Individual variation in information and its use

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Abstract.

Individuals within a population can vary in the way that they acquire, store, and act on information from the environment. Researchers have commonly looked at differences in genetic architecture, physical environment, or personality as possible causes of individual variation in cognition. Though cognition is defined as a suite of mechanisms involving the processing of information, we have yet to asses information (i.e. a numerical measure of the uncertainty of an outcome) as a possible cause of individual variation in cognition. This thesis seeks to understand the causes of individual variation in cognition by using approaches that allow quantifying and/or manipulating information acquisition or its use. In Chapter 1, I look at the link between information gathering and exploratory personality by testing the correlation between activity in a novel environment and attraction to novelty in wild-caught black-capped chickadees (*Poecile atricapillus*). My results validate exploratory personality assessed in an open field test as a measure of information gathering. Fast exploration of a novel environment was positively correlated with novelty seeking, suggesting that exploration is an information gathering strategy. In Chapter 2, I test for experience with informative vs non-informative cues as a cause for individual differences in decision making and learning performance. Here, I manipulated the informational properties (i.e. presence and number of reliable cues) of the developmental environment of juvenile captive zebra finches (*Taenopygia guttata*). This rare longitudinal and experimental examination of the effect of informative versus non-informative cues during development suggests that experience with informative cues can cause increased discrimination learning accuracy and decision-making speed later in life. Finally, in Chapter 3 I looked into individual variation in information use and decision making using a game theoretic approach. Using a producer-scrounger game, groups of zebra finches were exposed to varying seed distributions. Individual strategy choice in a social-foraging game was not significantly correlated with an individual’s experience with informative cues or learning performance. Still, contrary to my predictions, fear response significantly predicted strategy choice where more fearful individuals were more likely to choose a producer strategy. By addressing information as a parameter, my results suggest that information can affect individual variation depending on context.

Résumé

Les individus au sein d'une population peuvent varier dans la façon dont ils acquièrent, stockent et utilisent l'information de l'environnement. Les chercheurs ont généralement examiné les différences d'architecture génétique, d'environnement physique ou de personnalité comme causes possibles de la variation individuelle dans la cognition. Bien que la cognition soit définie comme une suite de mécanismes impliquant le traitement de l'information, l'information (c'est-à-dire une mesure numérique de l'incertitude d'un résultat) comme cause possible de variation individuelle dans la cognition n'a pas encore été examinée. Cette thèse cherche à comprendre les causes de la variation individuelle dans la cognition en utilisant des approches qui permettent de quantifier et/ou de manipuler l'acquisition d'information ou son utilisation. Dans le chapitre 1, j'examine le lien entre la collecte d'information et la personnalité exploratoire en testant la corrélation entre l'activité dans un nouvel environnement et l'attrait pour la nouveauté chez les mésanges à tête noire capturées dans la nature (Poecile atricapillus). Mes résultats valident le test d'« open field » de la personnalité exploratoire comme mesure de collecte d'information. L'exploration d'un nouvel environnement était positivement corrélée à l'attraction envers la nouveauté, suggérant que l'exploration est une stratégie de collecte d'information. Dans le chapitre 2, j'examine l'expérience avec des indices informatifs vs. non-informatifs comme cause de différences individuelles dans la prise de décision et la performance d'apprentissage. Ici, j'ai manipulé les propriétés informationnelles (c'est-à-dire la présence et le nombre d'indices fiables) de l'environnement de développement des jeunes diamants mandarins (*Taenopygia guttata*). Cette rare étude longitudinale et expérimentale de l'effet des indices informatifs par rapport aux indices non informatifs pendant le développement suggère que l'expérience avec des indices informatifs peut entraîner une augmentation de la précision de l'apprentissage (discrimination) et de la vitesse de prise de décision plus tard dans la vie. Enfin, au chapitre 3, j'ai examiné les variations individuelles dans l'utilisation de l'information et la prise de décision en utilisant une approche de la théorie des jeux. Des groupes de diamants mandarins ont été exposés à diverses distributions de graines dans le contexte d'un jeu producteur-chapardeur. Le choix de la stratégie individuelle n'était pas significativement corrélé avec l'expérience d'un individu en matière de signaux informatifs, ni avec sa performance d'apprentissage. Le choix de la stratégie individuelle dans un jeu producteur-chapardeur n'était pas significativement corrélé avec l'expérience d'un individu pendant le développement ou sa performance d'apprentissage. Contrairement à mes prédictions, la néophobie prédisait de manière significative le choix de stratégie où les individus plus craintifs face à de nouveaux objets étaient plus susceptibles de choisir une stratégie de producteur. En traitant l'information en tant que paramètre, ma thèse indique que l'information peut affecter la variation individuelle, mais seulement dans certains contextes.

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Statement of Contributions.

Chapter 1 of this thesis is adapted from a manuscript published as a research article in the journal Ethology (Rojas-Ferrer et al, 2019). The pronoun “we” is used within the manuscript to include additional authors, however this thesis was produced by myself. Myself, Megan Thompson, and Dr. Julie Morand-Ferron helped with the capture and banding of wild black-capped chickadees (*Poecile atricapillus*) led by Celia Bodnar and Dr. Julian Evans. Megan Thompson assisted with data collection and analysis for the open-field test. Dr. Julian Evans provided further support for data analysis. Experimental design, data collection, analysis and write-up were done by myself in collaboration with Dr. Julie Morand-Ferron.

Chapter 2 of this thesis is adapted from a manuscript published as a research article in the journal Philosophical Transactions of the Royal Society B (Rojas-Ferrer & Morand-Ferron 2020). The pronoun “we” is used within the manuscript to include additional authors, however this thesis was produced by myself. I designed the study, collected data, ran statistical analyses and drafted the manuscript with the help of Dr. Julie Morand-Ferron.

Chapter 3 of this thesis is being adapted for submission as a research article. The pronoun “we” is used within the manuscript to include additional authors, however this thesis was produced by myself. Sanjay Prasher and Rayyan Akhand helped with data collection for the PS game. I designed the study, collected data, ran statistical analyses and drafted the manuscript with the help of Dr. Julie Morand-Ferron.

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Introduction.

Cognition is defined as a mechanistic basis of behavior through which individuals process information (Shettleworth 2001; Rowe and Healy 2014). Because animals are not omniscient and commonly have incomplete information about their environment, individuals must acquire information in order to reduce the uncertainty about their environmental state (Fawcett and Frankenhuis 2015). By gaining information (i.e. sampling), individuals are better able to track variable environments and make optimal decisions in order to decrease predation and starvation risks, while increasing mating opportunities and fitness (Stephens 1989; Houston and McNamara et al. 1993; Dall and Johnstone 2002; Dall et al. 2004). However, acquiring information can be costly as it requires individuals to invest time and energy in physically sampling their environment. Additionally, information can deteriorate over time and become obsolete (Koops 2004). Theoretically individuals could respond the same way to these costs in their environment, however, there are observable differences among individuals within the same population in how they respond to changes in their environment (Dingemanse and Wolf 2013).

Individual variation in cognition can be due to external factors (abiotic, biotic) and/or internal factors such as inheritance of parental traits (see Boogert et al. 2018). For instance, environments with fluctuating food resources (low environmental certainty) will require individuals to sample regularly in order to adaptively adjust to the changing conditions (Stephens 1987; Shettleworth et al. 1988; Dunlap and Stephens 2012). Alternatively, animals should stop acquiring new information and rely on previous experience when environment is stable and food resources are constant (high environmental certainty) (McLinn and Stephens 2006; Fawcett and Frankenhuis 2015). On the other hand, experimental evolution experiments on fruit flies (*Drosophila melanogaster*) have demonstrated increased learning abilities with attached reproductive physiological costs to the individual when populations were reared in different environmental certainty (Mery and Kawecki 2003; Dunlap and Stephens 2014). Consequently, cognitive traits vary within populations when exposed to differing environments.

Individuals can vary in how they acquire information where exploratory personality can influence how an animal moves and gains knowledge from its environment. Within the animal personality literature, consistent individual differences across time and contexts are quantified using repeatability estimates (Bell et al. 2009; Griffin et al. 2015). Repeatability values calculate the proportion of phenotypic variance due to among individual differences. Among the many personality traits that have been measured, exploratory personality is commonly defined as the individual differences in the acquisition of information as the animal moves through a novel environment (Verbeek et al. 1994; Reader 2015). Great tits (*Parus major*), for instance, that had higher exploratory scores measured in terms of number of flights and hops in a novel environment, were also found to gather more information from their environment than slow explorers (van cOverveld and Matthysen 2013; Arvidsson and Matthysen 2016). Hypothetically, individuals can either explore larger quantities of their environment and collect less detailed information or explore less of their environment and gather more accurate information (Verbeek et al. 1994; Kramer and McLaughlin 2001; Sih and Del Giudice 2012). However, there is a disconnect in the way that exploration has been defined and measured; exploration is often defined in terms of information acquisition, while measured in terms of movement speed and diversity of contacted items. By correlating exploratory personality and attraction to novelty, one could test if exploration is indeed a metric for information gathering (Adriaenssens and Johnsson 2010; Herborn et al.2014; Arvidsson and Matthysen 2016). Though attraction to novelty and exploration have been looked at previously, activity rate has commonly been a confounding variable when addressing sampling and novelty seeking (more active individuals will encounter novelty more frequently through chance alone).

Individuals can vary in their experiences and how they process information in terms of learning and decision-making. As animals confront different conditions, they will gain experience and acquire information throughout their development that can influence behavioral traits (Niemela et al. 2015). The ‘Fanning-out’ hypothesis suggests that differences in environmental stimuli and developmental trajectories can result in a divergence in behavioral traits in individuals within the same group (Stamps and Biro 2016). For instance, jumping spider (*Marpissa muscosa*) siblings that were raised in either a food deprived environment, social environment, or physically complex environment, were observed to develop significant difference in their latency to emerge from hiding and mean level of exploratory tendencies (Liedtke et al. 2015). Similarly, as individuals collect information about their environment through time and experience different environmental parameters, they will be better able to track environmental changes and have increased learning performance (Dunlap and Stephens 2012). Consequently, models on information acquired during early development predict individual variation in cognitive traits later in life (Frankenhuis and Panchanathan 2011; Stamps and Krishnan 2014; English et al. 2016). For instance, juvenile African cichlid fishes (*Simochromis pleurospilus*) that experienced environmental fluctuation in the form of changes in feeding rations were found to outperform individuals that experienced stable feeding rations when tested in an associative learning task during adulthood (Kotrschal and Taborsky 2010). However, there are few empirical studies addressing the link between developmental environment to variation in cognitive traits later in life.

Individuals within the same group can vary in how they use information. Within social-foraging groups, individual foragers can differ in how they choose to acquire resources. In producer-scrounger (P-S) game-theoretic models, foragers have the choice between investing time and energy in searching for food (i.e. producer) or exploiting the efforts of others and joining them in their discoveries (Barnard and Sibly 1981; Vickery et al. 1991). The P-S model has three basic assumptions: (1) there is a negative frequency-dependent payoff for the scrounger strategy where the payoff increases when less individuals choose to scrounge, (2) there is complete incompatibility between strategies (individuals cannot search for food and observe other conspecifics simultaneously), and (3) producers get a proportion of resources before the arrival of scroungers known as the finder’s share. Additionally, individuals often have the ability to switch between strategies (Giraldeau and Dubois 2008). Studies have looked into determinants of strategy choice in terms of resource abundance and distribution (Beauchamp 2008), group size (Caraco and Giraldeau 1991; Coolen 2002), metabolic rate (Wu and Giraldeau 2005; Mathot et al. 2009), finder’s share (Hamilton 2002), and others. More so, models have focused on the evolution of learning by using the P-S game as a template to understand how learning as an adaptive strategy can act as mutation that can spreads through a population (Katsnelson et al. 2012; Dubois et al. 2010). However, there has been a limited number of studies addressing how cognitive traits and experience with information acquisition could serve as determinants of strategy choice in a P-S game.

The aim of this thesis is to understand the causes of individual variation in cognition by using approaches that allow quantifying and/or manipulating information acquisition or its use. I first look at the link between individual variation in information gathering and animal personality where I hypothesize that exploratory personality is a metric for information gathering using an open-field test. I then look at experience with informative cues throughout development (i.e. information processing) and its consequences on learning performance and decision speed later in life. I hypothesize that varying levels of informative cues in an individual's developmental environment will cause variation in cognitive traits and decision-making. Specifically, as experience with informative cues increases, so should learning performance later in life. Finally, I look at individual variation in information use using a game theoretic approach where I look at cognitive traits (i.e. experience with informative cues and learning performance) as well as individual reaction to novelty as possible determinants of strategy choice and plasticity of choice in a social-foraging game. Overall, I seek to address information as a parameter as a possible source of individual variation in cognitive traits among conspecifics.

References.

Adriaenssens, B., & Johnsson, I. “Shy trout grow faster: exploring links between personality and fitness-related traits in the wild.” *Behavioral Ecology* 22 (2011): 135–143.

Arvidsson, Lisa K., and Erik Matthysen. "Individual differences in foraging decisions: information-gathering strategies or flexibility?" *Behavioral Ecology* 27.5 (2016): 1353-1361.

Barnard, Chris J., and Richard M. Sibly. "Producers and scroungers: a general model and its application to captive flocks of house sparrows." *Animal behaviour* 29.2 (1981): 543-550.

Beauchamp, Guy. "What is the magnitude of the group-size effect on vigilance?" *Behavioral Ecology* 19.6 (2008): 1361-1368.

Bell, Alison M., Shala J. Hankison, and Kate L. Laskowski. "The repeatability of behaviour: a meta-analysis." *Animal behaviour* 77.4 (2009): 771-783.

Boogert, Neeltje J., et al. "Measuring and understanding individual differences in cognition." *Philosophical Transactions of the Royal Society B* (2018): 20170280.

Caraco, Thomas, and Luc-Alain Giraldeau. "Social foraging: producing and scrounging in a stochastic environment." *Journal of Theoretical Biology* 153.4 (1991): 559-583.

Coolen, Isabelle. "Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*)." *Behavioral Ecology and Sociobiology* 52.3 (2002): 232-238.

Dall, Sasha RX, Alasdair I. Houston, and John M. McNamara. "The behavioural ecology of personality: consistent individual differences from an adaptive perspective." *Ecology Letters* 7.8 (2004): 734-739.

Dall, Sasha RX, and Rufus A. Johnstone. "Managing uncertainty: information and insurance under the risk of starvation." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357.1427 (2002): 1519-1526.

Dingemanse, Niels J., and Max Wolf. "Between-individual differences in behavioural plasticity within populations: causes and consequences." *Animal Behaviour* 85.5 (2013): 1031-1039.

Dubois, Frédérique, Julie Morand-Ferron, and Luc-Alain Giraldeau. "Learning in a game context: strategy choice by some keeps learning from evolving in others." *Proceedings of the Royal Society B: Biological Sciences* 277.1700 (2010): 3609-3616.

Dunlap, Aimee S., and David W. Stephens. "Experimental evolution of prepared learning." *Proceedings of the National Academy of Sciences* 111.32 (2014): 11750-11755.

Dunlap, Aimee S., and David W. Stephens. "Tracking a changing environment: optimal sampling, adaptive memory and overnight effects." *Behavioural processes* 89.2 (2012): 86-94.

English, Sinead, et al. "Adaptive use of information during growth can explain long-term effects of early life experiences." *The American Naturalist* 187.5 (2016): 620-632.

Fawcett, Tim W., and Willem E. Frankenhuis. "Adaptive explanations for sensitive windows in development." *Frontiers in Zoology* 12.S1 (2015): S3.

Frankenhuis, Willem E., and Karthik Panchanathan. "Individual differences in developmental plasticity may result from stochastic sampling." *Perspectives on Psychological Science* 6.4 (2011): 336-347.

Giraldeau, Luc-Alain, and Frédérique Dubois. "Social foraging and the study of exploitative behavior." *Advances in the Study of Behavior* 38 (2008): 59-104.

Griffin, Andrea S., Lauren M. Guillette, and Susan D. Healy. "Cognition and personality: an analysis of an emerging field." *Trends in Ecology & Evolution* 30.4 (2015): 207-214.

Hamilton, Ian M. "Kleptoparasitism and the distribution of unequal competitors." *Behavioral Ecology* 13.2 (2002): 260-267.

Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. “Personality predicts behavioral flexibility in a fluctuating, natural environment.” *Behavioral Ecology* 25.6 (2014): 1374–1379.

Houston, Alasdair Ian, John M. McNamara, and John MC Hutchinson. "General results concerning the trade-off between gaining energy and avoiding predation." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 341.1298 (1993): 375-397.

Katsnelson, Edith, et al. "Individual-learning ability predicts social-foraging strategy in house sparrows." *Proceedings of the Royal Society B: Biological Sciences* 278.1705 (2011): 582-589

Koops, Marten A. "Reliability and the value of information." *Animal Behaviour* 67.1 (2004): 103-111.

Kotrschal, Alexander, and Barbara Taborsky. "Environmental change enhances cognitive abilities in fish." *PLoS Biol* 8.4 (2010): e1000351.

Kramer, Donald L., and Robert L. McLaughlin. "The behavioral ecology of intermittent locomotion." *American Zoologist* 41.2 (2001): 137-153.

Liedtke, Jannis, et al. "Early environmental conditions shape personality types in a jumping spider." *Frontiers in Ecology and Evolution* 3 (2015): 134.

Mathot, Kimberley J., et al. "Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of zebra finches." *Oikos* 118.4 (2009): 545-552.

McLinn, Colleen M., and David W. Stephens. "What makes information valuable: signal reliability and environmental uncertainty." *Animal Behaviour* 71.5 (2006): 1119-1129.

Mery, Frederic, and Tadeusz J. Kawecki. "A fitness cost of learning ability in *Drosophila melanogaster*." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270.1532 (2003): 2465 -2469.

Niemelä, Petri T., et al. "How does variation in the environment and individual cognition explain the existence of consistent behavioral differences?" *Ecology and Evolution* 3.2 (2013): 457-464.

Sih, Andrew, and Marco Del Giudice. "Linking behavioural syndromes and cognition: a behavioural ecology perspective." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367.1603 (2012): 2762-2772.

Reader, Simon M. "Causes of individual differences in animal exploration and search." *Topics in Cognitive Science* 7.3 (2015): 451-468.

Rowe, Candy, and Susan D. Healy. "Measuring variation in cognition." *Behavioral Ecology* 25.6 (2014): 1287 -1292.

Shettleworth, Sara J. "Animal cognition and animal behaviour." *Animal behaviour* 61.2 (2001): 277-286.

Shettleworth, Sara J., et al. "Tracking a fluctuating environment: a study of sampling." *Animal Behaviour* 36.1 (1988): 87-105.

Stamps, Judy A., and Peter A. Biro. "Personality and individual differences in plasticity." *Current Opinion in Behavioral Sciences* 12 (2016): 18-23.

Stamps, Judy A., and V. V. Krishnan. "Combining information from ancestors and personal experiences to predict individual differences in developmental trajectories." *The American Naturalist* 184.5 (2014): 647-657.

Stephens, D. W. "Variance and the value of information." *The American Naturalist* 134.1 (1989): 128-140.

van Overveld, Thijs, and Erik Matthysen. "Personality and information gathering in free-ranging great tits." *PloS one* 8.2 (2013): e54199.

Verbeek, Monica EM, Piet J. Drent, and Piet R. Wiepkema. "Consistent individual differences in early exploratory behaviour of male great tits." *Animal Behaviour* 48.5 (1994): 1113-1121.

Vickery, William L., et al. "Producers, scroungers, and group foraging." *The American Naturalist* 137.6 (1991): 847-863.

Wu, Gi-Mick, and Luc-Alain Giraldeau. "Risky decisions: a test of risk sensitivity in socially foraging flocks of *Lonchura punctulata*." *Behavioral Ecology* 16.1 (2005): 8-14.

Chapter 1: *Is exploration a metric for information gathering? Attraction to novelty and plasticity in black-capped chickadees*

Abstract.

