Examining the predictors of technical and consumer innovation in black-capped chickadees (*Poecile atricapillus*)

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

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Abstract

Behavioural innovation, the use of new behaviours or modification of existing ones in novel contexts, has been suggested to aid animals in meeting the demands of new or changing environments. Many researchers have studied intra-specific variation in the propensity for technical innovation (i.e. use of new or modified motor actions) using problem-solving tasks, but have found mixed results concerning the influence of individual and ecological variables. Relatively few researchers have investigated the predictors of consumer innovation (i.e. consumption of novel food). The aim of the work presented within this thesis is to ascertain which characteristics explain intra-specific variation in the propensity for technical and consumer innovation in black-capped chickadees. In chapter 2 I analyze dominance rank, exploratory tendency, and habitat urbanization as predictors of problem-solving performance and persistence. I found, for one of the tasks presented to the birds, that dominants outperform subordinates, particularly among rural individuals. This goes against predictions from the necessity drives innovation hypothesis, but may be explained by differences in experience, as adults were found to outperform juveniles in a follow-up analysis. There was also evidence for a positive relationship between exploratory tendency and lever-pulling performance. The lack of consistency in performance across tasks likely arose from differences in task characteristics. In chapter 3 I analyze the predictors of food neophobia and willingness to consume novel food using the same variables as before, as well as baseline levels of corticosterone. I found that birds responded differently to each novel food type and individuals became less neophobic and more willing to consume novel food items as the study progressed through autumn. Additionally, I found a negative relationship between baseline corticosterone levels and food neophobia, and a positive relationship between corticosterone levels and the propensity for consumer innovation. This finding is in line with the knowledge of higher baseline corticosterone driving foraging behaviour. Overall this work provides further insights into the characteristics that may drive innovation and allow animals to meet novel challenges or take advantage of novel opportunities in their environment.

Résumé

L'innovation comportementale, l'utilisation de nouveaux comportements ou la modification de comportements existants dans des contextes différents, peut aider les animaux à répondre aux environnements nouveaux ou changeants. De nombreux chercheurs ont étudié la variation intra-spécifique dans la propension à l'innovation technique (utilisation d'actions motrices nouvelles ou modifiées) en utilisant des tâches de résolution de problèmes, mais ont obtenu des résultats mitigés concernant l'influence des variables individuelles et écologiques. Relativement peu de chercheurs ont étudié les déterminants de l'innovation alimentaire (consommation d'aliments nouveaux). Le but des travaux présentés dans cette thèse est de déterminer quelles caractéristiques expliquent la variation intra-spécifique dans la propension à l'innovation technique et alimentaire chez les mésanges à tête noire. Au chapitre 2, j'analyse le rang de dominance, la tendance à l'exploration et l'urbanisation de l'habitat en tant que prédicteurs de la performance et de la persistance dans la résolution de problèmes. J'ai trouvé, pour l'une des tâches présentées aux oiseaux, que la performance des dominants surpasse celle les subordonnés, en particulier chez les individus ruraux. Cela va à l'encontre des prédictions de l'hypothèse de la nécessité, mais peut être expliquée par les résultats d'une analyse complémentaire indiquant que les adultes étaient plus performants que les jeunes, ce qui suggère un rôle de l'expérience dans la résolution de problèmes nouveaux. Cette analyse a également révélé une relation positive entre la tendance à l'exploration et la performance dans la tâche de ''lever-pulling''. Le manque de cohérence dans la performances des deux problèmes découlait probablement de différences dans les caractéristiques des tâches. Dans le chapitre 3, j'analyse les prédicteurs de la néophobie alimentaire et la consommation de nouveaux aliments en utilisant les mêmes variables qu'auparavant, en plus des niveaux de base de corticostérone. J'ai constaté que les oiseaux réagissaient différemment à chaque nouveau type d'aliment et que les individus devenaient moins néophobes et plus disposés à consommer de nouveaux aliments au fur et à mesure que la saison d’automne progressait. En outre, j'ai trouvé une relation négative entre les niveaux de base de corticostérone et la néophobie alimentaire, et une relation positive avec la propension à l'innovation alimentaire. Ce résultat est conforme aux connaissances indiquant qu’un taux de corticostérone de base plus élevé favorise la recherche de nourriture. Dans l'ensemble, ce travail fournit des informations supplémentaires sur les caractéristiques susceptibles de promouvoir l'innovation, qui permettent aux animaux de relever de nouveaux défis ou de tirer parti de nouvelles opportunités dans leur environnement.

Acknowledgements

A big thank you to my supervisor, Julie Morand-Ferron, for all of her advice and support over the past two years. I feel that I have had a fantastic start to my career as a researcher because of her commitment. I would also like to thank my committee members Jean-Guy Godin and Kathleen Gilmour for their helpful feedback on this project.

I thank the agencies (NSERC, the Human Frontiers Science Program and the Government of Ontario) that provided funding for this work. This project would also not have been possible without the help of our field assistants Celia Bodnar and Nicolas Bernier, and the numerous undergraduate students and volunteers that helped with running trials and conducting video analysis for both research chapters.

I am grateful to my lab mates, all of whom have contributed to my development as a scientist. Thank you for all of the advice regarding science and statistics, the games, snacks, sass, entertaining rants, adventures, and encouraging me to get out of my comfort zone. Thank you to all of the friends I have made here. I cannot imagine my time in Ottawa without all of you.

Finally, I am thankful for the constant love and support from my family. I could not have made it this far without the encouragement from my sisters, Priya and Shallu, in particular. Thank you so much!

Statement of Contributions

Chapters 2 and 3 of this thesis are adapted from manuscripts submitted to journals for publication (2 - PLoS ONE, 3 – Behavioral Ecology) and content overlaps between them. The pronoun “we” is used within manuscripts to include additional authors, however this thesis was prepared by myself.

Chapter 2: I made the problem-solving tasks, conducted trials, data handling, video and statistical analyses, and interpreted the findings. The quantification of urbanization by remote sensing via satellite imagery and the collection of dominance data was done by postdoctoral fellow Dr. Julian Evans. Megan Thompson conducted novel environment assays and analysis to assign exploration scores to birds. Honours student Kayla Humphreys, UROP student Sharon Yue, and undergraduate volunteers (Jean-Christophe Gosselin, Alec Michael Medd, and Andrea Parvan) assisted in video analysis of problem-solving trials.

Prasher, S., Evans, J.C., Thompson, M.J., and Morand-Ferron, J. Characterizing innovators: ecological and individual predictors of problem-solving performance. Invited for resubmission to PLoS ONE (PONE-D-18-26066; revision requested 12 October 2018).

Chapter 3: I collated data from my lab into a novel set of hypothesis tests, carried out statistical analyses, and interpreted the findings. Honours student Michael El-Nachef designed the novel food trials and conducted video analysis for these trials. The trials were conducted by myself as well as Michael El-Nachef, Megan Thompson, and Kayla Humphreys. Blood samples for corticosterone quantification were taken by Dr. Julie Morand-Ferron and Megan Thompson, and analyzed by Dr. Frances Bonier at Queen's University.

Prasher, S., Thompson, M.J., Evans, J. C., El-Nachef, M., Bonier, F., and Morand-Ferron, J. Innovative consumers: exploring behavioural, ecological, and physiological predictors of responses to novel food. Provisionally accepted by Behavioral Ecology (BEHECO-2018-0454; Provisionally accepted 12 November 2018).

NB: Work 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, and the Canadian Wildlife Service

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Chapter 1

General Introduction

Innovations have allowed humans to expand into and exploit environments around the world and they continue to improve our standard of living today. A wide variety of animals are also known to exhibit behavioural innovations in multiple contexts. These innovations involve the invention of new behaviours or the adjustment of old behaviours to meet new demands (Kummer and Goodall 1985). More recently, animal innovation has been defined as any new learned behaviour that occurs in a population (Reader and Laland 2003). This broad definition encompasses novel behaviours in various contexts including novel gestures or socially manipulative behaviour in primates, bird song variants, consumption of novel food, and new methods of accessing or processing food. Early observations of novel behaviours included milk bottle opening by British tits (Fisher and Hinde 1949) and the washing of food by Japanese macaques (Kawai 1965). Foraging innovations such as these have received the greatest amount of attention from researchers.

The study of innovation initially relied on taxonomic counts of novel behaviours from records published in ornithology and primatology journals. For example, Lefebvre et al. (1997) were the first to use rates of innovation across avian taxa as a measure of behavioural plasticity and examine its relationship with relative size of the forebrain. Reader and Laland (2002) took an analogous approach for primates and similarly found a positive association between innovation rates and executive brain (neocortex and striatum) size. These findings suggest that innovation relates to animal cognition (i.e. the mechanism involved in acquiring, processing and acting on information from the environment, Shettleworth 2001), and/or is more likely to arise in species equipped with relatively larger brains (Sol et al. 2016). Other studies have aimed to understand the ecological benefits of innovation. For example, researchers have found that innovation rates in birds positively correlate with invasion success (Sol and Lefebvre 2000; Sol et al. 2002) and the occupation of seasonally changing environments (Sol et al. 2005). These results support the idea that behavioural plasticity is favourable when confronting environmental variability. Innovation rates across taxa have also been used to investigate the relationship between behavioural plasticity and evolution. Wyles et al. (1983), with their behavioural drive hypothesis, first suggested that behavioural plasticity may promote evolutionary diversification. It was hypothesized that plasticity, in the form of innovative behaviours, exposes individuals to new selection pressures, which would favour the evolution of traits that increase fitness given the new circumstances. The exposure of animal populations to differing selection pressures would thus accelerate their evolutionary divergence. Nicolakakis et al. (2003) found support for this idea in birds, as innovation rates were positively associated with species richness.

As research on the subject has continued, distinctions have been made between technical innovations, which involve the use of novel foraging techniques, and consumer innovations, which are characterized by the consumption of novel foods (Overington et al. 2009). In both birds and primates it has been shown that rates of technical innovation more strongly associate with relative brain size compared to rates of consumer innovation (Overington et al. 2009; Navarrete et al. 2016). When investigating innovation as a potential explanation for the greater success of generalist species in anthropogenically modified environments, Ducatez et al. (2015) found that although dietary generalism positively related to both technical and consumer innovation rates, habitat generalism was only associated with rates of consumer innovation. Sol et al. (2016) also showed that consumer innovation, but not technical innovation, could explain variation in the brood values (a metric used to assess how much a species prioritizes future versus current reproduction) of bird species, with innovative species being more likely to prioritize future reproduction. These results suggest that these two types of innovation are distinct processes, and perhaps consumer innovation is a better reflection of opportunistic behaviour rather than greater cognitive ability (Overington et al. 2009; Ducatez et al. 2015).

Much effort has been put into investigating the traits predicting intra-specific variation in technical innovative ability. Studying the characteristics that associate with individual innovativeness may provide information on how innovations spread through a population (e.g. innovations may be less likely to spread if they are first exhibited by low ranking individuals that may not receive as much attention from conspecifics as higher ranking individuals; Nicol and Pope 1994; Galef and Laland 2005). Furthermore, we may learn about which individual characteristics (e.g. spatial exploration) are favoured in environments where innovations are beneficial, and the potential drivers of innovative behaviour. The propensity for technical innovation, or the efficiency with which individuals are able to innovate, has often been studied using extractive foraging tasks. These tasks require the manipulation of an object to gain access to a food reward. Performance on these types of tasks has been shown to be a valid proxy for innovativeness (Griffin and Guez 2014). Problem-solving performance on tasks for which the reward is gaining access to a nestbox or having a higher quality bower have been shown to be associated with proxies for fitness in great tits (*Parus major*, Cole et al. 2012; Cauchard et al. 2013) and satin bowerbirds (*Ptilonorhynchus violaceus*, Keagy et al. 2009). Some factors thought to contribute to innovation and that have often been studied in this context include novelty responses, asocial learning, social rank, and persistence (reviewed by Griffin and Guez 2014). Urbanization has also been considered as a potential promoter of innovative behaviour, as urbanized habitats are dynamic environments presenting novel resources and challenges to animals.

The predictors of individual variation in consumer innovation have been studied much less than those of technical innovation. Sol et al. (2011; 2012) showed that the variables associated with efficient technical problem solving in common mynas (*Acridotheres tristis*) did not predict latencies to eat novel food in consumer innovation trials. Research on the related topic of dietary wariness, the short-term (food neophobia) and long-term (dietary conservatism) avoidance of novel food (Marples & Kelly 1999), may provide clues about the potential predictors of consumer innovation. For example, some studies have shown that neophobic responses to novel foods can be decreased with continued exposure to palatable novel food items (Marples et al. 2007; Lecuelle et al. 2011; Adamová-Ježová et al. 2016). This suggests that animals living in environments with an abundance of novel food types (e.g. urbanized habitats) may be more likely to approach and consume novel foods compared to individuals that do not have the same experience. Additionally, the presence of a conspecific has been found to decrease the dietary wariness of birds, which may be caused by the perception of the conspecific as a competitor (Mcmahon et al. 2014; McMahon and Marples 2017). Thus, social rank would be expected to influence an individual's propensity for consumer innovation, because subordinates tend to be outcompeted for resources.

Despite potential benefits for individuals exhibiting novel behaviours, there are factors that may restrict the expression of innovation. Predation risk may constrain innovation as animals may be less vigilant of predators when attending to a novel problem (Morand-Ferron and Quinn 2011; van Schaik et al. 2016). Innovators may also lose their new resources to scroungers (Morand-Ferron et al. 2004), or receive aggressive behaviour from conspecifics (e.g. Cole and Quinn 2012). Additionally, social conformity may prevent individuals from exhibiting behaviours that are uncommon in their population (Galef 2003; Brosnan and Hopper 2014). Finally, innovating may bring individuals into contact with toxic substances (Papp et al. 2015; van Schaik et al. 2016), or increase their exposure to disease or parasites (Garamszegi et al. 2007; Vas et al. 2011; Mccabe et al. 2015). These costs and constraints further complicate the potential influences of individual and ecological characteristics on innovation.

The goal of this thesis is to understand the predictors of intra-specific variation in technical and consumer innovation in wild-caught black-capped chickadees. Chapter 2 provides an investigation of the individual and ecological predictors of technical innovation, measured as the latency to solve two distinct, food-motivated problem-solving tasks. The same variables are analyzed as predictors of persistence in a problem-solving context, as this has rarely been assessed in the literature. The predictors studied include dominance rank, spatial exploration, and habitat urbanization. Chapter 3 describes a similar analysis of the predictors of food neophobia (the latency to contact novel food) and consumer innovation (the likelihood of consuming novel food). In addition to the variables assessed in chapter 2, baseline corticosterone is included as a predictor in chapter 3 due to its effects on metabolism and foraging behaviour.

Chapter 2

Characterizing innovators: ecological and individual predictors of problem-solving performance

Abstract

Behavioural innovation, the use of new behaviours or existing ones in novel contexts, has important ecological and evolutionary consequences for animals. An understanding of these consequences would be incomplete without considering the traits that predispose certain individuals to exhibit innovative behaviour. Several individual and ecological variables are hypothesized to affect innovativeness, but empirical studies show mixed results. We examined the effects of dominance rank, exploratory personality, and urbanization on the innovativeness of wild-caught black-capped chickadees using a survival analysis of their performance in two problem-solving tasks. Additionally, we provide one of the first investigations of the predictors of persistence in a problem-solving context. For lever pulling, we found a trend for dominants to outperform subordinates, particularly in rural birds, which did not align with predictions from the necessity drives innovation hypothesis. When examining possible explanations for this trend we found that older chickadees outperformed younger birds. This follow-up analysis also revealed a positive effect of exploratory personality on the lever-pulling performance of chickadees. Our results suggest that experience may foster innovation in certain circumstances, for instance via the application of previously-acquired information or skills to a novel problem. As we found different predictors for both tasks, this suggests that task characteristics influence the innovative propensity of individuals, and that their effects should be investigated experimentally.

