University of Alberta

Animal cognition and animal personality: Individual differences in exploratory behaviour, learning, vocal output, and hormonal response in an avian model

by

Lauren Mary Guillette

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Psychology

Fall 2012
Edmonton, Alberta

Dedication

This thesis is dedicated to all the animals that made this research possible and to all the collaborators I worked with along the way.

Abstract

The foremost goal of this thesis is to integrate the study of animal cognition with the field of animal personality. In the early 20th century, Pavlov integrated these fields by describing an interaction between associative learning and dogs that exhibited different behavioural types. Since Pavlov, little work has been conducted to examine how differences in cognition may affect the development of personality, the converse, or the interaction between the two. In Chapters 2 and 3 I use wild-caught black-capped chickadees (*Poecile atricapillus*) to examine if individual differences in learning speed are related to exploratory behaviour. Results from Chapter 2 show that fast-exploring chickadees solve an acoustic operant discrimination task in fewer trials compared to slow-exploring chickadees. In Chapter 3, the acoustic operant discrimination task included a reversal phase. Once each bird had learned to perform the correct response to two different stimulus categories, the reward contingencies associated with each category were reversed. Here I found that the slow-exploring chickadees outperformed the fast-exploring chickadees suggesting that variation in cognition and behavior may be maintained through habitat-dependent selection. That is, slow and fast exploring chickadees may excel in different environments. In Chapter 4, I used black-capped chickadees to examine if vocal production was related to exploratory behaviour. I found that vocal production was consistent over time in a control context and in a stressful context, but vocal production was not consistent across contexts. Furthermore, vocal production of the namesake *chick-a-dee* call and *alarm* call in the stressful context were positively related to exploratory behaviour. In Chapter 5, I used domestic pigeons (*Columba livia*) to examine the relationship between accuracy of discrimination and exploration. I found, contrary to the predicted direction, that fast-exploring pigeons were better discriminators compared to slow-exploring pigeons. Taken together, the experiments that comprise this thesis suggest that different cognitive styles do co-vary with different behavioural styles (i.e., animal personalities). Ongoing and future research directions for studying individual differences in cognition are discussed.

Acknowledgements

I would like to thank my supervisor, Dr. Christopher Sturdy, for not only allowing me, but also pushing me to pursue my own research interests as well as his constant support and mentorship in both research and teaching. I would like to thank my examination committee, Dr. Dallas Triet, Dr. David Coltman, Dr. Dan Blumstein, Dr. Pete Hurd and Dr. Marcia Spetch. I would also like to thank Dr. Karen Hollis for her continued collaboration, mentorship and support.

I would like to thank my lab mates for the many long, but exciting and fun hours we spent together in and out of the laboratory: Dr. Marc Avey, Allison Hahn, Marisa Hoeschele, and Dr. Darren Proppe. I could not have collected all the data presented in this thesis without the help of the following undergraduate research assistants: Craig Anderson, Jillian Avis, Dawson Clary, Tara Farrelll, Jon Gaspar, Daniel Lee, Jeffrey Pisklak, Nicole Savignac and Shannon Wowk.

I would like to thank my collaborators: Dr. Michael Dawson, Danielle Lubyk, Dr. Scott MacDougall-Shackleton, Adam Reddon, and Dr. Hans Slabbekoorn for comments on an early version of Chapter 4. Special thanks to Allison Hahn for reading an early draft of this thesis. Thanks to Isaak Lank and Lou Omerzu for providing technical support. I would also like to thank Biosciences Animal Service at the University of Alberta, especially Simmone Kerswell for taking care of the birds. For the duration of this thesis I was supported by the Department of Psychology at the University of Alberta and the Isaak Walton Killam Memorial Scholarship.

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Chapter 1 General introduction

Animal personality

The study of animal personality is concerned with the behaviour of individuals in relation to one another (Stamps & Groothuis 2010). The term animal personality is operationally defined as individual differences in behaviour that are consistent across time and/or across situations (Réalé, Reader, Sol, McDougall & Dingenmanse 2007; Stamps & Groothuis 2010). The terms *temperament* and *coping style* have been used interchangeably with the term animal personality (Réalé et al. 2007; Koolhaas at el. 1999). Although the study of animal personality has become popular recently, empirical work dates back to Pavlov (1927), who identified four temperamental types in dogs (Gosling 2001, see below for more about Pavolv). The term *behavioural syndrome* refers to individual differences in behaviours that are correlated across time or context (Sih et al. 2004) at the level of the population (for recent reviews see Bergmüller 2010; Realé & Dingemanse 2010).

Prior to the recent surge in animal personality studies, individual variation in behaviour was assumed to represent noise around a maximally-adaptive mean arrived at through long-term selective pressures (e.g., Krebs & Davies 1997). This notion seems odd from a psychological perspective, since the study of human personality, defined as an individual’s characteristic style of behaving, thinking and feeling (Schacter, Gilbert & Wegner 2009) has been the focus of scientific study for more than a century. Another reason why it is odd that studying individual differences in behaviour has not become a popular topic until recently is because behavioural ecologists have long studied dichotomous behavioural traits (alternative behavioural strategies) that co-exist within the same population. For instance, producers versus scroungers in foraging behaviour (e.g., Barnard & Sibly 1981), holders versus sneakers for territorial defence or mating tactics (e.g., Clark & Ehlinger 1987), and hawk versus dove in the classic game theory example. Even so, studying alternative behavioural strategies does not reflect the true continuous nature of behaviour displayed by animals. Although it will not be discussed in any great detail, it is worth noting that a large literature exists on behavioural and physiological differences in mice that have been selected for the manner in which they deal with environmental stimuli (e.g., short-attack latency and long-attack latency lines, Benus, den Daas, Koolhaas & van Oortmerssen 1990; Benus, Koolhaas, van Oortmerrseen 1988) and in chickens selected for different behavioural styles (e.g., high-feather pecking frequency versus low-feather pecking frequency, Korte, Beuving, Ruesink & Blockhuis 1997).