Animals can learn about the value of resources and predation risk by exploring novel environments or exploring novel stimuli in their regular environments. Still, there is a disconnect in the way that exploration has been defined and measured; exploration is defined in terms of information acquisition, while measured in terms of movement speed and diversity of contacted items in a novel environment. If exploration is indeed a measurement of information gathering, fast explorers should seek to reduce uncertainty about their environment more than slow explorers. Exploration speed has also been linked to behavioral plasticity, where fast explorers move fast but collect less detailed information, thereby forming routines and expressing less plasticity than slow explorers. We test these two hypotheses by comparing exploration in a novel environment to individuals' attraction to novelty and behavioral plasticity. Our results support the view that exploration is a measurement of information-gathering tendencies as fast explorers were more likely to collect novel information, which should reduce uncertainty further than sampling familiar information sources, compared with slower explorers. Furthermore, faster explorers switched to sampling novel information more quickly than slow explorers when the value of the familiar option decreased, opposing the widely held view that faster explorers present more routine-like behavior. By providing familiar and novel foraging options in close spatial contiguity, we demonstrate an attraction to novelty in faster explorers that cannot be confounded by activity rate, thereby suggesting that these individuals seek to reduce uncertainty. In conclusion, our results support the biological validity of the term “exploration” through its association with information gathering.

Keywords. age differences, behavioral plasticity, experience, open field test, personality, sampling

Introduction.

By gaining information about its environment, an animal can reduce uncertainty which increases its likelihood of making more adapted choices about mates, predation, or resources (Mathot, Wright, Kempenaers, & Dingemanse, 2012; Schmidt, Dall, & van Gils, 2010; Shettleworth, Krebs, Stephens, & Gibbon, 1988; Stephens & Krebs, 1986). Uncertainty is caused by an animal's lack of knowledge about some aspect of its environment and should thus be maximum when encountering a new stimuli or location (Foley & Marjoram, 2017; Inglis, 2000). Individuals can gain knowledge via exploration, often defined as the acquisition of information as the animal moves through the environment (Verbeek, Drent, & Wiepkema, 1994). Under this definition, "fast explorers" seek novelty and thereby rapidly reduce uncertainty about their environment. Alternatively, slow explorers move through their environment more slowly and, as a consequence, are able to gather more detailed information in comparison with fast explorers; this would lead to a negative correlation between locomotion and information gathering, that is "slow but thorough" explorers (Mathot et al., 2012; Verbeek et al., 1994). To this point, little research has been done to formally assess whether traditional exploration measures gathered in open field tests reflect information-gathering processes (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Perals, Griffin, Bartomeus, & Sol, 2017), despite the key role of exploration tests in studies on the ecology and evolution of animal personality (Bergeron et al., 2013; Dingemanse, Both, Drent, & Tinbergen, 2004; Le Galliard, Paquet, Cisel, & Montes-Poloni, 2013). Indeed, exploration scores derived from novel environment tests have been used in studies investigating the fitness consequences of personality in natural populations (Dingemanse et al., 2004), artificial selection experiments (Baugh et al., 2012; van Oers, de Jong, Drent, & van Noordwijk, 2004), and assessments of genetic (van Oers & Mueller, 2010), physiological (Arnold et al., 2016; Baugh et al., 2012), and environmental (Edenbrow & Croft, 2013; Miller, Bugnyar, Pölzl, & Schwab, 2015) determinants of exploration- related behavior.

In 1994, Verbeek et al. found that male great tits (*Parus major*) that visited all five artificial trees in a novel environment more quickly also switched between trees more frequently, suggesting that they explored their environment faster but more superficially. Furthermore, while fast explorers in this study repeatedly chose a previously rewarding feeder regardless of changes in food availability, slow explorers switched to a different feeder when their current feeder proved to be unrewarding. These findings have served as the basis for many studies where fast explorers are predicted to be routine-like and slow explorers are predicted to be more plastic in their behaviors. Still, studies have found mixed results on the relationship between exploration and behavioral plasticity measured in the context of a change in the value of resources (e.g., reversal learning; Bebus, Small, Jones, Elderbrock, & Schoech, 2016; Guillette, Baron, Sturdy, & Spetch, 2017), abiotic conditions (e.g., temperature; Herborn, Heidinger, Alexander, & Arnold, 2014), or biotic conditions (e.g., predation risk; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). For instance, in Herborn et al. (2014) fast explorers were reported to change feeders more frequently in response to temperature changes, while slow explorers in Adriaenssens and Johnsson (2010) were suggested to have increased plasticity as they were observed to have higher activity rate with increased experience. A possible explanation for these mixed results is that fast explorers perceive environmental changes and novelty more quickly and adjust their behavior more readily than slow explorers (Mathot et al. 2012). More work is needed to understand how exploratory behavior correlates with behavioral plasticity.

Arvidsson and Matthysen (2016) described two hypotheses on the nature of the relationship between exploration, novelty seeking, and plasticity. In the “information-gathering strategy” hypothesis (IGS), exploratory tendency influences an individual's sampling behavior (Arvidsson & Matthysen, 2016). Sampling refers to the investment of time and energy in the gathering and storing of information (Mathot et al., 2012). We test this hypothesis in the context of attraction to novelty, a context where Arvidsson and Matthysen (2016) found no support for the IGS hypothesis, as their experiment with great tits revealed no relationship between exploration score and novelty seeking. We predict that when given a choice between a familiar and a novel option, fast explorers should preferentially select the novel option, as this novel option has yet to be sampled and its value should be the most uncertain (i.e., there is more information to be gained by sampling new over familiar options). The behavioral flexibility (BF) hypothesis assumes that slow explorers take their time to sample their environment and, in doing so, gain more detailed information ("slow but thorough" explorers; Verbeek et al., 1994). This sensitivity to information is then expected to cause slow explorers to respond to environmental changes such as the presence of predators, possible mates, and variation in food resources, more quickly and be more plastic in their behaviors (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Mathot et al., 2012; van Overveld & Matthysen, 2013). Conversely, fast explorers are assumed to be restrained from their lack of information and form routine-like behaviors (Coppens, De Boer, & Koolhaas, 2010; Verbeek et al., 1994); they are thus predicted to be more resistant to changes in the value of resources in their environment (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015; Sih & Del Giudice, 2012).

Our study aims to examine the link between exploratory behavior, novelty seeking, and behavioral plasticity by quantifying the movement and sampling tendencies of wild-caught black-capped chickadees (*Poecile atricapillus*). We test these two hypotheses by measuring the tendency to sample novel versus familiar information sources (IGS hypothesis) and the propensity to switch to a novel resource type when the value of the familiar resource decreases (BF hypothesis). We provide a multiple-choice scenario to individuals of known exploration score where spatially alternating familiar and novel options were presented to individuals (Figure 1). This design allows us, for the first time, to assess novelty seeking while experimentally controlling for individual differences in locomotion rate, as more active animals are not more likely to encounter novelty due to the contiguous placement of novel and familiar items. If exploration strategy is determined mainly by activity levels, then we would expect to see no significant difference in initial attraction to novelty between fast and slow explorers, because new and known items are equally distant in the environment. Alternatively, under the IGS hypothesis, we predict that faster explorers would be more likely than slower explorers to select the novel option over the familiar one at their first choice. We then examine the speed at which individuals decide to sample the novel option when the familiar option stops paying. Under the BF hypothesis, we predict slower explorers to be more plastic and change their behavior, that is, stop using the familiar option and switch to the novel option, more quickly than faster explorers. Here, we define behavioral plasticity as defined in Greenberg (2003), where plasticity is a modification in foraging behavior (Rockwell, Gabriel, & Black, 2012). Similar to Verbeek et al.

(1994), we use the “strength of a foraging habit” as the number of visits to a previously rewarding familiar option to measure behavioral plasticity. Finally, we examine the effect of recent experience with the familiar option and age, as it has been proposed that age might affect exploratory tendencies (Frankenhuis & Panchanathan, 2011), either via the time left to exploit knowledge (Eliassen, Jørgensen, Mangel, & Giske, 2007) and/or via its impact on the expected value of sampling a novel information source (Sherratt & Morand-Ferron, 2018).

Methods.

Study site and housing

We tested 69 black-capped chickadees of known age class during the non-breeding season from September 29, 2016 to December 1, 2016. We classified birds by age (juvenile, i.e. bird born last spring, or adult), based on shape and coloration of tail feathers (Meigs et al. 1983). Age class assessments are highly repeatable in the fall season, when we caught birds for this experiment. Indeed, 55/59 (93.2%) birds that were recaptured in our population within a fall season were blindly attributed the same age class by the same or a different observer. Birds were caught at 8 different sites within the region of Ottawa, Ontario, Canada, and were then individually housed in the Animal Care Facility at the University of Ottawa (day 1 of captivity). In the context of another study, birds were either captured from urban sites, which were partially forested city parks less than 10km from downtown Ottawa, or rural sites, completely forested areas more than 25km away from downtown Ottawa (Thompson et al. 2018). Individuals were housed singly and were visually isolated from other conspecifics, but were allowed auditory contact. Blood samples were collected from the brachial vein on the morning after all behavioral tests were completed to quantify baseline corticosterone levels, a covariate indicating baseline stress levels in captivity. All samples were collected within 3 minutes of capture from the home cage. Baseline corticosterone values fell within reported ranges for black-capped chickadees under both long-term captive (Pravosudov, Kitaysky, Wingfield, & Clayton, 2004) and wild (Montreuil-Spencer, 2017) conditions (for further details on the procedure, values, and confounding effects see Thompson et al. 2018). Blood samples were also used to obtain sex via PCR for most individuals, however as sex does not significantly impact exploration score either in black-capped chickadees (Thompson et al 2018) or the related great tit (Dingemanse et. al 2002; Arvidsson et al. 2017), we did not include this variable in our analyses.

Training

On day 2 of captivity, birds where trained to associate white 0.5cm cotton balls (“pompoms”) with food (i.e. sunflower seed with husks), and to remove pompoms from a single wooden block in their cage by using a gradual shaping procedure (free food, food partly hidden by half a pompom, food completely hidden behind a pompom).

On day 2, birds were further trained (6 trials) in their individual cage to remove pompoms from wooden blocks, this time with only one out of the 24 potential sites containing food. On day 3 and 4 of captivity, after the exploration test (see below), each bird was exposed to an “experience” task in which individuals first had 5 min to locate a freely-visible seed in a larger flight room (room A=3 x 3.3 x 2.3 m; room B=3.3 x 3 x 2.3 m). Successful birds (i.e. 95 out of 165 birds) re-entered the room 30min later and had to retrieve the food item, which was now hidden by a white pompom, as were all 59 other potential sites. We noted how many rewards (0, 1 or 2) were obtained by each individual during these two tests conducted in the flight room. These data on the number of rewards were used in the context of another study on spatial cognition (Thompson and Morand-Ferron 2019), but also served here to quantify variation in how rewarding the familiar option was for different individuals. It is to be noted that only one reward could be obtained per trial here, and thus birds experienced a low success rate with white pompoms.

Exploration test

On the third and fourth morning in captivity, we carried out a novel environment assay (a traditional test conducted with birds analogous to the open field test) to quantify exploration behaviours of individuals within the flight room that contained four artificial trees. The duration of hops (number of hops x 0.5s), duration of flights, number of visits to each of the 4 trees, and the number of visits to other features in the room (ceiling, floor, door handles, etc.) were recorded for 10 min (John L. Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). Behaviours were coded live by a single observer (MJT) using the software JWatcher (Blumstein et al. 2010). Inter-observer reliability was assessed by re-analysing 10 randomly chosen video-recorded trials and computing the sum of visits to the 4 trees, as well as the number of hops by a different observer (JMF). The Pearson correlation coefficients for the log-transformed number of tree visits and number of hops were: r=0.956 and r=0.953, respectively.

Information gathering and behavioral plasticity test

On the fourth day between 1300hr and 1730hr, individuals were given a choice between the familiar white 0.5cm cotton balls and novel colored 0.5cm cotton balls covering holes on artificial trees located in the flight room. Birds in room A (N=31) were exposed to blue as the novel colour, while the novel colour in room B was purple (N=38). Cotton balls were placed within each of the 59 holes in artificial trees, ensuring that each row and column alternated regularly between colored and white pompoms on all four artificial trees (Fig.1). We excluded the site where food was previously located in the experience test (no pompom). An individual bird was then allowed to enter the flight room for 8 minutes. We recorded the first choice (novel vs familiar pompom color) as a metric for initial attraction to novelty to test the IGS hypothesis. Additionally, we quantified the number of white pompoms removed before a novel colored pompom was selected (or the trial ended) to test the BF hypothesis. None of the pompom colors were rewarded during this test.

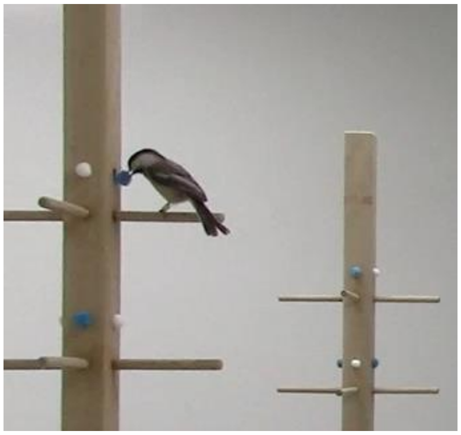

Figure 1. Individual black-capped chickadee removes a novel-colored pompom (out of 29 novel and 29 familiar-colored pompoms) in the information-gathering and behavioral plasticity test.

Statistical analysis.

We entered the 6 exploration variables (i.e. duration of hops, duration of flights, number of visits to tree 1, 2, 3 and 4) into a principal components analysis to generate an exploration score (John L. Quinn et al., 2009; Thompson, Evans, Parsons, & Morand-ferron, 2018). Exploration scores were generated using the first principal component (eigenvalue=2.21; Kaiser 1960) which explained 81.7% of the variance (see Table 1 for factor loadings). Individual exploration scores using this approach on a larger sample of birds were found to be significantly and moderately repeatable and are therefore inferred to be representative of an individual's exploratory personality (*N*=127, *R*=0.47, CI=0.41 ±0.51, *P*<0.001; Thompson et al. 2018). Baseline corticosterone, sex, date, and time of day were not found to affect exploration behaviours in this larger sample. As well, age was not found to affect mean exploration score in the novel environment, but juvenile birds were found to decrease exploration behaviours more rapidly over time during this assay than adults (Thompson et al. 2018).

We used binomial generalized linear models (GLM) to analyse first choice between white or colored pompoms (0, 1) in relation to the following fixed effects: age class (juvenile or adult), exploration PCA score, number of rewards with familiar pompoms (0, 1, 2), date, capture habitat (urban or rural), baseline corticosterone, novel color (blue or purple), and order tested. Baseline corticosterone was found to be non-significant (χ^2= 0.547, *P*=0.460) and was excluded from further models due to reduced sample size resulting from missing values (*n*=15). We built a model with all other fixed effects and included two-way interactions between exploration score, previous rewards with familiar pompoms, and age. Interactions were removed one-by-one by dropping the least significant effect until only significant or no interactions were retained.

Then we analyzed the number of white (i.e. familiar) pompoms that each individual chose before switching to a colored pompom. We applied the same procedure as outlined above for first choice, now using a Poisson GLMM including an observation-level random effect that successfully accounted for overdispersion (Harrison, 2014). Again, baseline corticosterone was not significant (χ^2=1.392, *P*=0.238) and was excluded from further models due to missing values. Due to convergence issues, we used a backward stepwise model reduction of the fixed-effect procedural variables (date, novel color, and order tested). We then separately tested each two-way interaction between exploration score, number of rewards with familiar pompoms (0, 1, 2), and age class (juvenile or adult), while controlling for each of these main effects and habitat (urban, rural). All analyses were conducted in R statistical software (R Development Core Team 2016), with the lme4 package (Bates et al. 2014), after mean-centering continuous predictors.

Ethics.

Individuals were deprived of food for 30min before beginning all training and test trials, excluding the exploration tests. They had ad libitum access to water at all times. For each test conducted in the flight room, birds moved out of their cage and into the room through a tunnel in the wall that connected each cage to the flight room, using the light to entice movement towards and away from the room, which prevented handling and associated stress before conducting the assays (see also Pravosudov and Clayton 2002). Observations were made behind a one-way glass. All birds were released at their capture site within 5 days of capture. Work was conducted under University of Ottawa Animal Care protocols (1758-1759), Canadian Wildlife Service Banding permit (10854), and Ministry of Natural Resources Scientific Permit (SC-42).

Results.

Out of 69 birds, 29 (42%) chose novel-colored pompoms at their first choice. Our results showed no significant effect of date, novel color, order of test, habitat, and previous rewarding experiences with white pompoms on the probability to first choose a novel-colored pompom (Table 2). None of the two-way interactions between previous rewarding experiences, age class, and exploration score were significant. The final model showed a significant positive effect for both exploration score and age, where faster explorers and juveniles had a higher tendency to choose novelty compared to slower explorers and adults, respectively (Table 2, Fig.2).

Table 1. Factor loadings extracted from six variables taken from an open-field, novel room exploration test using a principal components analysis (*N*=69)

Variables	***Loadings***
Flight duration	0.9163
Hop duration	0.8628
Visits to tree 1	0.9276
Visits to tree 2	0.8739
Visits to tree 3	0.944
Visits to tree 4	0.8949

Table 2. Final GLM (*N*=69) used to test the information-gathering hypothesis (IGS) using first choice (familiar/white) = 0, novel/blue or purple = 1) as the response variable evaluating initial attraction to novelty.

	Estimate ± SE	χ^2	***P-value***
Intercept	-1.206 ± 0.576		0.036
Exploration	0.339 ± 0.142	6.303	0.012
Number of rewards	-0.644 ± 0.343	3.713	0.054
Age (Adults)	1.568 ± 0.588	7.946	0.005
Habitat (Urban)	0.310 ± 0.604	0.263	0.608
Date	0.004 ± 0.015	0.091	0.762
Novel color (Purple)	-0.095 ± 0.572	0.027	0.869
Order tested	0.173 ± 0.185	0.088	0.348

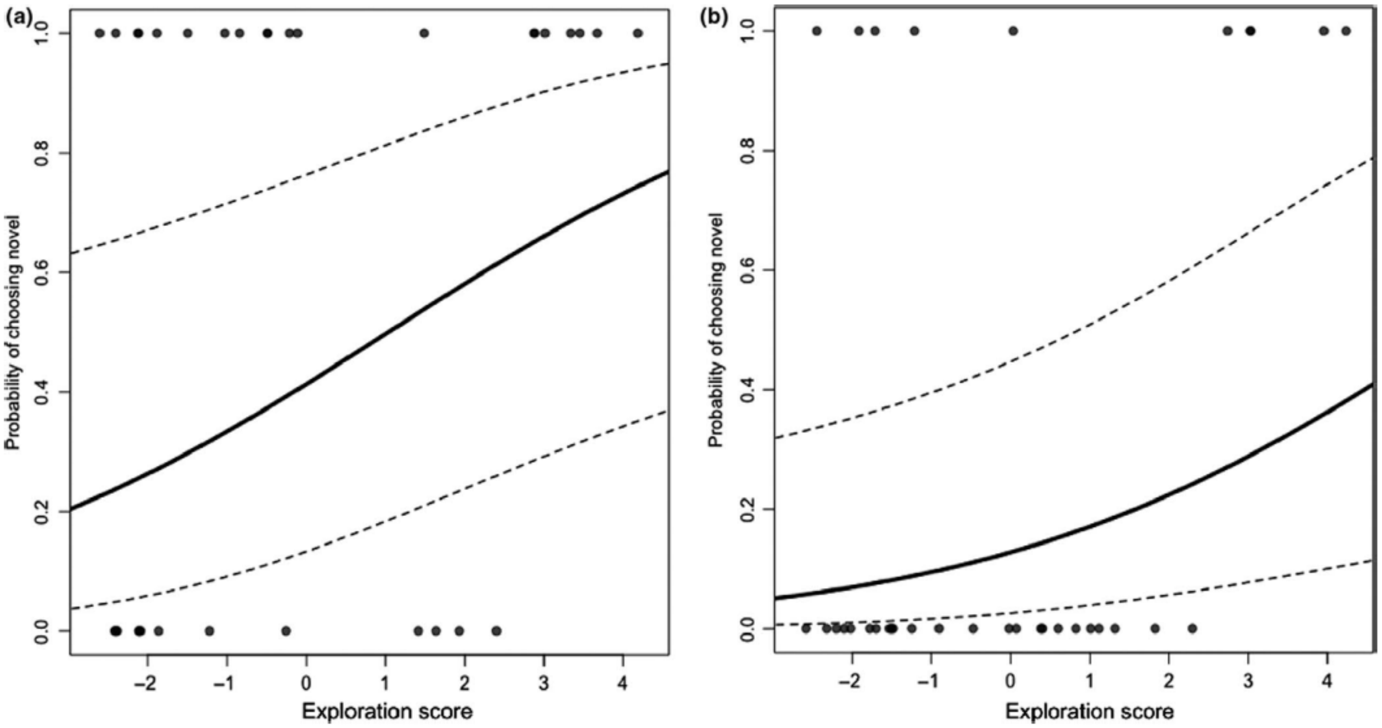

Figure 2. Probability of first choosing novel (1) over familiar white pompoms (0) in relation to the exploration score of each individual (*N*=69). (A) Juveniles and (B) Adults. Solid lines represent the final model prediction, while dashed lines are 95% confidence intervals.

