both habituation to novelty and spatial memory within-individuals. Due to lack of theory and mixed results on the topic, I did not make a priori predictions concerning the relationship between exploration and habituation. I did however predict that slow explorers would be more spatially accurate than fast explorers. Concerning urbanization, I hypothesized that urban scatter hoarders would be significantly faster explorers, habituate to novelty more quickly, and have inferior spatial memory in comparison to rural conspecifics.

I found significant between-individual differences in exploratory personality and habituation within a novel environment. A significant negative correlation between initial exploration and habituation slope suggests that fast explorers tended to habituate while slow explorers did not within the environment over time. As well, I report no significant relationship between exploratory personality and spatial memory within-individuals using the one-trial task. Results indicate a significant positive relationship between urbanization and exploratory personality, and therefore I conclude that faster exploring individuals occupy more urbanized areas. Urbanization did not significantly predict habituation to a novel environment and therefore we do not provide evidence for the prediction that urban individuals are more behaviourally plastic. Finally, spatial accuracy within the one-trial task was not predicted by urbanization and thus the adaptive specialization hypothesis (ASH) is not supported along an urban gradient.

Exploratory personality and its effects on cognition, or vice versa, may be affecting an individual's responsiveness to changes in the environment (Guillette *et al.* 2010; Mathot *et al.* 2012). As mentioned previously in this thesis, slower explorers may collect higher quality information via thorough searching strategies, and as a result, are predicted to be more behaviourally plastic to environmental changes (Verbeek *et al.* 1994; Sih & Del Guidice 2012; but see Arvidsson & Matthysen 2016). Alternatively, it is also predicted that fast exploratory personality and behavioural plasticity are beneficial for individuals in urban environments (Lowry *et al.* 2013; Sol *et al.* 2013; Miranda 2017). I found that urban individuals were significantly faster explorers as predicted, but no evidence that these individuals are also more behaviourally plastic. Exploratory personality may only affect the plasticity of certain behaviours, explaining the lack of a relationship between exploration and habituation in the current study. For example, fast explorers may be more likely to habituate to and exploit novel foods or habitats through faster learning abilities (Guillette *et al.* 2009, 2014), but may have more difficulty reversing a learned association due to superficial sampling of the environment (Guillette *et al.* 2010). Following this, food sources are suggested to be more predictable within urban environments (Lepczyk *et al.* 2004; Lowry *et al*. 2013; Tryjanowski *et al*. 2015), and therefore urban individuals may not need to be as plastic in their behaviours if urban environments are less variable in food or other resources. These explanations are speculative and work is needed to determine how exploration and cognition interact when examining different facets of behavioural plasticity within-individuals along an urban gradient.

I provide no evidence that slow explorers are collecting and storing higher quality spatial information to memory since slow explorers did not show superior spatial accuracy. Information sampling and utilization (i.e. cognition) is predicted to be the mechanism by which slow explorers are able to be more behaviourally plastic (Verbeek *et al.* 1994; Sih & Del Guidice 2012). Therefore, when examining the link between plasticity and personality within individuals, it may be important to also assess cognitive traits. Exploratory personality was not found to be associated with spatial cognition in the study, and since I found no evidence that slow explorers collect and store higher quality spatial information, this result may explain why no significant link between exploration and plasticity was found. I am the first to examine exploratory personality and spatial cognition using individual scatter hoarders, and the lack of a relationship found between these traits may be explained by the use of this model. Enhanced spatial memory is an adaptation that scatter hoarders use to survive during periods of food scarcity (Krebs 1990; McNamara *et al.* 1990), and as hypothesized in chapter three, spatial traits in scatter hoarders may be too important to develop associations with other traits like personality or plasticity. Since there is evidence that spatial cognition and personality are associated in other animals (Verbeek *et al.* 1994; Bousquet *et al.* 2015; Schuster *et al.* 2017), moving forward it will be important to confirm whether the absence of a relationship between these traits is scatter-hoarder specific. Future work should also aim to evaluate non-spatial aspects of cognition in scatter hoarders (like in Guillette *et al.* 2010), and the link with personality and plasticity traits.

The findings within this thesis contribute to both the cognitive and urban ecology fields. In the urban ecology literature, shifts in personality have previously been demonstrated in urban animals (Miranda *et al.* 2013). I also find personality differences along this gradient and join the only other study examining novel environment exploration (Atwell *et al.* 2012) in reporting that urban individuals are significantly faster explorers. I am among the first to examine habituation to spatial novelty in urban animals and find that urban individuals did not habituate more quickly. Although there is evidence that urban animals are more habituated to human presence (FIDs, Møller 2010; Evans *et al.* 2010; Atwell *et al.* 2012; Vincze *et al.* 2016), not all studies report this trend (Blumstein 2014). More work is needed to determine if urbanization is a significant predictor of habituation, and work in this area could join the current study in examining habituation responses of individuals to novel stimuli like spaces or objects.

In the cognitive ecology literature, there is growing evidence for inter-individual variation in the habituation process in wild animals (Montiglio *et al.* 2010; Bell & Peeke 2012; Dingemanse *et al.* 2012). I also found between-individual differences in habituation and therefore support these recent findings. Studies examining exploratory personality and habituation report that fast explorers habituate more quickly than slow explorers (Montiglio *et al.* 2010; Rodrigues-Prieto *et al.* 2011; Finger *et al.* 2016), which is also consistent with my results. The relationship between exploration and spatial cognition has never been examined in scatter hoarders. I provide the first evidence that spatial cognition and exploratory personality are not associated within scatter hoarders, and I hypothesize that this is because spatial memory may evolve independently of other traits within these individuals. As well, I am the first to examine ASH in scatter hoarders along an urbanized gradient, and conclude that this hypothesis is not supported along a gradient that differs in the degree of urbanization.

Moving forward it will be important to determine how behavioural modifications in urban wildlife arise. In agreement with others (Lowry *et al.* 2013; Sol *et al.* 2013; Miranda 2017), I believe it will be essential to examine the roles of microevolution and phenotypic plasticity in behavioural changes as a result of urbanization. I speculate that both evolutionary and plastic processes play a role in shaping behaviours of urban populations over time. A number of different approaches have been used in an attempt to determine if behavioural differences along this gradient are a result of local adaptation or plasticity. Some studies have utilized common garden approaches and confirmed that observed differences are likely a result of microevolution (Atwell *et al.* 2012; Miranda *et al.* 2013). More recently, studies have begun to examine genetic population structures in an attempt to explain behavioural differences between populations (e.g. Branch *et al.* 2017), but to my knowledge this approach has not been used to compare urban and non-urban populations. However, it has been suggested that genetic approaches may be unable to detect behavioural or cognitive differences between populations since the genetic underpinnings of behaviours are likely polygenic, and thus the use of population pedigrees are encouraged in the future (Branch *et al.* 2017). As well, utilizing systems where urbanization is still in its early stages may provide a unique opportunity for examining behavioural shifts in wildlife as they occur over time, and may help determine how these changes arise (Miranda 2017). Improving knowledge concerning the behavioural changes of urban animals, and more specifically the link between personality, cognition, and plasticity, should have important implications for both conservation and wildlife management moving forward.

Literature Cited

Abbott, M. L., Walsh, C. J., Storey, A. E., Stenhouse, I. J., & Harley, C. W. (1999). Hippocampal volume is related to complexity of nesting habitat in Leach's storm-petrel, a nocturnal Procellariiform seabird. *Brain, Behavior and Evolution*, *53*(5–6), 271–276. http://doi.org/10.1159/000006598

Andersson, M., & Krebs, J. R. (1978). On the evolution of hoarding behaviour. *Animal Behaviour*, *26*, 707–711.

Arvidsson, L. K., & Matthysen, E. (2016). Individual differences in foraging decisions: Information-gathering strategies or flexibility? *Behavioral Ecology*, *27*(5), 1353–1361. http://doi.org/10.1093/beheco/arw054

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., & Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology*, *23*(5), 960–969. http://doi.org/10.1093/beheco/ars059

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed- effects models using lme4. *Journal of Statistical Software*, 67, 1-48.

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. Anim. Behav. 77:771–783.

Bell, A. M., & Peeke, H. V. S. (2012). Individual variation in habituation: behaviour over time toward different stimuli in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour*, *149*(13–14), 1339–1365. http://doi.org/10.1163/1568539X-00003019

Blumstein DT, Daniel JC. (2007). Quantifying behavior the JWatcher way. Sunderland, MA: Sinauer.

Blumstein, D. T. (2014). Attention, habituation, and antipredator behaviour: implications for urban birds. In D. Gil & H. Brumm (Eds.), *Avian Urban Ecology: Behavioural and Physiological Adaptations.* (pp. 41–53). Oxford, UK: Oxford University Press. http://doi.org/10.1093/acprof:osobl/9780199661572.001.0001

Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour*, *120*(1), 255–262. http://doi.org/10.1016/j.anbehav.2016.05.012

Bókony, V., Kulcsár, A., Tóth, Z., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS ONE*, *7*(5). http://doi.org/10.1371/journal.pone.0036639

Bókony, V., Seress, G., Nagy, S., Lendvai, ádám Z., & Liker, A. (2012). Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows. *Landscape and Urban Planning*, *104*(1), 75–84. http://doi.org/10.1016/j.landurbplan.2011.10.006

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*(3), 127–135. http://doi.org/10.1016/j.tree.2008.10.008

Bousquet, C. A. H., Petit, O., Arrivé, M., Robin, J. P., & Sueur, C. (2015). Personality tests predict responses to a spatial-learning task in mallards, *Anas platyrhynchos*. *Animal Behaviour*, *110*, 145–154. http://doi.org/10.1016/j.anbehav.2015.09.024

Branch, C. L., Jahner, J. P., Kozlovsky, D. Y., Parchman, T. L., & Pravosudov, V. V. (2017). Absence of population structure across elevational gradients despite large phenotypic variation in mountain chickadees (*Poecile gambeli*) Author for correspondence: *Royal Society: Open Science*, *4*, 1–12. http://doi.org/10.1098/rsos.170057