Introduction

Animal innovation, defined as the use of novel behaviours to meet challenges or the application of existing behaviours to solve novel problems (Kummer and Goodall 1985), has been shown to play an important role in the ecology and evolution of diverse taxa. For instance, avian species characterized as successful invaders of novel environments tend to have higher innovation rates than unsuccessful species (Sol et al. 2002). Additionally, avian taxa with high innovation rates were found to contain a greater number of species (Nicolakakis et al. 2003), supporting the idea that innovative behaviours accelerate evolution by exposing animals to novel selection pressures (i.e. the behavioural drive hypothesis; (Wyles et al. 1983)). At the intra-specific level, innovative behaviour has been associated with increased reproductive success (Cole et al. 2012; Cauchard et al. 2013; Preiszner et al. 2017; Wetzel 2017). Despite these implications, the question of which characteristics make some individuals more innovative than others remains.

The ‘necessity drives innovation’ hypothesis suggests that individuals will be more likely to exhibit innovative behaviour when resources are scarce (Laland and Reader 1999; Reader and Laland 2003). Animals with a greater necessity for resources are expected to more readily approach and interact with tasks compared to less motivated individuals (Griffin and Guez 2014). Subordinates may have a greater necessity to innovate than dominant individuals and they may do so as an alternative to competing with dominant individuals for familiar resources. This pattern has been found in chimpanzees (*Pan troglodytes*, (Reader and Laland 2001)), meerkats (*Suricata suricata*, (Thornton and Samson 2012)), and great tits (*Parus major*, (Cole and Quinn 2012)). However, dominance rank was found not to influence problem-solving performance in pigeons (*Columba livia*, (Bouchard et al. 2007)) or spotted hyenas (*Crocuta crocuta*, (Benson-Amram and Holekamp 2012)).

Novelty responses may impact an individual's innovative potential by affecting its likelihood of being exposed to novel items or locations, and influencing the chances of gaining enough information to reach a solution (Reader and Laland 2003; Griffin and Guez 2014). These responses include object neophilia (the propensity to approach and interact with novel objects), spatial exploration (the speed and extent of an individual's movement through a novel space), and object neophobia (the tendency to avoid novel objects) (Griffin and Guez 2014). Conflicting results have been reported concerning the influence of novelty responses on individual innovativeness. For instance, more spatially exploratory and less neophobic carib grackles (*Quiscalus lugubris*) were found to outperform less exploratory and more neophobic individuals in an innovation task (Overington et al. 2011). Negative relationships between neophobia and innovativeness have also been shown in pigeons and common mynas (*Acridotheres tristis*;(Bouchard et al. 2007; Sol et al. 2012)). On the other hand, some studies have found no relationship between novelty responses and problem-solving performance, suggesting that these traits can vary independently (Boogert et al. 2008; Cole et al. 2011; Griffin and Diquelou 2015).

Habitat type, in particular the extent of urbanization of the environment, is an additional factor that has been explored in the context of intra-specific variation in problem-solving performance. Urban environments may contain fewer predators and more ecologically-novel resources (Sol et al. 2013). Thus, compared to rural individuals, animals in urban environments would be expected to exhibit less neophobia and a greater inclination to explore, which in turn is expected to increase their innovative performance. A study on common mynas (Sol et al. 2011), and one on mountain chickadees (*Poecile gambeli*, (Kozlovsky et al. 2017)), provide support for this idea. However, a recent study on house sparrows found that urban birds were no more likely to solve multiple problem-solving tasks compared to rural birds, perhaps reflecting aspects of urban environments that may reduce the tendency to innovate, such as new predators or toxins, and an abundance of accessible food (Papp et al. 2015).

We investigated the effects of dominance rank, exploratory tendency, and urbanization on the individual problem-solving performance of wild-caught black-capped chickadees (*Poecile atricapillus*) using two distinct foraging tasks. The black-capped chickadee belongs to Paridae, an avian family showing a high number of innovations in the wild (Overington et al. 2009), and is a widespread North American species occurring in rural and urban habitats (Smith 1991; Foote et al. 2010). In the non-breeding season, members of this species form stable groups with linear dominance hierarchies (Smith 1991; Devost et al. 2016). We predicted that the most efficient problem solvers would be those that are subordinates, faster to explore a novel environment, and originating from more urbanized habitats. Moreover, we provide an examination of individual and ecological determinants of persistence during problem-solving assays. The predictors of persistence are very poorly understood, despite its role in problem solving in various species (e.g. Sol et al. 2012; Thornton and Samson 2012), and its key importance in determining expertise, which itself can impact survival and reproductive success (Dukas 2018). To this end, we examine dominance, exploration, and habitat urbanization as potential predictors of the frequency of contacts made with the tasks.

Methods

Subjects and housing

From October to December 2016, a maximum of 12 birds were captured weekly using mist nets from one of seven sites in and around Ottawa, Ontario (Figure 2.1). The degree of urbanization at each site was assessed using remote sensing data (Congedo 2016; NASA Landsat Program 2016a, 2016b; Quantum GIS Development Team 2017) by quantifying the number of pixels classified as different land cover types (building, tarmac, forest, and bare earth) within a 1 km radius of capture sites. These variables were used in a principal components analysis (PCA) to generate a unique urban score that explained the degree of urbanization at each site (81.82% of variance explained by PC1, Thompson et al. 2018). Urban score was replaced with a binary habitat variable (urban/rural) in our final models to assess the robustness of our conclusions (Table S2.1).

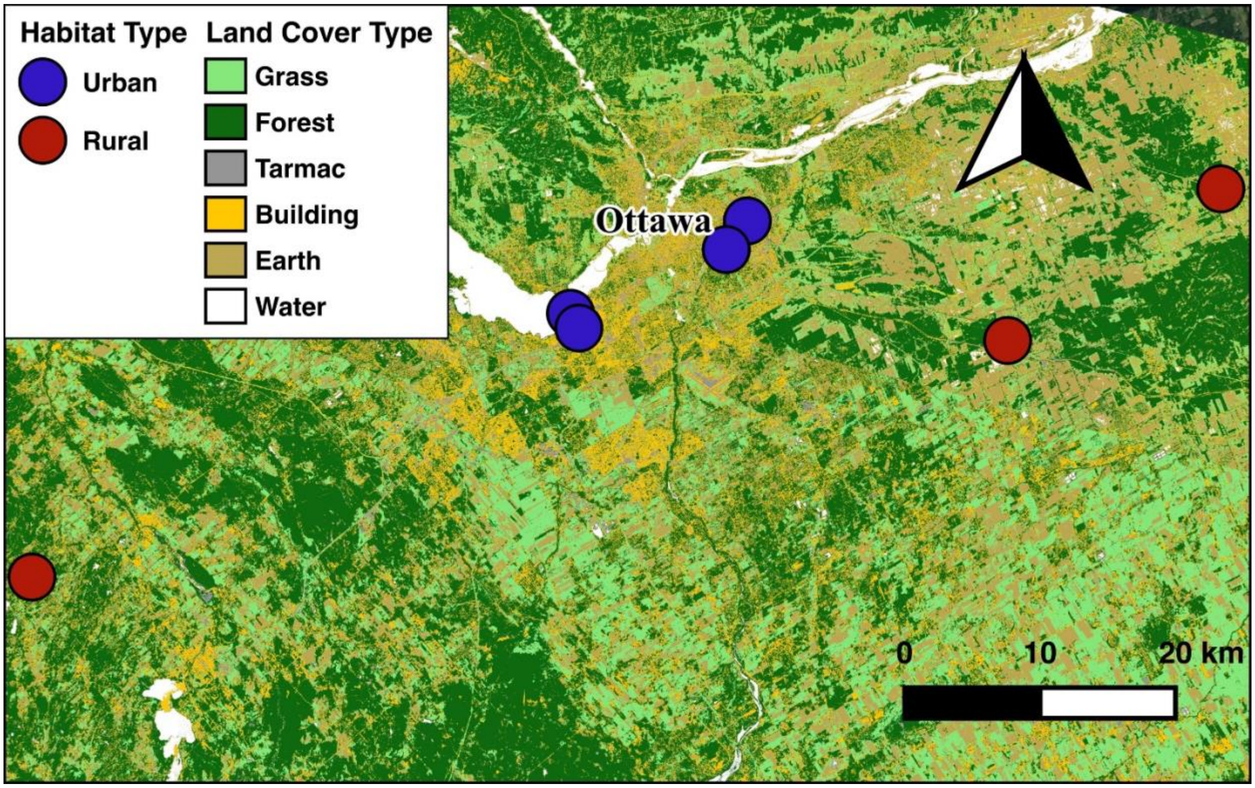

Figure 2.1. Land cover classification map showing the 4 urban (blue) and 3 rural (red) sites located in and around Ottawa, Ontario, Canada.

Upon capture, each individual was fitted with metal and coloured leg bands as well as a unique passive integrated transponder (PIT) tag (weighing less than 0.15 grams, about 1% of a bird's body weight). Birds were categorized as juvenile or adult by inspecting the shape and wear of their tail feathers (Pyle 1997). After capture, birds were transported and housed in individual cages, allowing only auditory contact between individuals, in the animal care facility of the University of Ottawa. Outside of testing periods, birds were given ad libitum access to food (sunflower seeds) and water, and mealworms at the end of each day. On the last day in captivity, before being released back at their site of origin, blood samples were taken from the brachial vein of each subject for molecular sexing (Griffiths et al. 1998; Thompson et al. 2018). Subjects were released at their site of capture after a total of 5 days at the university.

Problem-solving trials

In captivity, each bird underwent two problem-solving trials for each of two extractive foraging tasks that required the use of different motor actions to solve. The lever-pulling task consisted of a small Perspex tube in which two wax worms were held on top of a platform supported by a lever (Figure 2.2A; similar to Cole et al. 2011). To reduce accidental solutions the lever was placed in the task at a slight downward angle. Birds were required to pull the lever completely out of the tube, causing the food reward to fall out. The paper-ripping task consisted of the bottom half of a Petri dish, containing seeds and mealworms, wrapped with white paper towel (Figure2.2B; similar to Bókony et al. 2013). This task was solved when a bird ripped a hole through the paper that was big enough to extract a seed or worm.

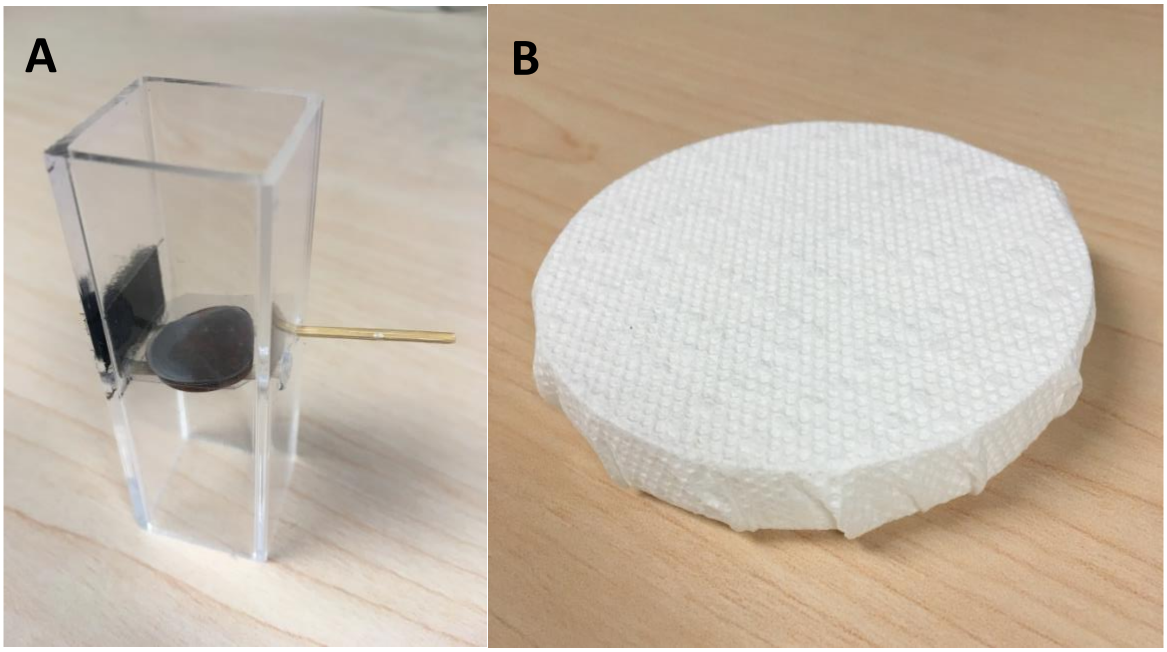

Figure 2.2. Two extractive foraging tasks used to measure problem-solving performance and persistence in chickadees. (A) The lever-pulling task required birds to pull a lever to cause a platform holding a food reward to fall out of the tube. (B) The paper-ripping task required birds to rip through the paper towel wrapping a Petri dish to gain access to the reward inside.

Lever-pulling trials took place on day 1 in captivity from 15:15 to 16:15 and day 2 from 15:00 to 16:00. Birds were not food deprived beforehand and a seed dish remained available during these trials. However, no worms other than those placed in the task were available. Paper-ripping trials occurred on day 3 from 14:15 to 15:15 and day 5 from 7:00 to 8:00. Birds were food deprived for 30 minutes prior to the first paper-ripping trial, and overnight (14 hours) prior to the second. At the start of each trial an experimenter turned off the lights of the housing room, entered with a red headlamp, and fixed a single task in each bird's cage. The trial began after the experimenter exited the room and turned the light back on. All trials were video recorded by a camera set up on shelves across the room from each cage for subsequent data collection.

Each bird's performance and persistence in the problem-solving trials were quantified using data extracted from video recordings. Performance was quantified as the latency to solve the task, measured as the time from the beginning of the trial to the time of solution. For birds that failed to solve the task in their first trial, but succeeded in their second, we added the duration of their first trial to their latency to solve in the second, effectively treating the two trials as a single extended test. Birds that did not solve in the time given were assigned latencies equal to the sum of the two trial durations. Persistence was quantified using the BORIS software (Friard and Gamba 2016) as the number of bill and foot contacts made with the task until it was solved (Intra-observer reliability: all Pearson's r > 0.988, Inter-observer reliability: all Pearson's r > 0.776). As with performance, the total number of contacts made with the task was added over both trials for birds that solved in the second trial or did not solve at all. Only performance and persistence data leading up to an individual's first solution were used for analysis, so as to consider only those instances of problem solving that reflect innovative behaviour.

Exploration in a novel environment

A spatial exploration assay was conducted on the third day in captivity to measure each individual's exploratory tendency in a novel environment. The novel room, containing four artificial trees, was accessible to birds from their home cages through an opaque sliding door. Light manipulation was used to move birds to and from the novel room, which avoided handling by the experimenter (Pravosudov and Clayton 2002). Each bird's number of visits to trees, number of visits to other features in the room, and the duration of their flights and hops were measured over a 10-minute period. A composite exploration score for each individual was generated by including these measures in a principal components analysis (similar to Quinn et al. 2009). Only the first principal component had an eigenvalue greater than one and it explained 67.84% of the variance (Thompson 2017). A similar measure of spatial exploration was found to be moderately repeatable after exposing each bird to a second exploration assay (on day 4) with new artificial trees placed in different positions (N = 70, R = 0.47, CI = 0.41 – 0.51 ; Thompson et al. 2018).