Birds picked on average 4.5 white pompoms before choosing a novel coloured one (range 0-30). When analyzing an individual's tendency to switch from now unrewarding familiar white pompoms to colored pompoms, we found no significant effect of date (GLMM: χ^2= 0.895, *P*=0.344), novel color (GLMM: χ^2= 2.79, *P*=0.094), and order of test (GLMM: χ^2= 0.511, *P*=0.475). Furthermore, we found no significant interaction between exploration score and previous rewarding experiences (GLMM: χ^2=0.478, *P*=0.48), or between exploration score and age (GLMM: χ^2=0.367, *P*=0.544). Our final model showed that exploration score significantly predicted the number of familiar items selected before switching to the novel color, where faster exploring individuals switched to the novel item more quickly than slower explorers (Fig.3, Table 3). An interaction between previous rewarding experiences and age was also found to be significant where the effect of previous rewarding experiences was stronger in juveniles than in adults (Table 3).

Table 3. Final GLMM (*N*=69) used to test the behavioral flexibility hypothesis (BF) using the number of familiar (white) pompoms removed before switching to novel colored pompoms (blue or purple).

	Estimate ± SE	χ^2	***P-value***
Intercept	0.135 ± 0.368		0.714
Exploration	-0.250 ± 0.116	4.682	0.030
Number of rewards	-0.216 ± 0.363	3.810	0.051
Age (Adults)	-0.132 ± 0.466	0.015	0.901
Habitat (Urban)	-0.069 ± 0.519	0.017	0.895
*Age * Rewards*	1.738 ± 0.560	9.645	0.002

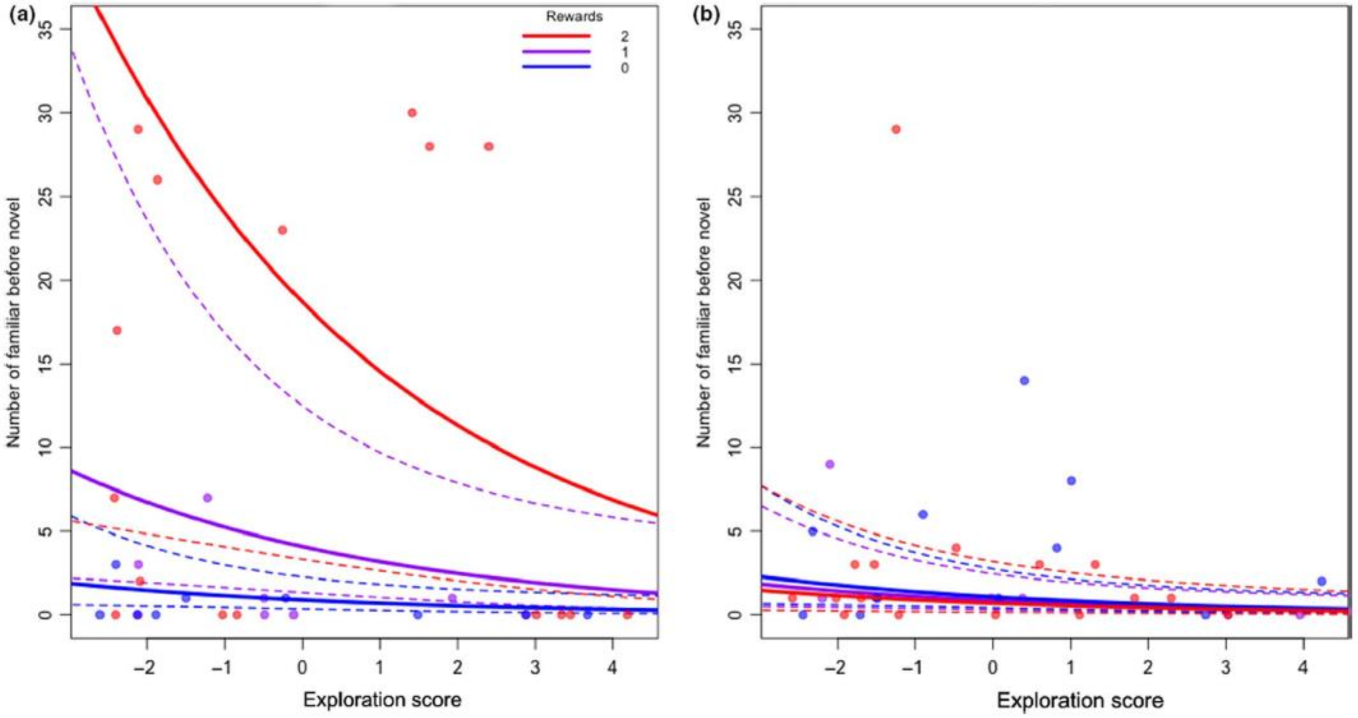

Figure 3. Number of familiar items chosen before switching to novel item type in relation to exploration score (*N*=69) for (A) Juveniles and (B) Adults. Different shades represent number of rewards recently experienced with familiar items (0 = blue, 1 = purple, 2 = red). Solid lines represent the final model prediction, while dashed lines are 95% confidence intervals.

Discussion.

Though exploration score has often been used as a proxy for information gathering, sampling is rarely measured in empirical studies. Despite several calls to investigate the construct validity of personality measurements used in evolutionary biology, few studies have examined the links between exploratory behaviour, novelty seeking, and behavioral plasticity. Our work suggests that individuals that show a higher overall exploration score in a novel environment test are more likely to sample novel over familiar information compared with slower explorers. Our results thus support the information-gathering hypothesis (IGS), where more exploratory individuals are expected to choose novel over known resources. In Arvidsson and Matthyssen (2016)'s work, wild-caught great tits were first provided with a binary choice between a profitable and non-profitable feeder. The experimenters then added a novel non-profitable feeder, thus giving the birds a choice between two familiar feeders and one feeder of uncertain profitability. In this experiment, fast explorers were not more likely to sample the novel option than slow-exploring great tits. Thus, our study is the first one to bring support to the IGS by showing a positive relationship between attraction to novelty and exploration score in a choice experiment. Moreover, we found that slower explorers continued to sample a previously known option longer than faster explorers when it had stopped paying, thereby paralleling some findings on great tits (Arvidsson and Matthyssen 2016). We interpret our results as suggesting that individual chickadees that initially chose an unfamiliar novel item are expressing an attraction to novelty and are also less resistant to switch to a novel option, although future studies would benefit from examining these two behavioural tendencies in separate assays. Our results do not support the BF hypothesis, and thus bring evidence against the long-held view that faster explorers are less behaviorally plastic.

Our results suggest that faster explorers are more attracted to novelty, which is consistent with studies that report a positive correlation between novel room exploration and novel object exploration (Réale et al.2010; Cole et al. 2014; Perals et al. 2017). In the current study we use an experimental design that minimized the effect of individual variation in locomotion rate and, interestingly, we come to the same conclusion as Perals et al. (2017) who controlled for variation in activity rates statistically. Providing multiple familiar and novel items located next to each other allowed us to reject a potentially confounding effect of locomotion rate in the relationship between exploration and novelty-seeking; if exploration strategy was determined mainly by activity levels, then we would expect to see no significant relationship between exploration score and initial attraction to novel information. This is because a high movement rate would not be more likely to expose individuals to the novel items by chance, as can be the case when presenting animals with novel objects in a familiar context and quantifying their latency or frequency of contact with the new item. Our results suggest that faster explorers displayed a stronger attraction to novel information compared with slower explorers despite the close spatial contiguity of both options, supporting the view that exploration score is intrinsically determined by an individual's attraction to novel information and not by its increased locomotion. Familiar white pompoms offered partial information as they were sometimes rewarding and other times unrewarding while the value of novel colored pompoms was completely unknown. Our results therefore suggest that faster explorers are choosing to reduce uncertainty, and are thus implementing an information-gathering strategy.

Under the BF hypothesis, less exploratory individuals should possess more accurate information about the familiar options and be more plastic (Arvidsson & Matthysen, 2016; Herborn et al., 2014). In contrast, our results suggest that faster explorers were more plastic as they removed fewer familiar pompoms (now unrewarding) before sampling the novel color option. Likewise, free-ranging great tits that were scored as faster explorers in a novel environment demonstrated a greater tendency to switch to a novel resource when a familiar resource was no longer profitable (van Overveld and Matthysen 2013). Since Verbeek et al. (1994) reported that more exploratory individuals were routine-like in their behaviors and less plastic than slower explorers, several studies have followed suit (Marchetti & Drent, 2000; Sih & Giudice, 2012). However, our work supports a growing number of studies which have observed that more exploratory individuals tend to show more behavioral plasticity (Mathot et al. 2012; Herborn et al. 2014, Thompson et al 2018). Studies on species from a different taxonomic group or with a different ecology than chickadees and great tits would allow assessing the generality of these findings, as both of these Paridae species are socially-foraging, habitat and dietary generalists, who may benefit from gathering information about food resources in their environment.

The extent to which animals are attentive to changes in their environment can be difficult to assess, as differences in behaviour may result from differences in detection (i.e. some individuals did not detect the change) and/or decision making (i.e. change is detected but the animal decides not to adjust behaviour). In our study, we can assume that at least some individuals detected the introduction of the new coloured items, as behavioral responses differed by exploration score and age class. If slower explorers did not detect the novel option and chose indiscriminately, this would go against the BF hypothesis, which assumes slower explorers to be more attentive to changes in the environment. Alternatively, if faster explorers did not detect the new colour and the difference in behavior stemmed from slower explorers discriminating against the novel colour, then this would support the idea that slower explorers are more attentive to changes in their environment, as assumed by the BF hypothesis. However, an increased attentiveness to changes in the environment would not have resulted in slower explorers expressing more plasticity as originally suggested by the BF hypothesis, because slower explorers were more reluctant to switch to the new stimuli type when the familiar option stopped being rewarded in our experiment. In a like manner, a study on captive great tits suggested that slow-explorers may rely on past information more than fast explorers as they were more likely to return to previous rewarding sample sites over novel sampling opportunities (Smit & Oers, 2019). Therefore, in either of these cases, our findings question some assumptions of the BF hypothesis. We encourage the development of new research paradigms that can distinguish between differential attentiveness and responsiveness to environmental change; some effort has already been made to improve our understanding of the relationship between exploration and responsiveness recently (Arvidsson, Adriaensen, Dongen, Stobbeleere, & Matthysen, 2017; Minderman et al., 2009).

Our results suggest that age and recent foraging experience can impact an individual’s attraction to novelty and affect their decision making. First, juveniles were more likely than adult birds to select the novel colored pompom over a familiar option at their first choice. Similarly, great tits were described to change their sampling tendencies with age, where juveniles sampled familiar feeders less often than adult birds (Herborn et al., 2014). This finding is also consistent with a study that showed an increased tendency for juveniles to pick a novel stimulus against a previously rewarded one in a touchscreen experiment with corvids and parrots (O'Hara et al., 2017), and aligns with similar findings in various taxa (e.g. Bergman and Kitchen 2009; Lafaille and Eron 2014; Carter et al. 2018). Second, juvenile chickadees seemed to be more influenced by recent experience than adult chickadees when switching from familiar to novel information. Due to their lack of experience juveniles should indeed be expected to pay more attention to novel information to inform decision making (English, Fawcett, Higginson, Trimmer, & Uller, 2016; Fawcett & Frankenhuis, 2015; Stamps & Krishnan, 2014). Our experiment provides rare empirical evidence supporting this prediction in non-human animals.

Our results bring support to the assumption that individuals that explore novel environments faster use a strategy to lower uncertainty (IGS), as faster explorers were more attracted to novelty when provided a choice between familiar and novel options. In contrast, we find no support for the BF hypothesis, as faster exploring individuals did not demonstrate the often-predicted routine-like behaviors, and more rapidly switched to the novel resource when known options were unrewarding compared with slower explorers. We have shown that in a situation where activity rate cannot bias decision making (multiple novel and familiar items located in close spatial contiguity), faster explorers are more likely than slower explorers to sample novel items preferentially over familiar ones. Thus, we find that novel room exploration assays do seem to capture individual differences in information-gathering strategies, as the name of the test implies, providing support for the construct validity of the open field test as a way to assess exploratory behaviour. Moreover, this personality trait seems to correlate positively, rather than negatively (i.e. routine-like behaviour), with behavioural plasticity. We propose that a deeper examination of the costs and benefits to movement-based information seeking, as well as the possibly diverse mechanisms underlying behavioral plasticity, could shed new light on the relationships between exploration and plasticity.

References

Adriaenssens, B., & Johnsson, I. (2011). Shy trout grow faster : exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, *22*, 135–143. doi.org/10.1093/beheco/arq185

Arnold, K. E., Herborn, K. A., Henderson, L. J., Adam, A., Alexander, L., & Evans, N. (2016). Individual variation in corticosterone and personality traits in the blue tit Cyanistes caeruleus. *Behaviour*, *153*, 1611–1637. doi.org/10.1163/1568539X-00003408

Arvidsson, L. K., Adriaensen, F., Dongen, S. Van, Stobbeleere, N. De, & Matthysen, E. (2017). Exploration behaviour in a different light : testing cross-context consistency of a common personality trait. *Animal Behaviour*, *123*, 151–158. doi.org/10.1016/j.anbehav.2016.09.005

Arvidsson, L. K., & Matthysen, E. (2016). Individual differences in foraging decisions: information-gathering strategies or flexibility? *Behavioral Ecology*, *00*, arw054. doi.org/10.1093/beheco/arw054

Baugh, A. T., Schaper, S. V, Hau, M., Cockrem, J. F., De Goede, P., & Van Oers, K. (2012). Corticosterone responses differ between lines of great tits (Parus major) selected for divergent personalities. *General and Comparative Endocrinology*, *175*, 488–494. doi.org/10.1016/j.ygcen.2011.12.012

Bebus, S. E., Small, T. W., Jones, B. C., Elderbrock, E. K., & Schoech, S. J. (2016). Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Animal Behaviour*, *111*, 251–260. doi.org/10.1016/j.anbehav.2015.10.027

Bergeron, P., Montiglio, P.-O., Réale, D., Humphries, M., Gimenez, O., & Garant, D. (2013). Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *Journal of Evolutionary Biology*, *26*, 766–774.

doi.org/10.1111/jeb.12081

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (Papio ursinus) and geladas (Theropithecus gelada). *Animal Cognition*, *12*(1), 63–73. doi.org/10.1007/s10071-008-0171-2

Carter, A. J. (2013). On validity and controls in animal personality research: a comment on Galhardo et al. (2012). *Biology Letters*, *9*(4).

Carter, G. G., Forss, S., Page, R. A., & Ratcliffe, J. M. (2018). Younger vampire bats (Desmodus rotundus) are more likely than adults to explore novel objects. *PLOS ONE*, *13*(5), e0196889. doi.org/10.1371/journal.pone.0196889

Cole, E. F., Quinn, J. L., & Cole, E. F. (2014). Shy birds play it safe : personality in captivity predicts risk responsiveness during reproduction in the wild, 8–11.

Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B., & Sih, A. (2011). Behavioural syndromes in fishes : a review with implications for ecology and fisheries management. *Journal of Fish Biology*, *78*, 395–435.

doi.org/10.1111/j.1095-8649.2010.02874.x

Coppens, C. M., De Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: towards underlying mechanisms. *Philosophical Transactions of the Royal Society B* , *365*, 4021–4028. doi.org/10.1098/rstb.2010.0217

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings. Biological Sciences*, *271*(1541), 847–852. doi.org/10.1098/rspb.2004.2680

Edenbrow, M., & Croft, D. P. (2013). Environmental and genetic effects shape the development of personality traits in the mangrove killifish Kryptolebias marmoratus. *Oikos*, *122*, 667–681. doi.org/10.1111/j.1600-0706.2012.20556.x

Eliassen, S., Jørgensen, C., Mangel, M., & Giske, J. (2007). Exploration or Exploitation: Life Expectancy Changes the Value of Learning in Foraging. *Oikos*, *116*(3), 513–523.

English, S., Fawcett, T. W., Higginson, A. D., Trimmer, P. C., & Uller, T. (2016). Adaptive Use of Information during Growth Can Explain Long-Term Effects of Early Life Experiences, *187*(5). doi.org/10.1086/685644

Fawcett, T. W., & Frankenhuis, W. E. (2015). Adaptive explanations for sensitive windows in development. *Frontiers in Zoology*, *12*, 1–14.

Frankenhuis, W. E., & Panchanathan, K. (n.d.). Balancing sampling and specialization: an adaptationist model of incremental development. doi.org/10.1098/rspb.2011.0055

Greenberg, R. (2003). The role of neophobia and neophilioa in the developmennt of innovative behaviour of birds. *Animal Innovation*.

Guillette, L.M., Baron, D. M., Sturdy, C. B., & Spetch, M. L. (2016). Fast- and slow-exploring pigeons differ in how they use previously learned rules. *Behavioural Processes*. doi.org/10.1016/j.beproc.2016.07.006

Guillette, Lauren M., Hahn, A. H., Hoeschele, M., Przyslupski, A.-M., & Sturdy, C. B. (2015). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition*, *18*(1), 165–178. doi.org/10.1007/s10071-014-0787-3

Harrison, X. A. (2014). Using observation-level random e ff ects to model overdispersion in count data in ecology and evolution. doi.org/10.7717/peerj.616

Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Personality predicts behavioral flexibility in a fluctuating, natural environment. *Behavioral Ecology*, *25*(6), 1374–1379. doi.org/10.1093/beheco/aru131

Kaiser, H. F. (1960). The Application of Electronic Computers to Factor Analysis. *Educational and Psychological Measurement*, *20*(1), 141–151. doi.org/10.1177/001316446002000116

Lafaille, M., & Eron, C. F. (2014). U-shaped relationship between ageing and risk-taking behaviour in a wild-type rodent. *Animal Behaviour*, *97*, 45–52. doi.org/10.1016/j.anbehav.2014.08.018

Le Galliard, J., Paquet, M., & Cisel, M. (2013). Personality and the pace-of-life syndrome : variation and selection on exploration , metabolism and locomotor performances. *Functional Ecology*, (27), 136–144. doi.org/10.1111/1365-2435.12017

Marchetti, C., & Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, *60*(1), 131–140. doi.org/10.1006/anbe.2000.1443

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

Meigs, B. Y. J. B., Smith, D. C., & Buskirk, J. V. A. N. (1983). Age Determination of Black-Capped Chickadees. *Journal of Field Ornithology*, *54*(3), 283–286.

Miller, R., Bugnyar, T., Pölzl, K., Schwab, C., & Miller, R. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology*, 1209–1220. doi.org/10.1007/s00265-015-1935-8

Minderman, J., Reid, J. M., Evans, P. G. H., Whittingham, M. J., Building, R., Building, Z., … Bridge, M. (2009). Personality traits in wild starlings : exploration behavior and environmental sensitivity. doi.org/10.1093/beheco/arp067

Montreuil-Spencer, C. (2017). *Relationships between winter energetic conndition and reproductive investment in a wild bird*.