Brennan, M. J., Allen, D., Aleman, D., Azmitia, E. C., & Quartermain, D. (1984). Age differences in within-session habituation of exploratory behavior: effects of stimulus complexity. *Behavioral and Neural Biology*, *42*(1), 61–72. http://doi.org/10.1016/S0163-1047(84)90436-9

Brodin, A. (2010). The history of scatter hoarding studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1542), 869–881. http://doi.org/10.1098/rstb.2009.0217

Carazo, P., Noble, D. W. a, Chandrasoma, D., & Whiting, M. J. (2014). Sex and boldness explain individual differences in spatial learning in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782). http://doi.org/0.1098/rspb.2013.3275

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? *Biological Reviews*, *88*(2), 465–475. http://doi.org/10.1111/brv.12007

Clayton, N. S., & Krebs, J. R. (1994). One-Trial Associative Memory - Comparison of Food-Storing and Nonstoring Species of Birds. *Animal Learning & Behavior*, *22*(4), 366–372. http://doi.org/Doi 10.3758/Bf03209155

Clergeau, P., Savard, J. L., Mennechez, G. G., & Falardeau, G. (1998). Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. *The Condor*, *100*(3), 413–425. Retrieved from http://www.jstor.org/stable/1369707

Cole, E. F., & Quinn, J. L. (2011). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1731), 1168–1175. http://doi.org/10.1098/rspb.2011.1539

Congedo L. (2016). Semi-Automatic Classification Plugin Documentation.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*(8), 734–739. http://doi.org/10.1111/j.1461-0248.2004.00618.x

Development Core Team, R. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Devost, I., Jones, T. B., Cauchoix, M., Montreuil-Spencer, C., & Morand-Ferron, J. (2016). Personality does not predict social dominance in wild groups of black-capped chickadees. *Animal Behaviour*, *122*(1), 67–76. http://doi.org/10.1016/j.anbehav.2016.10.001

Dingemanse, N. J., Both, C., Drent, P. J., Oers, K. V. A. N., & Noordwijk, A. J. V. A. N. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*(6), 929–938. http://doi.org/10.1006/anbe.2002.2006

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal Dispersal and Personalities in Great Tits. *Proceedings. Biological Sciences / The Royal Society*, *270*(1516), 741–7. http://doi.org/10.1098/rspb.2002.2300

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*(2), 81–89. http://doi.org/10.1016/j.tree.2009.07.013

Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E., & Quinn, J. L. (2012). Variation in personality and behavioural plasticity across four populations of the great tit Parus major. *Journal of Animal Ecology*, *81*(1), 116–126. http://doi.org/10.1111/j.1365-2656.2011.01877.x

Ellenberg, U., Mattern, T., & Seddon, P. J. (2009). Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour*, *77*(2), 289–296. http://doi.org/10.1016/j.anbehav.2008.09.021

Ensminger, A. L., & Westneat, D. F. (2012). Individual and Sex Differences in Habituation and Neophobia in House Sparrows (*Passer domesticus*). *Ethology*, *118*(11), 1085–1095. http://doi.org/10.1111/eth.12009

Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural Syndromes in Urban and Rural Populations of Song Sparrows. *Ethology*, *116*(7), 588–595. http://doi.org/10.1111/j.1439-0310.2010.01771.x

Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where, and when in the black-capped chickadee (Poecile atricapillus). *Animal Cognition*, *12*(6), 767–777. http://doi.org/10.1007/s10071-009-0236-x

Finger, J. S., Dhellemmes, F., Guttridge, T. L., Kurvers, R. H. J. M., Gruber, S. H., & Krause, J. (2016). Rate of movement of juvenile lemon sharks in a novel open field, are we measuring activity or reaction to novelty? *Animal Behaviour*, *116*(1), 75–82. http://doi.org/10.1016/j.anbehav.2016.03.032

Foote, R., Mennill, D. J., Ratcliffe L. M., Smith, S. M. (2010). Black-capped Chickadee (*Poecile atricapillus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.

Freas, C. A., LaDage, L. D., Roth, T. C., & Pravosudov, V. V. (2012). Elevation-related differences in memory and the hippocampus in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, *84*(1), 121–127. http://doi.org/10.1016/j.anbehav.2012.04.018

Galbraith, J. A., Beggs, J. R., Jones, D. N., & Stanley, M. C. (2015). Supplementary feeding restructures urban bird communities. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(20), E2648–E2657. http://doi.org/10.1073/pnas.1501489112

Gibelli, J., & Dubois, F. (2016). Does personality affect the ability of individuals to track and respond to changing conditions? *Behavioral Ecology*, *0*, arw137. http://doi.org/10.1093/beheco/arw137

GIS Development Team, Q. (2017). QGIS Geographic Information System. Open Source Geospatial Foundation. Retrieved from http://qgis/osgeo.org

Godfrey-Smith, P. (2001). Environmental Complexity and the Evolution of Cognition. In R. Sternberg & J. Kaufman (Eds.), *The Evolution of Intelligence* (pp. 233–249). London: Lawrence Elrbaum Associates. Retrieved from http://tamar.tau.ac.il/~eshel/Bio_complexity/1.Introduction/ComplexityCog.pdf

Griffin, A., Healy, S. D., & Guillette, L. M. (2015). Cognition and personality: An analysis of an emerging field. *Trends in Ecology & Evolution*, *30*(4), 207–214. http://doi.org/10.1016/j.tree.2015.01.012

Griffin, A. S., Netto, K., & Peneaux, C. (2017). Neophilia, innovation and learning in an urbanized world: A critical evaluation of mixed findings. *Current Opinion in Behavioral Sciences*, *16*, 15–22. http://doi.org/10.1016/j.cobeha.2017.01.00

Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, *77*(5), 419–450.

Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behavioural Processes*, *82*(3), 265–270. http://doi.org/10.1016/j.beproc.2009.07.005

Guillette, L. M., Reddon, A. R., Hoeschele, M., & Sturdy, C. B. (2010). Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proceedings. Biological Sciences / The Royal Society*, *278*(1706), 767–773. http://doi.org/10.1098/rspb.2010.1669

Guillette, L. M., Hahn, A. H., Hoeschele M, Przyslupski, A., & Sturdy, C. B. (2014). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition*, *18*(1), 165–178. http://doi.org/10.1007/s10071-014-0787-3

Hampton, R. R., Sherry, D. F., Shettleworth, S. J., Khurgel, M., & Ivy, G. (1995). Hippocampal volume and food-storing behavior are related in parids. *Brain, Behaviour and Evolution*, *45*(1), 54–61. http://doi.org/10.1159/000113385

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616. http://doi.org/10.7717/peerj.616

Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P., & Kelley, L. A. (2009). Explanations for variation in cognitive ability: Behavioural ecology meets comparative cognition. *Behavioural Processes*, *80*(3), 288–294. http://doi.org/10.1016/j.beproc.2008.10.002

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*(1), 20–29. http://doi.org/10.1111/j.1365-294X.2007.03428.x

Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L., & Arnold, K. E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour*, *79*(4), 835–843. http://doi.org/10.1016/j.anbehav.2009.12.026

Hoshooley, J. S. (2007). Neurobiology of spatial behaviour. In K. A. Otter (Ed.), *Ecology and Behavior of Chickadees and Titmice: An Integrated Approach*. Oxford: Oxford University Press. http://doi.org/10.1093/acprof

Huang, P., Kerman, K., Sieving, K. E., & St, C. M. (2016). Evaluating the novel-environment test for measurement of exploration by bird species. *Journal of Ethology*, *34*(1), 45–51. http://doi.org/10.1007/s10164-015-0444-6

Jones, T. B., Aplin, L. M., Devost, I., & Morand-Ferron, J. (2017). Individual and ecological determinants of social information transmission in the wild. *Animal Behaviour*, *129*, 93–101. http://doi.org/10.1016/j.anbehav.2017.05.011

Kaiser, H. F. (1960). The application of electronic computers to factor analysis. *Educational and Psychological Measurment, 20*, 141–151.

Kozlovsky, D., Branch, C., Freas, C. A., & Pravosudov, V. V. (2014). Elevation-related differences in novel environment exploration and social dominance in food-caching mountain chickadees. *Behavioral Ecology and Sociobiology*, *68*(11), 1871–1881. http://doi.org/10.1007/s00265-014-1796-6

Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H., & Vaccarino, a L. (1989). Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences of the United States of America*, *86*(4), 1388–1392. http://doi.org/10.1073/pnas.86.4.1388

Krebs, J. R. (1990). Food-storing birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions: Biological Sciences*, *329*(1253), 153–160.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). lmerTest: Tests in linear mixed effects models. R Foundation for Statistical Computing. Retrieved from https://cran.r-project.org/ %09package1⁄4lmerTest.