Dominance rank

Each site was equipped with a sunflower seed feeder two to seven weeks after releasing birds from captivity and they remained until the end of April 2017. The feeders were fitted with a single perch that restricted access to one individual at a time. These perches contained radio-frequency identification (RFID) antennae (Priority 1 Design, Australia), which recorded the arrival and departure of visits by PIT tagged individuals. We extracted displacement events automatically from these data and assigned each individual a dominance rank depending on the number of times they displaced others or were displaced themselves (Evans et al. 2018). A displacement was considered to have occurred when a bird landed on the feeder within one second of another individual leaving and then stayed for a minimum of five seconds. This method of calculating dominance automatically has been shown to correlate well with traditional methods of measuring dominance based on interactions extracted from video

(Evans et al. 2018). A linear model analyzing age and sex as predictors of dominance scores, while controlling for site as a fixed term, revealed that males have significantly higher dominance scores than females ($F_{1,26} = 12.783$, $P = 0.001$) and adults have significantly higher scores than juveniles ($F_{1,26} = 8.836$, $P = 0.006$). This is in agreement with previous findings of the correlates of social rank in chickadees (Desrochers et al. 1988; Smith 1991; Ratcliffe et al. 2007). We could not determine the overall linearity of the social hierarchies because not all pairs of birds interacted on the feeders and flock size varied. However, when determining the transitivity of triads (i.e. the linearity of relationships between sets of three individuals that all interacted) at each site using the methods of Shizuka and Mcdonald (2012; 2014) we found that all triads were transitive at three of the seven sites ($P_t = 1$, $t_{tri} = 1$), there were significantly more transitive triads than expected at an additional two sites (mean $P_t = 0.929$, mean $t_{tri} = 0.715$, $P < 0.05$), and the remaining two sites had significantly less transitive triads than expected (mean $P_t = 0.393$, mean $t_{tri} = 1.429$, $P > 0.39$). The lack of transitive triads probably reflects the fact that few individuals were detected at these two sites. We reran our statistical models that included dominance after removing birds from these last two sites to verify that our conclusions were not influenced by their inclusion (Table S2.3 and Table S2.4).

Analysis

When analyzing the predictors of problem-solving performance, we conducted an extended cox proportional hazards regression. This is a semi-parametric survival analysis approach that makes no assumptions about the distribution of the response variable (Therneau and Grambsch 2000). The ‘extended’ portion of the name refers to the fact that it includes time-dependent covariates (see below), which are variables whose value for a particular subject changes over the course of the study (Therneau et al. 2016). Assuming that every bird could solve the task given enough time, we coded individuals that failed to solve during the experiment as censored observations, since we do not know their true latency to solve (e.g. (Sol et al. 2011)). For instances in which birds solved with wings, or worms escaped from the lever pulling device (11/70 birds), we also assigned censored latencies up to the time of the incident. Individuals that had retrieved cached seeds during the paper-ripping trials (10/70 birds) were excluded from paper-ripping analyses.

We built a separate extended cox proportional hazards model for each task, setting the latency to solve as the response variable and capture site as a random intercept. We examined the influence of dominance, exploration, and urbanization scores on the problem-solving efficiency of birds in each task. An interaction term between dominance and urbanization was included in each model to account for the possibility that urbanization may influence the social dynamics of chickadees (Jones et al. 2017), and modify the impact of dominance on innovative tendencies. As persistence is often positively associated with problem-solving performance (e.g. Benson-Amram and Holekamp 2012; Sol et al. 2012; Thornton and Samson 2012; Griffin et al. 2014; Papp et al. 2015; Chow et al. 2016; Van Horik and Madden 2016), we controlled for the number of contacts made with the task throughout the two trials (persistence) as a time-dependent covariate.

In the case of the lever-pulling task, urbanization score was converted to a categorical variable (urban/rural) and stratified to meet the proportional hazards assumption (Therneau and Grambsch 2000). Stratification of a variable allows it to be controlled for, but prevents the model from returning an estimate. Inspection of the DFBETA residual plots (showing the impact of each observation on the model estimates) for each of the predictors allowed us to identify an influential observation (having a residual greater than one; Xue and Schifano 2017), and the lever-pulling analysis was conducted after removing it. The time-dependent contacts variable failed to meet the proportional hazards assumption for the paper-ripping task, so these data were analyzed after excluding three influential observations. Results of analyses before removing influential observations are provided in the supplementary information (Table S2.2). The random intercept of site was removed from each model as it was non-significant in likelihood ratio tests (lever pulling: $\chi 2=0.119$, df=1, *P*=0.731; paper ripping: $\chi 2=0.001$, df = 1, *P*=0.971). To check for multicollinearity issues, we calculated the variance inflation factor (VIF) for each variable and considered any values over five to indicate collinearity (Heiberger & Holland 2004). As all VIF values were below two, we proceeded with the analysis.

Following the precautions taken to meet model assumptions, a set of models with all combinations of the predictors was generated using the dredge function of the R package ‘MuMIn’ (Bartoń 2016). Model averaging was conducted on the subset of these models that were within 2 AICc units of the best fitting model (Symonds and Moussalli 2011). Model averaged estimates, calculated using the ‘zero method’ (Grueber et al. 2011), were used to ascertain the relative effects of our variables on performance in each task.

Following the results gained from the analyses above, we built an additional model to investigate predictors underlying the association between dominance and lever-pulling performance. We replaced the dominance variable with age and sex in this new model, and added an interaction between each of these and urbanization. Removing dominance increased our sample size by 13 individuals (33.33%). We then conducted model selection and averaging to understand the impacts of age and sex on lever-pulling performance.

When analyzing the characteristics associated with persistent individuals, we used each bird's total number of contacts (until the task was solved or the observation became censored) as our measure of persistence. Scores for dominance, exploratory tendency, and urbanization were used as predictors of the number of contacts in generalized linear mixed models with a negative binomial error structure to control for overdispersion (Zurr et al. 2009). Additionally, an interaction term between dominance and urbanization score was included for both tasks. We controlled for each bird's latency to solve or become censored, and their site of capture was included as a random intercept. We conducted the same steps for model selection and averaging as before to reach conclusions on the predictors of individual persistence.

To determine whether individuals performed consistently across tasks, we calculated the correlation-based repeatability of problem-solving latencies and overall persistence. Kendall's tau-b correlations are reported to account for violations of bivariate normality and for ties in performance and persistence (Hollander and Wolfe 1973). We also use a chi-square test of independence to investigate whether success in solving one task is associated with success in the other.

All continuous predictors were standardized (rescaled between 0 and 1, and mean-centred) prior to running survival and generalized linear mixed models (Schielzeth 2010). By rescaling the dominance variable we assumed that high ranking birds from different sized groups are equally dominant. Cox models were built using the 'coxme' (Therneau 2015a) and 'survival' (Therneau and Grambsch 2000; Therneau 2015b) packages in R, while the generalized linear mixed models were created using the 'lme4' package (Bates et al. 2015). All statistical analyses were completed using R version 3.4.3 (R Core Team 2017).

Results

Lever pulling

The lever-pulling task was solved by 54% (38/70) of individuals, 85% (33/38) of which solved in their first trial. The average latency to solve among solvers was 17.466 ± 5.103 SE minutes. When examining the determinants of performance in this task, our model selection procedure returned two top models (Table S2.5). Dominance score and the interaction between dominance and habitat type were found to be important predictors of lever-pulling performance (Table 2.1A). These results suggest that dominance has a greater effect on lever-pulling performance in rural habitats, with more dominant individuals having a higher probability of solving the task compared to subordinates (Table 2.1A, Figure 2.3). Exploration score was the least important predictor of performance that was retained in the top models.

Three top models were returned after replacing dominance with age and sex in a new global model (Table S2.6). We found an effect of age and exploratory tendency on the probability of solving the lever-pulling task (Table 2.1B). Adults had a higher probability of solving this task compared to juvenile birds, and more exploratory individuals were more likely to solve the task than less exploratory ones.

When examining the effects of individual characteristics on the total number of contacts made with the task (persistence) using a generalized linear mixed model, model selection returned five top models (Table S2.7). The second best fitting model was a null model, and none of the variables included were found to be important predictors after model averaging (Table 2.1C).

Table 2.1. Model averaged estimates assessing the influence of predictors on (A) lever-pulling performance (n = 38 individuals, solutions = 22), (B) lever-pulling performance after replacing dominance with age and sex in the global model (n = 52 individuals, solutions = 33), and (C) persistence in the lever-pulling task (n = 39 individuals).

	Parameter	*Estimate*	*Standard Error*	*Confidence interval*	*Relative importance*
A	Habitat (stratified)	--	--	--	1.00
	Contacts	3.039	0.961	**(1.155, 4.923)**	1.00
	Dominance	5.251	2.065	**(1.204, 9.298)**	1.00
	Dom*Habitat(Urban)	-4.825	2.328	**(-9.389, -0.262)**	1.00
	Exploration	0.803	0.896	(-0.953, 2.558)	0.60
B	Age(Adult)	0.969	0.409	**(0.167, 1.771)**	1.00
	Contacts	3.862	0.661	**(2.566, 5.157)**	1.00
	Exploration	1.677	0.609	**(0.484, 2.871)**	1.00
	Sex(Female)	-0.101	0.258	(-0.605, 0.404)	0.29
C	(Intercept)	3.250	0.130	**(2.986, 3.513)**	--
	Exploration	-0.491	0.553	(-1.592, 0.610)	0.59
	Urbanization	0.064	0.201	(-0.337, 0.464)	0.16
	Dominance	-0.115	0.286	(-0.687, 0.456)	0.27

The reference levels for habitat, age, and sex are rural, juvenile, and male, respectively. Variables not retained in the set of top models are not shown (B – urbanization, age*urbanization, sex*urbanization; C – latency to solve or censor, dominance:urbanization). Confidence intervals that exclude zero are shown in bold text.

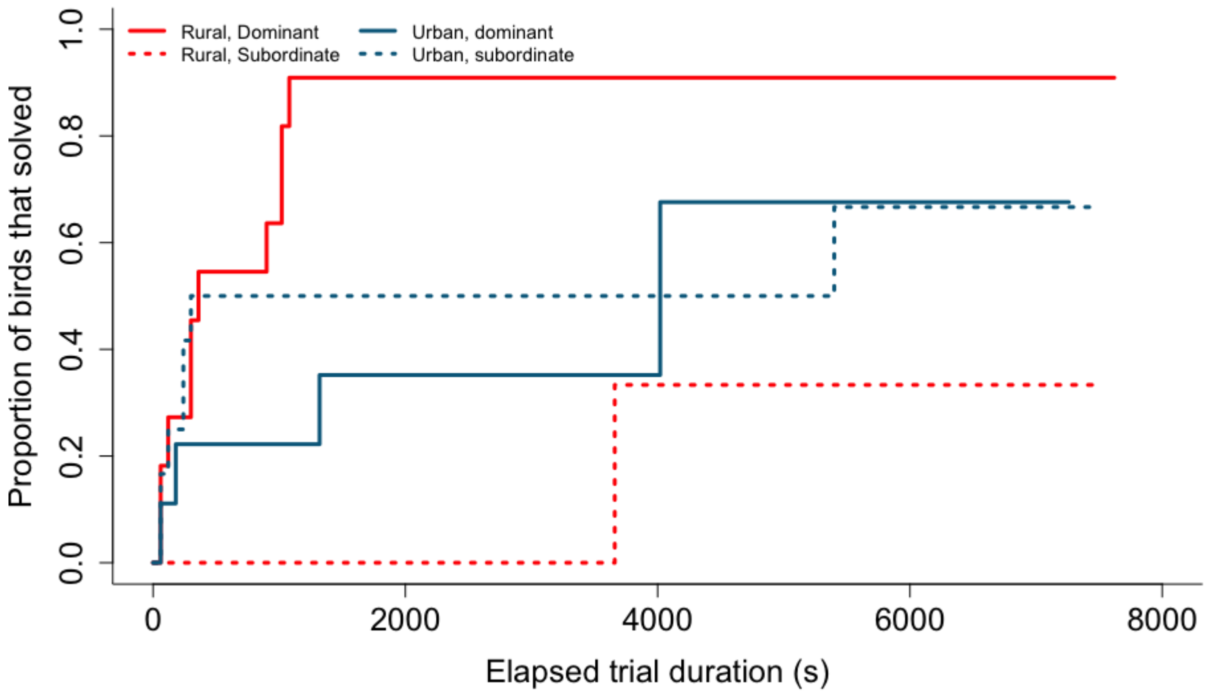

Figure 2.3. Relationship between dominance score and proportion of individuals that solved the lever-pulling task. This plot was created with a model including only the interaction term between habitat and a categorical dominance variable. Each step in a line represents a bird solving the task, and a steeper line indicates greater problem-solving efficiency. Blue lines represent birds from urban sites and red lines represent those from rural sites. Dominant individuals are defined as those with an above average dominance score (solid lines), while subordinates have a below average dominance score (dashed lines). Censored observations are not indicated.

Paper ripping

The paper-ripping task was solved by 41% (29/70) of individuals, 83% (24/29) of which solved in their first trial. The average latency to solve among solvers was 21.714 ± 6.267 SE minutes. When assessing the characteristics of innovative individuals, our model selection procedure returned four top models (Table S2.8). Model averaging results showed no strong effects of the predictors of interest (Table 2.2A).

Two top models (Table S2.9) were returned by model selection using our global generalized linear mixed model examining the predictors of persistence in the paper ripping task. We saw a negative effect of both the latency to solution or censoring (Figure 2.4) and urbanization score on the number of contacts with the task (Table 2.2B, Figure 2.5).

Table 2.2. Model average estimates assessing the influence of predictors on (A) paper-ripping performance (n=33 individuals, solutions=17), (B) persistence in the paper-ripping task (n = 36 individuals)

	Parameter	*Estimate*	*Standard Error*	*Confidence interval*	*Relative importance*
A	Contacts	23.438	4.584	**(14.454, 32.422)**	1.00
	Dominance	-0.075	0.483	(-1.022, 0.872)	0.17
	Urbanization	-1.756	1.450	(-4.598, 1.085)	0.79
	Exploration	0.167	0.646	(-1.100, 1.434)	0.20
B	(Intercept)	2.581	0.129	(2.317, 2.844)	--
	Latency to solve or censor	-1.871	0.410	**(-2.708, -1.035)**	1.00
	Urbanization	-0.887	0.367	**(-1.635, -0.139)**	1.00
	Dominance	0.562	0.432	(-0.544, 0.939)	0.35

Variables not retained in the set of top models (A – dominance*urbanization; B – exploration, dominance*urbanization) are not shown. Confidence intervals that exclude zero are shown in bold text.

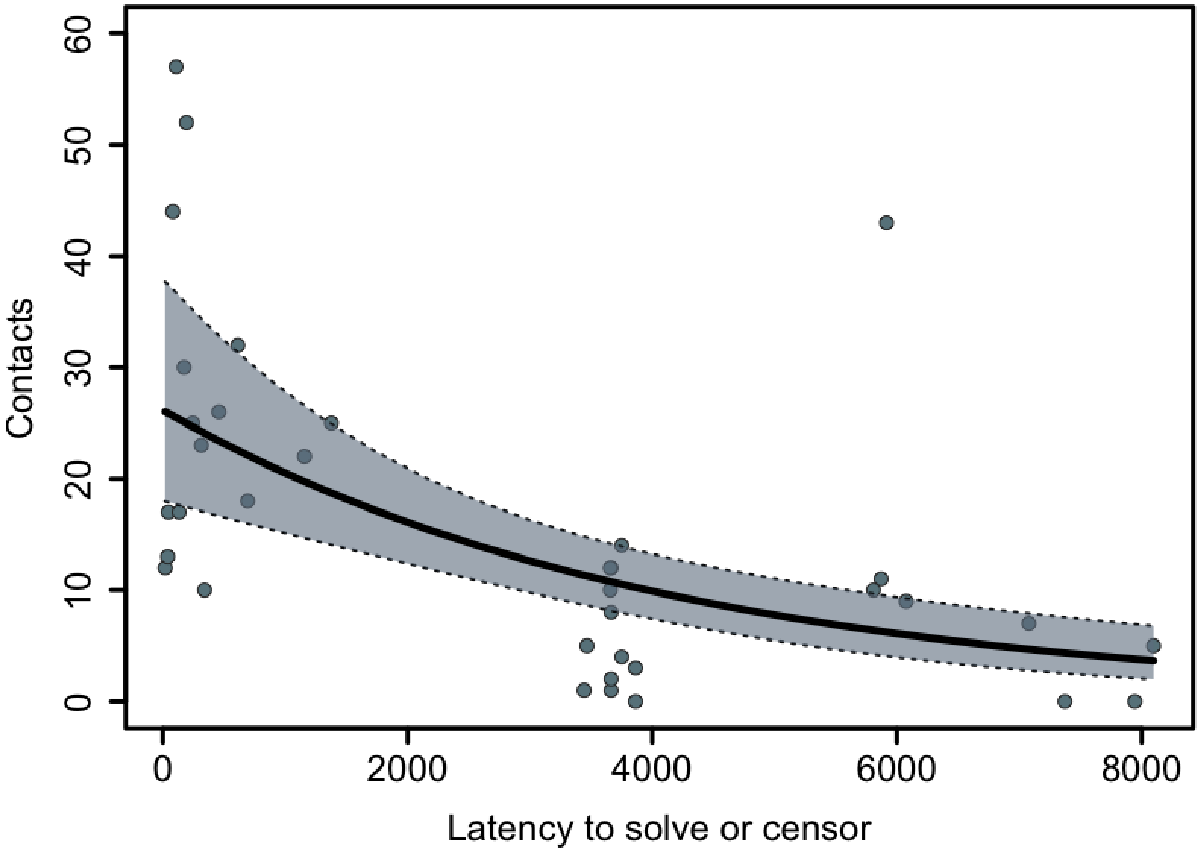

Figure 2.4. Relationship between number of contacts and latency to solve or censor in the paper-ripping task. The slope and 95% confidence interval reflect the model estimate for this variable when holding all other variables in the global model at their mean.