O'Hara, M., Mioduszewska, B., von Bayern, A., Auersperg, A., Bugnyar, T., Wilkinson, A., … Gajdon, G. K. (2017). The temporal dependence of exploration on neotic style in birds. *Scientific Reports*, *7*(1),

4742.
doi.org/10.1038/s41598-017-04751-0

Oers, K. Van, & Mueller, J. C. (2010). Evolutionary genomics of animal personality, 3991–4000.
doi.org/10.1098/rstb.2010.0178

Overveld, T. Van, & Matthysen, E. (2013). Personality and Information Gathering in Free-Ranging Great Tits, *8*(2).
doi.org/10.1371/journal.pone.0054199

Perals, D., Grif, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open- fi eld test : what does it really tell us about animal personality ?, *123*.
doi.org/10.1016/j.anbehav.2016.10.006

Pravosudov, V. V, & Clayton, N. S. (n.d.). A Test of the Adaptive Specialization Hypothesis: Population Differences in Caching, Memory, and the Hippocampus in Black-Capped Chickadees (Poecile atricapilla). doi.org/10.1037//0735-7044.116.4.515

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

Quinn, J L, Cole, E. F., Bates, J., Payne, R. W., & Cresswell, W. (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B* , *279*, 1919 1926.
doi.org/10.1098/rspb.2011.2227

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

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (n.d.). Personality and the emergence of the pace-of-life syndrome concept at the population level. doi.org/10.1098/rstb.2010.0208

Rockwell, C., Gabriel, P. O., & Black, J. M. (2012a). Bolder, older, and selective: factors of individual-specific foraging behaviors in Steller's jays. *Behav Ecol*, *23*, 676–683. doi.org/10.1093/beheco/ars015

Schmidt, K. A., Dall, S. R. X., & van Gils, J. A. (2010). The ecology of information: An overview on the ecological significance of making informed decisions. *Oikos*, *119*(2), 304–316. doi.org/10.1111/j.1600-0706.2009.17573.x

Sherratt, T. N., & Morand-Ferron, J. (2018). The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal Behaviour*, *138*, 59–67. doi.org/10.1016/J.ANBEHAV.2018.01.025

Shettleworth, S. J., Krebs, J. R., Stephens, D. W., & Gibbon, J. (1988). Tracking a fluctuating environment: a study of sampling. *Animal Behaviour*, *36*(1), 87–105. doi.org/10.1016/S0003-3472(88)80252-5

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

Smit, J. A. H., & Oers, K. Van. (2019). Personality types vary in their personal and social information use. *Animal Behaviour*, *151*, 185–193. doi.org/10.1016/j.anbehav.2019.02.002

Stamps, J. A., & Krishnan, V. V. (2014). Combining Information from Ancestors and Personal Experiences to Predict Individual Differences in Developmental Trajectories. *The American Naturalist*, *184*(5), 647-657. doi.org/10.1086/678116

Stephens, D., & Krebs, J. (1986). *Foraging theory*.

Thompson, M. J., Evans, J. C., Parsons, S., & Morand-ferron, J. (2018). Urbanization and individual differences in exploration and plasticity. *Behavioral Ecology*, *29*, 1415–1425. doi.org/10.1093/beheco/ary103

van Oers, K., De Jong, G., Drent, P. J., & Van Noordwijk, A. J. (n.d.). A Genetic Analysis of Avian Personality Traits: Correlated, Response to Artificial Selection.

van Overveld, T., & Matthysen, E. (2013). Personality and Information Gathering in Free-Ranging Great Tits. doi.org/10.1371/

Verbeek, M., Drent, P., & Wiepkema, P. (1994). Consistent individual differences in early exploratry behavior of male great tits.

Chapter 2: *The impact of learning opportunities on the development of learning and decision making: an experiment with passerine birds*

Abstract.

While it is recognized that species and populations vary broadly in their ability to learn, the existence and extent of individual variation in learning has just begun being assessed in animals. Learning abilities have been shown to be influenced by the developmental context, namely through experiments that imposed severe nutritional and/or environmental constraints (i.e. lack of enrichment). In contrast, we know very little on the impact of opportunities for learning on the development of cognition in animals, despite that such opportunities are known to influence human cognitive development. We exposed young zebra finches (*Taenopygia guttata*) (n=26) to one of three experimental conditions, i.e. an environment where (i) the presence of food was predicted by one colour cue (simple learning), (ii) a combination of two-colour cues (conditional learning), or (iii) colours cues were non-informative (control). After conducting two different discrimination tasks, our results show that experience with predictive cues cause increased learning performance and faster decision making. We found no support for a speed-accuracy trade-off. This novel dataset provides a rare longitudinal and experimental examination of the effect of exposure to learning opportunities during development on the cognition of adult animals.

Keywords. Information gathering, experience, individual differences, decision speed, speed-accuracy trade-offs

Introduction.

The developmental environment can shape how animals behave. Early life experiences can impact and even constrain morphology and behaviors displayed in adulthood. Such is the case with jumping spider (*Marpissa muscosa*) siblings that were raised with either physical enrichment (i.e. objects added), social enrichment (i.e. 15 individuals living together), or no enrichment (1). The authors found that the developmental environment in which the individuals were reared in caused personality differences, with higher exploratory behaviors observed in the enriched treatments.

The developmental environment can also affect cognitive abilities. Environments can vary in their degree of certainty, where stable environment have greater certainty of resource availability and fluctuating environments have lower certainty (2). When environmental certainty is high, individuals do not need to pay the time and energy cost associated to acquiring new information and rely more heavily on innate behaviors or prior experience. Comparatively, fluctuating resources require individuals to physically sample, gather information about their environment, store information, and adjust their behaviors accordingly by relying on additional cues to optimize their decisions (3). Juvenile African cichlid fishes (e.g. *Simochromis pleurospilus*) that experienced environmental fluctuation in the form of changes in feeding rations, were found to outperform individuals that experienced stable feeding rations when tested in an associative learning task during adulthood (4). Presumably, cichlids that acquired more information about their environment during development where better able to adjust to environmental changes encountered later in the learning test than those that had not experienced environmental changes in their lifetime. Models have suggested that experiencing environmental changes during development causes animals to gather more information about their environment which could lead to more optimal behavioral patterns (5). Through learning, an individual is able to increase its resource intake and energetic gain through experience (6). When the environment is uncertain, animals have been known to learn to use reliable cues in order to optimize their foraging decisions (7). Still, it is not yet well understood how experience can cause differences in behavior and cognition based on the informational properties (e.g. presence of cues predicting resources and their reliability) of the developmental environment.

In theory, the more information an individual has about their environment, the better they can adjust to it. However, acquiring information for accurate decisions can be time consuming and can affect the overall speed of choice. A speed-accuracy trade-off (SAT) has been suggested where physical and cognitive constraints hinder individuals from reaching high choice accuracy at high speeds (8). SATs have been studied in order to better understand the mechanisms of decision making and their relationship to the current environment, and are found across taxa including humans and invertebrates (9–11). When exposed to a color discrimination task, zebrafishes (*Danio rerio*) were found to have an increased average decision time as their choice accuracy increased, thus supporting the proposed SAT in cognitive performance (12). Still, the effects of the developmental environment and experience on the individual variation seen in SATs are not yet well understood.

We aim to address how early experience affects learning ability and speed of choice by manipulating the informational properties (i.e. presence and number of reliable cues) of the developmental environment of juvenile captive zebra finches (*Taenopygia guttata*). We exposed juvenile zebra finches to one of three experimental conditions; i.e. an environment where (i) colour cues reliably predicted the presence of food (simple learning), (ii) a combination of two-colour cues reliably predicted the presence of food (conditional learning), or (iii) colours cues were non-informative (control). We then measured learning performance in two discrimination tasks and predicted that birds with more experience with information acquisition during development would have increased choice accuracy (i.e. conditional learning treatment > simple learning treatment > control). Furthermore, we hypothesized that decision making would also be influenced by experimental manipulation of information acquisition during development; we predicted that birds will choose faster when they have had experience with more information acquisition (i.e. conditional learning treatment > simple learning treatment > control). Finally, we tested for a speed-accuracy trade-off during learning using individual variation in speed and accuracy of choice, where we predicted that speed of choice should decrease as choice accuracy increases.

Methods.

Subjects

We used a total of 26 (N=13 males, 13 females) captive juvenile zebra finches, aged approximately 3 months (13 females and 13 males), that were obtained from Oisellerie De L'Estrie Inc (Quebec). Individuals were caged (41w x 60L x 36h) in same sex dyads that were visually isolated from other birds, but were in auditory contact. Dyads were physically and visually isolated during experiments (~2.5hrs) and re-united upon the completion of trials. Birds were kept in a 11:13hr photoperiod and a temperature of 24-26°C. When experiments were not running, birds were given unlimited access to zebra finch seed mix (Canary and finch daily diet). Additionally, diet was supplemented with vegetables and boiled eggs twice a week, and birds were given vitamins (Nektons) in their water daily. Finches were deprived of food 30min before the lights turned off for the night (18hr) and for 1hr after the lights turned on and before the start of trials (8hr). All birds had ad libitum access to water at all times. Experiments were first conducted on a group of 12 (n=12) individuals from November 2017 to May 2018; experiments on the second group of birds (n=14) were completed from July 2018 to March 2019. Zebra finches were not handled during experiments to avoid associated stress.

Experience

Individuals from each of the two groups were randomly assorted into three experimental conditions while counterbalancing for sex. The three experimental treatments offered different information sources; i.e. an environment where (i) colour cues reliably predicted the presence of food (simple learning or 1-cue learning), (ii) a combination of two-colour cues reliably predicted the presence of food (conditional learning or 2-cues learning), or (iii) colours cues were non-informative (control). The three experimental conditions were achieved by using a silo bird feeder consisting of a top and bottom colors (i.e. green or white). Feeders could be matching or mismatched and had four possible feeder combinations: top green- bottom green (matching), top white- bottom green (mismatched), top white-bottom white (matching), top green- bottom white (mismatched). For the control treatment, all four feeder combinations had equal chance of being rewarding and thus have no informative cues. Individuals in the simple learning treatment only had to pay attention to the bottom color of the feeder (i.e. white or green) as this was the only informative cue. Only matching feeders (i.e. top green- bottom green and top white-bottom white) were rewarding for the conditional learning treatment, as the combination of both cues would be the reliable predictor of the correct feeder (Fig 1).

Birds were first exposed to both matching feeders (green-green and white-white) simultaneously for a habituation period of two days in order to reduce neophobia responses. During experiments, two feeders were presented simultaneously as a binary choice, each located close to a perch at the same height in the cage. The first four trials alternated between rewarded sides (i.e. R, L, R, L or L, R, L, R) in order for individuals to experience both sides as rewarding at least twice and prevent side biases. For the remainder of trials, the rewarded side was chosen randomly while ensuring that both sides were rewarded equally often. We also ensured that birds in the control and simple learning treatments would have an equal chance of matched and mismatched feeders to be rewarding. Because matching feeders would only be rewarding in the conditional learning treatment, we counterbalanced for color making sure that matching green and white feeders would be equally rewarding. Birds were exposed to 20 trials per day for a total of 500 trials, where trial is defined as a presentation of the binary feeder choice, whether a choice was made or not by the bird. Each bird was given a total of three minutes to choose (i.e. look at the contents within the feeder approached) before the trial was terminated and the feeders were removed. If a bird chose the rewarded feeder it was given 10 seconds to feed before the feeders were removed and we continued trials for the next bird. If a bird chose the unrewarded feeder, both feeders were removed immediately and the bird was not allowed to feed until the next trial, i.e. after all other birds were done with this trial. Individuals had to choose a feeder for a minimum of 400 trials to be included in the sample; all birds reached at least 400 choices (range: 400-500). Feeder chosen and latency to choose were recorded. Trials took 3-4 months to complete.

Learning

Zebra finches were subjected to the first learning task within 2 months after the experience phase finished; the second learning task took place within 2 months after the first task and 3-4 months after the experience phase had ended. Sample sized was reduced to 22 (N=22) as 4 birds died before the first learning phase. For both learning tasks individuals were exposed to 50 binary choices between a rewarding and non-rewarding feeder. Once again, the first four trials alternated between sides where individuals experienced each side as rewarding at least twice; rewarded side was then chosen randomly and counterbalanced for the remainder of trials. Birds would then be exposed to 10 trials per day for a total of 50 trials. Individuals were given a total of five minutes to choose before a trial was terminated, and trials proceeded as in the Experience phase where both feeders were removed either upon the bird reaching into the unrewarded feeder or after the bird had fed for 10 seconds in the rewarded feeder. Two birds died before the second learning task and sample size was further reduced to 20 (N=20). Individuals had to choose a feeder a minimum of 40 choices to be included in the sample; all birds reached at least 40 choices for both tasks. We recorded the feeder chosen and the latency to choose.

The first learning task was a discrimination task composed of a binary choice between two feeders: a rewarding purple bowl with vertical black electrical tape and an unrewarding purple bowl with a horizontal black electrical tape. The second learning task was based on three different shades of blue (e.g. dark blue, medium blue, light blue). Similar to the first task, birds were exposed to a discrimination task composed of a binary choice between two feeders: a rewarding bowl with a brown sticker and an unrewarding bowl with no sticker (Fig 2b). We ensured that all three shades were equally rewarding throughout the 50 choices.

Statistical Analysis.

Experience

We used binomial generalized linear mixed model (GLMM) to analyze choice accuracy (0=incorrect, 1=correct) during training, in relation to trial number, experimental treatment (control, simple learning, conditional learning), sex, and group (1, 2). Trial number was rescaled and mean-centered before all analyses.

Learning

We used a binomial GLMM to analyze choice accuracy (0=incorrect, 1=correct) in the associative learning trials in relation to task number (1, 2), trial number, experimental treatment, sex, and group. We also tested for a trial number by experimental treatment interaction, to assess if the change in choice accuracy over successive trials was different for each experimental treatment.

Speed of choice

We used the latency from start of the trial (both feeders installed on the cage) to actual choice (bird looks at the contents within the feeder approached) to measure speed of choice. Latency was log transformed before all analyses to improve normality. For the experience phase, latency was analyzed using a linear mixed model to (LMM) in response to trial number, experimental treatment, sex, and group. Only the first 50 choices were used for consistency between the experience phase and the learning phase. For the learning phase, we analyzed choice latency in all trials of each associative learning task in response to trial number, experimental treatment, sex, and group. In order to test for a speed-accuracy trade-off (SAT), we used latency to choose as our dependent variable and choice accuracy in the current trial as a fixed predictor (0=incorrect, 1=correct), while controlling for trial number, experimental treatment (simple learning, conditional learning), sex, and group. Here we only used the simple and conditional learning treatments as the SAT hypotheses is based on learning and the control treatment is thus irrelevant for this specific analysis.

All models controlled for individual as a random intercept. Non-significant interactions were removed before re-running the model. We ran all analyses using the package lme4 (13) from R version 2017 (14).

Ethics

Individuals were deprived of food for 0.5hr before the lights turned off for the day and the birds rested for the night. Birds where further deprived for 1hr the next morning before beginning test trials. They had ad libitum access to water at all times. Tests were conducted in the bird's home cages and dyads were separated by a white divider which prevented handling and associated stress before conducting the assays. Work was conducted under University of Ottawa Animal Care protocol 1758.

Results

Experience

Trial number was significant and positive, indicating that choice accuracy increased with successive trials (Figure 2; Table 1). We found support for a treatment effect where both simple and conditional learning treatments were significantly different from the control treatment, with birds in these treatments expressing more correct choices. Furthermore, there was a significant difference between the simple learning and conditional learning treatment (GLMM: Estimate= -1.66 $\pm$ 0.20, χ^2=121.54, $P< 0.001$) where there were fewer correct choices in the conditional learning than in the simple learning treatment. There was no significant effect of sex or group.

Learning

We found a strong and significant difference in mean accuracy between the two learning tasks (GLMM: Estimate= 1.02 $\pm$ 0.12, χ^2=74.81, $P<0.001$). For these reasons, we decided to separate our initial model into two separate models, one for each learning task (Figure 3). For task 1, we found a significant interaction between trial number and experimental treatments (GLMM: Estimate= 0.03 $\pm$ 0.01, χ^2=7.64, $P=0.02$) (Table 2). Though there was a significant difference between the slope of control treatment and simple learning over trials, there was no difference between the slope of simple and conditional learning treatments over trials (GLMM: Estimate= -0.0002 $\pm$ 0.01, χ^2= 0.98, $P=0.99$). There was no significant effect of sex or group (Table 2). For task 2, we found no significant trial by treatment interaction (GLMM: Estimate= -0.003 $\pm$ 0.02, χ^2=0.26, $P=0.88$). After eliminating the interaction, we found that trial was positive and significant; treatment, sex, task, and group were not significant (Table 3).

Speed of choice

We examined the effect of the developmental environments on latency of choice during the experience phase and both learning tasks. For the experience phase, trial number had a significant effect on choice latency where latency decreased over the first 50 trials (Table 4). We found no effect of treatment or sex but group was significant. Upon analyzing choice latency for task 1 of the associative learning trials, we found no support for an effect of trial number, experimental treatment, sex, or group (Table 5A). Task 2 of the associative learning trials revealed no effect of trial number, sex, or group (Table 5B), yet, we find a significant effect of experimental treatment for task 2 (GLMM: Estimate= -0.82 ± 0.41, χ^2=8.92, P=0.01). The conditional learning treatment had significantly shorter choice latencies than control birds and a similar non-significant trend was found for the simple learning treatment, but there was no significant difference between the simple and conditional learning treatments (Table 5B).

Finally, we test the SAT hypothesis using data from the experience and learning phases. During the experience phase, trial number was significant with a negative slope, thus suggesting that latency to choose decreased as trial number increased (Table 6). Group was also significant but we found no significant effects of choice accuracy in the current trial, experimental treatment, or sex. For the learning phase we separated the analysis into the two different tasks in accordance with our previous analyses. We found no support for an effect of choice accuracy, experimental treatment (simple vs conditional learning), sex, and group as predictors of latency to choose (Table 7) in either task. Trial number was significant for learning tasks 1 with a negative slope (Table 7A).

Figure 1. Experience phase. Female zebra finch given a binary choice between a matching feeder (left) and a mismatched feeder (right).

Figure 2. Experience phase. Proportion of correct choices in relation to trial number (1 block = 10 trials) for a total of 500 trials and 26 individuals (*N=26*). Solid lines represent treatment slopes. [Blue= Control; Green=Simple learning; Red= Conditional learning]

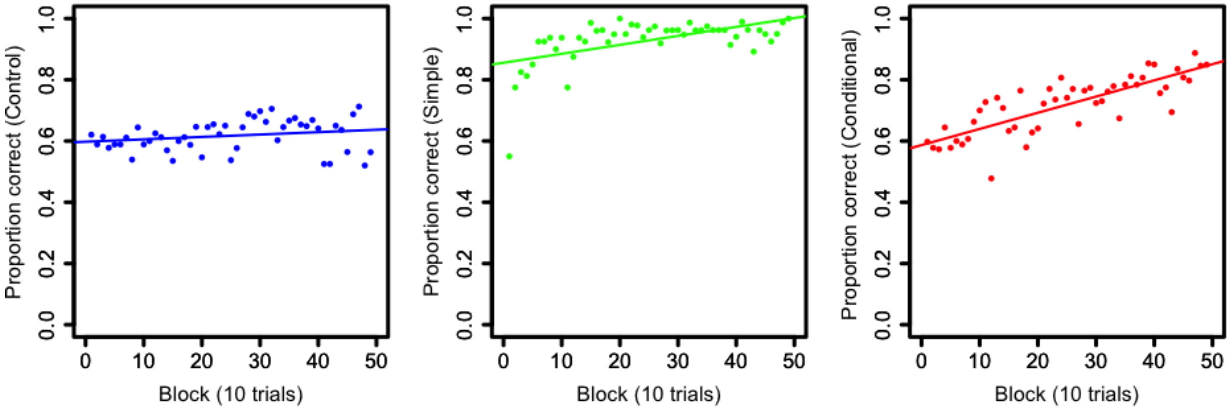

Table 1. Experience phase. GLMM (*N*=26 individuals) used to analyze choice accuracy using binary choice (incorrect = 0, correct = 1) as the response variable. Reference category is ‘control’ for treatment, and females for ‘sex’.

	Estimate ± SE	χ^2	***P-value***
Intercept	0.68 ± 0.18		< 0.001
Trial	0.92 ± 0.08	127.31	< 0.001
Treatment $_{Simple}$	2.14 ± 0.20	121.51	< 0.001
Treatment $_{Conditional}$	0.48 ± 0.19	121.51	0.01
Sex $_{Males}$	0.01 ± 0.16	0.001	0.97
Group $_2$	-0.29 ± 0.16	3.25	0.07

Figure 3. Learning phase. Proportion of correct choices in relation to the bin trial number (1 bin = 5 choices) for a total of 50 choices and 22 individuals (*N=22*). (A) Task 1 and (B) Task 2. Solid lines represent treatment slopes. [Blue= Control; Green=Simple learning; Red= Conditional learning]. Data points are jittered slightly to show superimposed values.