Lepczyk, C. A., Mertig, A. G., & Liu, J. (2004). Assessing Landowner Activities Related to Birds Across Rural-to-Urban Landscapes. *Environmental Management*, *33*(1), 110–125. http://doi.org/10.1007/s00267-003-0036-z

Liker, A., Papp, Z., Bókony, V., & Lendvai, Á. Z. (2008). Lean birds in the city: Body size and condition of house sparrows along the urbanization gradient. *Journal of Animal Ecology*, *77*(4), 789–795. http://doi.org/10.1111/j.1365-2656.2008.01402.x

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. http://doi.org/10.1111/brv.12012

Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, Tamias striatus. *Animal Behaviour*, *75*(1), 309–318. http://doi.org/10.1016/j.anbehav.2007.05.026

Marzluff, J. M. J., Bowman, R., & Donnelly, R. (2001). A historical perspective on urban bird research: trends, terms, and approaches. *Avian Ecology and Conservation in an Urbanizing World*, 1–17. Retrieved from http://www.oglethorpe.edu/faculty/~r_donnelly/urban.pdf

Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, *121*(7), 1009–1020. http://doi.org/10.1111/j.1600-0706.2012.20339.x

McDonnell, M. J., & Hahs, A. K. (2015). Adaptation and Adaptedness of Organisms to Urban Environments. *Annual Review of Ecology, Evolution, and Systematics*, *46*(1), 261–280. http://doi.org/10.1146/annurev-ecolsys-112414-054258

Mcnamara, J. M., Houston, A. I., & Krebs, J. R. (1990). Why hoard? The economics of food storing in tits, Parus spp. *Behavioral Ecology*, *1*(1), 12–23. http://doi.org/10.1093/beheco/1.1.12

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: A result of microevolution or phenotypic plasticity? *Global Change Biology*, *19*(9), 2634–2644. http://doi.org/10.1111/gcb.12258

Miranda, A. C. (2017). Mechanisms of behavioural change in urban animals: The role of microevolution and phenotypic plasticity. In E. Murgui & M. Hedblom (Eds.), *Ecology and Conservation of Birds in Urban Environments* (pp. 113–132). Springer. http://doi.org/10.1007/978-3-319-43314-1

Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology*, *21*(2), 365–371. http://doi.org/10.1093/beheco/arp199

Montiglio, P. O., Garant, D., Thomas, D., & Réale, D. (2010). Individual variation in temporal activity patterns in open-field tests. *Animal Behaviour*, *80*(5), 905–912. http://doi.org/10.1016/j.anbehav.2010.08.014

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews*, *91*(2), 367–389. http://doi.org/10.1111/brv.12174

Moule, H., Michelangeli, M., Thompson, M. B., & Chapple, D. G. (2016). The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity-exploratory behavioural syndrome. *Journal of Zoology*, *298*(2), 103–111. http://doi.org/10.1111/jzo.12288

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, *85*(4), 935–956. http://doi.org/10.1111/j.1469-185X.2010.00141.x

NASA Landsat Program. (2016a). Landsat ETM+ scene LC80150292016072LGN00, L1T, USGS, Sioux Falls, 12/03/2016.

NASA Landsat Program. (2016b). Landsat ETM+ scene LC80160292016079LGN00, L1T, USGS, Sioux Falls, 19/03/2016.

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, *20*(3), 831–844. http://doi.org/10.1111/j.1420-9101.2007.01300.x

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*(2), 118–122. http://doi.org/10.1111/j.2041-210X.2010.00021.x

Odum, E. P. (1942). Annual cycle of the black-capped chickadee: 3. *The Auk*, *59*(4), 499–531.

Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: what does it really tell us about animal personality? *Animal Behaviour*, *123*, 69–79. http://doi.org/10.1016/j.anbehav.2016.10.006

Pinheiro, J. C., & Bates, D. M. (2000). Mixed-effects models in S and S-PLUS. New York, NY: Springer-Verlag

Poucet, B., Durup, M., & Thinus-Blanc, C. (1988). Short-term and long-term habituation of exploration in rats, hamsters and gerbils. *Behavioural Processes*, *16*, 203–211.

Pravosudov, V. V, & Clayton, N. S. (2001). Effects of demanding foraging conditions on cache retrival accuracy in food-caching mountain chickadees (Poecile gambeli). *Proceedings of the Royal Society B: Biological Sciences*, *268*(1465), 363–368. http://doi.org/10.1098/rspb.2000.1401

Pravosudov, V. V, & Clayton, N. S. (2002). A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience*, *116*(4), 515–522. http://doi.org/10.1037/0735-7044.116.4.515

Pravosudov, V. V., Kitaysky, A. S., Wingfield, J. C., & Clayton, N. S. (2004). No latitudinal differences in adrenocortical stress response in wintering black-capped chickadees (*Poecile atricapilla*). *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *137*(1), 95–103. http://doi.org/10.1016/S1095-6433(03)00264-2

Pravosudov, V. V, & Roth, T. C. (2013). Cognitive Ecology of Food Hoarding: The Evolution of Spatial Memory and the Hippocampus. *The Annual Review of Ecology, Evolution, and Systematics*, *44*, 173–193. http://doi.org/10.1146/annurev-ecolsys-110512-135904

Pyle, P. (1997). *Identification of North American birds. Part I: Columbidae to Ploceidae.* Bolinas, CA: Slate Creek Press.

Quantum GIS Development Team. (2017). QGIS Geographic Information System (Version 2.18.0). Open Source Geospatial Foundation. http://qgis/osgeo.org

Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A., & Sheldon, B. C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology*, *78*(6), 1203–1215. http://doi.org/10.1111/j.1365-2656.2009.01585.x

Quinn, J. L., Cole, E. F., Patrick, S. C., & Sheldon, B. C. (2011). Scale and state dependence of the relationship between personality and dispersal in a great tit population. *Journal of Animal Ecology*, *80*(5), 918–928. http://doi.org/10.1111/j.1365-2656.2011.01835.x

R Development Core Team. (2017). R: A language and environment for statistical computing (Version 3.3.2). Vienna, Austria: R Foundation for Statistical Computing http://www.r-project.org.

Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., Coppola, G., Geyer, M. A., Glanzman, D. L., Marsland, S., McSweeney, F. K., Wilson, D. A., Wu, C., Thompson, R. F. (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, *92*(2), 135–138. http://doi.org/10.1016/j.nlm.2008.09.012

Réale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 3937–3946. http://doi.org/10.1098/rstb.2010.0222

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. http://doi.org/10.1111/j.1469-185X.2007.00010.x

Rejt, Ł., Turlejski, K., Bronche, K., & Topczewski, A. M. (2000). Can Food Caching Increase Frequency of Chicks' Feeding in Urban Kestrels *Falco tinnunculuc*? *Acta Ornithologica*, *35*(2), 217–221.

Rodriguez-Prieto, I., Martin, J., & Fernandez-Juricic, E. (2011). Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1703), 266–273. http://doi.org/10.1098/rspb.2010.1194

Roth, T. C., LaDage, L. D., Freas, C. a., & Pravosudov, V. V. (2012). Variation in memory and the hippocampus across populations from different climates: a common garden approach. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1727), 402–410. http://doi.org/10.1098/rspb.2011.1020

Russell, P. A. (1973). Relationships between exploratory behaviour and fear: A review. *British Journal of Pyschology*, *64*(3), 417–433.

Sanford, K., & Clayton, N. S. (2008). Motivation and memory in zebra finch (*Taeniopygia guttata*) foraging behavior. *Animal Cognition*, *11*(2), 189–198. http://doi.org/10.1007/s10071-007-0106-3

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., & Hickling, G. J. (2005). Restitution of Mass – Size Residuals : Validating Body Condition Indices. *Ecology*, *86*(1), 155–163. http://doi.org/doi:10.1890/04-0232

Schuster, A. C., Zimmermann, U., Hauer, C., & Foerster, K. (2017). A behavioural syndrome, but less evidence for a relationship with cognitive traits in a spatial orientation context. *Frontiers in Zoology*, *14*(1), 19. http://doi.org/10.1186/s12983-017-0204-2

Shaw, R. C., Boogert, N. J., Clayton, N. S., & Burns, K. C. (2015). Wild psychometrics: Evidence for "general" cognitive performance in wild New Zealand robins, *Petroica longipes*. *Animal Behaviour*, *109*, 101–111. http://doi.org/10.1016/j.anbehav.2015.08.001

Sherry, D. (1984). Food storage by black-capped chickadees: Memory for the location and contents of caches. *Animal Behaviour*, *32*(2), 451–464. http://doi.org/10.1016/S0003-3472(84)80281-X

Sherry, D. F. (1985). Food Storage by Birds and Mammals. In J. S. Rosenblatt (Ed.), *Advances in the Study of Behavior* (Vol. 15, pp. 153–188). Orlando: Academic Press Incorporated. http://doi.org/10.1016/S0065-3454(08)60489-1

Sherry, D. F., & Vaccarino, A. L. (1989). Hippocampus and memory for food caches in black-capped chickadees. *Behavioral Neuroscience*, *103*(2), 308–318. http://doi.org/10.1037/0735-7044.103.2.308

Shettleworth, S. J. (1998). *Cognition, Evolution, and Behavior*. Oxford, UK: Oxford University Press.

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology*, *79*(3), 241–277.

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*(2), 367–387. http://doi.org/10.1111/j.1752-4571.2010.00166.x

Sih, a., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2762–2772. http://doi.org/10.1098/rstb.2012.0216

Smith, S. M. (1991). *The black-capped chickadee: Behavioral ecology and natural history.* Ithaca, NY: Cornell University Press.

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or Avoiding Novel Food Resources? The Novelty Conflict in an Invasive Bird. *PLoS ONE*, *6*(5), e19535. http://doi.org/10.1371/journal.pone.0019535

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*(5), 1101–1112. http://doi.org/10.1016/j.anbehav.2013.01.023

Thompson, D. C., & Thompson, P. S. (1980). Food habits and caching behavior of urban grey squirrels. *Canadian Journal of Zoology*, *58*(5), 701–710. http://doi.org/10.1139/z80-101

Tillé, Y., Newman, J. a., & Healy, S. D. (1996). New tests for departures from random behavior in spatial memory experiments. *Animal Learning & Behavior*, *24*(3), 327–340. http://doi.org/10.3758/BF03198981

Tryjanowski, P., Skórka, P., Sparks, T. H., Biaduń, W., Brauze, T., Hetmański, T., Martyka, R., Indykiewicz, P., Myczk,o K., Kunysz, P., Kawa, P., Czyz, S., Czechowski, P., Polakowski, M., Zduniak, P., Jerzak, L., Janiszewski, T., Golawski, A., Dudus, L., Nowakowski, J. J., Wucyzynski, A., Wysocki, D. (2015). Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environmental Science and Pollution Research*, *22*, 15097. http://doi.org/10.1007/s11356-015-4723-0

van der Merwe, M., Burke, A. M., & Brown, J. S. (2007). Foraging ecology of North American tree squirrels on cacheable and less cacheable foods: A comparison of two urban habitats. *Evolutionary Ecology Research*, *9*(4), 705–716.