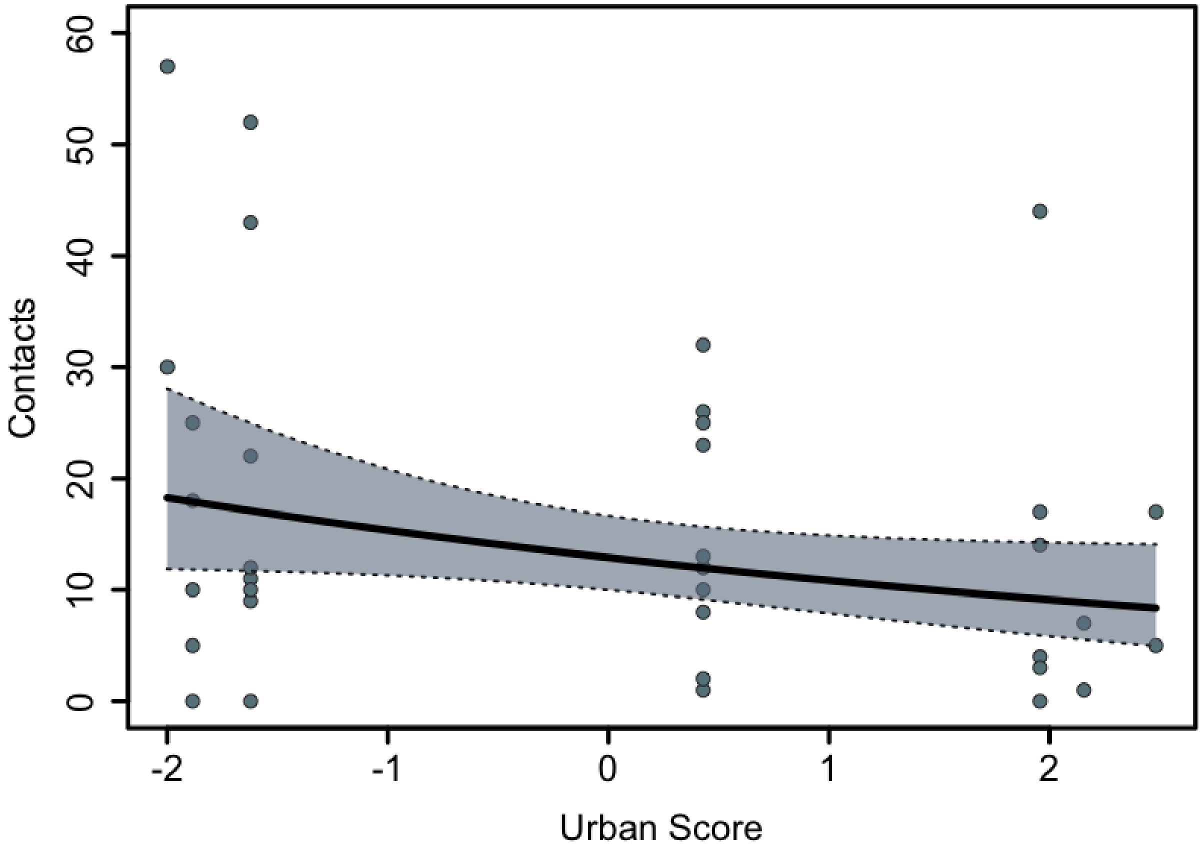

Figure 2.5. Relationship between number of contacts with the paper-ripping task and urbanization of the habitat. A higher urban score corresponds to more urbanized habitats. The slope and 95% confidence interval reflect the model estimate for this variable when holding all other variables in the global model at their mean.

Repeatability

We found no significant within-individual correlation in the latency to solve or censor (τ_b = 0.034, P = 0.713) or the total number of contacts (τ_b = 0.073, P = 0.445) in each of our tasks. Additionally, our chi-square test of independence showed that the success in solving the lever-pulling task was not associated with success in the paper-ripping task ($\chi^2 = 0.001$, df = 1, P = 0.969).

Discussion

Animal innovations have potential implications for the fitness of individuals, and the ecology and evolution of species, but the traits that characterize innovative individuals are not fully understood. We examined the predictors of innovativeness in black-capped chickadees using their performance on two food-motivated problem-solving tasks. We found that dominant individuals were more efficient than subordinates in the lever-pulling task, especially if they were captured from rural habitats. We also found evidence for a positive association between spatial exploration and lever-pulling performance. Furthermore, when analyzing the predictors of persistence, we found that individuals originating from less urbanized habitats tended to have a greater total number of contacts with the paper-ripping task.

When assessing the effect of dominance rank on problem-solving performance, our results did not align with predictions from the necessity drives innovation hypothesis. In fact, our analysis showed that higher ranking individuals outperformed lower ranking birds in the lever-pulling task, and this effect was stronger in birds originating from rural compared to urban habitats. This is contrary to previous findings that less competitive individuals tend to be more likely to innovate than the more competitive dominants, even when individuals are tested in an isolated context as in our study (e.g. Cole and Quinn 2012). Our result should be taken with caution since the interaction effect was only found to be influential when excluding an influential observation (cf. Table S2.2A and Table S2.3A). However, dominants have been found to be more efficient in a lever pulling task compared to subordinates in our population previously (Devost 2015). There could be two potential explanations for dominant individuals outperforming subordinates. The first possibility is that the costs of innovating vary between individuals of different competitive abilities. Less competitive individuals are at greater risk of losing newly discovered resources to conspecifics (Duffield et al. 2015; Lee et al. 2016), thereby potentially decreasing the benefits of innovating. Alternatively, individuals of different competitive abilities may differ in the value that they place on available food items in isolated versus social contexts (Cole and Quinn 2012). O'Shea et al. (2017) found that less competitive great tits were more likely to perform a string-pulling task in dyadic trials, but innovativeness in an isolated context was not associated with competitive ability. This suggests that less competitive individuals may forego a high quality food resource available through novel means, but competition for established resources in a social context may drive them to innovate. If the costs of innovating are high for subordinate chickadees, or competition is required to elicit their problem-solving attempts, then we would predict that subordinate chickadees would interact with the lever-pulling task less than dominant individuals in the solitary context of our tests. However, dominance scores did not predict the level of persistence exhibited by individuals in the lever-pulling trials, so these explanations seem unlikely.

To investigate other explanations for this trend, we replaced dominance with age and sex in our model and found that adult chickadees outperformed younger individuals. This pattern matches findings in multiple species where adults tend to be more innovative than nonadults (Reader and Laland 2001; Kendal et al. 2005; Thornton and Samson 2012). It may be that experience plays a role in the performance of individuals. Adult chickadees may have more information from their previous interactions with objects that can be applied to the new context of lever pulling. Another possibility is that adults employ a greater diversity of motor actions or contact a variety of task components when interacting with objects, which is known to predict innovation in some taxa (Benson-Amram and Holekamp 2012; Thornton and Samson 2012; Griffin et al. 2014). Previous experience and/or greater motor diversity might allow adults to recognize functional components of a task or use the appropriate motor actions sooner than juveniles. The role of experience or motor tactics may be especially evident if juveniles interact with tasks more than adults, but still do not outperform them (e.g. in meerkats, Thornton and Samson 2012; and hyenas, Benson-Amram and Holekamp 2012).

The weaker effect of dominance on problem-solving performance in urban birds may be explained by reduced competition between conspecifics resulting from the presence of ample resources year-round (Preiszner et al. 2017). For example, a study on zenaida doves (*Zenaida aurita*) found that an urban population of these birds had begun to exhibit unaggressive scramble competition for food rather than interference competition as seen in other habitats (Carlier and Lefebvre 1997). Thus in chickadees, both dominant and subordinate individuals from urban habitats may be less motivated to access novel resources, thereby explaining the steeper relationship between dominance and problem-solving in rural birds. Further studies into the relationship between dominance and problem-solving performance would benefit from a deeper investigation into the behavioural and cognitive characteristics distinguishing individuals of varying dominance ranks, comparisons of problem solving in isolation versus in the presence of competitors, and larger sample sizes to enable robust conclusions.

When running our analyses with maximal sample size, we found, as predicted, a positive association between the spatial exploratory tendency of an individual and its probability of solving the lever-pulling task. This result is in line with the findings of Overington et al. (2011), but see Cole et al. 2011; Lermite et al. 2017) and provides support for the idea that novelty responses contribute to the innovative propensity of animals. Presumably individuals that show a greater tendency for spatial exploration are also more likely to approach and interact with novel objects. The lack of an association between exploratory tendency and the number of contacts made with the lever-pulling task suggests that our exploratory chickadees may be more efficient at solving the task because they approach the task sooner rather than interacting with it more; this highlights the value of analyzing predictors of contact rate to gain an understanding of the drivers of innovation at different stages of the process.

When assessing the predictors of the total number of contacts made with the tasks, we only found a negative effect of urbanization in the paper-ripping task. However, this was not detected when excluding birds from sites with less transitive triads than expected and must therefore be interpreted with caution. This result is in contrast to a positive effect of urbanization on the frequency of pecks directed at a problem by common mynas (Sol et al. 2011). A possible explanation for this trend is that urban chickadees may not have a need to be persistent when foraging in the wild as they are likely to come across freely accessible resources such as bird feeders (Papp et al. 2015). The presence of these resources may also make urban chickadees less likely to exhibit bark-pulling behaviour (foraging for food hidden under bark in natural environments, Smith 1991), which resembles the motor actions needed to solve the paper-ripping task. Foraging for hidden food may be a more natural behaviour for rural compared to urban birds, but this idea would need to be tested explicitly. Across species, individuals that persist in their interaction with a task, especially using appropriate motor actions, tend to be the most successful problem solvers (e.g. Cauchard et al. 2013; Griffin et al. 2014), and those that persist in activities that may not be immediately beneficial are expected to be able to develop expertise in those behaviours (Dukas 2018). Thus, further investigation of the characteristics associated with persistence is merited.

We found that an individual's problem-solving success, efficiency, and persistence were not consistent across tasks. This inconsistency suggests that the protocols and characteristics of the problems used (e.g. visibility of the food reward, motor actions required to solve, and food deprivation) may have a significant impact on the relative performance of individuals. A study on house sparrows found that problem-solving performance was significantly repeatable across four tasks, but the tasks used all had visible rewards (Papp et al. 2015). Griffin and Diquelou (2015) also found that problem-solving success was consistent across three tasks, one of which was opaque. Additionally, Van Horik and Madden (2016) found that problem solving success was consistent across two similar tasks, but not on a third one that differed in its structure. Future work on problem solving in animals may benefit from an experimental assessment of the effect of task characteristics on individual performance.

In conclusion, we found a trend in rural birds for dominants to outperform subordinates in a lever-pulling task. Moreover, we found that rural birds were slightly more persistent in the paper-ripping task compared to birds from urbanized areas. Individual performance and persistence was not repeatable across tasks, and the traits defining the most innovative and persistent individuals in each task were not consistent. Overall, our findings point to the possibility that different individual characteristics may facilitate innovative behaviour in different ecological contexts.

Chapter 3

Innovative consumers: ecological, behavioural and physiological predictors of responses to novel food

Abstract

Consumer innovation, i.e. the acquisition and consumption of novel food types using existing behaviours, has received little attention despite its predominance among animal innovations, and its potential implications for the ecology and evolution of species in a changing world. Results of the few studies that have investigated individual responses to novel foods suggest that various ecological, behavioural, and physiological variables may impact individual propensity for consumer innovation, but further work is needed to clarify these relationships. We investigated if urbanization, social rank, exploratory personality, and baseline levels of corticosterone predict food neophobia and consumer innovation responses of wild-caught black-capped chickadees (N=169) from 14 sites along an urbanization gradient. Our analyses do not support a link between food neophobia or consumer innovation and urbanization, dominance or exploratory personality. However, birds with higher levels of baseline corticosterone were quicker to contact novel food types, and more likely to consume novel foods than individuals with lower levels of the hormone. This finding suggests that physiological states that promote foraging behaviour might drive individual responses to novel food.

Introduction

Animals living in newly colonized or changing environments are faced with novel challenges and opportunities. Rather than ignoring potentially profitable resources, or exploiting them relatively inefficiently with existing behaviours, these challenges may be met, through innovation (i.e. displaying new learned behaviours that were not previously exhibited by any members of the population, Reader and Laland 2003). A common form of innovative behaviour involves the consumption of novel foods (e.g. 50.8% of innovations in the Overington et al. 2009 database). These are referred to as food type or consumer innovations, as opposed to technical innovations, which involve the use of novel behaviours (Overington et al. 2009; Sol et al. 2011; Sol et al. 2012).

In birds, rates of consumer innovations are associated with levels of habitat generalism and dietary generalism (Ducatez et al. 2015). It has been suggested that the success of habitat generalists in colonizing new environments may arise from their willingness to incorporate novel foods into their diet (Ducatez et al. 2015). Individuals exhibiting these innovative behaviours may experience benefits, such as an added source of energy and the avoidance of competition for familiar resources, which may allow them to survive when familiar resources are scarce (Reader and Laland 2003; Sol et al. 2011; Mcmahon et al. 2014). On the other hand, the consumption of novel food types takes time away from other activities (e.g. foraging for familiar resources), and puts individuals at risk of eating toxic items, or being exposed to parasites (Marples et al. 1998; Reader and Laland 2003; Garamszegi et al. 2007; Brosnan and Hopper 2014). These costs would favour the avoidance of novel foods, referred to as dietary wariness. Thus, consumer innovation potentially has important implications for animals.

However, little research has investigated the characteristics associated with intraspecific variation in dietary wariness and consumer innovation.

One factor thought to influence individual differences in innovative propensity is the level of urbanization of an animal's habitat. Urban environments may promote innovative behaviour if they contain fewer predators and more ecologically-novel resources, factors that would be expected to favour potentially risky exploratory behaviour (Sol et al. 2011; Sol et al. 2013). These effects may be counteracted by factors such as the presence of abundant and easily accessible anthropogenic resources (e.g. bird feeders), or risks associated with novel items (e.g. risk of ingesting toxins) in urban environments (Papp et al. 2015). Previous work on dietary wariness in a variety of species has shown that prior experience with novel foods decreases the neophobic responses to other novel food items encountered in the future (Marples et al. 2007; Lecuelle et al. 2011; Adamová-Ježová et al. 2016). This suggests that animals living in habitats where they would be exposed to novel foods repeatedly may exhibit lower food neophobia, and greater consumer innovation, than conspecifics from other habitats. However, this expectation was not met in a study on common mynas (*Acridotheres tristis*), which found that birds from urban and suburban habitats did not differ in the time they took to consume a novel food item (Sol et al. 2011). Additionally, Liebl and Martin (2014) found that house sparrows (*Passer domesticus*) from more urbanized sites took longer to eat novel food compared to birds from less urbanized areas. More empirical work is needed to understand the relationship between urbanization and the response of animals to novel food.