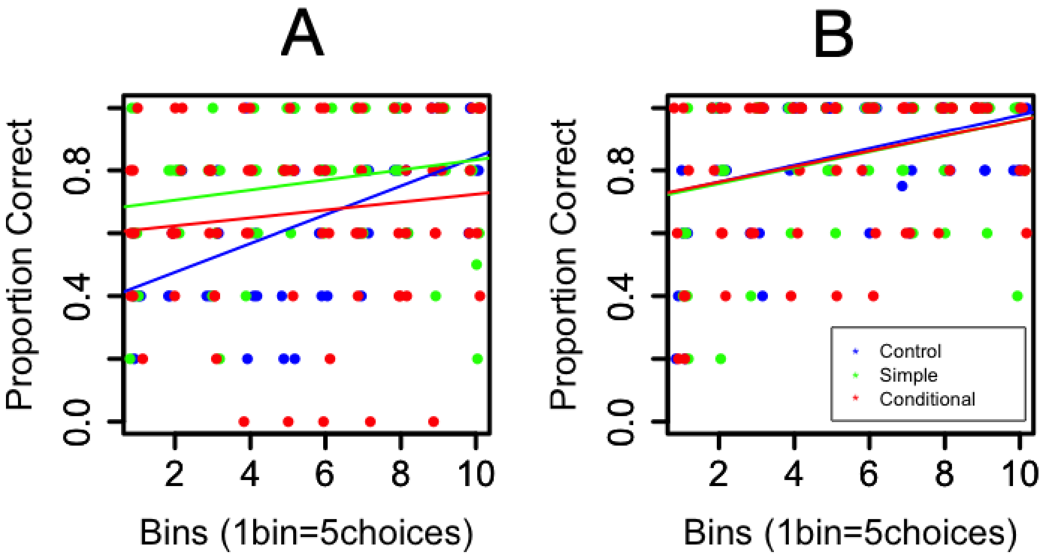

Table 2. Learning phase. GLMM (*N*=22 individuals) used to analyze learning task 1 using binary choice (incorrect = 0, correct = 1) as the response variable. Reference category is ‘control’ for treatment, and females for ‘sex’.

	Estimate ± SE	χ^2	***P-value***
Intercept	1.46 ± 0.42	12.32	0.04
Trial	0.04 ± 0.01	21.68	< 0.001
Treatment	0.55 ± 0.30	3.66	0.16
Sex_{Males}	-0.13 ± 0.24	0.30	0.59
Group	-0.20 ± 0.23	0.77	0.38
Treatment*trial Control vs Simple	-0.03 ± 0.01	7.64	0.02
Treatment*trial Control vs Conditional	-0.03 ± 0.01	7.64	0.01
Treatment*trial Simple vs Conditional	-0.0002 ± 0.01	0.98	0.99

Table 3. Learning phase. GLMM (*N*=20 individuals) used to analyze learning task 2 using binary choice (incorrect = 0, correct = 1) as the response variable. Reference category is 'control' for treatment, and females for 'sex'.

	Estimate ± SE	χ^2	***P-value***
Intercept	3.09 ± 0.78	17.09	< 0.001
Trial	0.05 ± 0.01	42.32	< 0.001
Treatment *Control vs Simple*	-0.14 ± 0.53	0.34	0.79
Treatment *Control vs Conditional*	0.15 ± 0.5	0.34	0.77
Treatment *Simple vs Conditional*	0.29 ± 0.5	0.34	0.79
Sex *Males*	-0.54 ± 0.42	1.62	0.20
Group	-0.50 ± 0.41	1.43	0.23

Table 4. Experience phase. LMM (*N*=26 individuals) used to analyze choice latency as the response variable. Reference category is 'control' for treatment, and females for 'sex'.

	Estimate ± SE	χ^2	***P-value***
Intercept	1.58 ± 0.22	-	< 0.001
Trial	-0.01 ± 0.001	57.63	< 0.001
Treatment $_{\textit{Simple}}$	0.35 ± 0.24	3.62	0.17
Treatment $_{\textit{Conditional}}$	-0.09 ± 0.24	3.62	0.703
Sex $_{\textit{Males}}$	-0.11 ± 0.20	0.34	0.56
Group	-0.55 ± 0.20	7.18	0.01

Figure 4. Learning phase. Choice latency in seconds (log transformed) in relation to treatment for (A) tasks 1 and (B) 2 for the associative learning trials.

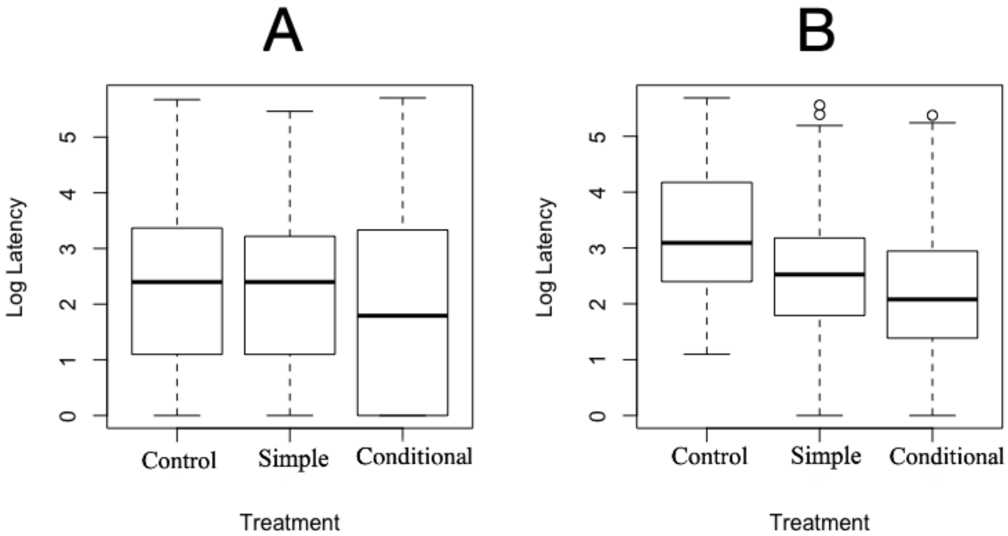

Table 5. Learning phase. LMM used to analyze latency for learning task 1 (A) and learning task 2 (B) using latency to choose as the response variable. Reference category is ‘control’ for treatment, and females for ‘sex’.

(A)

	Estimate ± SE	χ^2	***P-value***
Intercept	3.20 ± 0.82		0.001
Trial	-0.003 ± 0.002	1.33	0.25
Treatment $_{Simple}$	-0.17 ± 0.55	0.89	0.76
Treatment $_{Conditional}$	-0.50 ± 0.55	0.89	0.38
Sex $_{Males}$	-0.75 ± 0.44	2.92	0.09
Group	-0.23 ± 0.43	0.28	0.60

(B)

	Estimate* ± *SE	χ^2	***P-value***
Intercept	3.85 ± 0.61		< 0.001
Trial	-0.004 ± 0.002	2.63	0.11
Treatment $_{Simple}$	-0.82 ± 0.41	8.92	0.06
Treatment $_{Conditional}$	-1.14 ± 0.38	8.92	0.009
Sex $_{Males}$	-0.57 ± 0.33	3.02	0.08
Group	-0.11 ± 0.33	0.10	0.75

Table 6. Experience phase. LMM (*N*=17 individuals, simple vs. conditional learning treatments only) used to analyze latency to choose as a response variable in function of accuracy in the current trial (speed-accuracy trade-off). Reference category is 'simple' for treatment, and females for 'sex'.

	Estimate ± SE	χ^2	***P-value***
Intercept	2.09 ± 0.27		< 0.001
Choice accuracy	-0.05 ± 0.06	0.65	0.42
Trial	-0.01 ± 0.002	36.50	< 0.001
Treatment $_{\textit{Conditional}}$	-0.43 ± 0.26	2.71	0.10
Sex $_{\textit{Males}}$	-0.15 ± 0.26	0.32	0.57
Group$_2$	-0.75 ± 0.26	8.05	0.004

Table 7. Learning phase. LMM (*N*=16 individuals, simple vs. conditional learning treatments only) used to analyze latency to choose as a response variable in function of accuracy in the current trial (speed-accuracy trade-off in learning task 1 (A) and learning task 2 (B). Reference category is 'simple' for treatment, and females for 'sex'.

(A)

	Estimate ± SE	χ^2	***P-value***
Intercept	3.14 ± 0.89		0.004
Choice accuracy	0.10 ± 0.10	0.97	0.32
Trial	-0.01 ± 0.003	22.74	< 0.001
Treatment $_{Conditional}$	-0.32 ± 0.51	0.40	0.52
Sex $_{Males}$	-0.93 ± 0.51	3.27	0.07
Group$_2$	-0.29 ± 0.51	0.32	0.57

(B)

	Estimate ± SE	χ^2	***P-value***
Intercept	3.53 ± 0.63		< 0.001
Choice accuracy	0.04 ± 0.11	0.15	0.70
Trial	-0.005 ± 0.003	3.38	0.07
Treatment $_{\textit{Conditional}}$	-0.28 ± 0.34	0.66	0.42
Sex $_{\textit{Males}}$	-0.45 ± 0.38	1.39	0.23
Group $_2$	-0.54 ± 0.39	1.91	0.17

Discussion.

The goal of this research was to understand how the informational properties of the developmental environment could affect decision making and cognitive abilities. Our learning treatments proved to be successful as individuals that had experience with information gathering (i.e. simple and conditional learning treatments) had higher choice accuracy than control birds in the experience phase. Furthermore, experience with information caused differences in learning rate as well as decision-making speed when tested several weeks later. Overall we demonstrate, for the first time using an experimental approach, that experience with predictive cues during development can cause cognitive variation in terms of learning and decision making later in life.

During training, when the environment provided information (simple and conditional learning treatments), choice accuracy increased when compared to individuals reared in an environment with no information, supporting the predicted effect of our experimental treatments. Still, there was a significant difference in choice accuracy contingent on the amount of information provided. Juvenile birds that developed with only one source of information (i.e. simple learning treatment) had higher choice accuracy than individuals with two sources of information (conditional learning treatment). This result suggests that too much information could constrain choice accuracy as the task of paying attention to two different sources could be more difficult than paying attention to just one. Indeed, when given the choice between paying attention to one primary source of information or a second conditional signal, captive blue Jays (*Cyanocitta cristata*) preferentially chose to pay attention to one information source unless the certainty of the primary source of information decreased (15). There seems to be a cost associated to acquiring too much information which could in turn limit choice accuracy and even learning (16).

In order to test our prediction that experience with an increasing number of information sources would lead to higher learning performance (i.e. conditional treatment > simple treatment > control) we ran two different learning tasks several weeks after the experience phase. Our first learning task resulted in significant differences in learning rates between treatments as shown by a significant treatment by trial number interaction. Birds that had developed with one or two sources of information about food were faster to learn than birds that did not experience information and only had access to cues that were not predictive. Though it is commonly predicted that greater experience with environmental information can lead to greater learning performance (17), and that providing opportunities for learning contributes to increases in general intelligence in young mice (18) and humans (19), this is to our knowledge the first experimental demonstration of a link between experience with predictive vs non-predictive cues and learning performance. Our results for the second task showed that though learning took place, there was no difference between treatments in learning rates. Lack of significant difference between treatments here may be due to a high choice accuracy being reached much faster than in task 1, thereby leaving less variation in learning slopes to be explained by predictor variables.

Our results show that zebra finches in the learning treatments decided on a feeder faster in comparison to birds in the control treatment. Shorter latencies in learning treatments support our predictions that birds that have more experience with information gathering should be faster decision makers, although this result was apparent only in one of the two learning tasks. The mechanisms involved with the speed of choice are yet to be well understood and may be associated with individual differences in animal personalities (20,21). Another possible mechanism for the decrease in latency in the learning treatments may involve the detection and perception of information. Theoretically, once individuals have experienced informative cues they should be able to detect and perceive information quicker, which could lead to faster choices and potentially, more optimal behaviours (22).

Our results also suggest that accumulating experience in a given feeding situation causes individuals to choose faster, as latency to express a choice decreased over successive trials in the experience phase. It is assumed that animals can have a belief or an estimate about the state of their current environment or the value of a given resource (23). The degree of belief can fluctuate between uncertain where an individual is unsure of the estimate and its choice, and certain where the individual will be more confident about its estimate and its choice (24). It is possible that the decrease in choice latency over experience trials observed in our experiment indicates a higher certainty in the bird’s belief as they gradually gain knowledge on the task presented to them. Little is known about the link between the speed of choice and the certainty of belief; we suggest this would be a topic worthy of investigation. However, an alternative explanation for the decreased choice latencies with trial number in the experience phase could be related to a reduction of neophobia (fear of novelty) towards the new feeders or experimental set-up over successive trials.

Learning can imply costs and constraints (25,26). One of the implied constraints of learning is a cognitive and/or physiological trade-off between speed and accuracy where individuals can choose fast with minimal amount of information, or slowly with more information which should result in higher accuracy (9). We predicted that the latency to choose should increase with choice accuracy in the current trial, because birds would then take more time to choose accurately. We found no support for a speed accuracy trade-off in our results, however it is possible that these results are due to a lack of statistical power. Similarly, work on jumping spiders (*Portia labiate*) found no support for a speed-accuracy trade-off on prey choice, and suggested that faster decision makers may also gather information faster (27). In our experiment, individuals that developed in environments that provided information were found to be more accurate than controls in learning task 1, and although they were not more accurate in learning task 2 they did choose faster. Together, these results seem to indicate that these individuals could express higher accuracy or speed, but maybe not both at the same time, providing indirect evidence for a SAT.

Our experiment provides empirical evidence for theoretical models that predict that experience with information early in life should lead to distinct phenotypic variation (26). We conclude that experience with predictive cues can lead to individual differences in decision making and learning performance, which are important components in how animals respond to their environment. By exposing young birds to either predictive or non-predictive cues and testing them on learning months after, we provide a rare longitudinal and experimental examination of the effect of exposure to learning opportunities on the development of cognitive traits. Our results emphasize the fact that learning abilities are not fixed, but that learning is a developmental process that can be shaped by information gathering opportunities in the environment. Though work still needs to be done on the evolution of learning at an empirical level, we suggest that the informational properties of the developmental environment can work as a factor that could promote phenotypic variation that may have long-term adaptive consequences (29).

References.

1. Liedtke J, Redekop D, Schneider JM, Schuett W. Early Environmental Conditions Shape Personality Types in a Jumping Spider. 2015 Dec 22;3:134.
2. Dunlap AS, Stephens DW. Components of change in the evolution of learning and unlearned preference. Proceedings of the Royal Society B: Biological Sciences. 2009 Jun 17;276(1670):3201-8.
3. Stephens DW. On Economically Tracking a Variable Environment. Theoretical Population Biology. 1987 Aug 1;32(1):15-25.
4. Kotrschal A, Taborsky B. Environmental Change Enhances Cognitive Abilities in Fish. PLoS biology. 2010 Apr 6;8(4):e1000351.
5. Frankenhuis WE, Nettle D, Dall SRX, Nettle D, Frankenhuis WE. A case for environmental statistics of early-life effects. Philosophical Transactions of the Royal Society B. 2019 Feb 25;374(1770):20180110.
6. Durisko Z, Dukas R. Effects of Early-Life Experience on Learning Ability in Fruit Flies. Ethology. 2013 Dec;119(12):1067-76.
7. McLinn CM, Stephens DW. What makes information valuable: signal reliability and environmental uncertainty. Animal Behaviour. 2006 May 1;71(5):1119-29.
8. Ducatez S, Applications F, Audet J, Lefebvre L. Problem-solving and learning in Carib grackles : individuals show a consistent Problem-solving and learning in Carib grackles : individuals show a consistent speed – accuracy trade-off. Animal cognition. 2015 Mar 1;18(2):485-96.
9. Chittka L, Skorupski P, Raine NE. Speed – accuracy tradeoffs in animal decision making. Trends in ecology & evolution. 2009 Jul 1;24(7):400-7.
10. Onagawa R, Shinya M, Ota K, Kudo K. Risk aversion in the adjustment of speed-accuracy tradeoff depending on time constraints. Scientific reports. 2019 Aug 13;9(1):1-2.
11. Chittka L, Dyer AG. Bees trade off foraging. Nature. 2003 Jul;424(6947):388.
12. Wang M, Brennan CH, Lachlan RF, Chittka L. Speed–accuracy trade-offs and individually consistent decision making by individuals and dyads of zebrafish in a colour discrimination task. Animal Behaviour. 2015 May 1;103:277-83.

13. Bates D, Maechler M, Bolker B, Walker S, Christensen RH, Singmann H, Dai B, Scheipl F, Grothendieck G. Package 'lme4'. Linear mixed-effects models using S4 classes. R package version. 2011 Mar 7:1-.

14. Team RC. R: A language and environment for statistical computing.2013.

15. Mclinn CM, Stephens DW, Mclinn CM, Stephens DW. An experimental analysis of receiver economics: cost, reliability and uncertainty interact to determine a signal's value. Oikos. 2010 Feb;119(2):254-63.

16. Thornton A, Boogert NJ. The Nature and Nurturing of Animal Minds : Beyond Nature-Nurture The Nature and Nurturing of Animal Minds. In: Genes and Behaviour: Beyond Nature Nurture, DJ Hosken, N Wedell, and J Hunt, eds(Wiley). 2019. Apr 1:181-202.

17. Dukas R. Animal expertise: mechanisms, ecology and evolution. Animal behaviour. 2019 Jan 1;147:199-210.

18. Light KR, Kolata S, Wass C, Denman-brice A, Zagalsky R, Matzel LD. Report Working Memory Training Promotes General Cognitive Abilities in Genetically Heterogeneous Mice. Current biology. 2010 Apr 27;20(8):777-82.

19. Protzko J. Intelligence The environment in raising early intelligence : A meta-analysis of the fadeout effect. Intelligence. 2015 Nov 1;53:202-10.

20. Guillette LM, Hahn AH, Hoeschele M, Przyslupski A-M, Sturdy CB. Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. Animal Cognition. 2015 Jan 1;18(1):165-78.

21. Mamuneas D, Spence AJ, Manica A, King AJ. Bolder stickleback fish make faster decisions , but they are not less accurate. Behavioral Ecology. 2014 Sep 15;26(1):91-6.

22. Abbott KR, Sherratt TN. Optimal sampling and signal detection : unifying models of attention and speed – accuracy trade-offs. Behavioral Ecology. 2013 Jan 28;24(3):605-16.

23. Stamps JA, Frankenhuis WE. Bayesian Models of Development. Trends in Ecology & Evolution. 2016 Apr 1;31(4):260-8.

24. Stamps JA, Krishnan V V. Age-dependent changes in behavioural plasticity : insights from Bayesian

models of development. Animal Behaviour. 2017 Apr 1;126:53-67.

25. Jaumann S, Scudelari R, Naug D. Energetic cost of learning and memory can cause cognitive impairment in honeybees. Biology letters. 2013 Aug 23;9(4):20130149.

26. Kotrschal A, Rn Rogell B, Bundsen A, Svensson B, Zajitschek S, Brä Nnströ M I, et al. Report Artificial Selection on Relative Brain Size in the Guppy Reveals Costs and Benefits of Evolving a Larger Brain. Current Biology. 2013 Jan 21;23(2):168-71.

27. Chang C, Ng PJ, Li D. Aggressive jumping spiders make quicker decisions for preferred prey but not at the cost of accuracy. Behavioral ecology. 2016 Dec 20;28(2):479-84.

28. English S, Fawcett TW, Higginson AD, Trimmer PC, Uller T. Adaptive Use of Information during Growth Can Explain Long-Term Effects of Early Life Experiences. The American Naturalist. 2016 May 1;187(5):620-32.

29. Laland KN. Animal learning as a source of developmental bias. Evolution & development. 2019 Aug 26:e12311.

Chapter 3: *What makes a scrounger? Experience, learning performance, and fear as predictors for social-foraging strategy*

Abstract.