Current proximate and ultimate theories of the cause and maintenance of animal personalities are the constraint hypothesis and the adaptive hypothesis, respectively (Realé & Dingemanse 2010; Bergmüller 2010). The former hypothesis suggests that genetic mechanisms such as pleiotrophy or linkage disequilibrium produce a common gene-physiology-behaviour pathway that serves to constrain behavior (i.e., behaviours cannot evolve independently because of the common pathway). The latter hypothesis suggests that consistency in behaviour is adaptive because of the trade-offs associated with life-history traits, that may be maintained by habitat-dependent selection or negative-frequency-dependent selection.

There are five main behavioural axes that have been identified in the animal personality literature: exploration, boldness, activity, sociability, and aggressiveness (Gosling 2001; Realé et al. 2007; Sih et al. 2004). Chapters 2 – 4 in this thesis focus on the exploration axis, and Chapter 5 examines boldness and activity in addition to exploration. The benefits of studying animal personality include; (1) a more holistic picture of understanding why animals behave the way they do, (2) improved experimental design (e.g., medical, psychological) if we understand how animals with different behavioural profiles may react to the same treatment, (3) improved welfare for laboratory-housed and farmed animals, (4) conservation efforts can be improved (e.g., reintroduction efforts).

Cognition and personality

In Pavlov's studies on associative learning he classified dogs as possessing one of four types of nervous systems: excitable, lively, quiet or inhibited. Pavlov described how these different nervous systems affected how animals of each type differed in their ability to form excitatory or inhibitory associations. For instance, the *excitable* type learned excitatory conditioning very quickly, but acquiring inhibitory conditioning was very difficult. For the *quiet* type, the equilibrium between excitatory and inhibitory conditioning was balanced and these individual displayed consistent, but slower learning compared to the *excitable* type (Locurto 2007; Carere & Locurto 2011). In fact, this classification of the different types of nervous systems later influenced Eysenck's (1967) human personality theory (Locurto1997).

Since Pavlov’s seminal studies, individual differences in learning ability represent one aspect of animal personality that has received relatively limited attention to date (Sih & Bell 2008). Most studies that have examined the relationship between learning ability and personality have used either associative or spatial tasks (but see Coleman, Tully & McMillan 2005). Evidence from several species supports the idea that an animal’s boldness or willingness to explore directly mediates the instance or degree of contact than an individual has with unconditioned and conditioned stimuli. For example, rainbow trout that are more willing to enter into an unprotected open area acquired a classically conditioned task more quickly compared to shyer trout (Sneddon 2003). Dugatkin and Alfieri (2003) found that bolder guppies, those that were more willing to inspect predators, learned an associative task faster than guppies that were less willing to inspect predators. Rhesus macaques that avoid novel food are more difficult to train to perform instrumental learning tasks, like retrieving food from an experimenter for positive reinforcement or learning to touch a goal object for a food reward (Coleman et al. 2005). In sum, studies that focus on associative learning are driving most of the correlations between learning and other personality traits studied in non-human animals to date. In the studies that comprise the body of this thesis (Chapters 2 through 5) I aim to control for the differential effects that neophobia and exploratory tendencies of individuals may have on individual performance in cognitive tasks.

Great tits (*Parus major*) and the Exploration task

Great tits (*Parus major*) are one of the best-studied models of animal personality and, to date, the novel environment task is one of the most widely used behavioural assays to study animal personality. A series of studies (Verbeek et al. 1994, 1996, 1999) demonstrated that wild-caught, lab-reared male great tits differed from one another, but were individually consistent in exploratory behaviour. Breeding studies with great tits have found exploratory behaviour to be heritable (54 ± 5%; Drent, van Oers & van Noordwijk 2003) and to be related to several behaviours in the wild that affect fitness such as natal dispersal (Dingemanse et al 2003), dominance (Dingemanse & de Goede, 2004), offspring recruitment (Dingemanse et al. 2004), nest defence (Hollander et al. 2008), mate-choice and extrapair behaviour (van Oers et al. 2008), singing behaviour (Naguib et al. 2010) and that fitness advantage for males and females fluctuated over several years in accordance with local abundance or shortage of food (i.e., beech masting, Dingemanse, Both, Drent & Tinbergen 2004). In sum, the study of animal personality using great tits has demonstrated that: 1) behaviours are stable across parts of an individual's life 2) similar behaviours are correlated across different contexts, 3) different behaviours are correlated 4) these behaviours are linked to underlying physiological profiles, 5) these behaviours are heritable, and 6) these behaviours affect the fitness of individuals.

Why use exploratory behaviour? I chose to use exploratory behaviour as the main proxy for animal personality in my thesis mainly because exploration seems to be related to so many other ecologically relevant behaviours (see previous paragraph). Moreover, exploratory behaviour has been tested in a large number of species, which facilitates cross-species comparisons using standardized testing.

Fig. 1-1 is a screen shot taken from the novel environment used to test exploratory behaviour in black-capped chickadees in Guillette et al. (2011). This is a modified design based on Verbeek et al.'s (1994, 1996, 1999) studies with great tits. In these studies, each great tit's home cage was located on the opposite side of the same walls of the novel environment room. A mechanical door was opened, and the room containing the home cage was darkened with the intention of making the bird enter the lighted novel environment room. The novel environment room contained five artificial trees, each with four branches. Observations occurred in real time through a one-way screen. At the end of the observation period, the light in the room containing the home cage was lit, and the lights in the novel environment room were darkened to facilitate the bird to move back to the home cage. Our novel environment assay was conducted in a different room for the experiments in Chapters 2, 3 and 4, but each experiment consisted of the same five artificial trees (same dimensions as in Verbeek et al. 1994) and the same basic design. Each chickadee was placed, in its home cage against the novel environment room. A transparent barrier controlled the birds' physical access to the room. We allowed birds to visually assess the room for one hour because in pilot testing, chickadees failed to leave the home cage if the barrier was opaque. After one hour with visual access to the novel environment room, the transparent barrier was removed. We did not manipulate the lights, but rather chose to let birds enter the novel environment, or stay in their home cages. Fig. 1-2 is a picture of the novel environment test used for testing pigeons in Chapter 5. See Fig. 5-1 for schematic of this novel environment apparatus. For Chapters 2, 3, 4 and 5 all trials in the novel environment were recorded so they could be scored at a later date.