Necessity brought about by the scarcity of existing resources may also promote innovative behaviour (i.e. necessity drives innovation; Laland and Reader 1999; Reader and

Laland 2003). For instance, social rank may affect an individual's access to resources and push subordinate individuals to innovate rather than compete with more dominant conspecifics. When studying technical innovations (i.e. problem solving), researchers have found conflicting results in relation to this hypothesis. For example, lower ranking individuals were found to be more innovative in chimpanzees (*Pan troglodytes*, Reader and Laland 2001) and meerkats (*Suricata suricata*, Thornton and Samson 2012), but not in pigeons (*Columba livia*, Bouchard et al. 2007) or spotted hyenas (*Crocuta crocuta*, Benson-Amram and Holekamp 2012). Some research on dietary wariness has suggested that the presence of a competitor reduces the dietary wariness of juvenile domestic chickens (*Gallus gallus domesticus*, McMahon et al. 2014) and blue tits (*Cyanistes caeruleus*, McMahon and Marples 2017). Although wariness may be decreased via social learning, McMahon and Marples (2017) controlled for this possibility by training competitor birds to avoid both familiar and novel foods to ensure that the decisions of focal individuals did not depend on the feeding behaviour of conspecifics. Focal individuals were more likely to consume novel foods in the presence of another bird, which was interpreted as the focal bird having a higher perceived cost of remaining wary of novel food in the presence of a potential competitor. This explanation is in line with the hypothesis that necessity drives innovation, and raises the possibility that subordinate individuals, given that they are outcompeted for existing resources, may be more likely to exhibit consumer innovation compared to dominants.

An individual's response to novelty is another characteristic thought to be central in determining the innovative ability of animals. Individuals that more readily move through novel areas (i.e. exhibit greater spatial exploration) and approach novel objects (i.e. are less neophobic), are expected to be more innovative than less exploratory or more neophobic conspecifics (Griffin and Guez 2014). In the context of novel food assays, Exnerová et al. (2010) found that great tits (*Parus major*) selected for fast spatial exploration were quicker to attack aposematic firebugs (*Pyrrhocoris apterus*, a novel prey type for the individuals tested) compared to slow explorers. On the other hand, some researchers found no relationship between latency to consume a novel food item and object neophobia (Sol et al. 2012) or spatial exploration (Liebl and Martin 2014). The disparity in these results may arise from differences in methodology. For example, Exnerová et al. 2010 used captive birds artificially selected to be more or less exploratory and used a live novel prey, while the other studies used wild-caught birds and inanimate novel food items. Given the scarcity of studies on these relationships and the mixed results they show, further research would help to elucidate the effects of exploratory personality on the consumer innovation propensity of wild animals.

Physiological variables, such as levels of the hormone corticosterone, may relate to innovative behaviour as well. Expectations for associations between corticosterone and innovation differ depending on the level of the hormone being investigated. At baseline concentrations, one of corticosterone’s primary functions is as a metabolic hormone, regulating appetite and metabolism (Dallman et al. 1993; Sapolsky et al. 2000; Remage-Healey and Romero 2001). Thus, baseline corticosterone might influence consumer innovation through its direct stimulatory effects on appetite and foraging behaviour (Dallman et al. 1993; Landys et al. 2004; Lohmus et al. 2006; Crossin et al. 2012). These effects might generate a positive association between baseline concentrations of corticosterone and consumer innovation. In contrast, acute increases in corticosterone in response to stressors (most often measured via the response to capture stress) tend to be more highly repeatable within individuals than baseline concentrations (Schoenemann and Bonier 2018) and have been found to be correlated with stable personality traits. For example, in a review across several well-studied vertebrates, Koolhaas et al. (1999) reported that individuals with more reactive coping styles, which are characterized by more flexible behaviour, exhibited higher stress-induced glucocorticoid concentrations. In the context of technical innovation, a study on juvenile greylag geese (*Anser anser*) found that successful problem solvers had higher levels of fecal corticosterone than unsuccessful individuals (Pfeffer et al. 2002). In contrast, Medina-García et al. (2017) found no relationship with either baseline or stress-induced corticosterone and problem solving ability in budgerigars (*Melopsittacus undulatus*). The relationship between consumer innovation and levels of corticosterone has yet to be investigated~~.~~

Here we aim to understand what ecological, behavioural, and physiological factors predict individuals' responses to novel food types. We investigated the associations of urbanization, dominance, exploratory personality, and baseline levels of corticosterone with food neophobia and consumer innovation responses exhibited by wild-caught black-capped chickadees (*Poecile atricapillus*). Black-capped chickadees are habitat generalists found throughout North America (Smith 1991; Foote et al. 2010), belonging to an avian family that has exhibited a relatively large number of innovations in the wild (Overington et al. 2009). We predicted that individuals would exhibit greater food neophobia and be less likely to innovate if they come from less urbanized habitats, are low in their social hierarchy, are less exploratory, and have low baseline corticosterone.

Methods

Capture sites and housing

A total of 169 chickadees were captured using mist nets installed near a feeder filled with black-oil sunflower seeds. Birds were caught from one of fourteen sites located in and around Ottawa, Ontario (Figure 3.1) from October to December of 2015 and 2016 (seven sites each year, up to 12 birds per week). The degree of urbanization at each site was assessed using remote sensing data (NASA Landsat Program 2016a, 2016b; Quantum GIS Development Team 2017, Congedo 2016) by quantifying the number of pixels classified as different land cover types (building, tarmac, forest, and bare earth) within a 1 km radius of capture sites (large enough to encompass the winter home range of chickadees, Smith 1991). These variables were combined in a principal components analysis (PCA) to generate a score that explained the degree of urbanization at each site (with 81.82% of variance explained by PC1, Thompson et al. 2018). We assessed the robustness of our conclusions by replacing urban score with a dichotomous habitat variable (urban/rural) in our final models (Table S3.1).

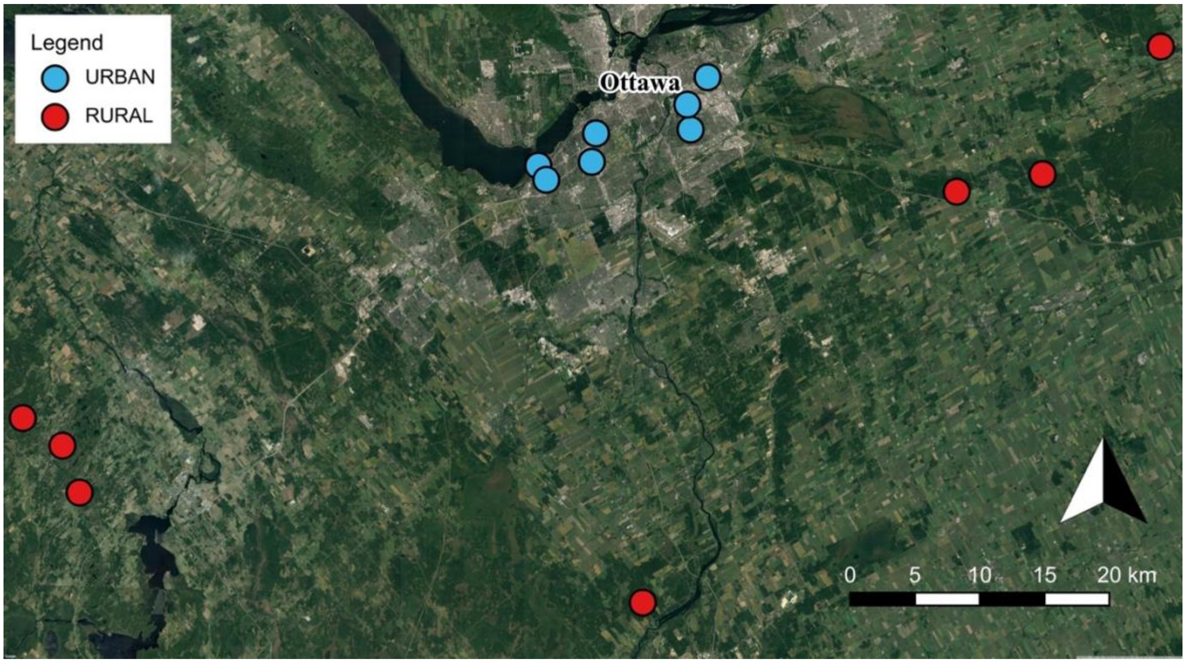

Figure 3.1. Remote sensing map showing 7 urban (blue) and 7 rural (red) sites located in and around Ottawa, Ontario, Canada. Taken from Thompson (2017).

Upon capture, each individual was fitted with metal and coloured leg bands as well as a unique passive integrated transponder (PIT) tag (weighing less than 0.15 grams, about 1% of a bird's body weight). Birds were categorized as juvenile or adult by inspecting the shape and wear of their tail feathers (Pyle 1997). The body condition of each bird was calculated as the residuals from a multiple linear regression of body mass on tarsus length and time of capture (Schulte-Hostedde et al. 2005; Liker et al. 2008; Herborn et al. 2010). After capture, birds were transported and housed in individual cages (40 x 60 x 40 cm), allowing only auditory contact between individuals, in the indoor aviaries of the animal care facility of the University of Ottawa. Outside of testing periods, birds were given ad libitum access to food (sunflower seeds) and water, as well as mealworms at the end of each day. On the last day in captivity, between

10:00 and 11:00, blood samples were taken from the brachial vein of each subject for molecular sexing (Griffiths et al. 1998; Thompson et al. 2018) and to collect plasma for measurement of baseline corticosterone. Enzyme-linked immunosorbent assay (EIA) kits (Cayman Chemical Co. Item 510320, Ann Arbor, Michigan, United States) were used to measure total plasma corticosterone. Diluted plasma samples (7.5 μL, 1:16 buffer) were assayed in duplicate. Five assays were run with two replicates per plate. Mean intra-assay variation was 10.74% and inter-assay variation was 60.24% (see Thompson et al. 2018 for a more detailed description of these methods). An analysis on a large subset of these birds (N = 127) found that year, order of testing, and sampling time (mean = 122 sec, range = 63 – 180 sec) did not significantly predict corticosterone values (Table S3.3 in Thompson et al. 2018). The range of baseline corticosterone levels (0.44 – 13.74 ng/mL) resembled those reported in both captive and wild chickadees (Pravosudov et al. 2004; Montreuil-Spencer 2017). Birds were weighed at the time of capture and on the last day in captivity to determine the change in their body mass. Subjects were released at their site of capture near a filled feeder after a total of 5 days in captivity.

Novel food trials

The neophobic response of chickadees toward three types of novel food (almond, scrambled egg, and rice), and their propensity for consumer innovation was tested in three novel food trials. To begin a trial, the experimenter turned off the lights of the housing room, entered with a red headlamp, and simultaneously placed two pieces of novel food and one sunflower seed (familiar food) in separate petri dishes at the bottom of each individual's cage. Almonds and eggs were cut into pieces roughly the size of sunflower seeds to control for the size of food items. The trial started once the experimenter exited the room and switched the lights back on. Almond trials began at approximately 10:30 on day 2 in captivity, egg trials on day 2 at 16:15 in 2015 and 15:45 in 2016, and rice trials at 09:00 on day 5. All trials were 15 minutes in length, preceded by a period of food deprivation (1 hour for almond and rice trials, and 30 minutes for egg trials). Differences in timing of trials and lengths of food deprivation periods resulted from the accommodation of concurrent studies (Thompson et al. 2018; Thompson & Morand-Ferron 2018). All trials were video recorded for later data collection.

Information about the order of food items contacted (novel or familiar), latency to contact a novel food item, and whether sunflower seeds and novel food items were consumed (partially or completely) were extracted from the video recordings of the novel food trials. A bird's neophobic response is reflected by its latency to contact a novel food item, which was defined as the time from the beginning of the trial to the time that the bird first pecked the food. Individuals that did not contact the novel food were assigned capped latencies equal to the duration of the trial (900 seconds). A bird that at least partially consumed a novel food item was considered to have exhibited consumer innovation. To account for the fact that individuals may not have been motivated to feed in some trials, we excluded data from trials in which the sunflower seed was not consumed (15 trials) or the bird retrieved previously cached seeds before contacting the novel food (18 trials). Three trials were excluded because the view of the food was obstructed. For trials in which birds were hidden in their roost box for some time, we subtracted that time from their latency to contact novel food (2 trials). An additional eight trials were excluded from the consumer innovation analyses, because the birds had cached rather than consumed novel food items.

Exploration in a novel environment

A spatial exploration assay was conducted on day 3 in captivity to measure each individual's exploratory tendency in a novel environment. The novel room, containing four artificial trees, was accessible to birds from their home cages through an opaque sliding door. Light manipulation was used to move birds to and from the novel room, which avoided handling by the experimenter (Pravosudov and Clayton 2002). Each bird's number of visits to trees, number of visits to other features in the room, and the duration of their flights and hops were measured over a 10-minute period. A composite exploration score for each individual was generated by combining these measures in a principal components analysis (similar to Quinn et al. 2009). This first component explained 67.84% of variance (Thompson 2017). Exploration score was found to be moderately repeatable after exposing each bird to a second exploration assay conducted the next day with new artificial trees placed in different positions (N = 70, R = 0.47, CI = 0.41 – 0.51; Thompson et al. 2018).

Dominance rank

Black-capped chickadees form stable groups with linear dominance hierarchies in the non-breeding season (Smith 1991; Devost et al. 2016). Following the 2016 assays in captivity, each site was equipped with a sunflower seed feeder, fitted with a single perch that restricted access to one individual at a time. These perches contained radio-frequency identification (RFID) antennae (Priority 1 Design, Australia), which recorded the presence of PIT tagged individuals every second. This allowed for the detection of arrivals and departures by birds, and we extracted displacement events automatically from these data. Displacements were defined as instances in which a bird landed on the perch within one second of another bird leaving and remained for at least 5 seconds. Each individual was assigned a dominance rank depending on the number of times they displaced others or were displaced themselves (Evans et al. 2018). This method of calculating dominance automatically has been shown to correlate well with traditional methods of measuring dominance based on interactions extracted from video (Evans et al. 2018). We calculated the proportion of all triads (sets of 3 birds that interacted with each other on feeders) that were transitive (P_t, i.e. bird A > B > C) and the triangle transitivity metric (t_{tri}) using methods set out by Shizuka and Mcdonald (2012, 2014). All of the triads at three of seven sites were transitive ($P_t = 1$, $t_{tri} = 1$), two other sites had significantly more transitive triads than expected by chance (mean $P_t = 0.929$, mean $t_{tri} = 0.715$, $P < 0.05$), and the final two sites had significantly fewer transitive triads than expected (mean $P_t = 0.393$, mean $t_{tri} = -1.429$, $P > 0.39$). The lack of transitive triads at two sites is probably due to the detection of relatively few individuals, leading to an inability to produce robust dominance hierarchies. Birds from these last two sites were not included in our models analyzing dominance as a predictor of food neophobia or consumer innovation.

Analysis

To analyze the relationships between individual and ecological characteristics and the neophobic response of chickadees to novel food, we used Cox proportional hazards regression. This type of analysis does not make assumptions about the distribution of the response variable. In addition, it accounts for individuals that did not contact the novel food during the trial by labelling them as censored observations. When building our models, we set the latency to contact novel food as the response variable and individual ID nested within site as random effects. A generalized linear mixed model with a binomial error structure was used to analyze the relationships between variables and the consumer innovation propensity of chickadees. This model incorporated a binary response (novel food eaten or not) and individual ID nested within site as random effects. All models included date of capture, and novel food type as fixed effects.

Since the incorporation of dominance score as a predictor in our models dramatically reduced the sample size by over 130 out of 170 individuals (135 for food neophobia and 136 for consumer innovation), we built two separate models for each response variable. In the first we used age and sex as proxies for dominance (Desrochers et al. 1988; Smith 1991; Ratcliffe et al. 2007; our population: Devost et al. 2016) and aimed to determine whether urbanization, exploratory tendency, and baseline corticosterone predicted food neophobia and consumer innovation ability while controlling for year. We included interactions between capture date and each of age, sex, and urbanization to account for the possibilities that individuals of different social rank respond to changes in food availability across the season differently and that food availability changes differently in habitats of varying levels of urbanization. Year had to be stratified in the Cox proportional hazards model for food neophobia as it failed to meet the statistical assumption of proportional hazards. Stratification allows for the effects of a variable to be controlled for, but it is not possible to get an estimate for this variable (Therneau and Grambsch 2000). Additionally, all three interaction terms with capture date were removed from the consumer innovation model due to convergence issues. Our second model for food neophobia included dominance score and an interaction effect between capture date and dominance, in addition to the same effects as above, i.e. date of capture and novel food type as fixed effects, and ID nested within site as random effects. The interaction between dominance and date was removed from the equivalent model for consumer innovation due to convergence issues.