van Overveld, T., & Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, *6*(2), 187–90. http://doi.org/10.1098/rsbl.2009.0764

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., & Van Tienderen, P. H. (1995). Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology & Evolution*, *10*(5), 212–217. http://doi.org/10.1016/S0169-5347(00)89061-8

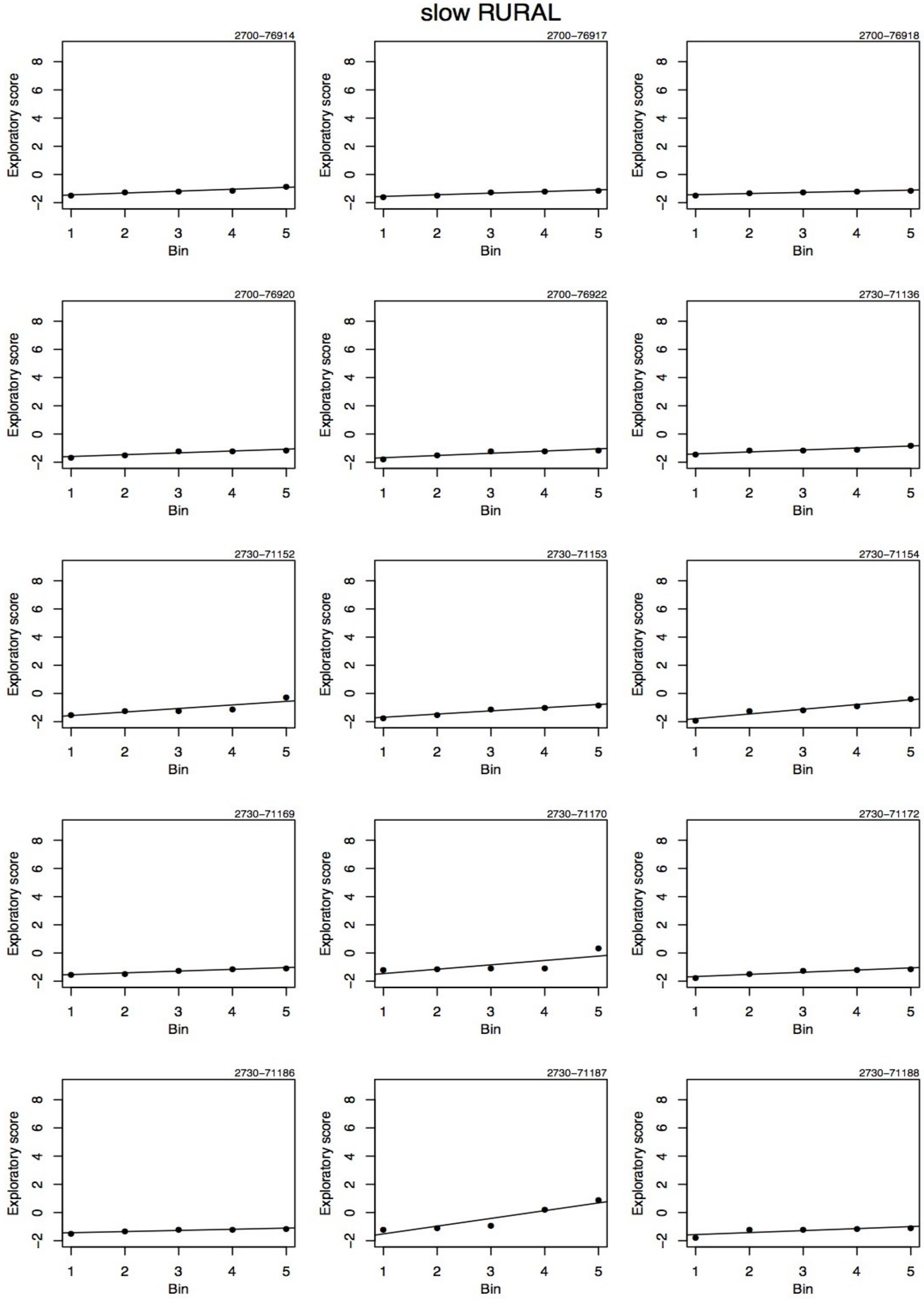
Verbeek, M. E. M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behavior of male great tits. *Animal Behaviour*, *48*(5), 1113–1121.

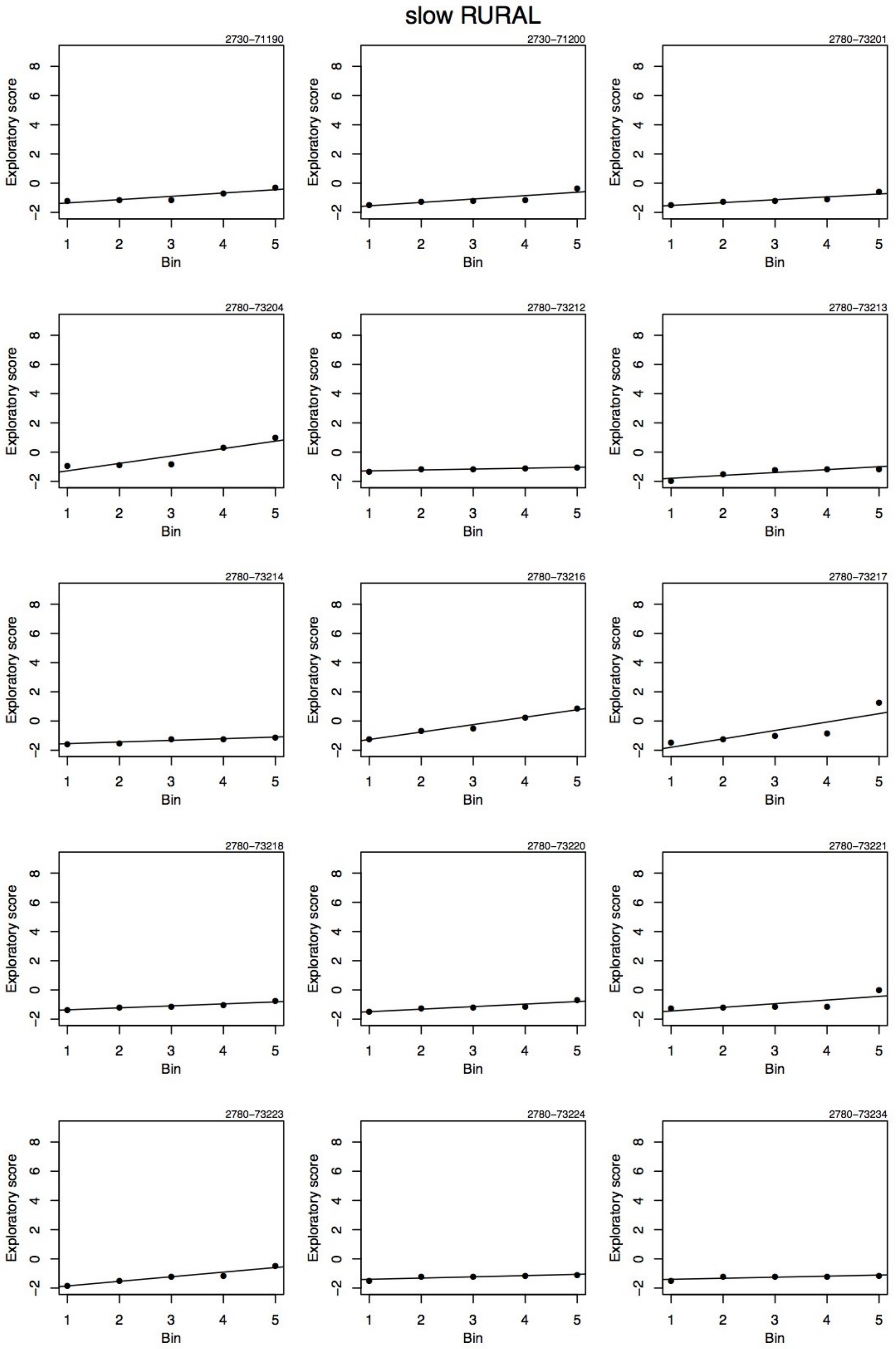
Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V., & Liker, A. (2016). Habituation to human disturbance is faster in urban than rural house sparrows. *Behavioral Ecology*, *27*(5), 1304–1313. http://doi.org/10.1093/beheco/arw047