Animals in social foraging groups can choose between two foraging strategies: producers, who invest in searching and finding resources, and scroungers who profit from the investment of producers. Though it has been hypothesized that individuals choose a foraging strategy solely on resource availability and the strategies of others, factors such as experience with information, learning performance, and fear of novelty could also contribute to foraging strategy choice. We hypothesize that individuals that prefer to use a producer strategy should be individuals that have had experience learning from cues, have better performance in associative learning tasks, and are less fearful of novelty; the opposite should be true for scroungers that profit from the experience of the producers. Furthermore, we look at behavioral plasticity in alternative strategy choice by quantifying the adjustment in strategy use over different seed distributions. We predict that individuals that show greater adjustment in strategy use are more likely to detect and/or respond to change in their environment due to their greater experience with information, learning performance, or lower fear response. We exposed groups of zebra finches (n=19) to three experimental conditions of varying number of seeds per patch and measured the frequency of producer/ scrounger use for each individual. Social foraging data were then combined with data on developmental experience with information, learning performance, and fear of novelty (neophobia). Results show that zebra finches meet the prediction established by the producer-scrounger model in the response to varying seed distributions, but we found no support for our hypothesis that experience with informative cues and learning performance serve as predictors of strategy choice. Interestingly we found that, contrary to our predictions, more fearful foragers were more likely to choose a producer strategy when compared to less fearful individuals. We also found that individuals significantly vary from one another in their plasticity when switching between foraging strategies.

Keywords. development, plasticity, neophobia, individual variation, game theory

Introduction.

Animals in social foraging groups can choose to either search for food or join others' discoveries. Accordingly, the producer-scrounger (P-S) game states that foraging groups are composed of producers that invest in searching for food, and scroungers that profit from the investment of producers by following them to food sources. These two foraging strategies are mutually exclusive and an individual can only choose one strategy at a time, as they cannot look for food and look at what their conspecifics are doing simultaneously (Barnard and Sibly 1981; Vickery et al. 1991; Giraldeau and Caraco 2000). In an experiment done with ground-feeding birds, researchers found that individuals that look for food hopped with their head down, while individuals that joined others hopped with head up (Coolen et al. 2001). Though the predictions of the P-S game assume that the least common strategy has a better payoff in terms of food intake and energetic gain (Vickery et al. 1991) [i.e. negative-frequency dependence payoff (Mottley and Giraldeau 2000)], we have yet to fully understand what causes individuals to choose among these social foraging strategies.

An individual's strategy choice can be dependent on their environmental conditions, physical condition, and social environment (reviewed in Afshar and Giraldeau 2014). In order to maximize payoffs, decisions should be based on the food distribution where the proportion of scrounging should increase with food clumpiness (i.e. density of food per patch) (Caraco and Giraldeau 1991). Such was the case in European starlings (*Sturnus vulgaris*), where these birds where shown to join more than they look for resources (scrounger use) as food clumpiness increased (Koops and Giraldeau 1996). However, though individuals have been observed to alternate between strategies, it has been shown that individuals vary in their consistency of strategy use and some individuals alternate between strategies more than others (Morand-Ferron et al. 2011; Barou-Dagues et al. 2020). Various studies have calculated repeatability (i.e. proportion of total variance explained by between individual variation (Dingemanse and Dochterman 2013)) values for the consistency of strategy use and have found low to moderate repeatability values (Beuchamp 2000: R=0.94, p<0.025; David et al. 2014: R=0.23, CI=[−0.08,0.62]; Aplin and Morand-Ferron 2017: R=0.50, CI=[0.46–0.5].

Individuals can choose a foraging strategy based on past experiences. Through positive feedback, some individuals will be successful in finding food and become more likely to adopt a producer strategy on future foraging bouts (Katsnelson et al. 2008). Alternatively, some individuals may have negative experiences when searching for food alone and choose a scrounger strategy the next time they forage. Nestling house sparrows (*Passer domesticus*) that were reared to associate conspecifics to food and received positive feedback for joining others in their search (i.e. scrounging) for food were more likely to choose a scrounger strategy in future foraging bouts (Katsnelson et al. 2008). Thus, the authors suggest that experience through learning could be a key component of strategy preference. Through learning, an individual can make predictive associations between a stimulus and a behavior (Eliassen et al. 2009; Shettleworth 2009). Due to the nature of the producer strategy, where they must search for food alone and acquire information directly from their environment, it has been suggested that individuals that chose to search for food will have better learning abilities (Katsnelson et al. 2011; Barou-Dagues et al. 2020). Comparatively, individuals that acquire information from the experience of others are more likely to adopt a scrounger strategy. Still, it is unclear how experience with informative cues and learning ability outside a social foraging context may shape strategy choice.

The P-S model can also be used as risk-sensitive model where it is predicted that individuals use a risk-averse strategy when choosing to scrounge (Caraco and Giraldeau 1991; Koops and Giraldeau 1996). Scroungers are assumed to bypass the costs associated with producing in terms of predation and starvation risks. In Egyptian fruit bats (*Rousettus aegyptiacus*) producers had to attain food from a feeder and scroungers would eat directly from the mouth of the producers; producing was directly correlated to higher predation risk as producers had to leave to safety of their shelter (Harten et al. 2018). Hence, foraging strategy choice could be a byproduct of an individual’s risk aversion and, by extension, reaction to novelty, because contacting novelty entails uncertainty and can thus be risky. In accordance with this, a study done in barnacle geese (*Branta leucopsis*) showed that bolder individuals (scored using a novel object test) had a higher proportion of searching for food over joining (Kurvers et al. 2010). To my knowledge, this is the only study to examine the relationship between neophobia and P-S strategy choice.

Strategy choice in animals can be a result of behavioral plasticity (i.e. change in behavior). Changes in the environment may require individuals to adjust their foraging strategy accordingly. Interestingly, Dubois et al. (2012)'s model predicts that not all individuals will be plastic in order to retain group equilibrium since adjustment by plastic individuals restore equilibrium after environmental change. When exposed to two different seed distributions, nutmeg mannikins (*Lonchura punctulata*) exhibited variation on their plasticity in alternative tactic use (Morand-Ferron et al. 2011). Hypothetically, individuals that detect and/or respond to changes in their environment more quickly will be more likely to show greater adjustment in strategy choice. Plasticity can possibly be driven by associative learning and, presumably, individuals that make associations faster may also be able to respond quicker to their environmental changes. Furthermore, plasticity in strategy use may be driven by fear reactions. More neophobic zebra finches where found to be more plastic where the authors argue that the fear response constrains foragers to specific parameters within their environment (e.g. 'familiar environments with low predation') which would cause the individual to be more willing to adjust their behaviors accordingly (Gibelli and Dubois 2016). Additionally, a study done in female Bengalese finches (*Lonchura striata*) found that birds that learned slower in a colour discrimination task showed greater adjustment in foraging strategy when compared to faster learners (Barou-Dagues et al. 2020). Thus, we could predict that individuals that are more neophobic will also be more plastic. Alternatively, individuals that are less neophobic and have more information about their environment (as they are less affected by novelty) could respond to their environment quicker and be more plastic.

In our study, we first aim to understand why some individuals invest more in searching for resources (i.e. producer strategy), while others choose to profit from the investment of others. To do this, we look at experience with informative cues about food, learning performance, and neophobia as possible predictors of strategy choice in zebra finches (*Taeniopygia guttata*). Individuals that tend to choose a producer strategy should be individuals that have had experience learning individually from cues and have better performance in associative learning tasks. We also predict that individuals that choose to find resources and prefer a producer strategy should be risk-prone and less fearful of novelty. Finally, we looked at experience with informative cues, learning, and neophobia, as possible predictors of plasticity by quantifying adjustment in strategy use over different seed distributions. We predict that individuals that show greater adjustment in strategy use are more likely detect and/or respond to change in their environment due to their increased experience with information and learning performance, or decreased fear response.

Methods.

Study subjects

We used a total of 19 (N=9 females, 10 males) captive juvenile zebra finches, that were obtained from Oisellerie De L'Estrie Inc. (Quebec). Birds were kept in a 11 h light: 13 h dark photoperiod and a temperature of 24–26°C. When experiments were not running, birds were given unlimited access to zebra finch seed mix (Canary and finch daily diet). Additionally, diet was supplemented with vegetables and boiled eggs twice a week, and birds were given vitamins (Nektons) in their water daily. Finches were deprived of food 30 min before the lights turned off for the night (at 18.00 h) and for 1 h after the lights turned on and before the start of trials (at 8.00 h). All birds had ad libitum access to water at all times. Zebra finches were not handled during experiments to avoid associated stress.

Experience with informative cues

We used data obtained from a previous experiment using the same individual birds (see Rojas-Ferrer and Morand-Ferron 2020), in which we manipulated experience with informative cues during development. Experimental treatments consisted of three different developmental environments where an individual was exposed to (i) one colour cue that reliably predicted the presence of food (1-cue learning), (ii) a combination of two-colour cues that reliably predicted the presence of food (2-cue learning), or (iii) colour cues that were non-informative (control). We used a silo bird feeder that could have matching or mismatched colours, with four possible feeder combinations: top green–bottom green (matching), top white–bottom green (mismatched), top white–bottom white (matching), top green–bottom white (mismatched) (see Rojas-Ferrer and Morand-Ferron 2020). For the control treatment, all four feeder combinations had equal chance of being rewarding and thus had no informative cues. Individuals in the 1-cue learning treatment only had to pay attention to the bottom colour of the feeder (i.e. either white or green) as this was the only informative cue. While in the 2-cue learning treatment only matching feeders (i.e. top green–bottom green and top white–bottom white) were rewarding and the combination of both cues would be the reliable predictor of the correct feeder. Juvenile birds (aged approx. 3 months old) were exposed to 20 trials per day for a total of 500 trials, where a trial is defined as a presentation of a binary feeder choice, whether or not a choice was made by the bird. Trials took three to four months to complete.

Learning performance

Approximately 2 months after the experience phase ended, individuals had to complete an associative learning task where birds had to make 50 binary choices between a rewarding and non-rewarding feeder. This learning task was a discrimination task composed of a binary choice between two feeders: a rewarding purple bowl with vertical black electrical tape and an unrewarding purple bowl with a horizontal black electrical tape. Learning performance was quantified using the proportion correct of all 50 choices.

Neophobia

Neophobia score was defined as the difference between the latency to approach food in the presence (i.e. neophobic response) and absence of a novel object (i.e. baseline response). We added 100 to these values and log transformed them to help normalize the distribution. We found neophobia scores to be moderately repeatable in two repeated trials using two different objects (i.e. yellow bottle; brown Lego structure) with an R=0.38, CI=[0.108, 0.62], p-value<0.003 (Rpt R package; Stoffel et al. 2019). We used the first neophobia score for our analyses.

Social foraging

We used a total of four same-sex groups of finches consisting of two female groups of 3 and 5 individuals and two male groups of 4 and 6 individuals for the social foraging experiments (2 from September to October 2018 and 2 from May to July 2019). Groups were housed in one of two indoor flight rooms (room A=3 × 3.3 × 2.3 m; room B=3.3 × 3 × 2.3 m) over a roughly three-week period per group. The flight room contained two open cages (with three nest boxes and two water dishes each) stacked on a rack against the wall furthest from the door. An artificial tree was placed on each side of the cages and a foraging grid was placed on two tables directly in front of the flight room door. For the training and experimental trials, we used a foraging grid consisting of two plywood boards (~95 x 95 cm) with each 100 evenly spaced wells (i.e. 200 wells total) per board (~10.0 cm apart, ~0.8 cm deep, and ~1.4 cm diameter). A camera was placed at each of the two corners of the room closest to the foraging grid to record activity on each board in case anything was missed during live observations. Live behavioural observations were made through the one-way glass of the flight room door.

Training

Before starting the training phase, birds were weighed and marked on the crown of the head with a unique colour of non-toxic acrylic paint to assist in identification. The training focused on habituating the birds to the experimental set up by associating the foraging grid with food rewards. On day 1, hulled millet seeds and regular bird feed was spread throughout the foraging grid (inside and outside of wells) and four food dishes containing food were placed on the grid. On day 2, we placed only hulled millet seeds inside each well of the foraging grid, with two water dishes but no food dishes on the surface. After 2-3 days of habituating to the foraging grid, birds were exposed to the experimental protocol by covering the foraging grid with a tablecloth and removing it a few times per day. The evening before the final training day, all food was removed, the grid was covered with the tablecloth, and water dishes were placed on top of the covered grid until the next day.

Birds were further trained by exposing them to the complete experimental protocol for six training trials. After the training, ad libitum food dishes were provided and placed on the covered foraging grid for about three hours. Food dishes were removed at 17:30h on the evening prior to experimental trials and birds were food deprived until the next day (~15 hours). Water dishes in the open cages were available to birds at all times.

Experimental trials

Social foraging experiments lasted 18 days for each group of birds, with six days for each of three different food distribution: (i) 5 seeds x 40 wells (ii) 10 seeds x 20 wells, (iii) 20 seeds x 10 wells (*see* Giraldeau et al. 1990). All groups of birds were first exposed to intermediate (10 seeds x 20 wells), low (5 seeds x 40 wells), and then high resource clumpiness (20 seeds x 10 wells).

Six social foraging trials were conducted daily at one-hour intervals (8:30h – 13:30h). Using focal sampling, one focal individual was observed live by the experimenter for each of the foraging trials. The order of focal birds observed was randomly determined and then counterbalanced across the four to six days of trials to ensure that each individual was observed at different times of the day.

For each trial , millet seeds were placed in randomly selected wells out of view of the birds (under the tablecloth covering the foraging grid); trails began when the tablecloth was pulled off of the foraging grid and the foraging grid was exposed. We recorded the focal bird's time of first landing on the foraging grid, and all producing (feeding from an unoccupied well) and scrounging (feeding from a well occupied by at least one conspecific) events. Focal observation continued until focal individual left the grid for one minute or until a maximum of 5 minutes had elapsed since the start of the trial All live observations were recorded using BORIS v. 4.1.4 (Friard and Gamba 2016). When the final trial was completed, food was returned and placed in dishes on the covered foraging grid for about three hours (~14:20h – 17:30h). At 17:30h food dishes and all traces of food were removed from the foraging grid and floor of the flight room and birds were deprived until the next day (~15 hours).

Statistical analysis.

We ran all analyses using the package lme4 [24] from R v. 2017 [25] and a total of 265 focal observations (N=265) taken from a total of 19 individuals (females=9; males=10) using four different groups (females=2, males=2).

Individual strategy choice

We used strategy choice as a response variable where we combined the frequency that a focal individual chose to produce and scrounge using cbind (produce, scrounge). We used a Binomial Generalised Mixed Model (GMM) to analyse individual strategy choice as a function of number of seeds per patch(5, 10, 20 seeds per patch), trial number, group size, sex, experience with informative cues, learning performance, and neophobia score. All fixed effects were rescaled. Group was included as a random factor with ID nested within each group. We ran a variance inflation factor (VIF) and found no evidence of collinearity between the covariates.

Plasticity

We used random slopes in order to quantify how individuals vary in their plasticity of strategy use over the different seed distributions, with strategy choice as the response variable. We aimed to test two-way interactions with seed distributions and experience, learning performance, and neophobia, while controlling for random slopes but encountered convergence issues. Consequently, we first tested a simpler model including seed distribution, trial number, sex, and random slopes for individuals over seed distribution. We then ran a Likelihood Ratio Test (LRT) using this simple model to compare models with and without random slopes. Finally, because we could not fit all interactions at once due to convergence issues, we tested interactions between number of seeds per patch and experience with informative cues, learning performance, and neophobia, one by one (i.e. in three separate models). Groups were included as a random intercept and number of seeds per patch by ID was included as a random slope. All fixed effects were rescaled.

Repeatability

We calculated repeatability for individual strategy choice using the RptR package (Stoffel et al. 2019). The proportion of patches scrounged by each individual was used as a response variable, while number of seeds per patch and trial number were used as fixed effects. ID and group were included as random intercepts.

Ethics.

Individuals were deprived of food for 0.5 h before the lights turned off for the day and the birds rested for the night. Birds were further deprived for 1 h the next morning before beginning test trials. They had ad libitum access to water at all times. Work was conducted under University of Ottawa Animal Care protocol 1758.

Results.

The proportion of scrounging was significantly and moderately repeatable: R=0.22 ± 0.08, CI=[0.06, 0.38], p-value < 0.001 while group was not significant which suggests consistent individual differences within the groups. As predicted by P-S models, our results show that there is a significant increase in proportion of patches scrounged as the number of seeds per patch, and thus resource clumpiness, increases (see Table 1 for all results). There was no significant effect of experimental treatment; thus, we found no support for our prediction that individuals with more experience with informative cues during development would produce more. Additionally, we found no support for trial number, group size, sex, or learning performance as predictors of strategy choice.

Due to model convergence issues, we were unable to run a model using random slopes with an interaction between number of seeds per patch and experience with informative cues. For our model including random slopes and learning performance we found no significant interaction while controlling for random slopes (see see Table 2 for results); however, there was a significant difference between models with and without random slopes (LRT: X^2=6.97, *p*=0.03). Finally, we were unable to estimate the covariance between the intercept and the slope when analyzing an interaction between number of seeds per patch and neophobia using random slopes (see Table 3 for results).

Table 1. GLMM (N=19 individuals; 4-6 trials/seed distribution; 264 focal observations) used to analyse individual strategy choice [cbind (produce, scrounge] as a response variable for individual zebra finches.

Fixed effects	***Estimate ± se***	X^2	***p-value***
Number of seeds per patch	-1.81 ± 0.20	85.54	< 0.001
Trial	-0.01 ± 0.04	0.08	0.78
Group size	-2.03 ± 1.18	2.95	0.09
Sex $_{Male}$	1.57 ± 0.88	0.002	0.96
Experience	0.39 ± 0.66	1.21	0.54
Learning performance	-1.01 ± 0.57	3.06	0.08
Neophobia	2.48 ± 1.21	4.21	0.04

Table 2. GLMM (N=19 individuals; 4-6 trials/seed distribution; 264 focal observations) used to analyse individual strategy choice [cbind (produce, scrounge] as a response variable for individual zebra finches using an interaction between number of seeds per patch and learning performance [proportion of correct choices over 50 binary choices between a rewarding and non-rewarding feeder] including groups as a random intercept and number of seeds per patch by ID as a random slope.

Fixed effects	***Estimate ± se***	***X^2***	***p-value***
*Number of seeds per patch * Learning performance*	1.41 ± 1.57	0.80	0.37
Learning performance	-1.72 ± 0.90	3.69	0.05
Trial	-0.01 ± 0.04	0.06	0.80
Sex $_{Male}$	-0.18 ± 0.86	0.04	0.84

Table 3. GLMM (N=19 individuals; 4-6 trials/seed distribution; 264 focal observations) used to analyse individual strategy choice [cbind (produce, scrounge] as a response variable for individual zebra finches using an interaction between number of seeds per patch and neophobia [[latency to approach food in the presence – latency to approach food in the absence of a novel object] including including groups as a random intercept and number of seeds per patch by ID as a random slope.