We simplified our models first by testing the random effect of capture site using likelihood ratio tests. Capture site was removed from all models as it was found to be nonsignificant (all $P > 0.921$; Bolker et al. 2009). To check for multicollinearity issues, we calculated the variance inflation factor (VIF) for each variable and considered any values over five to indicate collinearity (Heiberger & Holland 2004). All VIF values were below three, so we proceeded with the analysis. We then followed a model selection procedure for all of our initial models. First, we generated a set of models with all combinations of predictors using the dredge function of the R package 'MuMIn' (Barton 2016). Model averaging was then conducted on the subset of these models that fell within 2 AICc units of the best fitting model (Symonds and Moussalli 2011). Conclusions were based on model averaged estimates calculated using the 'zero method' (Grueber et al. 2011).

To gain a deeper understanding of the relationship between baseline corticosterone and the food neophobia and consumer innovation propensity of chickadees, we checked for Pearson correlations between corticosterone levels and body condition, as well as change in body mass over the week. Corticosterone levels were square-root transformed to improve normality because log-transformation was not as effective.

Finally, we calculated the adjusted repeatability of both food neophobia and consumer innovation. For food neophobia, we used a linear mixed model with latency to contact novel food as the response variable. All latencies were increased by one second to allow for log-transformation to improve normality. A generalized linear mixed model with a binomial error structure was used to calculate the repeatability of consumer innovation. Both of these models contained year, date, and trial number as fixed effects and the random effect of individual. These analyses were run with 1000 bootstrap simulations using the ‘rptR’ package in R (Stoffel et al. 2017).

All continuous predictors in our food neophobia and consumer innovation models were standardized prior to running analyses (Schielzeth 2010). Standardization involved rescaling the variable between zero and one (i.e. for each variable subtracting the minimum value from each observation and dividing by its range), and then mean-centring such that the mean of the variable is zero. By rescaling the dominance variable we assumed that high ranking birds from different sized groups are equally dominant. Cox models were built using the ‘coxme’ (Therneau 2015a) and ‘survival’ (Therneau and Grambsch 2000; Therneau 2015b) packages in R, while the generalized linear mixed models were created using the ‘lme4’ package (Bates et al. 2015). The ‘DHARMa’ package (Hartig 2018) was used to assess diagnostics for our generalized linear mixed models. All statistical analyses were conducted using R version 3.4.3 (R Core Team 2017).

Results

Food Neophobia

Birds showed a preference for the familiar food item over each of the three novel food types tested, as the sunflower seed was the first food item contacted in 85.2% (379/445) of trials (Almond: 115/159 $\chi^2 = 109.03$, df = 1, $P < 0.001$; Egg: 140/154 $\chi^2 = 230.11$, df = 1, $P < 0.001$; Rice: 124/132 $\chi^2 = 218.53$, df = 1, $P < 0.001$). The average latency to contact a novel food item was 5.073 ± 0.267 SE minutes (Almond: 3.581 +/- 0.362 SE minutes, Egg: 5.649 ± 0.482 SE minutes, Rice: 6.171 ± 0.519 SE minutes).

When examining the predictors of the neophobic response of individuals, our model selection procedure returned eight top models (Table S3.2). After model averaging, birds that were tested later in the season were found to have a higher probability of contacting a novel food item (Figure 3.2, but see Table S3.1A). There was also a difference in the probability of contacting each novel food item, with birds being the most likely to contact almonds, compared to egg or rice (Figure 3.3). A positive relationship was also seen between baseline levels of corticosterone and the probability of contacting the novel food (Figure 3.4). No other main effects or interactions proved to be important predictors of food neophobia in chickadees (Table 3.1A).

For the global model using dominance score as a predictor, our model selection procedure returned two top models (Table S3.3). Neither dominance score nor its interaction with date were found to be important terms after model averaging. However, the effects of date and food type were again present in the same direction (Table 3.1B).

Table 3.1. Model averaged estimates assessing the influence of predictors on the latency to contact a novel food item from a survival analysis (A: Full model: n=327 observations of 125 individuals, B: Dominance model: n=79 observations of 35 individuals).

	Parameter	*Estimate*	*Standard Error*	*Confidence interval*	*Relative importance**
A	Strata(Year)	--	--	--	1.00
	Age(juvenile)	-0.150	0.161	(-0.465, 0.165)	0.88
	Sex(female)	-0.305	0.165	(-0.627, 0.018)	1.00
	Trial(egg)	-0.588	0.154	**(-0.890, -0.286)**	1.00
	Trial(rice)	-0.723	0.164	**(-1.045, -0.402)**	1.00
	Date	0.878	0.410	**(0.074, 1.682)**	1.00
	Corticosterone	1.103	0.459	**(0.203, 2.004)**	1.00
	Urban score	0.401	0.214	(-0.018, 0.819)	1.00
	Age(juvenile):Date	-0.444	0.570	(-1.561, 0.673)	0.64
	Urban score:Date	0.080	0.437	(-0.776, 0.936)	0.33
	Exploration	-0.029	0.143	(-0.310, 0.251)	0.09
	Sex(female):Date	-0.013	0.270	(-0.542, 0.251)	0.18
B	Trial(egg)	-0.648	0.286	**(-1.209, -0.087)**	1.00
	Trial(rice)	-1.948	0.500	**(-2.928, -0.968)**	1.00
	Date	1.177	0.414	**(0.366, 1.465)**	1.00
	Dominance	0.510	0.487	(-0.445, 1.465)	0.73

Confidence intervals that do not contain zero (i.e. no effect) are indicated in bold text. The reference levels for trial, age, and sex are almond, adult, and male, respectively. Variables not retained in the set of top models (B: dominance:date) are not shown.

*Relative importance reflects how many top models included each variable while accounting for the weight of these models. A value of 1.00 indicates that the variable appeared in all of the top models.

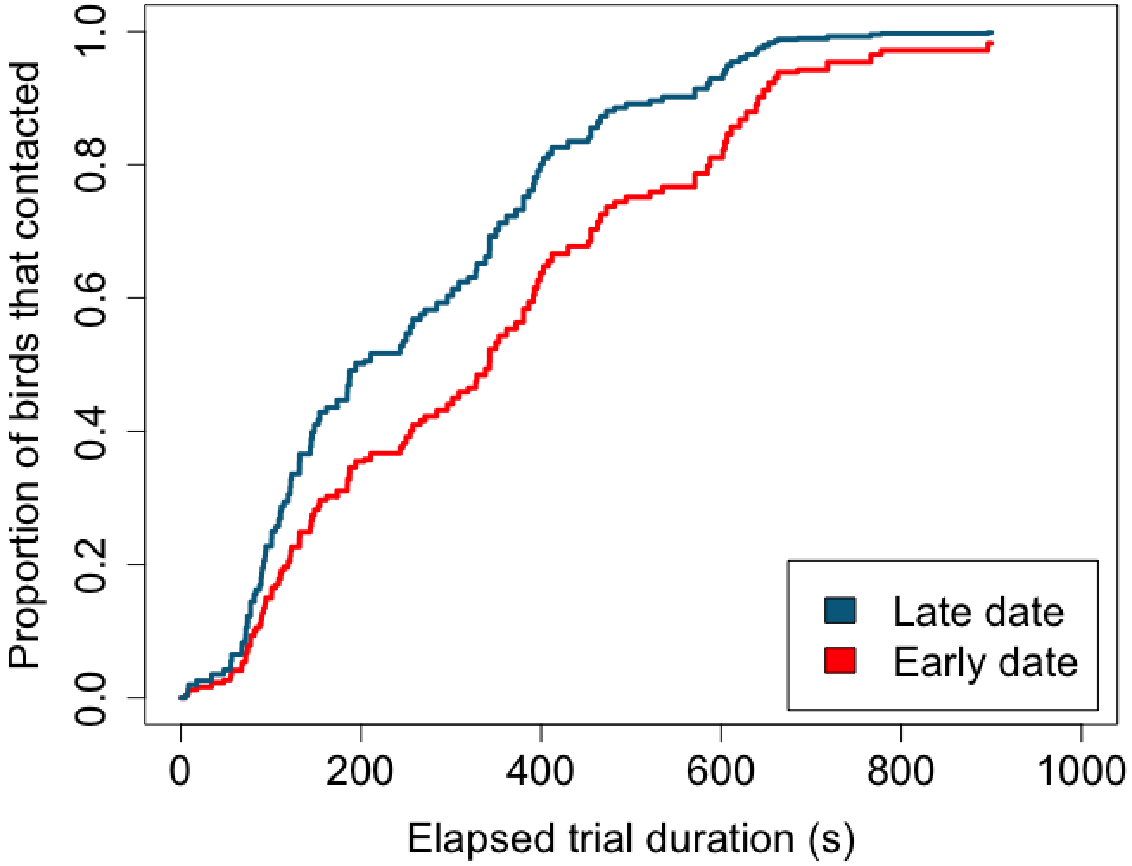

Figure 3.2. Relationship between Julian date and the proportion of birds that contacted a novel food item over the trial. The 25th percentile (red) and 75th percentile (blue) of dates are shown (reflecting the model estimate for this variable) while holding all other predictors at their mean. To control for the repeated trials per individual, average latencies to contact a novel food were used for this plot, although analyses were conducted at the level of trials.

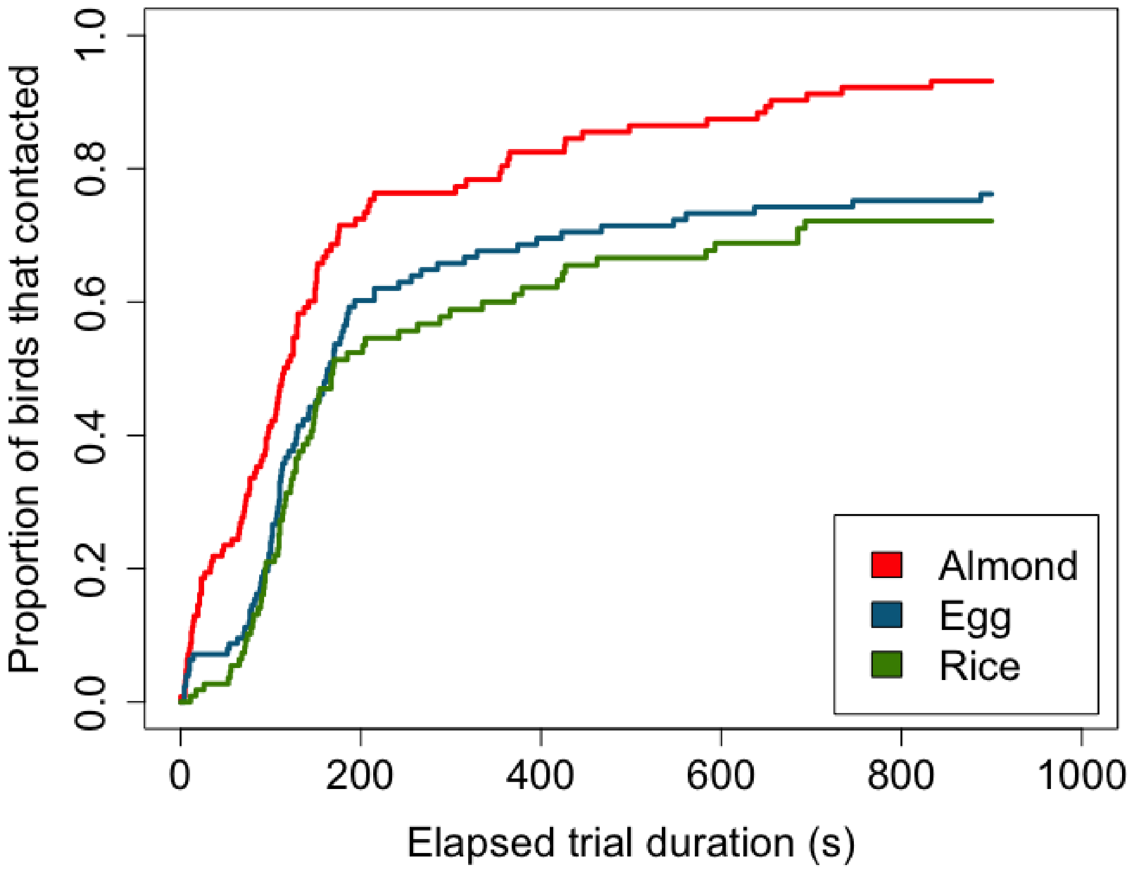

Figure 3.3. Survival plot showing the relationship between novel food type and the proportion of birds that contacted a novel food item over time. Almond, egg, and rice trials are represented by the red, blue, and green lines respectively.

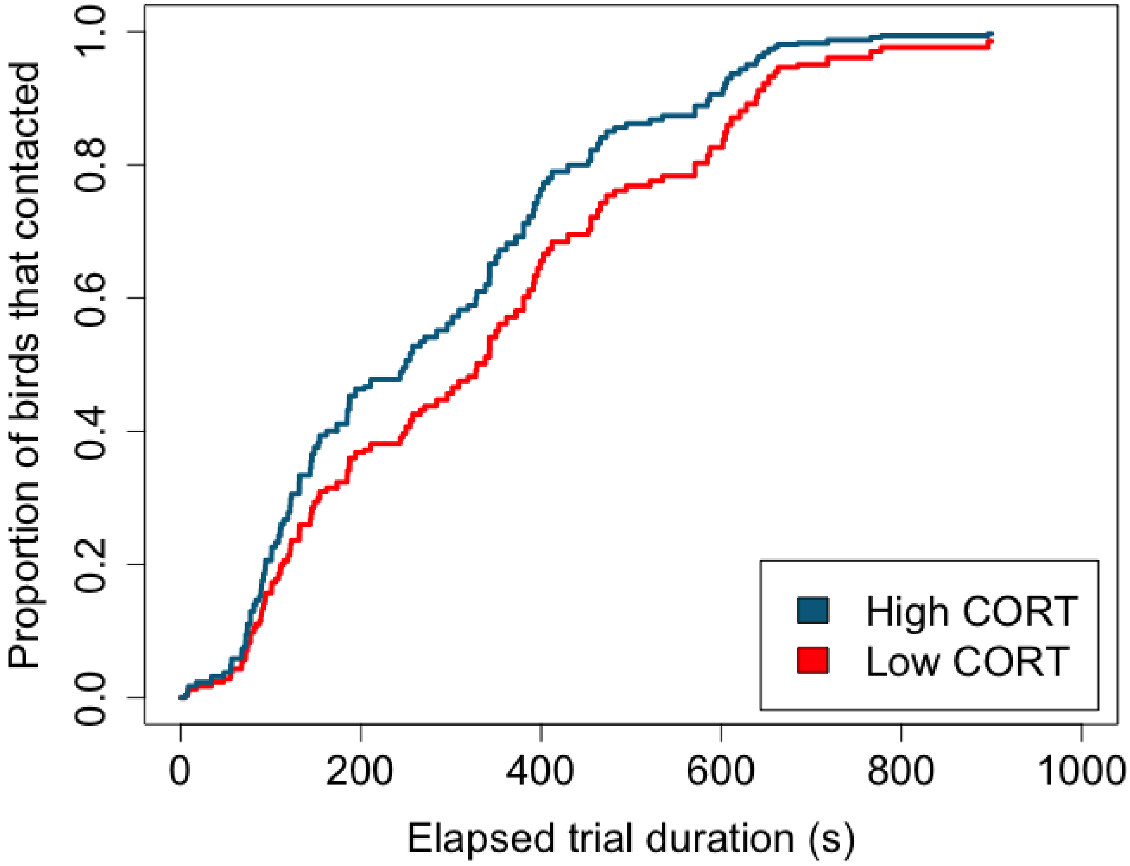

Figure 3.4. Relationship between baseline levels of plasma corticosterone and the proportion of birds that contacted a novel food item over the trial. The 25th percentile (red) and 75th percentile (blue) of corticosterone values are shown (reflecting the model estimate for this variable) while holding all other predictors at their mean. To control for the repeated trials per individual, average latencies to contact a novel food were used for this plot, although analyses were conducted at the level of trials.