Model species

Chickadees have long been used as models to examine vocal production and perception (e.g., Hailman & Ficken 1996; Nowicki 1983; Bloomfield, Charrier & Sturdy 2004) because they are one of a few groups, including humans, which learn their vocalizations (Doupe & Kuhl 1999). In addition to studies concerned with vocal production and perception, chickadees have also been used as a model to study a host of cognitive functions, such as episodic-like memory (Feeney, Roberts & Sherry 2009), spatial learning and spatial orientation (Gray, Bloomfield, Ferrey, Spetch & Sturdy 2005; Batty, Bloomfield, Spetch & Sturdy 2009), vocal category perception (e.g., Sturdy, Phillmore & Weisman 2000; Bloomfield, Sturdy, Phillmore & Weisman 2003; Charrier, Lee, Bloomfield & Sturdy 2005), cue competition in cache recovery (LaDage, Roth, Fox & Pravosudov 2009), abstract concept formation (Hoeschele, Cook, Guillette, Hahn & Sturdy, under review) and seasonal effects of neuronal recruitment (Hoshooley & Sherry 2004) to name but a few.

In addition to the studies I present in the follow chapters, two additional studies have used chickadees as model species to investigate other aspects of animal personality, one from our lab group, in collaboration with the Hurd Laboratory group at the University of Alberta and another from the Pravosudov laboratory group (Fox et al. 2009) at the University of Nevada at Reno. Fox et al. (2009) demonstrated that low-exploring male mountain chickadees (*Poecile gambeli*) were more likely to become dominant in pairwise encounters with high-exploring males. They found that novel environment and novel object approach score were not correlated, in contrast with the findings in great tits, where these scores are considered to measure the same trait (Verbeek, Boon & Drent 1996). We (Guillette, Bailey, Reddon, Hurd & Sturdy 2010) tested sympatric black-capped and mountain chickadees and allopatric mountain chickadees for repeatability in capture order. In same species/sex groups, chickadees were released into a room and then captured by an experimenter. The same process was repeated a week later. The males of both species, but not the females showed consistency in capture order over both sessions.

Because of their history as a model of learning, their phylogenetic relationship to a key model of animal personality (the great tit, Verbeek et al. 1994, 1996, 1999) and their recent use as an animal personality model themselves, we advocate the use of chickadees as a model for studying the relationship between learning and personality. In addition, chickadees are year-round resident species; they do not migrate, allowing the same individuals to be easily tracked in the field from year to year. In Alberta, Canada the closely related (sister species) black-capped and mountain chickadees live both in areas of sympatry (Kananaskis Country; 50°37′05″N 115°09′15″W) and allopatry (53°32′N 113°30′W, black-capped chickadees only). These different populations in close proximity of one another allow for investigating the phylogenetic and learned difference in species-typical behaviour and cognition.

The personality-based research conducted by our laboratory group was motivated in part by the intra-specific variation observed in black-capped and mountain chickadees learning an acoustic operant discrimination. My initial goal was to examine learning speed (the number of trials needed to learn an acoustic GO/NOGO discrimination) as a personality trait and see if learning speed varied consistently along other known personality traits (i.e., novel environment exploration).

Current studies

My first goal was to test if novel environment exploration, a standard animal personality assay (Verbeek et al. 1994; Sih et al. 2004) is related to learning. The data presented in Chapter 2 differs from previous experiments that examined the relationship between learning and personality because I used an operant learning paradigm, rather than an associative (classical conditioning) paradigm. Faster exploring animals may have an advantage in associative-based tasks because these animals may have more contact with important information, and therefore learn the associative tasks more quickly than slower exploring animals. Therefore associative tasks may be measuring the same underlying behavioural axis (i.e., personality trait) as the novel environment test. A second goal of Chapter 2 is to establish the black-capped chickadee as a model species to study individual differences in behaviour.

Each chickadee was first released into a room containing five artificial trees. Each bird received a score that reflects the number of trees visited within the allotted time. This test is called the novel environment test (see brief description, above) and was adapted from a novel environment test previously conducted with great tits (e.g., Verbeek et al. 1994). Next, each black-capped chickadee was trained in an acoustic operant discrimination task. In this task each bird learned to discriminate between two different conspecific vocalizations. The number of trials each bird required to learn this task varied, and this number served as the learning score. Lower learning scores represented faster learners. We found that birds that visited more trees in the novel environment had lower learning scores, that is, they learned the discrimination task faster, compared to birds that visited fewer trees in the novel environment test.

The study presented in Chapter 2 is significant for at least two reasons: First, it established two behavioural tests, novel environment and operant discrimination, that can be used to assay exploration and learning, respectively, in a new model species. Second, this is the first study in the field of animal personality to explicitly test the relationship between a non-associative based form of learning and personality. Other studies (e.g., Sneddon 2003; Dugatkin & Alfieri 2003) demonstrated that learning speed is related to exploratory behaviour, however, in these studies, learning speed may have been influenced by an animal's willingness to explore in such a way that both the learning task and the novel environment task were measuring the same underlying trait. We believe that our study is one of the first to measure a more general capacity for learning that is not mediated by the exploration tendencies of an individual.

In Chapter 2, we found that fast-exploring chickadees have an advantage; they learned an operant task more quickly than slow-exploring individuals. For variation in exploratory behaviour to remain in a population, there must be some advantage to being a slow-explorer. That is, slow-explorers must excel in some areas where fast-explorers do not, or fast-exploring birds would outperform slow-exploring birds. The habitat-dependent selection hypothesis suggests that different personality types (e.g., fast and slow-exploring birds) may fare better in different environments. Previous research (e.g., Verbeek et al. 2004; Dall, Houston & McNamara 2004) and theoretical work (e.g., Wolf et al. 2007; Cockrem 2007) has suggested that fast-exploring animals may fare better in stable environments where these animals can form a routine and stick to it, while slow-exploring animals may fare better in unpredictable environments where flexibility is favored. In the current study we tested this idea by reversing learned rules in an operant discrimination tasks and examined whether fast or slow-exploring birds learned the new rules more quickly.