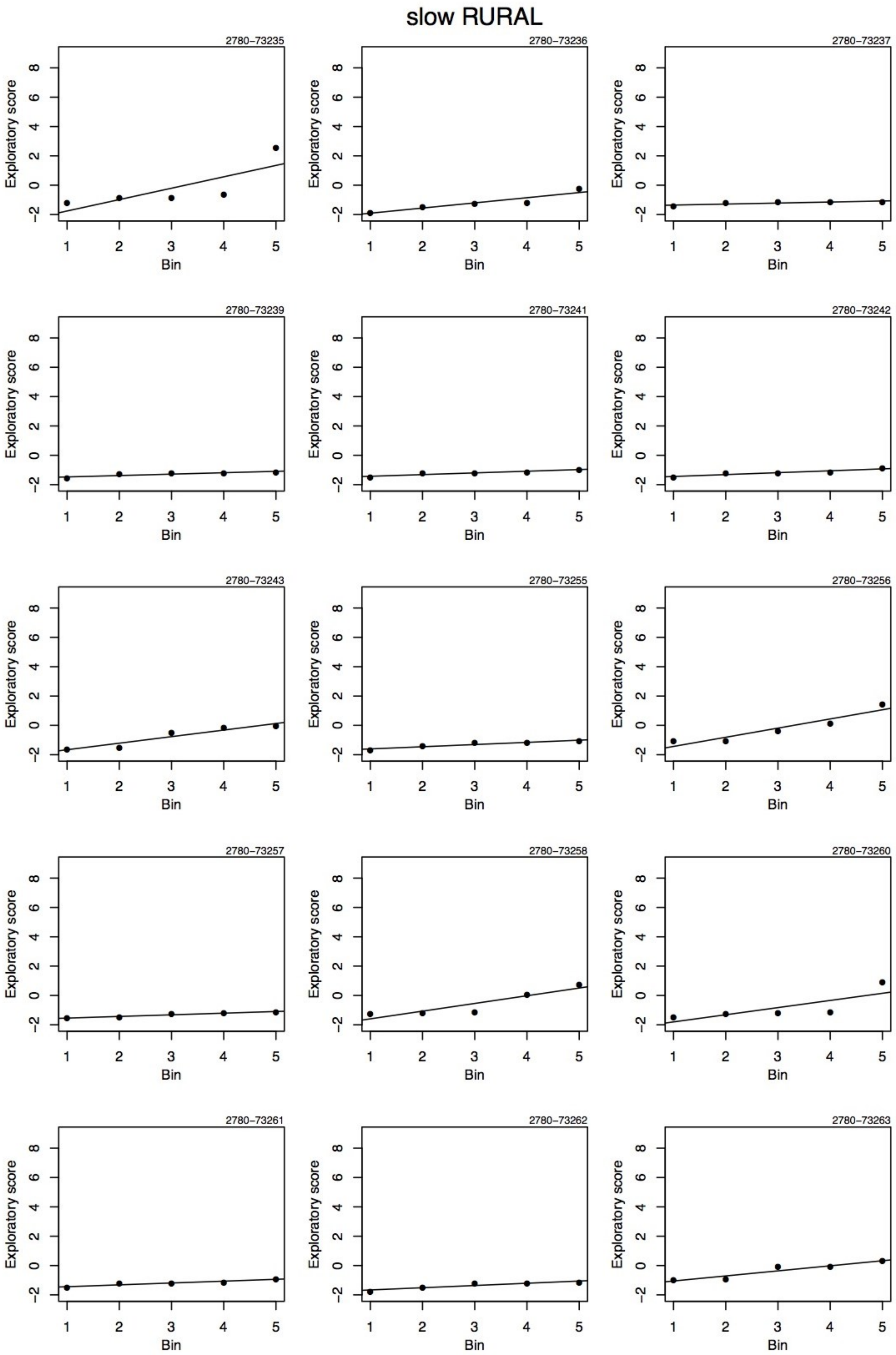
Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution*, *27*(8), 452–461. http://doi.org/10.1016/j.tree.2012.05.001

Appendix

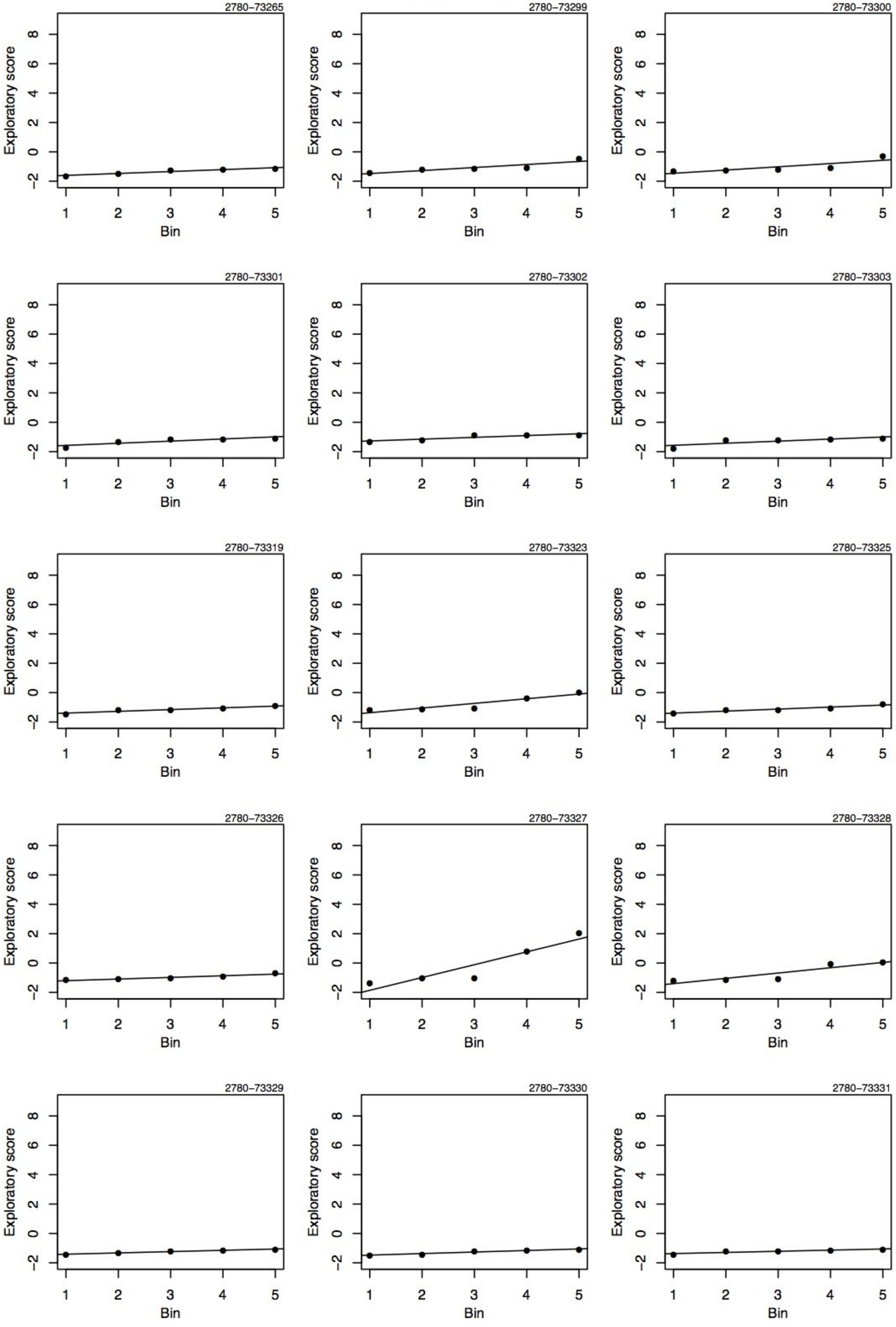
The linear relationship between exploration scores over time bins during the novel environment assay for each individual (individual identifications on top right of plots). Individuals have been sorted by exploration score category (slow < 0, fast > 0) and habitat category (URBAN vs. RURAL).

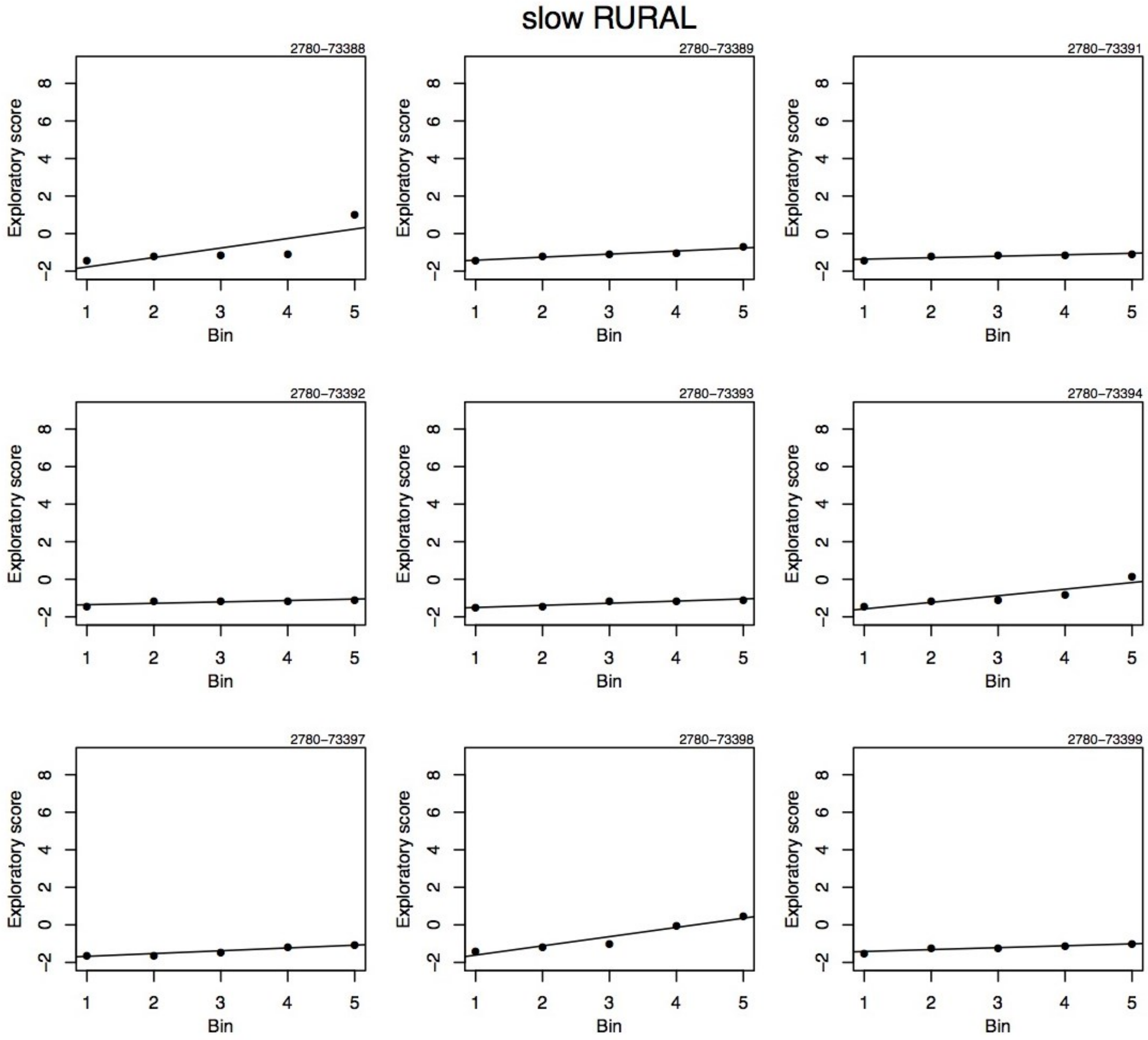



slow RURAL
2730–71190
2730–71200
2780–73201
2780–73204
2780–73212
2780–73213
2780–73214
2780–73216
2780–73217
2780–73218
2780–73220
2780–73221
2780–73223
2780–73224
2780–73234
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