Consumer Innovation

Chickadees ate the available sunflower seed in 96.6% (431/446) of trials in which at least one food item was contacted. The novel food item was at least partially eaten in 59.1% (233/394) of trials (Almond: 110/131, Egg: 54/140, Rice: 69/123).

When assessing the characteristics of innovative consumers, our model selection procedure returned four top models (Table S3.4). Birds showed the highest probability of consuming novel food in the almond trials compared to both egg and rice trials (Figure 3.5). As was the case for the analysis on food neophobia, the results of model averaging show a positive relationship between corticosterone levels and the probability of consuming a novel food item (Figure 3.5). However, there was no relationship between capture date and probability of consuming novel food. Additionally, year was influential, with birds tested in 2016 being less likely to consume novel food than those tested in 2015 (Table 3.2A).

When investigating dominance score as a predictor, our model selection procedure returned two top models (Table S3.5). Dominance and year were not found to be important predictors following model averaging (Table 3.2A). However, birds that were tested later in the season had a higher probability of tasting a novel food item.

Table 3.2. Model averaged estimates assessing the influence of individual and ecological characteristics on the probability of tasting a novel food item. (A: Full model: n=312 observations for 124 individuals, B: Dominance model: n=72 observations for 34 individuals)

	Parameter	*Estimate*	*Standard Error*	*Confidence interval*	*Relative importance*
A	(Intercept)	1.991	0.342	**(1.319, 2.663)**	--
	Trial(egg)	-2.443	0.399	**(-3.227, -1.659)**	1.00
	Trial(rice)	-1.965	0.392	**(-2.736, -1.195)**	1.00
	Year	-0.969	0.300	**(-1.560, -0.378)**	1.00
	Date	0.771	0.600	(-0.407, 1.948)	0.80
	Corticosterone	2.733	0.889	**(0.984, 4.482)**	1.00
	Age(Juvenile)	0.065	0.178	(-0.284, 0.415)	0.24
	Sex(Female)	-0.023	0.123	(-0.265, 0.219)	0.16
B	(Intercept)	1.334	0.558	**(0.219, 2.449)**	--
	Trial(egg)	-1.872	0.737	**(-3.343, -0.401)**	1.00
	Trial(rice)	-3.041	1.042	**(-5.121, -0.960)**	1.00
	Date	2.182	0.998	**(0.190, 4.174)**	1.00
	Dominance	-0.281	0.695	(-1.659, 1.097)	0.32

Confidence intervals that do not contain zero (i.e. no effect) are indicated in bold text. The reference levels for trial, and age are almond, and adult, respectively. Variables not retained in the set of top models (A: exploration, urban score) are not shown

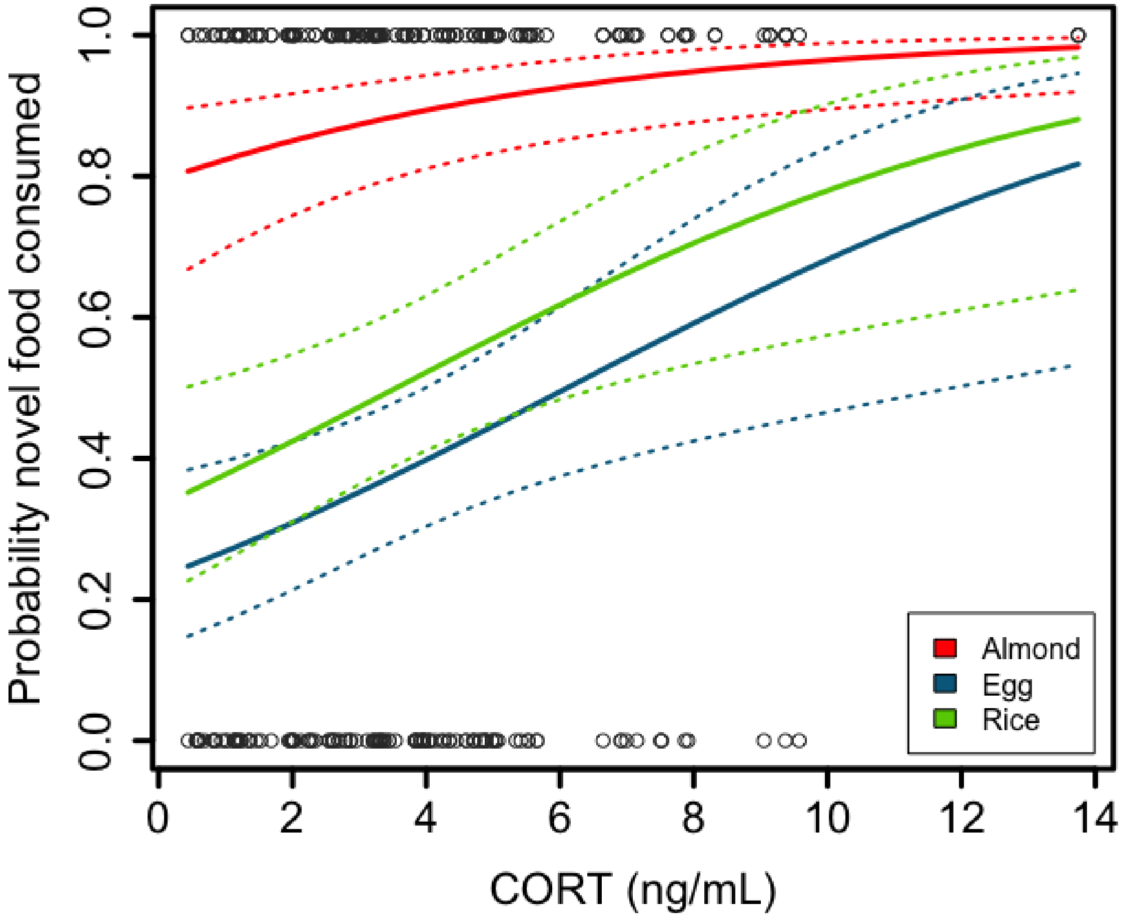

Figure 3.5. Relationship between baseline levels of plasma corticosterone and the probability of consuming a novel food item. Slopes for each food type reflect model estimates and were plotted while holding all other variables from the global model at their mean. Almond, egg, and rice trials are represented by the red, blue, and green lines respectively.

Correlates of baseline corticosterone

We found no significant correlation between body condition and corticosterone levels (Pearson's r=0.038, t=0.443, df=133, P=0.659). However, birds with higher corticosterone levels had more positive changes in body mass over the five days in captivity (Figure S3.1; Pearson's r = 0.210, t=2.468, df=132, P=0.015)

Repeatability

Food neophobia was found to be significantly repeatable across food types (R = 0.20, CI = 0.098 – 0.325, P < 0.001), while consumer innovation was not (R = 0.027, CI = 0 – 0.121, P = 0.299). Food neophobia was still significantly repeatable after removing all ceiling values for the latency to contact novel food (further improving normality, R = 0.268, CI = 0.144 – 0.406, P < 0.001).

Discussion

Here we provide an examination of the ecological, behavioural, and physiological predictors of the responses to novel food in individuals from a natural population. We tested the neophobic response exhibited by black-capped chickadees toward three novel food types and their propensity to taste each novel food as a measure of their consumer innovation response. The neophobic response was found to be predicted by food type, date, and baseline corticosterone levels of birds, while we found no support for a relationship with urbanization, dominance, or exploratory personality. The probability of tasting a novel food was also found to be predicted by food type and baseline corticosterone, but none of the other hypothesized effects were supported.

The level of urbanization of a bird's habitat did not predict its food neophobia or propensity for consumer innovation. This result matches the lack of relationship found by Sol et al. (2011) in common mynas. We expected that urban chickadees, as they are presumably being exposed to novel foods consistently in their habitat, would be more likely to approach and eat novel foods. However Marples et al. (2007) found that, although dietary wariness could be reduced with exposure to palatable novel food, this effect was easily reversed when the food was made unpalatable. So it may be the case that urban birds do not eat novel food more readily than their rural counterparts because they are consistently being exposed to unpalatable novel food types in addition to palatable ones. We also expected urban birds to be less neophobic than rural individuals because urban birds tend to be more exploratory than rural birds in our population (Thompson et al. 2018). However, it may be that animals do not respond to different types of novelty (e.g. environments, objects, foods) in the same way. This idea is also supported by the findings that spatial exploration was not associated with latency to consume novel food in house sparrows (Liebl and Martin 2014) and object neophobia did not predict consumer innovation in common mynas (Sol et al. 2012).

We found no evidence for a relationship between dominance, or its proxies (sex and age), and the responses of chickadees to novel food. Though dominance is meant to reflect differential access to resources, it may not have had an effect here because birds were tested in isolation and did not experience competition for familiar resources during their time in captivity. Experiments conducted in a social setting may allow relationships with dominance to emerge. For example, Visalberghi et al. (2003) gave a wild group of capuchins (*Cebus apella*) access to familiar and novel foods simultaneously and found that low-ranking monkeys manipulated and ate novel foods more frequently than high ranking individuals. However, the potential for socially facilitated consumption of novel food would need to be considered in such studies, as this has been demonstrated in multiple species (e.g. Forkman 1991; Ralphs et al. 1994; Visalberghi and Fragaszy 1995; Sherwin et al. 2002).

Baseline corticosterone levels were associated with both food neophobia and consumer innovation. Birds with higher levels of corticosterone were faster to contact novel foods and more likely to sample them. Additionally, higher baseline corticosterone levels were associated with larger increases in mass while in captivity. Together these results match expectations of baseline corticosterone as a metabolic hormone that increases foraging activity (Lohmus et al. 2006; Angelier et al. 2007; Crossin et al. 2012). Pravosudov et al. (2001) showed that mountain chickadees (*Poecile gambeli*) given access to unpredictable food resources had increased baseline corticosterone levels, and increased their body mass over the experimental period. These authors suggested that elevated baseline corticosterone levels may serve to promote adaptive behaviours associated with energy management that improve the chances of survival for animals in challenging environments. Perhaps increased baseline corticosterone levels improve survival in wintering chickadees via decreased food neophobia and an increased willingness to eat novel food items. Alternatively, there is a possibility that our baseline corticosterone values reflect differences in individual responses to captivity. However, they may demonstrate longer lasting differences between individuals particularly because the values were within the range observed in wild black-capped chickadees (Montreuil-Spencer 2017).

Furthermore, baseline corticosterone values have been found to be repeatable in chickadees (R = 0.28, Schoenemann & Bonier 2018).

Chickadees responded differently to the three food types that we used, and birds that were tested later in the season were less neophobic than those tested earlier. Individuals had the shortest latencies to contact, and highest probabilities of tasting novel food items, in the almond trials compared to both egg and rice trials. This may reflect the perception of almonds as being similar to the familiar sunflower seeds, but since the foods and trials differed in many aspects we are unable to determine if there is one in particular that led to these differences. The relationship between food neophobia and date of capture may be explained by a decrease in food availability across the season leading birds to become less neophobic. This explanation would further suggest that metabolic needs drive consumer innovation in chickadees. Although our study did not find changes in the willingness to consume novel food items across the season, lowered food neophobia may facilitate innovation in the wild and allow resident birds to survive through the winter (Sol et al. 2005). It is interesting to note that the relationship with date was detected despite birds being kept under standardized conditions in indoor aviaries, which may reflect a persistence of their natural motivations while in captivity.

We found that food neophobia was significantly repeatable across food types in chickadees, but consumer innovation was not. This is surprising given that these two responses were associated with some of the same predictors, but perhaps shows that they are indeed distinct responses to novel food. Studies showing that dietary wariness can be deactivated and reactivated with exposure to different foods would suggest that propensity for consumer innovation is not a repeatable trait. However, some researchers (e.g. Marples et al. 1998;

Thomas et al. 2010) have identified a dichotomy separating dietarily conservative consumers (those that show a long lasting reluctance to incorporate novel foods into their diet even after sampling them) and adventurous consumers (those that consume novel foods once their initial neophobic response is overcome). Additionally, genetic variation in dietary conservatism has been demonstrated in Japanese quail (*Coturnix coturnix japonicus*, Marples and Brakefield 1995). Investigation into the level of repeatability of consumer innovation in other species would be an interesting avenue for future research.

In conclusion, we found that physiological state is associated with individual differences in both food neophobia and consumer innovation. These responses to novel food also relate to the type of food presented. Furthermore, food neophobia was found to be related to the date that individuals are tested during the fall season. These similarities and differences in the predictors of food neophobia and consumer innovation, as well as the fact that only food neophobia was found to be significantly repeatable, show that there is still much to learn about the factors that affect these responses to novel food, and the relationships between different facets of them. Experimental manipulations of food availability would allow for a deeper investigation of the relationships between these responses and the predictors studied here. Further research into this area would also allow for a deeper understanding of the differences between different types of innovation and how these may relate to the success of animals facing different environmental challenges.

Chapter 4

General Conclusion

As environments continue to be altered by human activity animals around the globe will need to adjust to these changes. Behavioural innovation may be one method to deal with changing habitats. Researchers have put much attention into trying to ascertain which individual or environmental characteristics facilitate the use of innovative behaviour. Individual problem-solving performance is often used to understand the propensity for technical innovation within species, but the studies employing this method have shown mixed results concerning the predictors of problem-solving performance. Intra-specific variation in the propensity for consumer innovation has not received as much attention, but past research would suggest that it may not be associated with the same characteristics as technical innovation. My work aimed to contribute to this literature by examining the relationship between individual and ecological characteristics and the individual propensity for technical and consumer innovation in black-capped chickadees. In chapter 2 of this thesis I predicted that greater problem-solving performance and persistence would be associated with greater exploratory tendency and urbanization, and lower dominance rank. In chapter 3 I predicted that a greater willingness to contact and eat novel food items would be associated with greater exploratory tendency, urbanization, and baseline levels of corticosterone, and lower dominance rank.

I found that characteristics predicting innovative propensity differ between two tasks with different features and between technical and consumer innovation. For the lever-pulling task, dominant individuals tended to outperform subordinates if they were caught at rural, but not urban sites. This goes against expectations from the necessity drives innovation hypothesis, and may be partly explained by adults (with potentially relevant past experience) outperforming juveniles in this task. Additionally, I found that more exploratory individuals were better performing lever pullers than less exploratory birds, which matched my prediction. None of the predictors studied were associated with performance in the paper-ripping task. When examining the predictors of problem-solving persistence, rural birds were found to be more persistent paper rippers than individuals from urbanized habitats. The differing results for each task likely reflect their unique characteristics, including whether the food reward was visible, the different motor actions required to solve each one, and the presence or absence of a food-deprivation period before the trials. When analyzing the predictors of food neophobia and consumer innovation I found that higher baseline corticosterone levels were associated with both shorter latencies to contact novel food and greater probabilities of consuming it. However, dominance, exploration, and urbanization did not predict either food neophobia or consumer innovation.

The differing results of each research chapter provide support for the idea that technical and consumer innovation reflect distinct processes. Innovation may be a domain-specific rather than domain-general ability. In other words, individuals that are innovative in the context of consuming novel food may not be innovative when solving problems or in their social interactions. It may be that these two types of innovation are alternative strategies for dealing with energy demands, with technical innovation allowing for increased foraging efficiency and consumer innovation allowing for the addition of new resources to the diet (Lee 2003). Studies investigating the effect of manipulating resource availability on technical and consumer innovation may shed light on this possibility.

My work suggests that the likelihood of both technical and consumer innovation depend on the type of problem or food that is presented to an animal. Future studies would benefit from testing the consistency of innovation using tasks or foods that differ in well-defined ways. For example, Tebbich et al. (2016) suggest one way researchers should begin to test the generalizability of innovativeness is by presenting animals with perceptually different tasks (e.g. food visible vs. food hidden) that require the same motor actions to solve. This is thus an interesting avenue for further research assessing individual consistency in innovativeness.