In Chapter 3, black-capped chickadees were tested in a novel environment and received a score that reflected the number of trees visited, just as in Chapter 2. Then, each bird completed an acoustic operant discrimination task, as in Chapter 2. However, in the current operant discrimination task, once each bird had learned the category rules, that is, which vocal signal was rewarded, and which vocal signal was unrewarded, the rules were reversed. The learning score in this experiment was the number of trials required to learn the task with the reversed rules, compared to the number of trials needed to learn the initial task. A lower learning score reflected individuals who learned to respond to the new rules the fastest. We found that birds that were faster at reversing previously learned rules also visited fewer trees in the novel environment, compared to birds that were slower at reversing previously learned rules.

The study presented in Chapter 3 is significant for at least two reasons: First, it supports the habitat-dependent selection hypothesis for the maintenance of individual variation in behaviour (Réale et al. 2007). This hypothesis suggests that fast-exploring birds may perform better in stable, predictable environments where forming a routine is advantageous, while slower-exploring birds are favoured in unstable, unpredictable environments where task demands often change. Second, the data also support a hypothesis derived from previous work with great tits suggesting that slow-exploring birds may be generally more flexible, and able to modify their behaviour in accordance with changes in environmental stimuli (Exnerová, Svádová, Fucíková, Drent & Stys 2010).

The focus of Chapter 4 shifts from learning, to vocal behaviour, namely the production of songs and calls and their relationship with exploratory behaviour. Previous work with great tits has examined the relationship between songs and personality (Naguib, Kazek, Schaper, van Oers & Visser 2010; Amy, Sorau, de Geode & Naguib 2010). Songs are sexually-selected traits that function in territorial defense and mating. Therefore, in temperate species, songs are produced mainly by males during certain times in the annual and circadian cycle.

No studies yet have examined if calls are related to personality. Calls serve a variety of functional roles, are critical to daily survival, and are given by both males and females through the year. The goals of this study are to extend previous research done with great tits and to also examine the vocal output of bird calls and the relationship to personality. Previous work in great tits have demonstrated that males' song is related to exploratory behaviour (e.g., Naguib et al. 2010; Amy et al. 2010), and although yet untested, a link between individual differences in exploratory behaviour and bird calls may also exist.

In Chapter 4, I examine the relationship between songbird vocalizations, analyzing both song and call output in baseline and playback conditions, and exploratory behaviour in a novel environment, once again, using the black-capped chickadee as a model. The goals were to (1) test if the vocalizations produced in different settings (silence versus playback of *chick-a-dee* mobbing calls) are repeatable across time, and (2) test is the vocal output is related to an individual's exploratory behaviour. First, black-capped chickadees were tested in a novel environment and received a score that reflected the number of trees visited, just as in Chapter 2 and Chapter 3. Next, each bird was housed individually in a sound attenuating chamber for four days. On the second and fourth day we played *chick-a-dee* mobbing calls of black-capped chickadees back to each bird. I measured the number and type of vocalizations each bird gave before, during, and after each of the two playbacks. I also recorded the amount of overall activity of each bird and the amount of time each bird spent in an agonistic threat display.

I found that the vocal output of black-capped chickadees was repeatable across time and that an individual’s vocal output was related to its exploration score only during the playback condition, but not during the control condition (pre-playback). The study presented in Chapter 4 is significant because it demonstrates that call production may reflect a stable behavioural trait in a songbird, and that call production is related to other behavioural aspects, such as exploration of a novel environment. This is important because calls, unlike songs, are produced year round, by both sexes, and function in day to day survival.

Chapter 5 is the last study in this thesis. In Chapter 5 the focus moves from vocalizations, back to the interaction between animal personality and animal cognition, although as in Chapters 2 and 3 the aim of Chapter 5 was not to examine differences in learning rate, but to examine learning in a finer grained manner by asking how expert different individuals are at discriminating visual test stimuli from stimuli they were trained with. As in Chapters 2, 3 and 4, individuals in Chapter 5 were run in a novel environment task to assess whether discrimination ability was related to exploratory behaviour. In this chapter I used pigeons as a model species because they are best suited for the cognitive test paradigm.

The cognitive task in the current study is an adaptation of a classic psychological test, designed to test for a phenomenon called the *Peak Shift Effect*. This effect is the result of a discrimination training procedure where the reinforced and non-reinforced stimuli differ from one another along a single dimension, for example, wavelength of light (e.g., Hanson 1959). Hanson (1959) trained pigeons in an operant box to peck in response to one color (e.g., 550 nm) and withhold pecking to another color (e.g., 590 nm). When the pigeons were tested for their responses in the presence of a variety of different colors (e.g., ranging from 480 to 620 nm), the pigeons had generalization gradients that usually peaked (the highest proportion of response) not to the trained color (550 nm) but to the color that was shifted away from the previously unrewarded color (e.g., 540 nm). I used a modified version of this task, where the stimuli vary in line orientation (different degrees of rotations, with 90° as horizontal, similar to Bloomfield 1967). The resulting generalization gradients allow comparison of discrimination performance (i.e., sensitivity to change in environmental stimuli) among birds.

I also took blood samples from each bird, after completing the novel environment task, to examine potential proximate mechanisms, such as levels of plasma corticosterone. This study is significant because it integrates the study of animal personality, cognition and proximate mechanisms under hormonal control into one experiment. Furthermore, while most studies of animal personality and animal cognition examine learning rate, this study measures a different aspect of learning; expertise of discrimination. Elucidating a different aspect of learning, as Chapter 5 does, allows for a better understanding of the interactions between animal personality and animal learning.

Chapters 2, 3 and 4 have been published in three different peer-reviewed journals (see chapter headings for details) and the complete manuscripts (minus abstracts) appear (with permission) in this thesis. Chapter 5 is currently under preparation for submission. Each chapter contains its own introduction, methods, results, discussion and reference section. The last chapter of this thesis is the general discussion which summarizes the findings of Chapters 2-5 and highlights where these data fit into the current theories and future directions are suggested.