Fixed effects	***Estimate ± se***	X^2	***p-value***
*Number of seeds per patch * Neophobia*	-0.37 ± 1.36	7.27	< 0.01
Neophobia	4.73 ± 1.72	7.55	< 0.01
Trial	-0.01 ± 0.04	0.09	0.76
Sex $_{Male}$	0.42 ± 1.04	0.16	0.69

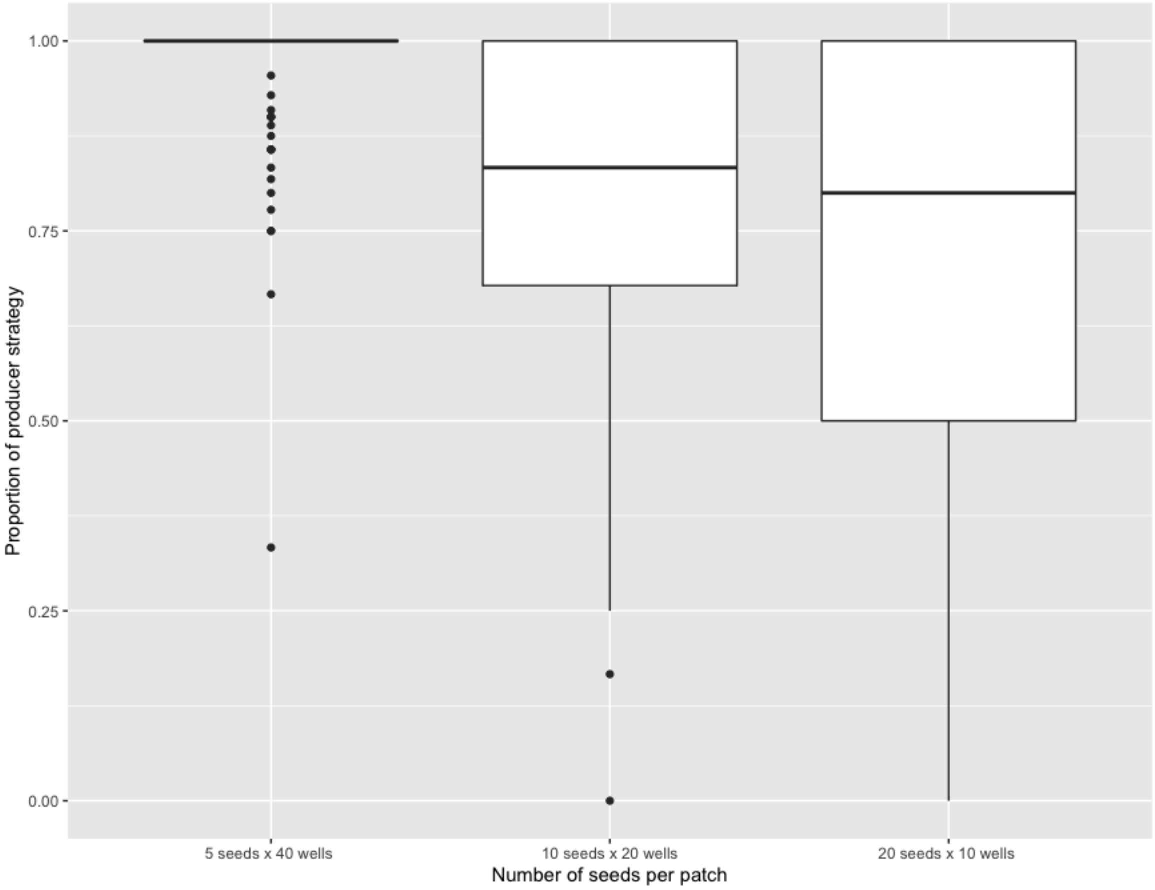

Figure 1. Individual proportion of patches produced (feeding from an unoccupied well) as a response to varying number of seeds per patch (i.e. 5 seeds x 40 wells, 10 seeds x 20 wells, 20 seeds x 10 wells) (N=19 x 4-6 trials/number of seeds per patch; observations=264).

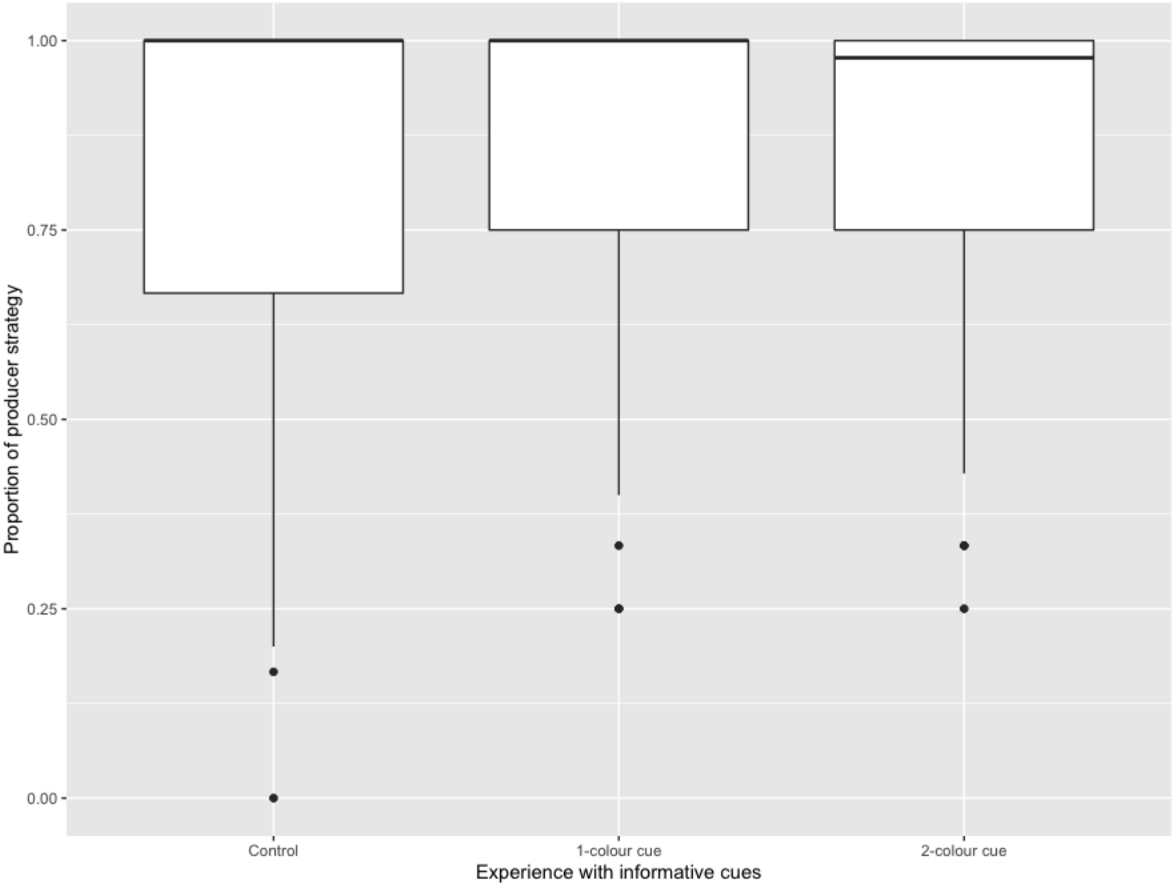

Figure 2. Proportion of patches produced (feeding from an unoccupied well) as a response to varying levels of experience with informative cues during development [i.e. control, 1-colour cue, 2-colour cue] (N=19 birds x 4-6 trials/number of seeds per patch; observations=264).

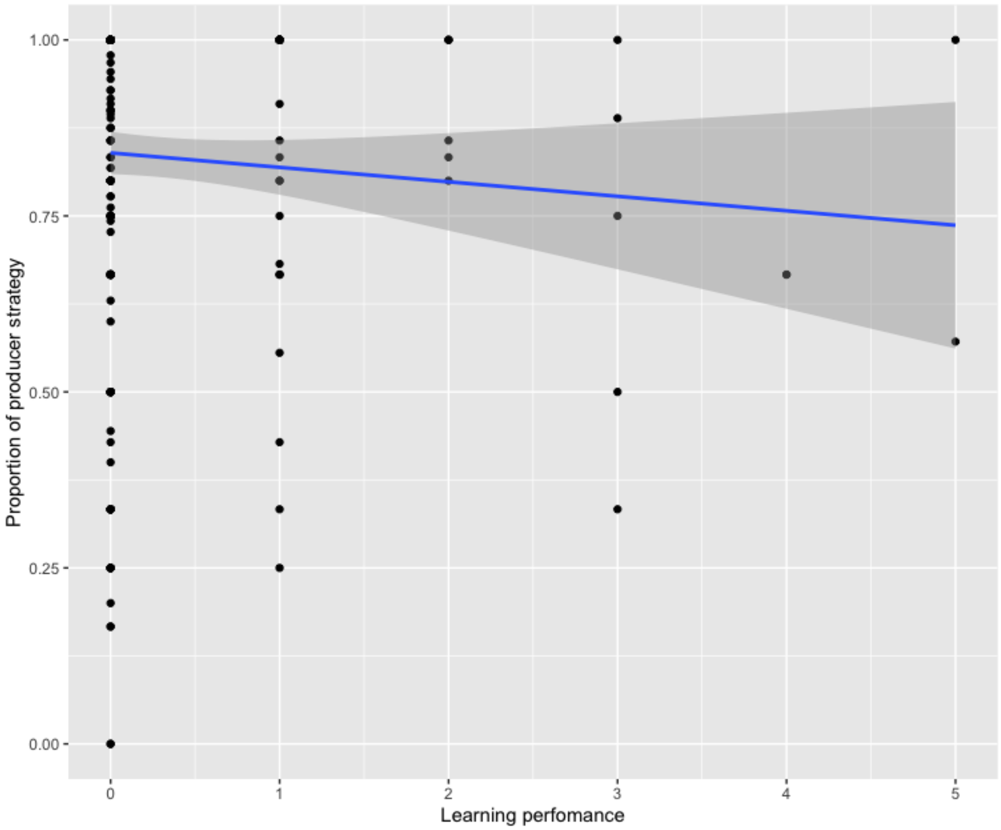

Figure 3. Proportion of patches produced (feeding from an unoccupied well) as a response of learning performance obtained from a discrimination task [proportion of correct choices over 50 binary choices between a rewarding and non-rewarding feeder] (N=19 individuals x 4-6 trials/seed distribution; observations=264).

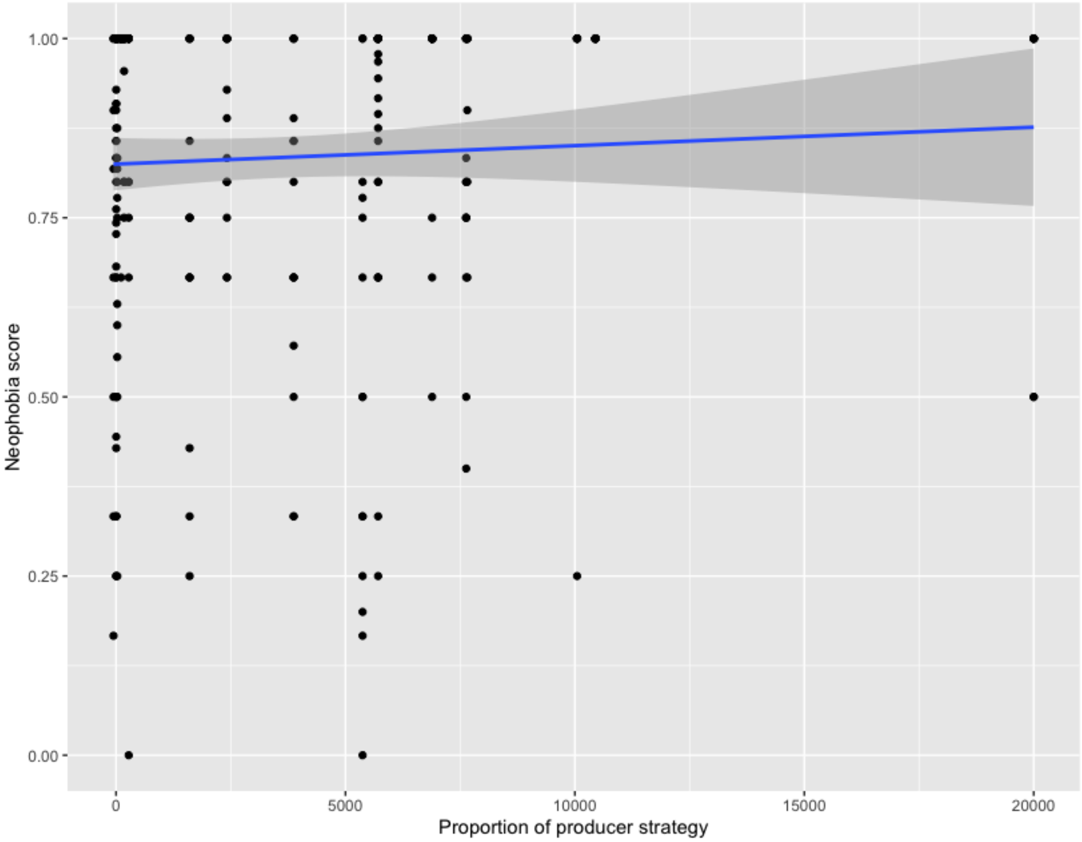

Figure 4. Proportion of patches scrounged as a response of neophobia obtained from a novel object test [latency to approach food in the presence – latency to approach food in the absence of a novel object] (N=19 individuals x 4-6 trials/seed distribution; observations=264).

Discussion.

In this experiment, we found that choosing a social foraging strategy is not mediated by previous experience with informative cues or learning performance, but may be influenced by fear response. Thus, foragers that use a producer strategy and gather information asocially are not necessarily individuals that have experience with information gathering and perform better in an associative learning task. Yet, choosing to produce was associated with increased fear of novelty. Additionally, our findings suggest that choosing to search or join others in their discoveries is impacted by resource distribution, where increased clumpiness leads to increased use of the scrounger strategy. Finally, our results add to the repeatability literature on individual consistency in strategy choice as we found significant moderate repeatability values.

Our work looked at individual-level determinants of strategy choice such as experience with informative cues and learning performance, and found that they were not good indicators of strategy choice. It is possible that experience with informative cues reliably predicting food in an associative learning task may not be transferable to a social foraging context and affect whether a forager will choose to look for food or join others' discoveries. It has been suggested that social-foraging games may require more complex learning abilities than simple learning tasks (Barou-Dagues et al. 2020); for instance, individuals in a producer-scrounger game must pay attention to social and non-social cues simultaneously. In accordance with this suggestion, studies done in stickleback species (*Gasterosteus aculeatus* and *Pungitius pungitius*) suggest that individuals must have prior experience with social information use in a social-foraging task in order to choose between searching for food or following a demonstrator fish to food (Webster and Laland 2018). Furthermore, learning performance in an associative learning task did not significantly predict strategy choice. House sparrows tested in a P-S game where variable food rewards were hidden under different coloured sand suggests that individuals use current information about their environment (i.e. colour of sand) significantly more than the experience with the variance of food patches (Ilan et al. 2013). Consequently, our birds may be giving more weight to their current environmental conditions over experience with previously informative cues.

Though there have been studies that have shown that animal personalities can affect strategy choice (e.g, David et al. 2011; Kurvers et al. 2010; Kurvers et al. 2012), they have rarely addressed neophobia or fear of novelty. Using a novel items test, our results show a negative and significant relationship between neophobia and a producer strategy. Contrary to our predictions, our results suggest that more fearful zebra finches are producing more. In comparison to our zebra finches, barnacle geese tested in a P-S game found that more fearful foragers (scored using the minimal distance and latency to approach a novel object) scrounged more; the authors suggest that this relationship could be a result of (1) higher activity in a novel environment in bold individuals, which takes them to the edge of foraging groups, and (2) the sociability of shy individuals which leads them to join discoveries, as scroungers tend to stay closer to their conspecifics. We do not know why our results with the zebra finches differ from the findings in the barnacle geese study, by adding more studies on neophobia on P-S games could be helpful to uncover the biological mechanisms driving these findings.

When measuring individual behavioral plasticity using random slopes, we found that individuals did significantly differ in how they adjust their foraging strategies depending on food availability; this finding has only been reported in Morand-Ferron et al. (2011) and Barou-Dagues et al. (2020). Still, our results should be interpreted carefully due to a small sample size. We found no support for learning performance or neophobia as the causes for these differences in plasticity. Interestingly, zebra finches tested in a P-S game that were observed to have greater adjustment between strategies were slower at learning in a colour discrimination as opposed to the authors' predictions (Barou-Dagues et al. 2020). The authors suggest that plasticity in strategy use in a social foraging context may require different cognitive processes than those needed to solve a simple discrimination task. Overall, I found no support for my hypotheses that individuals that adjust their strategy choice do so because of high learning performance in a discrimination task, or a weak reaction to novelty, and could not test my prediction on the effect of previous experience with informative cues due to convergence issues.

Using a producer strategy has been linked to dominance hierarchies (Barta and Giraldeau 1998; Liker and Barta 2002; Beauchamp 2006), body condition (Mathot et al. 2009; Biro and Stamps 2010; David and Giraldeau 2012), centrality and group composition (Aplin and Morand-Ferron 2017), competition among group members (Laskowski and Bell 2013), and animal personalities (David et al. 2011). Our study looks at individual-level cognitive traits and neophobia in an asocial context to understand their role in a social foraging game and found no support for any of the cognitive variables tested; however, we found evidence for an effect of neophobia and current environmental conditions (i.e. seed distribution) on strategy use. Our experiment is the first to experimentally bias the developmental experience of individuals with informative cues in order to look at social-foraging strategy choice. When testing for individual differences in plasticity, we found no significant relationship between level of adjustment in strategy use and our predictors, despite suggestions of possible individual differences in plasticity. We suggest that group phenotypic composition may play an important role in strategy choice and may be masking any possible relationships between strategy choice and the cognitive traits used in our experiment; an effect that could potentially be more pronounced in smaller groups similar to our experiment.

References.

Afshar, Mohammad, and Luc-Alain Giraldeau. "A unified modelling approach for producer–scrounger games in complex ecological conditions." *Animal behaviour* 96 (2014): 167-176.

Aplin, Lucy M., and J. Morand-Ferron. "Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour." *Proceedings of the Royal Society B: Biological Sciences* 284.1852 (2017): 20162872.

Bates, Douglas, et al. "The lme4 package." R package version 2.1 (2007): 74.

Barou-Dagues, Marie, Carolyn Louise Hall, and Luc-Alain Giraldeau. "Individual differences in learning ability are negatively linked to behavioural plasticity in a frequency-dependent game." *Animal Behaviour* 159 (2020): 97-103.

Barnard, Chris J., and Richard M. Sibly. "Producers and scroungers: a general model and its application to captive flocks of house sparrows." *Animal behaviour* 29.2 (1981): 543-550.

Barta, Zoltán, and Luc-Alain Giraldeau. "The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game." *Behavioral Ecology and Sociobiology* 42.3 (1998): 217-223.

Beauchamp, G. "Learning rules for social foragers: implications for the producer–scrounger game and ideal free distribution theory." *Journal of Theoretical Biology* 207.1 (2000): 21-35.

Beauchamp, G. "Phenotypic correlates of scrounging behavior in zebra finches: role of foraging efficiency and dominance." *Ethology* 112.9 (2006): 873-878.

Biro, Peter A., and Judy A. Stamps. "Do consistent individual differences in metabolic rate promote consistent individual differences in behavior?" *Trends in Ecology & Evolution* 25.11 (2010): 653-659.

Briffa, Mark, Danielle Bridger, and Peter A. Biro. "How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs." *Animal Behaviour* 86.1 (2013): 47-54.

Caraco, Thomas, and Luc-Alain Giraldea. "Social foraging: producing and scrounging in a stochastic environment." *Journal of Theoretical Biology* 153.4 (1991): 559-583.

Coolen, Isabelle, and Luc-Alain Giraldeau. "Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins, *Lonchura punctulata*." *Animal Behaviour* 66.4 (2003): 657-664.

Coolen, Isabelle, Luc-Alain Giraldeau, and Myriam Lavoie. "Head position as an indicator of producer and scrounger tactics in a ground-feeding bird." *Animal Behaviour* 61.5 (2001): 895-903.

David, Morgan, and Luc-Alain Giraldeau. "Zebra finches in poor condition produce more and consume more food in a producer–scrounger game." *Behavioral Ecology* 23.1 (2012): 174-180.

David, Morgan, et al. "Individual differences in behavioral consistency are related to sequential access to resources and body condition in a producer-scrounger game." *Frontiers in Ecology and Evolution* 2 (2014):19.

David, Morgan, Frank Cézilly, and Luc-Alain Giraldeau. "Personality affects zebra finch feeding success in a producer–scrounger game." *Animal Behaviour* 82.1 (2011): 61-67.

Dingemanse, Niels J., and Ned A. Dochtermann. "Quantifying individual variation in behaviour: mixed-effect modelling approaches." *Journal of Animal Ecology* 82.1 (2013): 39-54.

Dubois, Frédérique, and Étienne Richard-Dionne. "Consequences of multiple simultaneous opportunities to exploit others' efforts on free riding." *Ecology and Evolution* 10.10 (2020): 4343-4351.

Dubois, Frédérique, Luc-Alain Giraldeau, and Denis Réale. "Frequency-dependent payoffs and sequential decision-making favour consistent tactic use." *Proceedings of the Royal Society B: Biological Sciences* 279.1735 (2012): 1977-1985.

Eliassen, Sigrunn, et al. "Quantifying the adaptive value of learning in foraging behavior." *The American Naturalist* 174.4 (2009): 478-489.

Friard, Olivier, and Marco Gamba. "BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations." *Methods in Ecology and Evolution* 7.11 (2016): 1325-1330.

Galhardo, Leonor, A. Vitorino, and Rui Filipe Oliveira. "Social familiarity modulates personality trait in a cichlid fish." *Biology Letters* 8.6 (2012): 936-938.