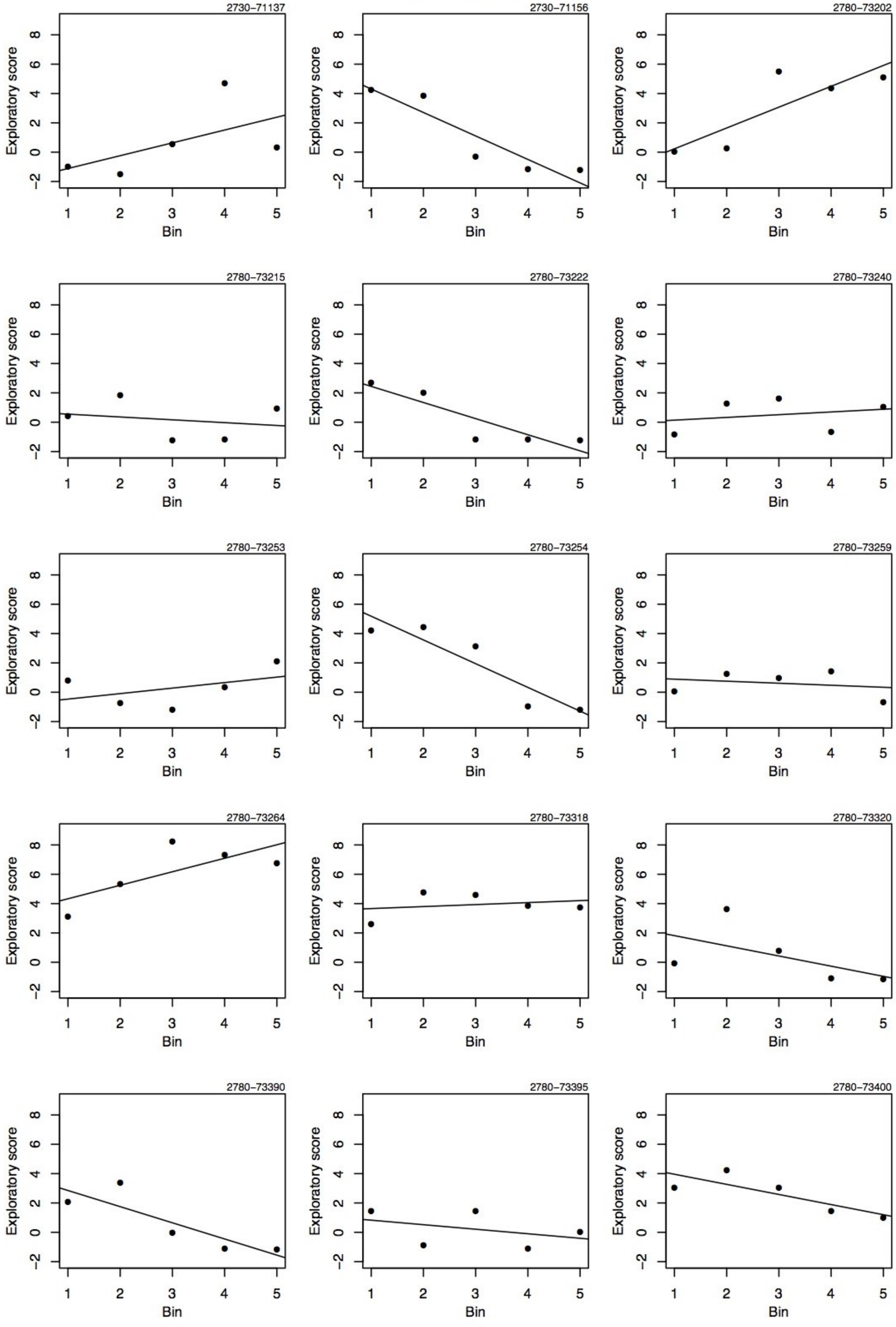

slow RURAL
2780−73235
2780−73236
2780−73237
2780−73239
2780−73241
2780−73242
2780−73243
2780−73255
2780−73256
2780−73257
2780−73258
2780−73260
2780−73261
2780−73262
2780−73263
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