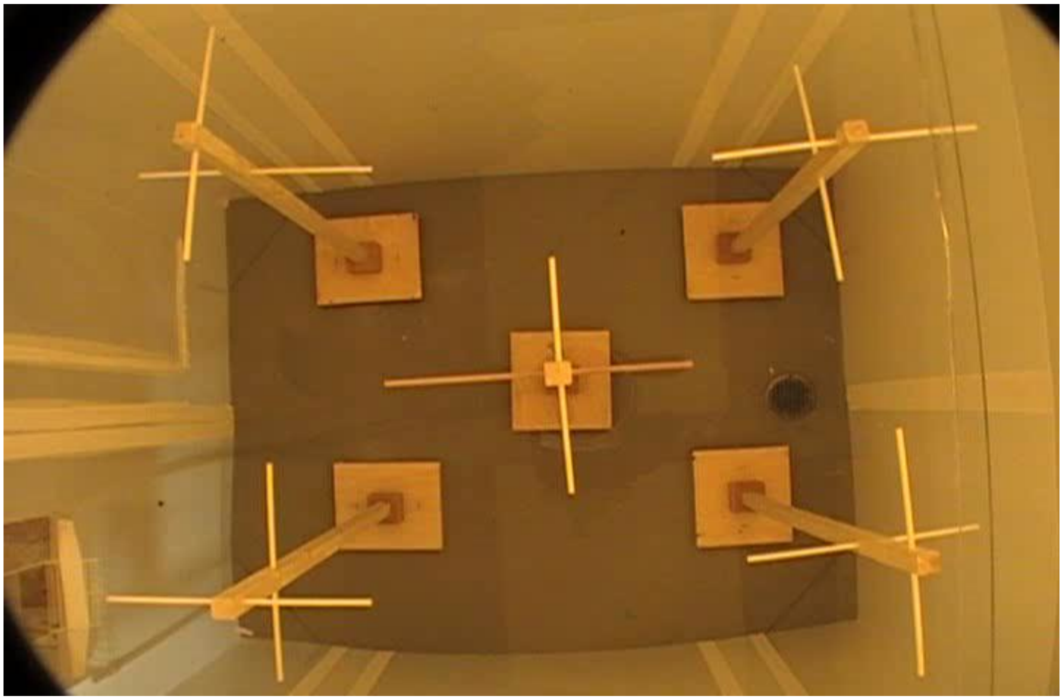

Figure 1-1.

Figure 1-2.

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Chapter 2 Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees (*Poecile atricapillus*)[1]

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[1] *A version of this chapter has been published. Guillette, L. M., Reddon, A. R., Hurd, P. L. & Sturdy, C. B. 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees (Poecile atricapillus). Behavioural Processes. 82(3) 265-270.*

Introduction

Darwin wrote about emotion in human and nonhuman animals as early as 1872 (Wilson 2005). The experimental study of individual differences in animal temperament, and how temperament interacts with learning, dates back at least to Pavlov's work with conditioned reflexes in dogs (1927). In another classic early study, Hall (1934) measured the defecation and urination rate of rats in an open field to assess individual differences in emotionality, and validated his findings with behavioural assays involving eating in a novel setting. In addition to studying individual differences in emotionality, open field studies have also been used to assess related personality traits such as fearfulness and exploration (Gosling 2001). With these and other historical accounts of personality, there is a continuing, and perhaps growing, interest in the study of personality traits in nonhuman animals (for a thorough review see Gosling 2001).

To date, individual variation in exploratory behaviour represents one of the best-studied personality characteristics in nonhuman animals (e.g., Verbeek et al., 1994; Sih et al. 2004a; Sih et al. 2004b; Dingemanse & Réale 2005; Groothuis & Carere 2005; Réale et al. 2007; Sih & Bell 2008). Individual variation in this trait may represent a life-history strategy trade off between growth and mortality maintained by frequency- or habitat-dependent selection (Wilson et al. 1994; Stamps 2007; Biro & Stamps 2008; Wolf et al. 2007; Wolf et al. 2008). If exploration is a component of a broader life-history strategy, then we ought to find correlations with individual variation in other behavioural and physiological traits at the population level, such as the observation that faster explorers also tend to be bolder and more aggressive (a behavioural syndrome *sensu* Sih et al. 2004a).

The relationship between personality characteristics and individual variation in cognitive ability has received limited attention in animals (Koolhaas et al. 1999; Moreira et al. 2004; Øverli et al. 2007; Sih & Bell 2008). However, exploratory style is one personality characteristic that is related to learning speed in specific tasks. This relationship is supported by evidence from several, diverse species and learning tasks. Sneddon (2003) found that rainbow trout which are more willing to venture into an unprotected open area acquired a classical conditioning task more quickly than shyer trout. Guppies that are more willing to inspect predators, an index of boldness, learn associative tasks faster than guppies that are less willing to inspect predators (Dugatkin & Alfieri 2003). Rhesus macaques that avoid novel food in their home environment are more difficult to train to perform instrumental learning tasks like retrieving food from an experimenter for positive reinforcement or learning to touch a goal object for a food reward (Coleman et al. 2005). Similarly, trait anxiety may reduce cognitive performance in nonhuman primates in certain tasks (Toxopeus et al. 2005). Finally, fast and slow exploring great tits do not differ significantly in their speed of acquisition in either associative learning or spatial memory tasks, although fast explorers demonstrated better retention (unpublished data cited in: Groothuis & Carere 2005).

Great tits (*Parus major*) are one of the best-studied models of animal personality. Wild-caught, hand-reared, male great tits show consistent individual differences in exploratory behaviour, approach to a novel object, aggression, and dominance behaviour (Verbeek et al. 1994; Verbeek et al. 1996; Verbeek et al. 1999). Birds that explored a novel environment, or approached a novel object more readily were also more likely to return to a location where food had previously been available, while birds that were slow to explore a novel environment or approach a novel object altered their foraging habits more rapidly when food locations varied (Verbeek et al. 1994). Field work has expanded these findings in natural populations (e.g., Dingemanse et al. 2004) demonstrating that personality may influence individual fitness through mate choice, extrapair behaviour (Van Oers et al. 2008), natal dispersal (Dingemanse et al. 2003), and nest defence (Hollander et al. 2008).