Gibelli, Julie, and Frédérique Dubois. "Does personality affect the ability of individuals to track and respond to changing conditions?" *Behavioral Ecology* (2016): arw137.

Giraldeau, Luc-Alain, Jerry A. Hogan, and Michael J. Clinchy. "The payoffs to producing and scrounging: what happens when patches are divisible?" *Ethology* 85.2 (1990): 132-146.

Giraldeau, Luc-Alain, and Thomas Caraco. Social foraging theory. Vol. 73. Princeton University Press, 2000.

Ha, Renee Robinette, and James C. Ha. "Effects of ecology and prey characteristics on the use of alternative social foraging tactics in crows, *Corvus caurinus*." *Animal Behaviour* 66.2 (2003): 309-316.

Harten, Lee, et al. "Persistent producer-scrounger relationships in bats." *Science Advances* 4.2 (2018): e1603293.

Ilan, Tomer, et al. "The role of beginner's luck in learning to prefer risky patches by socially foraging house sparrows." *Behavioral Ecology* 24.6 (2013): 1398-1406.

Katsnelson, Edith, et al. "Early experience affects producer–scrounger foraging tendencies in the house sparrow." *Animal Behaviour* 75.4 (2008): 1465-1472.

Katsnelson, Edith, et al. "Individual-learning ability predicts social-foraging strategy in house sparrows." *Proceedings of the Royal Society B: Biological Sciences* 278.1705 (2011): 582-589.

Koops, Marten A., and Luc-Alain Giraldeau. "Producer–scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models." *Animal Behaviour* 51.4 (1996): 773-783.

Kurvers, Ralf HJM, et al. "Boldness affects foraging decisions in barnacle geese: an experimental approach." *Behavioral Ecology* 23.6 (2012): 1155-1161.

Kurvers, Ralf HJM, et al. "The effect of personality on social foraging: shy barnacle geese scrounge more." *Proceedings of the Royal Society B: Biological Sciences* 277.1681 (2010): 601-608.

Laskowski, Kate L., and Alison M. Bell. "Competition avoidance drives individual differences in response to a changing food resource in sticklebacks." *Ecology Letters* 16.6 (2013): 746-753.

Liker, András, and Zoltán Barta. "The effects of dominance on social foraging tactic use in house sparrows." *Behaviour* 139.8 (2002): 1061-1076.

Mathot, Kimberley J., and Luc-Alain Giraldeau. "Increasing vulnerability to predation increases preference for the scrounger foraging tactic." *Behavioral Ecology* 19.1 (2008): 131-138.

Mathot, Kimberley J., et al. "Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of zebra finches." *Oikos* 118.4 (2009): 545-552.

Mottley, Kieron, and Luc-Alain Giraldeau. "Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria." *Animal Behaviour* 60.3 (2000): 341-350.

Morand-Ferron, Julie, Elisabeth Varennes, and Luc-Alain Giraldeau. "Individual differences in plasticity and sampling when playing behavioural games." *Proceedings of the Royal Society B: Biological Sciences* 278.1709 (2011): 1223-1230.

Morand-Ferron, Julie, Gi-Mick Wu, and Luc-Alain Giraldeau. "Persistent individual differences in tactic use in a producer–scrounger game are group dependent." *Animal Behaviour* 82.4 (2011): 811-816.

Ohtsuka, Yasunori, and Yukihiko Toquenaga. "The patch distributed producer–scrounger game." *Journal of Theoretical Biology* 260.2 (2009): 261-266.

Rojas-Ferrer, Isabel, and Julie Morand-Ferron. "The impact of learning opportunities on the development of learning and decision-making: an experiment with passerine birds." *Philosophical Transactions of the Royal Society B* 375.1803 (2020): 20190496.

Shettleworth, Sara J. Cognition, evolution, and behavior. Oxford university press, 2009.

Stamps, Judy A., Mark Briffa, and Peter A. Biro. "Unpredictable animals: individual differences in intraindividual variability (IIV)." *Animal Behaviour* 83.6 (2012): 1325-1334.

Stoffel, Martin A., Shinichi Nakagawa, and Holger Schielzeth. "rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models." *Methods in Ecology and Evolution* 8.11 (2017): 1639-1644.

Vickery, William L., et al. "Producers, scroungers, and group foraging." *The American naturalist* 137.6 (1991): 847-863.

Webster, Mike M., and Kevin N. Laland. "Experience shapes social information use in foraging fish." *Animal Behaviour* 146 (2018): 63-70.

Conclusion.

My work suggests that information acquisition can cause among-individual variation in animal personality and learning performance, but does not affect strategy choice in a social-foraging game. When individuals have incomplete information about their environment, they find themselves in need to reduce environmental uncertainty by sampling their environment. By sampling novel stimuli representative of uncertainty and unfamiliarity, individuals are better able to make adaptive decisions tailored to their current environment (Stephens 1989; Houston and McNamara et al. 1993; Dall and Johnstone 2002; Dall et al. 2004). However, my results suggest that not all individuals respond the same to their environment. In my first chapter I find that individuals vary in the way they lower environmental uncertainty due to their reactions to novelty. By correlating individual novelty reactions to exploratory personality using the classic open field test, I conclude that variation in exploration is linked to variation in information gathering strategies. In my second chapter, I use a rare longitudinal study to understand how experience with informative cues can cause variation in learning performance and decision-making later in life. My results suggest that experience with informative cues (i.e. learning opportunities during ontogeny) leads to increased learning performance in a simple discrimination task; additionally, experience with learning opportunities may also affect speed of choice. Finally, my third chapter examines how individual cognitive traits can affect information use in a producer-scrounger (P-S) game-theoretic model. Here my results show that experience with informative cues and learning performance have no detectable effect on individual strategy choice or plasticity in strategy use, yet neophobia significantly influences social-foraging strategy choice.

Exploratory personality is commonly defined as the individual differences in the acquisition of information as the animal moves through a novel environment (Verbeek et al. 1994; Reader 2015). Though individual exploration is often described as a metric of information gathering, it is rarely measured as a strategy to reduce environmental uncertainty. In fact, exploratory personality has been frequently measured in terms of activity rate in a novel environment (van Overveld and Matthysen 2013; Arvidsson and Matthysen 2016). Consequently, it has been largely assumed that higher activity rate makes a coincidental effect of encountering novelty. In my own work, I first scored individual exploratory personality using a standard open field test which measures activity rate in a novel environment (Carter et al. 2013; Perals et al. 2017); I then quantified repeatability values (proportion of phenotypic variance explained by among-individual differences) for exploration score. Exploration score was then used as an explanatory variable for individual first choice between a familiar stimulus previously associated with a food reward and a novel stimulus representing uncertainty. I hypothesize that individuals that move through their environment quicker are actively seeking novelty in order to reduce environmental uncertainty. I predicted that if exploratory personality is indeed an information gathering strategy, then individuals that move through their environment faster (faster explorers) should be more attracted to novelty as a way to reduce uncertainty. Alternatively, it has been proposed that exploratory personality could result from behavioral plasticity where faster explorers are constrained by their lack of knowledge due to a speed-accuracy trade-off since they are assumed to have less accurate information about their environment (Verbeek et al. 1994; Mathot et al., 2012; Arvidsson and Matthysen 2016). Consequently, if exploratory personality were a result of behavioral plasticity, then faster explorers would be more routine-like and more resistant to changing from a familiar resource to a novel resource. My results validate exploratory personality as an information-gathering strategy since faster explorers were more likely to choose novel stimuli and switched from a familiar to novel stimuli more readily when compared to slow explorers. More so, my results suggest that experience with previously rewarding options interacts with age, where juvenile birds were more influenced by recent experience than older birds. This finding counters the long-held idea that fast explorers are routine-like and less plastic than slow explorers. Still, it is important to highlight the lack of independence between our alternative hypotheses where behavioral plasticity analysis encompasses novelty seeking. Thus, future work should aim to disentangle novelty seeking from plasticity. Additionally, my study highlights a positive correlation between locomotion and sampling where higher activity rates correlate to novelty seeking in an open-field test. Furthermore, my work provides support for causal direction of exploratory behavior where information seeking drives locomotion. In conclusion, my results suggest that exploratory personality as assessed in the traditional open field test can be used as a measurement for individual variation in information gathering. Within the animal personality literature, researchers commonly ask about the causes of variation in personality traits within a group and how these differences are maintained across time (Carter et al. 2013). How animals respond to novelty within their environment is of particular interest to many that study animal personalities. Réale et al. (2007) suggest that an individual's response to a novel stimulus (i.e. neophobia and neophilia) may be a mechanism underlying exploratory personality (i.e. response to a novel environment) which natural selection could act upon. My results support the idea of novelty response as a causal effect of exploratory behavior and a mechanism for individual variation within groups.

My second chapter provides empirical support for the hypothesis that an individual's developmental environment can influence cognitive traits and decision-making later in life. Models have predicted that variation in environmental certainty during development can lead to individual variation later in life; stable environments with consistent food resources are commonly associated with decreased learning performance as individual can rely on previously learned experiences or innate preferences (Stephens 1987; Dunlap and Stephens 2009). Comparatively, environments with low certainty and fluctuating food resources can lead to increased learning performance as individual foragers must learn to track their changing environments (Kotrschal and Taborsky 2010). In my work I address how experience with informative cues in the developmental environment can cause variation in cognitive traits. Specifically, I use learning opportunities which allow individuals to learn to form associations, a type of experience that can then be transferred to optimize learning later in life. Hypothetically, forming associations using informative cues during development could cause better learning performance later in life and quicker decision-making since individuals should be more familiar making associations. I exposed juvenile birds to three different experimental treatments of varying cue reliability: (i) one-colour cue reliably predicted the presence of food (associative learning), (ii) a combination of two-colour cues reliably predicted the presence of food (conditional learning), or (iii) colour cues were non-informative (control). After the experience phase was completed, I exposed each bird to two separate discrimination tasks in order to test for learning performance (choice accuracy) and speed of choice. My results indicate that the experimental learning treatments (associative and conditional learning treatments) caused an increase in initial (higher intercept) and overall accuracy in the first learning task, and shorter choice latencies in the second learning task. I further tested for speed-accuracy trade-offs in my learning treatments, but found no support. Overall, my experiment provides rare empirical evidence for theoretical models that predict that experience with informative cues early in life should lead to distinct phenotypic variation in the development of cognitive traits. Moreover, my work provides evidence that learning is a developmental process that can be shaped by information gathering opportunities in the environment. By looking into learning performance later in life, I was able to make inferences about how the informational properties of the environment are integrated into an individual's behavioral repertoire. This study answers the call of many researchers (e.g. Stamps and Krishnan 2014; Fawcett and Frankenhuis 2015; Stamps and Frankenhuis 2016) trying to understand the interplay between learning, ontogeny, and plasticity.

Within the same environmental conditions, individuals can differ in how they use information and make decisions. Presumably, individuals differ in their decision-making partly due to previous experience and differing cognitive traits. Under this assumption, I used the P-S game to understand if differing experience with informative cues, learning performance, and fear reactions (neophobia scores) could explain individual strategy choice. In a P-S game, foragers can choose between investing energy and time in searching for novel food resources and use a producer strategy; alternatively, foragers can join others in their discoveries and use a scrounger strategy (Barnard and Sibly 1981; Vickery et al. 1991). Though strategy choice is highly influenced by negative frequency-dependent payoffs where the least common strategy within the group will have the greatest payoff, other factors such as group size, and resource abundance and distribution have also been shown to influence individual strategy choice (Caraco and Giraldeau 1991; Coolen 2002; Hamilton 2002; Beauchamp 2008). Presumably, searching for food alone requires individual learning more than joining other's discoveries. Hypothetically, experience forming associations is useful when searching for food asocially and can lead to individuals choosing to search for resources more than they join other's discoveries. Thus, cognitive traits could also contribute to a forager's choice of strategy since individuals that choose to search for food should be better at tracking changes in their environment by forming associations using informative cues and have better learning performance. Fear response, measured in terms of neophobia, could also affect strategy choice as foragers that are less fearful of novelty should also be more willing to seek novel resources. In order to understand the relationship between strategy choice and the previous factors mentioned, I first exposed groups of birds to three different seed distribution of varying resource density and quantified the frequency of scrounger use for each individual. I then tested for experience with informative cues, learning performance, and neophobia as possible predictors. Additionally, I looked into these predictors as explanatory variables for strategy adjustment between seed distributions, i.e. behavioral plasticity in strategy choice. My results provide no support for experience with informative cues or learning performance as predictors for individual strategy choice and behavioral plasticity. However, contrary to my predictions, neophobia was significantly and negatively correlated to the producer strategy where more neophobic foragers chose a producer strategy more than a scrounger strategy. Additionally, I found significant moderate repeatability values for strategy choice which supports individual consistency in social-foraging strategy.

Few empirical studies have looked at individual variation in plasticity in a P-S game (i.e. Morand-Ferron et al. 2011; Barou-Dagues et al. 2020). My random slopes analysis found significant variation in individual behavioral plasticity across the different seed distributions. I conclude that my chosen cognitive traits, which were quantified in an asocial context, may not be transferable to a social-foraging context and affect whether a forager will choose to look for food or join others' discoveries. Still, I found a significant correlation between increased neophobia and increased producer strategy choice which could suggests a possible confound of social hierarchy where less dominant foragers may be displaced more easily from novel resources by more dominant foragers that choose to scrounge. In social-foraging games with divisible resources (i.e. more than one piece of food per patch) interference competition may occur, particularly in groups with social hierarchies maintained through aggressive encounters. Zebra finches are known to have strong dominance hierarchies (Morgan et al. 2011) and were observed to be aggressive with their conspecifics during the experiment. Consequently, when food availability is reduced and the number of food items per patch decreases, competition may increase as well as aggressive encounters (Liker and Barta 2002). In a previous study, zebra finches that were found to be more neophobic where also found to be the subordinates within their groups (Morgan et al. 2011), thus, neophobia could be linked to dominance hierarchies which could constrain their strategy choice into a higher frequency of producer strategy. Much work is still needed to clearly understand the relationship between neophobia and social foraging strategy choice. My study is the first to experimentally bias the learning and experience of individual birds in order to look at social-foraging strategy choice, and one of the few studies to address neophobia. Furthermore, this work suggests that complex social-foraging games may require a different set of cognitive skills than simple associative learning task. Future studies could test for performance in discrimination tasks of increasing complexity (i.e. social and asocial contexts) and difficulty (i.e. variable options) and see if that serves as a better predictor of social foraging strategy.

My thesis addresses two of Niko Tinbergen's four questions (i.e. causation and ontogeny) on the understanding of animal behaviour (Tinbergen 1963; Bateson and Laland 2013), where I address information acquisition as a mechanism for individual variation in decision-making, learning, and animal personality. Additionally, my work looks at ontogeny as a source of individual variation in cognitive traits and decision-making by providing a rare empirical quantification and manipulation of information (a numerical measure of the uncertainty of an outcome). My first chapter concludes that individuals vary in the way they gather information which can be observed via exploratory personality. Subsequently, my second chapter highlights the importance of experiences with informative cues in an animal's developmental environment which can cause differences in cognitive traits such as learning and decision-making later in life. Finally, my third chapter found no effect of cognitive traits, but a significant effect of fear response, in a P-S game where individuals must choose between searching for food or exploiting the efforts of other foragers. In general, I suggest that the effect of information on subsequent behavior may be context-specific and information which has been acquired may not be transferable to every context (Dukas 2013).

References.

Arvidsson, Lisa K., and Erik Matthysen. "Individual differences in foraging decisions: information-gathering strategies or flexibility?" *Behavioral Ecology* 27.5 (2016): 1353-1361.

Barou -Dagues, Marie, Carolyn Louise Hall, and Luc-Alain Giraldeau. "Individual differences in learning ability are negatively linked to behavioural plasticity in a frequency-dependent game." *Animal Behaviour* 159 (2020): 97-103.

Barnard, Chris J., and Richard M. Sibly. "Producers and scroungers: a general model and its application to captive flocks of house sparrows." *Animal behaviour* 29.2 (1981): 543-550.

Bateson, Patrick, and Kevin N. Laland. "Tinbergen's four questions: an appreciation and an update." *Trends in ecology & evolution* 28.12 (2013): 712-718.

Beauchamp, Guy. "What is the magnitude of the group-size effect on vigilance?" *Behavioral Ecology* 19.6 (2008): 1361-1368.

Caraco, Thomas, and Luc-Alain Giraldeau. "Social foraging: producing and scrounging in a stochastic environment." *Journal of Theoretical Biology* 153.4 (1991): 559-583.

Carter, Alecia J., et al. "Animal personality: what are behavioural ecologists measuring?" *Biological Reviews* 88.2 (2013): 465-475.

Coolen, Isabelle. "Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*)." *Behavioral Ecology and Sociobiology* 52.3 (2002): 232-238.

Dall, Sasha RX, Alasdair I. Houston, and John M. McNamara. "The behavioural ecology of personality: consistent individual differences from an adaptive perspective." *Ecology Letters* 7.8 (2004): 734-739.

Dall, Sasha RX, and Rufus A. Johnstone. "Managing uncertainty: information and insurance under the risk of starvation." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357.1427 (2002): 1519-1526.

David, Morgan, Yannick Auclair, and Frank Cézilly. "Assessing short-and long-term repeatability and stability of personality in captive zebra finches using longitudinal data." *Ethology* 118.10 (2012): 932-942.

Dukas, Reuven. "Effects of learning on evolution: robustness, innovation and speciation." *Animal Behaviour* 85.5 (2013): 1023-1030.

Dunlap, Aimee S., and David W. Stephens. "Components of change in the evolution of learning and unlearned preference." *Proceedings of the Royal Society B: Biological Sciences* 276.1670 (2009): 3201-3208.

Fawcett, Tim W., and Willem E. Frankenhuis. "Adaptive explanations for sensitive windows in development." *Frontiers in Zoology* 12.1 (2015): 1-14.

Hamilton, Ian M. "Kleptoparasitism and the distribution of unequal competitors." *Behavioral Ecology* 13.2 (2002): 260-267.

Houston, Alasdair Ian, John M. McNamara, and John MC Hutchinson. "General results concerning the trade-off between gaining energy and avoiding predation." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 341.1298 (1993): 375-397.

Kotrschal, Alexander, and Barbara Taborsky. "Environmental change enhances cognitive abilities in fish." *PLoS Biol* 8.4 (2010): e1000351.

Liker, András, and Zoltán Barta. "The effects of dominance on social foraging tactic use in house sparrows." *Behaviour* 139.8 (2002): 1061-1076.

Mathot, Kimberley J., et al. "Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity." *Oikos* 121.7 (2012): 1009-1020.

Morand-Ferron, Julie, Gi-Mick Wu, and Luc-Alain Giraldeau. "Persistent individual differences in tactic use in a producer–scrounger game are group dependent." *Animal Behaviour* 82.4 (2011): 811-816.

Perals, Daniel, et al. "Revisiting the open-field test: what does it really tell us about animal personality?" *Animal Behaviour* 123 (2017): 69-79.

Reader, Simon M. "Causes of individual differences in animal exploration and search." *Topics in Cognitive Science* 7.3 (2015): 451-468.

Réale, Denis, et al. "Integrating animal temperament within ecology and evolution." *Biological reviews* 82.2 (2007): 291-318.

Stamps, Judy A., and V. V. Krishnan. "Combining information from ancestors and personal experiences to predict individual differences in developmental trajectories." *The American Naturalist* 184.5 (2014): 647-657.

Stamps, Judy A., and Willem E. Frankenhuis. "Bayesian models of development." *Trends in ecology & evolution* 31.4 (2016): 260-268.

Stephens, D. W. "On economically tracking a variable environment." *Theoretical Population Biology* 32.1 (1987): 15-25.

Stephens, D. W. "Variance and the value of information." *The American Naturalist* 134.1 (1989): 128-140.

Tinbergen, Niko. "On aims and methods of ethology." *Zeitschrift für tierpsychologie* 20.4 (1963): 410-433.

van Overveld, Thijs, and Erik Matthysen. "Personality and information gathering in free-ranging great tits." *PloS one* 8.2 (2013): e54199.

Verbeek, Monica EM, Piet J. Drent, and Piet R. Wiepkema. "Consistent individual differences in early exploratory behaviour of male great tits." *Animal Behaviour* 48.5 (1994): 1113-1121.

Vickery, William L., et al. "Producers, scroungers, and group foraging." *The American Naturalist* 137.6 (1991): 847-863.