Another question that has not received much attention is whether innovative ability is heritable. Quinn et al. (2016) found that problem-solving performance was not heritable in great tits and individual variation in innovativeness resulted from environmental variables. Innovation has usually been considered as a distinct trait, but has recently been thought of as being an emergent property arising from an array of traits that impact responses to environmental variation (Griffin 2016, Sol et al. 2016). If innovation is an emergent property then it would not itself be heritable or under selection (Griffin 2016). Investigation into the heritability of the traits associated with innovativeness would help in understanding the evolution of innovative abilities.

Overall the work communicated in this thesis contributes to our understanding of which individuals within a species are likely to innovate in different circumstances. I am hopeful that this work will promote further investigation into the understudied topic of consumer innovation, and the relationship between different facets of innovation, which should contribute to our understanding of its evolution and underlying mechanisms.

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Appendix

Table S2.1. Model averaged estimates assessing the influence of predictors on (A) lever-pulling persistence (n = 39 individuals), (B) paper-ripping performance (n = 33 individuals, solutions = 17), and (C) paper-ripping persistence (n = 36 individuals). The reference level for habitat is rural. Variables not retained in the set of top models are not shown (A – latency to solve or censor, dominance:habitat; B – dominance:habitat; C – exploration, dominance:habitat). Confidence intervals that exclude zero are shown in bold text.

	Parameter	Estimate	Standard Error	Confidence interval	Relative importance
A	(Intercept)	3.232	0.150	**(2.928, 3.536)**	--
	Exploration	-0.476	0.548	(-1.568, 0.616)	0.57
	Dominance	-0.119	0.289	(-0.698, 0.460)	0.28
	Habitat (Urb)	0.035	0.133	(-0.232, 0.302)	0.13
B	Contacts	22.795	4.325	**(14.319, 31.271)**	1.00
	Habitat (Urb)	-0.707	0.831	(-2.337, 0.922)	0.60
	Exploration	0.273	0.780	(-1.255, 1.802)	0.29
	Dominance	-0.071	0.455	(-0.964, 0.821)	0.13
C	(Intercept)	2.959	0.200	**(2.551, 3.367)**	--
	Latency to solve or censor	-1.950	0.417	**(-2.801, -1.099)**	1.00
	Habitat(Urb)	-0.643	0.271	**(-1.196, -0.091)**	1.00
	Dominance	0.144	0.324	(-0.505, 0.793)	0.30

Table S2.2. Model averaged estimates assessing the influence of predictors on (A) lever-pulling performance (n = 39, solutions = 23) and (B) paper-ripping performance (n = 36, solutions = 20) prior to removing influential observations. Variables not retained in the set of top models (B – dominance:urbanization) are not shown. The reference level for habitat is rural. Confidence intervals that exclude zero are shown in bold text.

	Parameter	Estimate	Standard Error	Confidence interval	Relative importance
A	Habitat (stratified)	--	--	--	1.00
	Contacts	3.286	0.969	**(1.387, 5.185)**	1.00
	Dominance	3.281	1.748	(-0.145, 6.706)	1.00
	Dom:habitat(Urb)	-2.531	2.247	(-6.934, 1.872)	0.74
	Exploration	1.094	0.933	(-0.736, 2.923)	0.74
B	Contacts	10.394	2.388	**(5.714, 15.073)**	1.00
	Dominance	0.176	0.545	(-0.892, 1.243)	0.28
	Urbanization	-0.056	0.330	(-0.703, 0.590)	0.13
	Exploration	0.689	0.891	(-1.056, 2.435)	0.55

Table S2.3. Model averaged estimates assessing the influence of predictors on (A) lever-pulling performance (n = 34, solutions = 20) and (B) paper-ripping performance (n = 32, solutions = 17) after removing individuals from sites that did not meet requirements for transitivity. Variables not retained in the set of top models (B – dominance:urbanization) are not shown. Confidence intervals that exclude zero are shown in bold text.

	Parameter	Estimate	Standard Error	Confidence interval	Relative importance
A	Habitat (stratified)	--	--	--	1.00
	Contacts	2.811	1.184	**(0.492, 5.131)**	1.00
	Dominance	5.190	2.022	(1.227, 9.153)	1.00
	Dom:habitat(Urb)	-5.335	2.328	**(-9.898, -0.772)**	1.00
	Exploration	0.920	1.050	(-1.137, 2.977)	0.59
B	Contacts	17.306	3.401	**(10.640, 23.972)**	1.00
	Dominance	-0.079	0.485	(-1.030, 0.872)	0.17
	Urbanization	-1.696	1.340	(-4.322, 0.931)	0.81
	Exploration	0.159	0.648	(-1.111, 1.430)	0.20

Table S2.4. Model averaged estimates assessing the influence of predictors on (A) lever-pulling persistence (n = 34 individuals) and (B) paper-ripping persistence (n = 32 individuals) after removing individuals from sites that did not meet requirements for transitivity. The interaction term was removed from the lever-pulling model due to convergence issues. Variables not retained in the set of top models (A – latency to contact or censor, urbanization; B – exploration, dominance:urbanization) are not shown.

	Parameter	Estimate	Standard Error	Confidence interval	Relative importance
A	(Intercept)	3.235	0.147	(2.935, 3.536)	--
	Exploration	-0.279	0.515	(-1.305, 0.747)	0.33
	Dominance	-0.114	0.304	(-0.723, 0.494)	0.23
B	(Intercept)	2.537	0.152	**(2.225, 2.849)**	--
	Latency to solve or censor	-1.730	0.481	**(-2.714, -0.745)**	1.00
	Urbanization	-0.378	0.465	(-1.307, 0.551)	0.52
	Dominance	0.247	0.441	(-0.635, 1.130)	0.37

Table S2.5. Top candidate models assessing the predictors of lever-pulling performance.

Model	Predictors	df	logLik	AICc	ΔAICc	ω_i
1	Cont + dom + explor + str(hab) + dom:str(hab)	4	-40.251	88.5	0.00	0.6
2	Cont + dom + str(hab) + dom:str(hab)	3	-41.661	89.3	0.81	0.4

Table S2.6. Top candidate models assessing the predictors of lever-pulling performance after replacing dominance with age and sex.

Model	Predictors	df	logLik	AICc	ΔAICc	ω_i
1	Age + cont + explor	3	-94.566	195.1	0.00	0.512
2	Age + sex + cont + explor	4	-94.135	196.3	1.14	0.289
3	Age + cont + explor + urban	4	-94.510	197.0	1.90	0.199

Table S2.7. Top candidate models assessing the predictors of lever-pulling persistence.

Model	Predictors	df	logLik	AICc	ΔAICc	ω_i
1	explor	4	-164.663	338.5	0.00	0.308
2	NULL	3	-166.080	338.8	0.34	0.260
3	Explor +urban	5	-163.998	339.8	1.31	0.160
4	dom	4	-165.366	339.9	1.41	0.153
5	Dom + explor	5	-164.293	340.4	1.90	0.119

Table S2.8. Top candidate models assessing the predictors of paper-ripping performance.

Model	Predictors	df	logLik	AICc	ΔAICc	ω_i
1	Cont + urban	2	-18.138	40.3	0.00	0.426
2	Cont	1	-19.853	41.7	1.43	0.209
3	Cont + explor + urban	3	-17.910	41.8	1.55	0.196
4	Cont + dom + urban	3	-18.059	42.1	1.85	0.169

Table S2.9. Top candidate models assessing the predictors of paper-ripping persistence.

Model	Predictors	df	logLik	AICc	ΔAICc	ω_i
1	Cont + urban	5	-128.623	269.2	0.00	0.648
2	Cont + dom + urban	6	-127.787	270.5	1.22	0.352

Table S3.1. Model averaged estimates assessing the influence of variables on **(A)** food neophobia and **(B)** consumer innovation when replacing urban score with a binary habitat variable. Confidence intervals that do not contain zero are indicated in bold text. Variables not retained in the set of top models (A: exploration; B: exploration, habitat) are not shown.

	Parameter	*Estimate*	*Standard Error*	*Confidence interval*	*Relative importance*
A	Year (stratified)	--	--	--	1.00
	Age (juvenile)	-0.173	0.163	(-0.493, 0.147)	1.00
	Sex (female)	-0.294	0.164	(-0.616, 0.028)	1.00
	Trial (egg)	-0.586	0.154	**(-0.888, -0.284)**	1.00
	Trial (rice)	-0.715	0.164	**(-1.037, -0.393)**	1.00
	Habitat (urban)	0.277	0.170	(-0.056, 0.610)	1.00
	Date	0.783	0.429	(-0.058, 1.624)	1.00
	CORT	1.100	0.458	**(0.202, 1.997)**	1.00
	Date:Age (juvenile)	-0.508	0.599	(-1.683, 0.667)	0.69
	Date:Habitat (urban)	0.278	0.552	(-0.804, 1.361)	0.64
	Date:Sex (female)	-0.014	0.257	(-0.518, 0.491)	0.16
B	(Intercept)	2.382	0.387	**(1.621, 3.143)**	--
	Trial (egg)	-2.443	0.399	**(-3.227, -1.659)**	1.00
	Trial (rice)	-1.965	0.392	**(-2.736, -1.195)**	1.00
	Year	-0.969	0.300	**(-1.560, -0.378)**	1.00
	Date	0.771	0.600	(-0.407, 1.948)	0.80
	CORT	2.733	0.889	**(0.984, 4.482)**	1.00
	Age(Juvenile)	0.065	0.178	(-0.284, 0.415)	0.24
	Sex(Female)	-0.023	0.123	(-0.265, 0.219)	0.16

Table S3.2. Top candidate models assessing the predictors of food neophobia

Model	*Predictors*	*df*	*logLik*	*AICc*	*ΔAICc*	*ω_i*
1	Age + Sex + Trial + Date + CORT + str(year) + Urban + age:date	44	-1124.854	2352.6	0.00	0.209
2	Age + Sex + Trial + Date + CORT + str(year) + Urban + age:date + urban:date	43	-1125.653	2353.0	0.42	0.170
3	Age + Sex + Trial + Date + CORT + str(year) + Urban	44	-1124.907	2353.2	0.58	0.156
4	Sex + Trial + Date + CORT + str(year) + Urban	44	-1124.791	2353.7	1.12	0.119
5	Age + Sex + Trial + Date + CORT + str(year) + Urban + age:date + sex:date	44	-1125.018	2354.1	1.48	0.100
6	Age + Sex + Trial + Date + CORT + Explo + str(year) + Urban + age:date	45	-1123.649	2354.4	1.80	0.085
7	Age + Sex + Trial + Date + CORT + str(year) + Urban + urban:date	44	-1125.187	2354.5	1.88	0.082
8	Age + Sex + Trial + Date + CORT + str(year) + Urban + age:date + sex:date + urban:date	44	-1125.811	2354.5	1.92	0.080

Table S3.3. Top candidate models assessing the predictors of food neophobia (when including dominance in the global model).

Model	*Predictors*	*df*	*logLik*	*AICc*	*ΔAICc*	*ω_i*
1	Trial + Date + Dominance	4	-203.665	415.9	0.00	0.726
2	Trial + Date	4	-204.180	417.9	1.95	0.274

Table S3.4. Top candidate models assessing the predictors of consumer innovation

Model	*Predictors*	*df*	*logLik*	*AICc*	*ΔAICc*	*ω_i*
1	Trial + Year + Date + CORT	7	-171.477	357.3	0.00	0.402
2	Age + Year + Trial + Date + CORT	8	-170.959	358.4	1.07	0.235
3	Year + Trial + CORT	6	-173.203	358.7	1.36	0.204
4	Sex + Year + Trial + Date + CORT	8	-171.346	359.2	1.84	0.160

Table S3.5. Top candidate models assessing the predictors of consumer innovation when including dominance in the global model.

Model	*Predictors*	*df*	*logLik*	*AICc*	*ΔAICc*	ω_i
1	Trial + Date	5	-39.896	90.7	0.00	0.684
2	Trial + Date + Dominance	6	-39.478	92.2	1.55	0.316

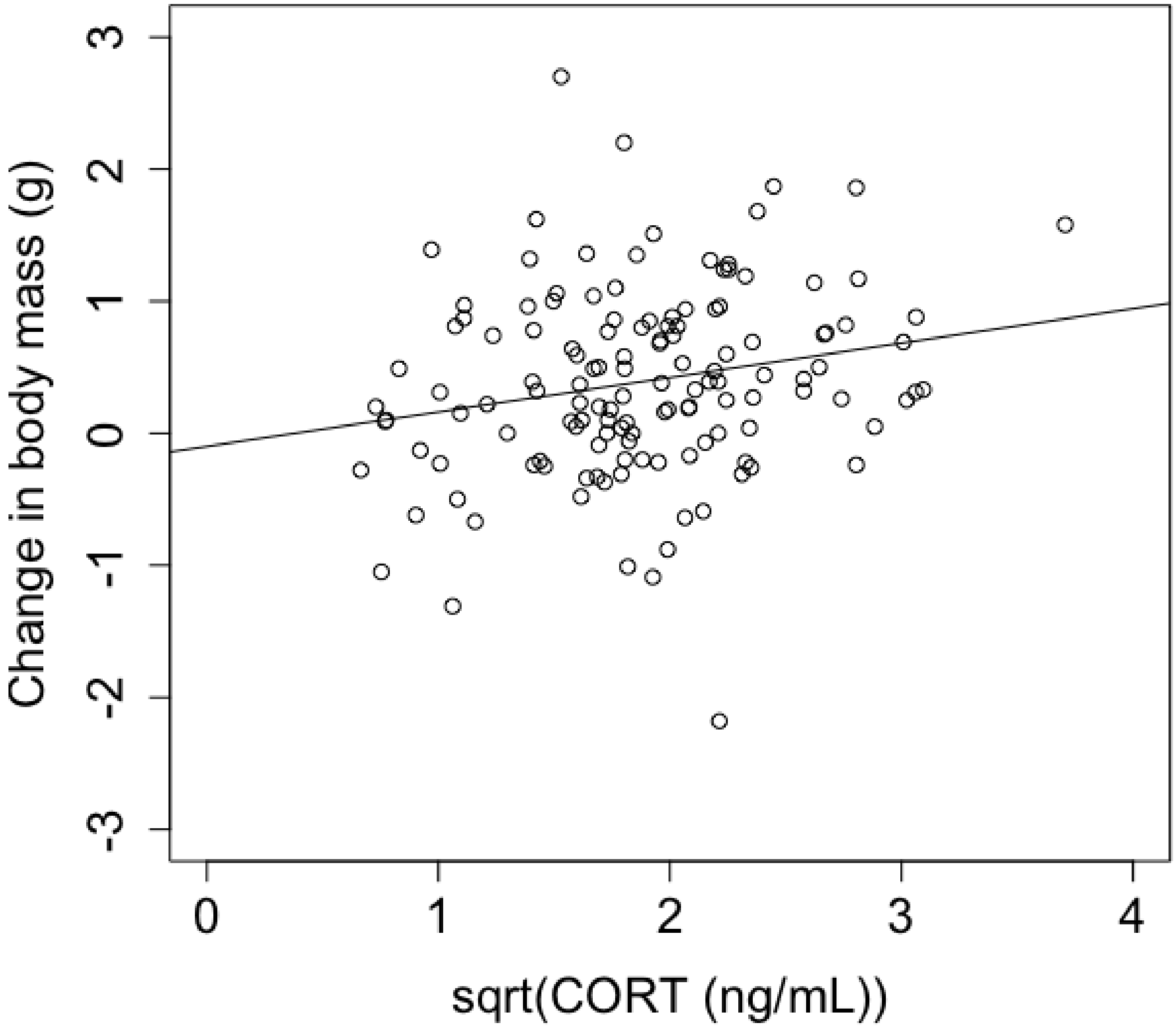

Figure S3.1. Relationship between the change in body mass while in captivity and baseline levels of plasma corticosterone.