All studies, of which we are aware, that have explicitly examined the relationship between learning ability and personality characteristics involve either associative (i.e., classical or Pavlovian conditioning) or spatial memory tasks (but see Coleman et al. 2005). Here we investigate the relationship between individual variation in exploratory behaviour and the acquisition of an instrumental note-type discrimination task in wild-caught black-capped chickadees (*Poecile atricapillus*), a North-American relative of the great tit. Our instrumental conditioning paradigm requires animals to respond to S+ (rewarded) stimuli and withhold responding to S− (non-rewarded) stimuli belonging to different note-type categories from their namesake *chick-a-dee* call. The goal of the present study is to examine the association between an individual's learning speed and their exploratory behaviour in a novel environment.

Methods

Subjects

Twenty-four adult black-capped chickadees were trained in an acoustic discrimination task in 2007 or 2008. Nineteen of these birds (12 males, 7 females) were captured from sites around Edmonton, Alberta (53°30′N, 113°W) in 2006 and 2007. The remaining birds (1 male, 4 females) were captured in Alberta at the Barrier Lake Field Station (51°02′N, 115°03′W) in 2004 and 2006. Of the initial 24 birds, 22 birds were available to test in the novel environment task. All birds were adults when captured and were naïve to all experimental procedures. Sex was determined by DNA analysis.

Apparatus

A detailed description of the instrumental discrimination apparatus can be found in Sturdy and Weisman (2006). In brief, birds lived and worked in a modified budgerigar cage (30 cm × 40 cm × 40 cm) that had several perches, grit cup, cuttle bone, water tube, an opening in one side to allow access to the food hopper and plastic mesh suspended from the bottom so that birds could not eat spilled food. A request perch with an infrared beam was situated 5 cm from the opening to the food hopper; another infrared beam spanned the entrance to the food hopper. A speaker which broadcast stimuli was at perch height next to the food hopper on the outside of the cage. This apparatus was housed in a ventilated sound attenuating chamber.

The novel environment room (3.15 m × 2.0 m × 2.87 m) housed five artificial trees. The artificial trees consisted of a 2 cm × 2 cm ‘trunk’ that was 1.4 m high. There were four 1 cm diameter ‘branches’ that extended 20 cm from the trunk. Two upper branches were 5 cm from the top of the trunk, and other two branches were 20 cm lower and perpendicular to the top branches (following Verbeek et al., 1994). In one corner of the room was a false wall with a 35 cm × 24 cm opening behind which the bird is placed in home cage (30 cm × 40 cm × 40 cm). Each session was recorded via a wireless camera so behavioural data could be scored at a later date.

Stimulus preparation

A detailed description of stimulus preparation can be found in Charrier et al. (2005). Briefly, notes were taken from high-quality recordings of black-capped chickadee *chick-a-dee* calls. Twenty exemplars each, of three note types (i.e., A, B, C) were recorded, one call per track, to a CDR for discriminative stimuli in the instrumental discrimination task.

Instrumental discrimination task

Nondifferential training. Once a bird had learned to use the request perch and food hopper to obtain food, nondifferential training began. To start a trial, a bird had to wait on the request perch, thus breaking an infrared beam, for a randomly selected interval of between 900 and 1100 ms. Following this, a note from the pool of 20 notes (10 each of two note types) was randomly selected from the pool and played (between about 70 and 80 dB SPL (A)). If the bird left the request perch before the note had finished playing, the trial terminated and a 30 s inter-trial interval (ITI) with the houselights off ensued (termed a zap). This was to train birds to remain on the perch and attend to each stimulus in its entirety before making a response. If the bird remained on the perch until the note was played in its entirety and then flew to the feeder within 1 s from the termination of the stimulus, it was given 1 s access to food followed by a 30 s ITI, with the houselights on. If the bird listened to the entire note, left the request perch within 1 s of stimulus termination but did not enter the feeder, the trial ended after 1 s. If the bird listened to the entire call note and remained on the request perch, the trial ended after 1 s and a 60 s ITI followed, with the houselights on. We used nondifferential training to train birds to create high, uniform, responding to all training stimuli that would be used in the initial acquisition phase of the experiment, and to train the birds to listen to each stimulus in its entirety while also training them to leave the request perch after each stimulus was played (see Charrier et al. 2005 for details). This step also ensured that birds approached all stimuli prior to discrimination training, thus eliminating any bias that neophobia may have imposed on initial acquisition performance. The criteria to complete nondifferential training was 6–500 trial blocks with over 60% responding to all stimuli, and no more that 3% difference in response to future S+ and S− exemplars.

Discrimination Acquisition. For detailed description of acoustic discrimination and transfer training procedure refer to Charrier et al. (2005). In this phase, breaking the infrared beam in the food hopper after food-rewarded (S+) notes resulted in 1 s access to food whereas visits to the feeder following non-rewarded (S−) notes resulted in a 30 s ITI with the houselights extinguished and no food access. All other procedures from nondifferential training (e.g., random selection of notes, remaining on the perch until stimulus completion, etc.) remained in effect during discrimination training.

Discrimination training (i.e., acquisition) was initiated immediately following nondifferential training. Birds were trained on one of six discrimination tasks: birds learned to discriminate between either A and B notes (A S+ and B S− or A S− and B S+), B and C notes (B S+ and C S− or B S− and C S+) or A and C notes (A S+ and C S− or A S− and C S+) of the *chick-a-dee* call. In this way, we tested a more general ability of note type discrimination, to increase the generalizability of our findings, rather than focusing on one or two particular discriminations.

Birds were initially trained to discriminate between 10 S+ and 10 S− stimuli (initial acquisition). Each of these notes was heard and responded to previously during nondifferential training, removing any possible influence of neophobia on discrimination performance. Next, the birds were presented with the remaining 10 S+ and 10 S− stimuli (transfer 1). Finally, the birds were presented with all 20 S+ and 20 S− stimuli (transfer 2). The criterion to complete each of the three (initial acquisition, transfer 1, and transfer 2) phases of the discrimination task was 6–500 trial blocks with a discrimination ratio [DR; calculated by dividing the average percentage of response to S+ notes by the average percentage of response to all (both the S+ and S−) notes corrected for zaps] of 0.8 or greater with the last two blocks of 0.8 or greater occurring consecutively.