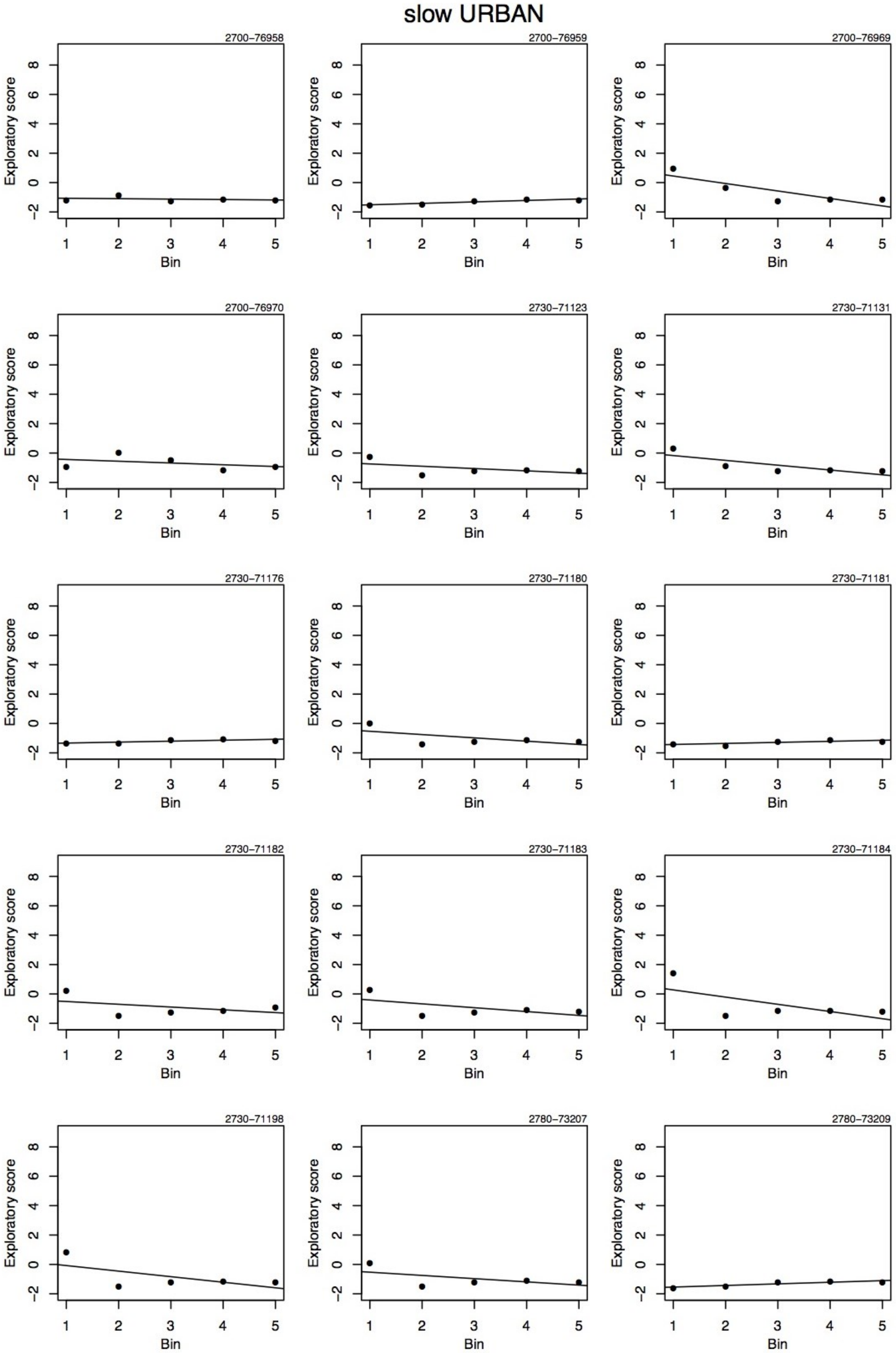
slow RURAL

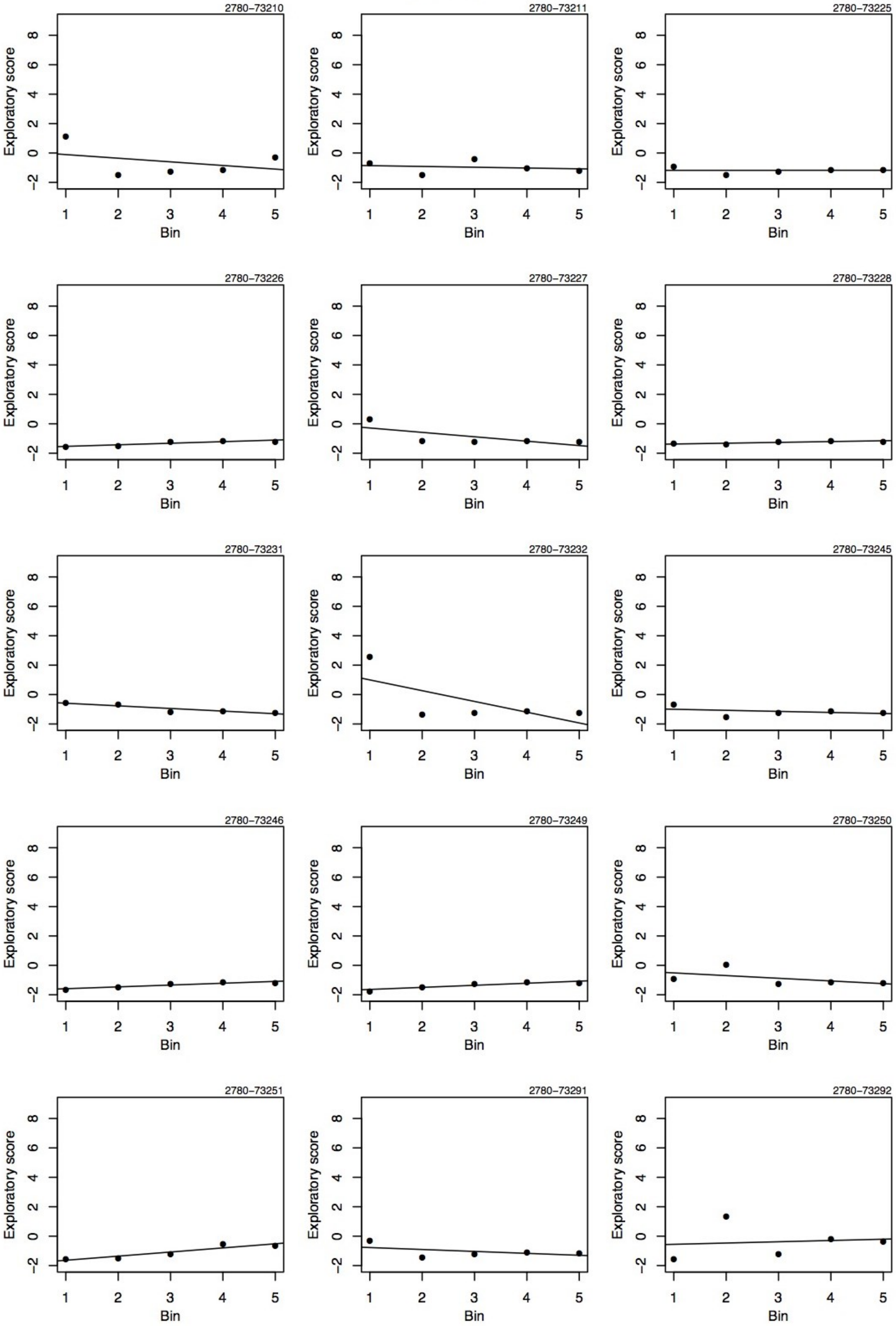

2780−73265
2780−73299
2780−73300
2780−73301
2780−73302
2780−73303
2780−73319
2780−73323
2780−73325
2780−73326
2780−73327
2780−73328
2780−73329
2780−73330
2780−73331
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5


slow RURAL
2780−73388
2780−73389
2780−73391
2780−73392
2780−73393
2780−73394
2780−73397
2780−73398
2780−73399
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

fast RURAL

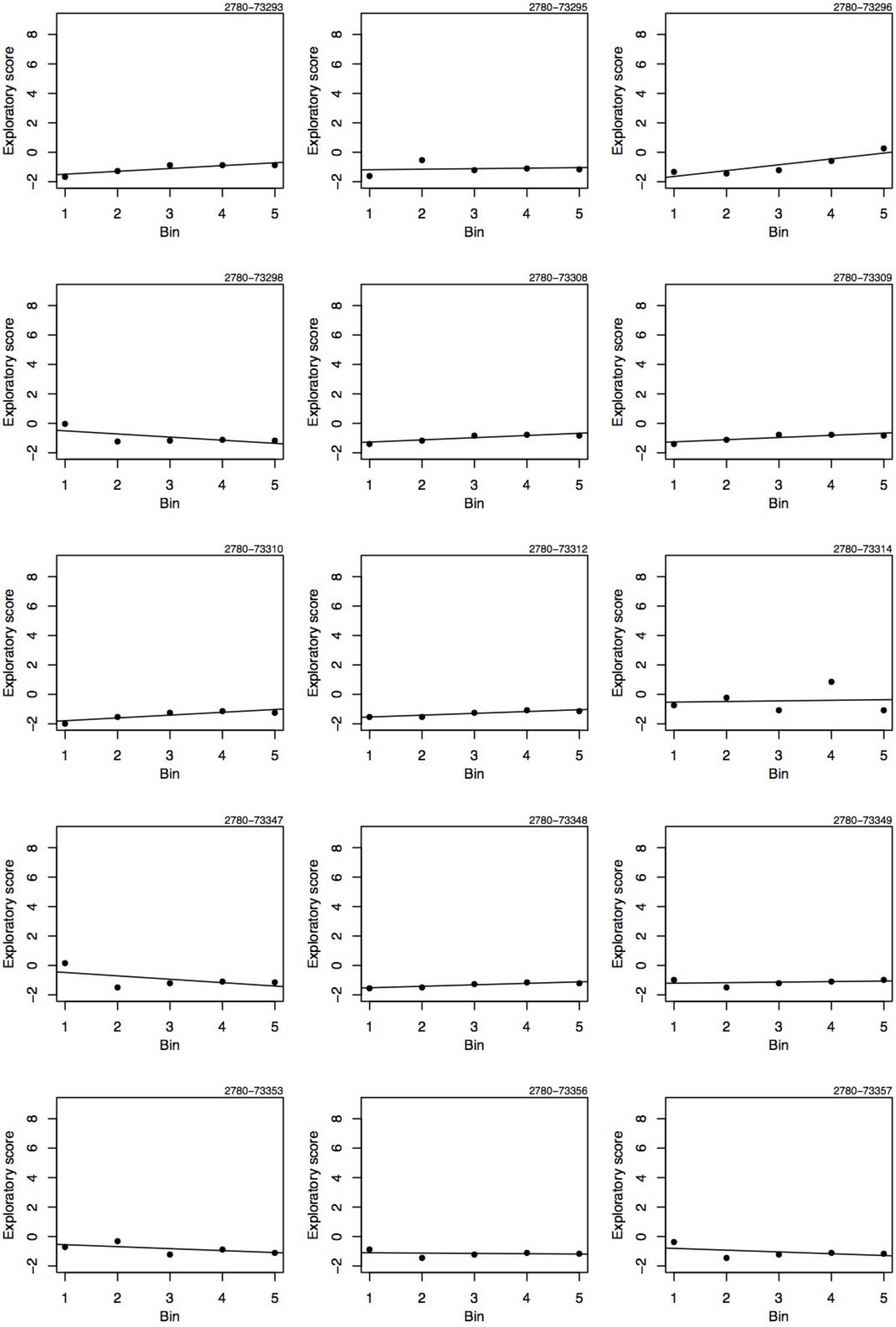

2730−71137
2730−71156
2780−73202
2780−73215
2780−73222
2780−73240
2780−73253
2780−73254
2780−73259
2780−73264
2780−73318
2780−73320
2780−73390
2780−73395
2780−73400
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5


slow URBAN
2700−76958
2700−76959
2700−76969
2700−76970
2730−71123
2730−71131
2730−71176
2730−71180
2730−71181
2730−71182
2730−71183
2730−71184
2730−71198
2780−73207
2780−73209
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

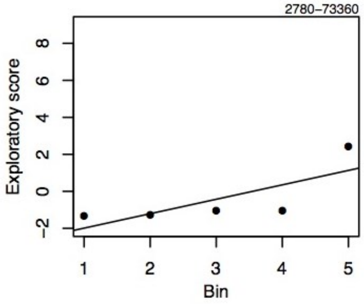

slow URBAN

2780−73210
2780−73211
2780−73225
2780−73226
2780−73227
2780−73228
2780−73231
2780−73232
2780−73245
2780−73246
2780−73249
2780−73250
2780−73251
2780−73291
2780−73292
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