Discrimination is at chance level when the discrimination ratio is 0.5 and perfect when the ratio is 1, therefore, birds' performance in these tasks was based on how accurately they were able to discriminate, and in so doing, respond differentially, to the two classes of rewarded (S+) and non-rewarded (S−) notes. Performance accuracy did not vary based on other physiological, motivational, or behavioural measures, such as how many times they were able to request a note or how often they flew to the feeder, as personality and metabolism may be related (Careau et al., 2008). The lights came on at 09:00 h and the duration of the lights on followed the natural cycle for Edmonton, AB.

Following the instrumental discrimination task, birds were returned to colony rooms where they were housed in individual cages (30 cm × 40 cm × 40 cm), but were in visual and vocal contact with conspecifics. Birds were tested for exploratory behaviour in the novel environment task no less than 3 months after they completed the acoustic discrimination task. Individual birds in their home cages were placed behind a false wall in the novel environment room. One hour later the cage door was opened, allowing the bird access to the room. Each bird was recorded via a wireless camera suspended from the ceiling, for 15 min. All trials were conducted between 10:00 and 15:00 h. Birds were returned to the colony room after testing, and the length of the left tarsus was measured as an index of body size.

Scoring

The number of novel trees visited by each bird in the novel environment room was scored from the recording of each trial. A score of zero was awarded to a bird that failed to leave the home cage. The range of possible scores was 0–5. A visit to a novel tree was defined as perching on a branch, or the trunk of a tree that had not yet been visited.

In the instrumental discrimination task, standardized scores (Z-scores) were computed for each individual, separately for each of the three discrimination groups (AB, AC, and BC). The standardized score was computed from the sum of the number of blocks to criterion for initial acquisition, transfer 1 and transfer 2. Standardized scores were computed because previous work has demonstrated that it takes chickadees more trials to discriminate between A and B notes, than to discriminate A and C notes (Guillette et al., 2010, see Fig. 2-1 for the number of blocks to criterion for each subject). This standardized score was the learning score for each bird. Birds that took longer to learn the operant discrimination had positive standardized scores, while birds that finished the task in fewer trials had negative standardized learning scores (range: −1.604 to 2.292).

Results

Performance in the instrumental discrimination task showed no effect of sex on the number of blocks to criterion in any discrimination group (AC: t_6 = 1.042, P = 0.338; AB: t_6 = −1.01, P = 0.350; BC: t_6 = 0.96, P = 0.372). We therefore collapsed across sex to calculate the standard score from the mean blocks to criterion and the standard deviation of each group (n = 8 for AC, n = 8 for BC, n = 8 for AB). A general linear model repeated measures ANOVA was conducted to compare discrimination ratios during the last block of initial acquisition and the first 500 trial block of transfer 1 for the 22 birds tested in the novel environment task. These 22 birds showed generalization in their discrimination ratios during discrimination training for notes previously heard during nondifferential training (last block of initial acquisition, 0.877 ± 0.014) and novel notes (first block of transfer 1, 0.857 ± 0.015; $F_{1,21}$ = 2.828, P = 0.107).

A linear regression predicting the standardized learning score using the number of novel trees perched on (0, 1, 2, 3, 4, or 5) and including sex and tarsus length as covariates showed a significant effect of the number of trees visited on learning speed (R^2 = 0.497, $F_{5,16}$ = 3.168, P = 0.036, Fig. 2-2). All analyses were conducted in SPSS v 15.0. All values are reported as mean ± s.e.m.

Discussion

Black-capped chickadees that readily entered a novel environment within a 15 min trial were also faster at learning an acoustic instrumental discrimination task compared to conspecifics that did not readily enter a novel environment.

These effects are not related to sex, or size (tarsus length). We used tarsus length as a control for the size of each black-capped chickadee because tarsus length is significantly correlated with body mass for black-capped chickadees in our study populations (Pearson r(102) = 0.201, P = 0.04), and in at least some species, body size is related to boldness (Brown & Braithwaite 2004; Réale et al. 2007).

Our results are comparable with previous research showing that bolder animals learned an association between a visual cue and food delivery faster than shyer animals (Dugatkin & Alfieri 2003; Sneddon 2003). Sneddon (2003) attributed this difference to the fact that bolder animals more readily acquire information about novel situations and as a result may learn the requirements of novel task more quickly than shyer animals (Sih & Bell 2008). However, solving our instrumental task in fewer trials is not directly aided by a birds willingness to explore and hence, greater exposure to relevant information. If willingness to explore also served as driving force behind the operant discrimination, then it could be hypothesized that birds that are more likely to explore a novel environment would approach the feeder more frequently, making more errors (incorrectly going to the feeder in an S− [unrewarded] trial). This would result in a lower discrimination ratio, and is not the case. We see that birds that are more willing to explore a novel environment also reach criteria in the operant discrimination task in fewer trials. We are suggesting that willingness to explore a novel space and a bird's ability to learn an acoustic discrimination task are two personality traits that vary consistently among individuals in our study sample; whether this is representative of the population as a whole and thus represents a behavioural syndrome (Sih et al. 2004a; Sih et al. 2004b) will require further investigation.

Our results are also comparable with Arnold et al. (2007) who found a relationship between novel object approach and spatial learning ability in a population of blue tits. Individuals that succeeded at a spatial learning task (i.e., remembering the location of hidden food) demonstrated intermediate levels of risk taking (time to approach a novel object). Individual that were more risk prone (approached novel object more readily) were the least successful at the spatial learning task, while individuals that were risk averse (slowest in approach of a novel object) avoided the spatial learning apparatus and therefore failed to learn the spatial task. There was also an interaction between the levels of taurine an individual received as a juvenile and performance on the novel object approach and spatial learning task. Future research with black-capped chickadees should explore the effect of nutrition deprivation/supplementation on performance of tasks that are known to vary consistently at the level of the population, such as exploration of a novel environment, and learning speed, as suggested by the current study.