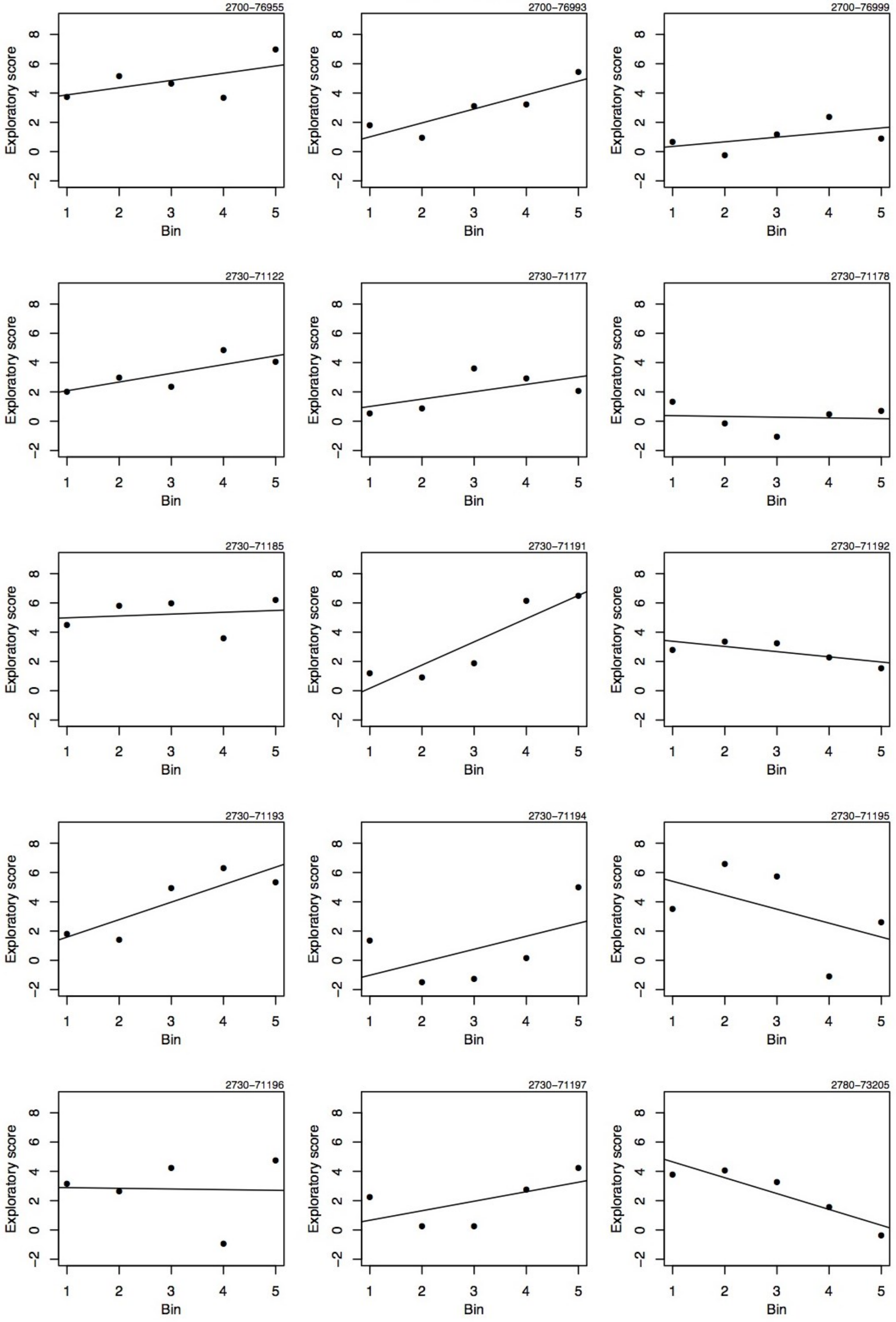
slow URBAN


2780−73293
2780−73295
2780−73296
2780−73298
2780−73308
2780−73309
2780−73310
2780−73312
2780−73314
2780−73347
2780−73348
2780−73349
2780−73353
2780−73356
2780−73357
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

slow URBAN

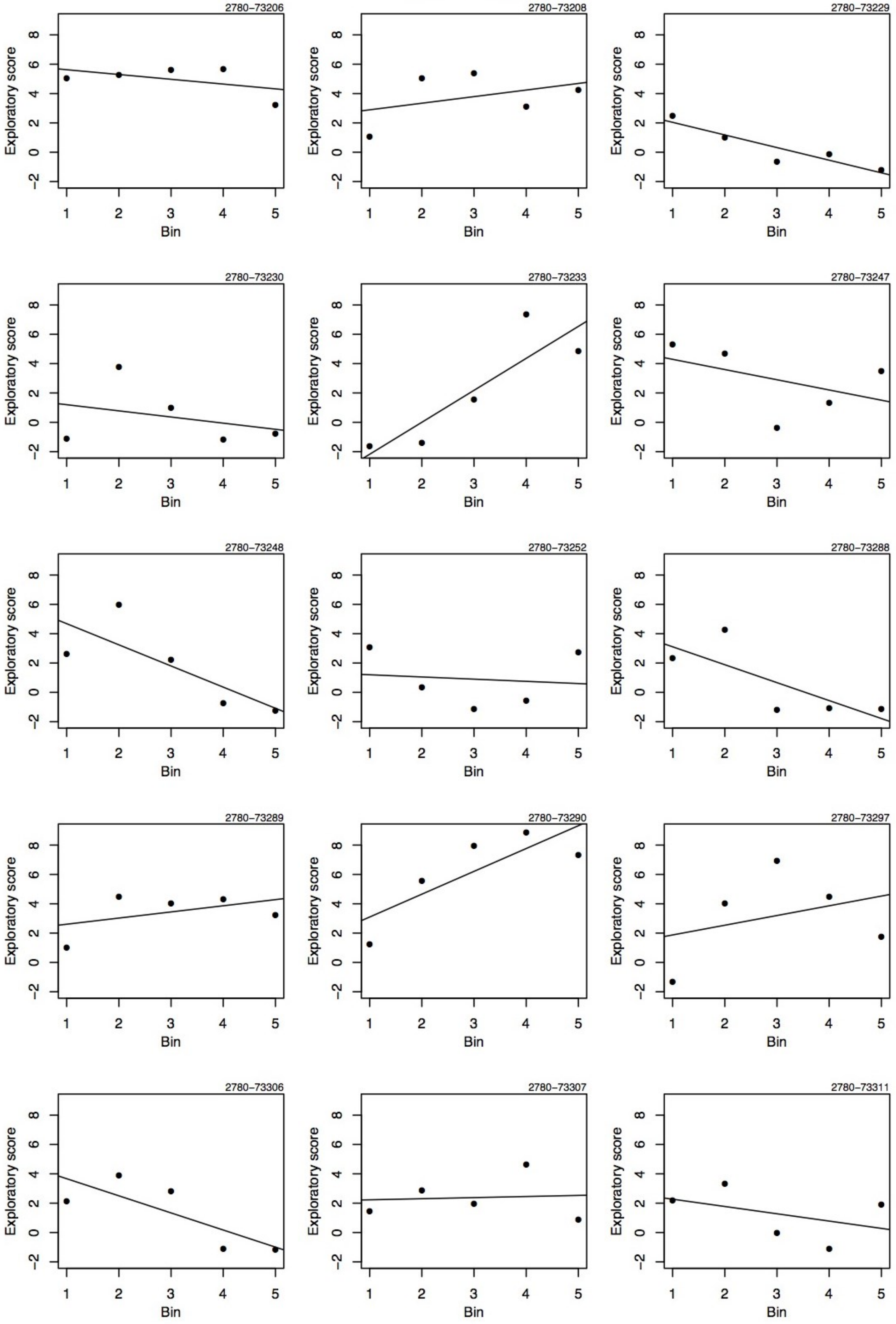


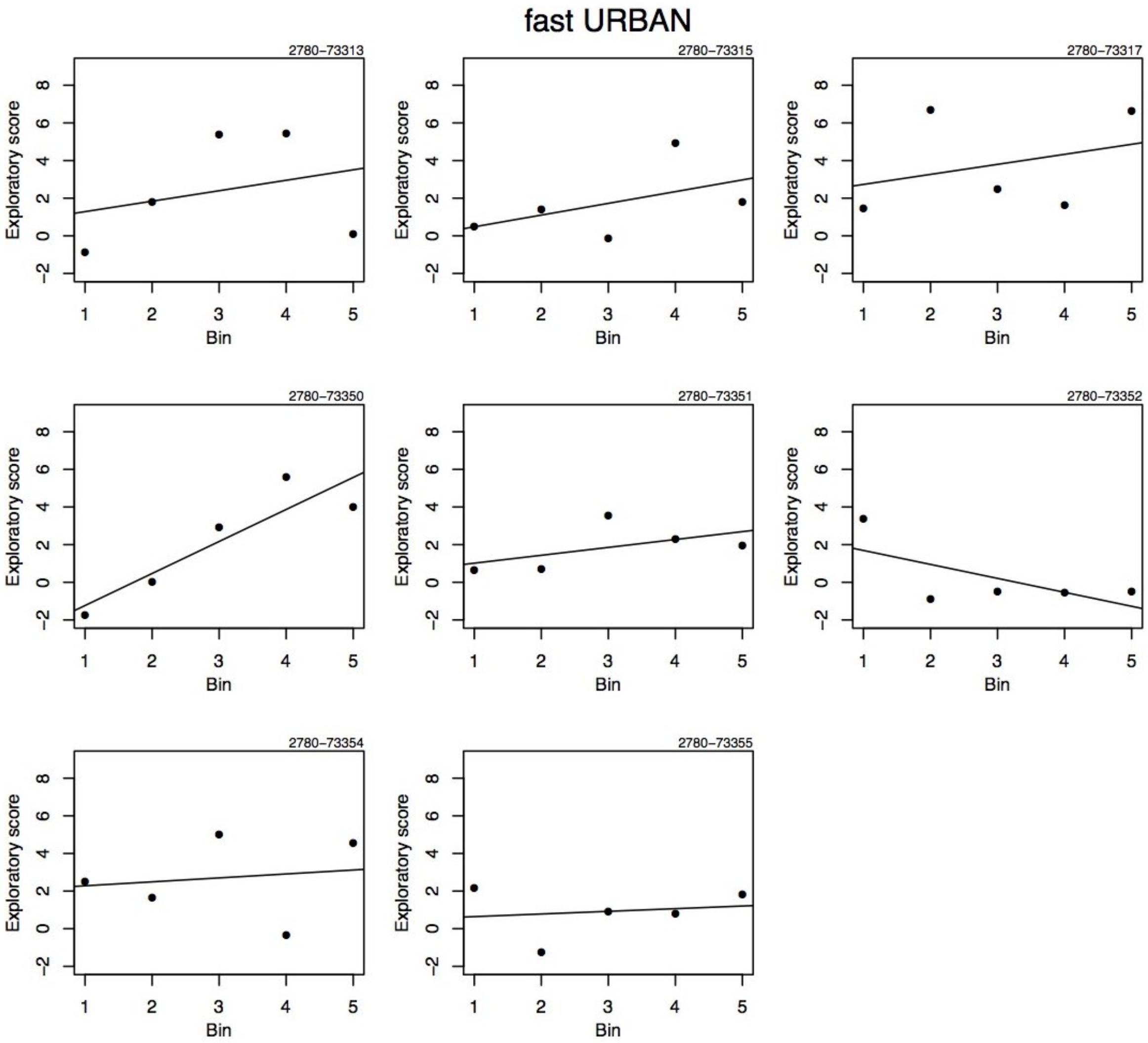
fast URBAN



2700−76955
2700−76993
2700−76999
2730−71122
2730−71177
2730−71178
2730−71185
2730−71191
2730−71192
2730−71193
2730−71194
2730−71195
2730−71196
2730−71197
2780−73205
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5

fast URBAN


2780−73206
2780−73208
2780−73229
2780−73230
2780−73233
2780−73247
2780−73248
2780−73252
2780−73288
2780−73289
2780−73290
2780−73297
2780−73306
2780−73307
2780−73311
Exploratory score
−2
0
2
4
6
8
Bin
1
2
3
4
5


fast URBAN
2780−73313
2780−73315
2780−73317
2780−73350
2780−73351
2780−73352
2780−73354
2780−73355
Exploratory score
Bin
−2
0
2
4
6
8
1
2
3
4
5