We reject the idea that neophobia is the driving force behind the birds behaviour on both the novel environment and acoustic discrimination task. While birds that are neophobic may be less likely to explore a novel environment, neophobia cannot explain why birds require more trials to learn an acoustic discrimination task. In our operant design, birds live and work in the operant chamber for the duration of the experiment, therefore, they must respond to acoustic stimuli to receive food rewards. During nondifferential training, all of the birds were trained to respond equally to each stimulus that was subsequently played during the initial acquisition phase of discrimination training. Thus, birds were trained until there was no behavioural evidence of neophobia. Finally, all birds demonstrated transfer (i.e., showed significant generalization) when presented with novel notes during the various phases of discrimination training. Taken together, although neophobia may play a role in our novel environment assay, it appears unlikely that it plays any role in our operant discrimination task.

In an attempt to uncover the mechanism for the consistent differences we observed in our study population, and to further explore the possibility that neophobia may have contributed to the differences we observed in operant performance, we analyzed the errors that each bird made over the course of initial acquisition. There are two types of errors a bird can make; going to the feeder on a punished (S−) trial (false alarm), or not going to the feeder on a rewarded (S+) trial (miss). For each 500 trial block during initial acquisition of discrimination learning, we calculated an error ratio (the number of misses/the number of misses + the number of false alarms). If this number is near one, the errors are almost exclusively misses, and if the number is close to zero, the errors are mostly false alarms. It follows that a neophobic animals should have more misses (and a larger error value) compared to a non-neophobic animals. If an animal adopts a “go-bias” then their errors will be mostly false alarms (and a small error value). We found no relationship between this new error ratio and either learning speed or the number of trees visited. To test this, we ran several regressions predicting the standardized learning score from different error values (i.e., the error value averaged over all blocks of initial acquisition, the error value average over the first five blocks of initial acquisition, the error value at the first block of criterion performance during initial acquisition, and the average error value for the five blocks prior to the first block at criterion during initial acquisition, all $r^2 < 0.12$, all ps > 0.10). We likewise ran several different regressions predicting the type of errors made from the number of trees each bird perched on and found no relationship (all $r^2 < 0.29$, all ps > 0.25). Therefore, neophobia is not a satisfactory explanation for our findings, and the mechanism linking increased wiliness to enter a novel environment to faster learning in an acoustic discrimination task remains obscure.

Our results contrast with those reviewed by Groothuis and Carere (2005) who reported that fast and slow exploring great tits, derived from lines bidirectionally selected for exploratory behaviour, did not differ in their speed of acquisition of two types of learning tasks (associative and spatial). The discrepancy between Groothuis and Carere's and the current study might arise due to the difference in learning task demands. In our study, birds had to make fine-scale discriminations among biologically relevant acoustic stimuli and in doing so, demonstrate open-ended classification (generalization) of note-type categories by continuing to correctly respond to novel exemplars of each note-type category during successive transfers (e.g., initial acquisition → transfer 1 → transfer 2). The demands of the present task may have made the difference in learning speed easier to detect (e.g., greater variability in learning scores). However, we cannot rule out the possibility that the differences between great tits and black-capped chickadees result from intrinsic differences between the species. Groothuis and Carere do report a difference between fast and slow exploring great tits in the retention of learned information, suggesting that fast exploring birds retain information better than slow exploring birds. They attribute this finding to the fact that fast explorers are quicker to form routines then are slow explorers (Verbeek et al. 1994).

While our design did not examine consistencies in an individuals behaviour over time, which is one aspect of a behavioural syndrome, our results are consistent with the idea that personality characteristics tend to coalesce within individuals in a predictable way resulting in behaviours consistent with a general life-history strategy (Sih et al. 2004a; Sih et al. 2004b; Groothuis & Carere 2005; Stamps 2007; Biro & Stamps 2008; Wolf et al. 2007; Wolf et al. 2008; Sih & Bell 2008). These different ‘behavioural profiles’ (Groothuis & Carere 2005) may be maintained by frequency- (Wilson et al. 1994; Wolf et al. 2007; Wolf et al. 2008; Stamps 2007; Biro & Stamps 2008) or habitat-dependent (Dingemanse et al. 2004; Groothuis & Carere 2005; Dingemanse & Réale 2005; Duckworth & Badyaev 2007; Réale et al. 2007) selection, as different personality types may do better if rare compared to other personality types or in different local habitats. For instance, fast explorers may do better in stable environments in which it is adaptive to learn new tasks quickly and commit them to a routine (Verbeek et al. 1994; Dall et al. 2004), while slower exploring animals may benefit in unpredictable environments where the demands of a specific task may change quickly and remaining behaviourally plastic is favoured (Nussey et al. 2007; Groothuis & Carere 2005). A test of this hypothesis would be to reverse the S+ and S− contingencies in the instrumental task such that the previously rewarded note-type was punished and vice versa. If slower exploring animals are more sensitive to changes in task demands, they may learn this change faster than the animals that may be more set in their routine.

The current study is the first to examine the relationship between exploration and learning in black-capped chickadees. We acknowledge however that there may be other important factors that need to be explored understand the nature of this relationship. For instance, a necessary next step in this line of research is an assessment of the consistency of these behaviours within an individual over time. Furthermore, determining the particular demands of our discrimination task (i.e., expert, fine-grained discrimination between note types) and mechanisms (i.e., behavioural and neural) that lead to our observation of a relationship between exploratory behaviour and learning speed, where others have failed to find such an effect, will necessarily require further experimentation (see Mercado 2008 for a review of factors impacting learning and plasticity). Additionally, other factors may interact with personality, including nutrition and parental provisioning during development (Arnold et al. 2007), age or maturity (Verbeek et al. 1994) and predation regime (Bell & Sih, 2007). Understanding what effect these variables have on the behaviour we observe in this species is fertile ground for future research.

In conclusion, there is a positive relationship between exploration and learning in wild-caught black-capped chickadees. Individuals that learn an acoustic operant discrimination task quickly are also more likely to readily enter a novel environment. Differences among individuals in learning speed or learning strategy may be components of a general life-history strategy in which some individuals learn fast, but adapt slowly, while others learn more slowly, but remain more plastic. Our results suggest that variation in personality characteristics extends to learning speed in a passerine bird.

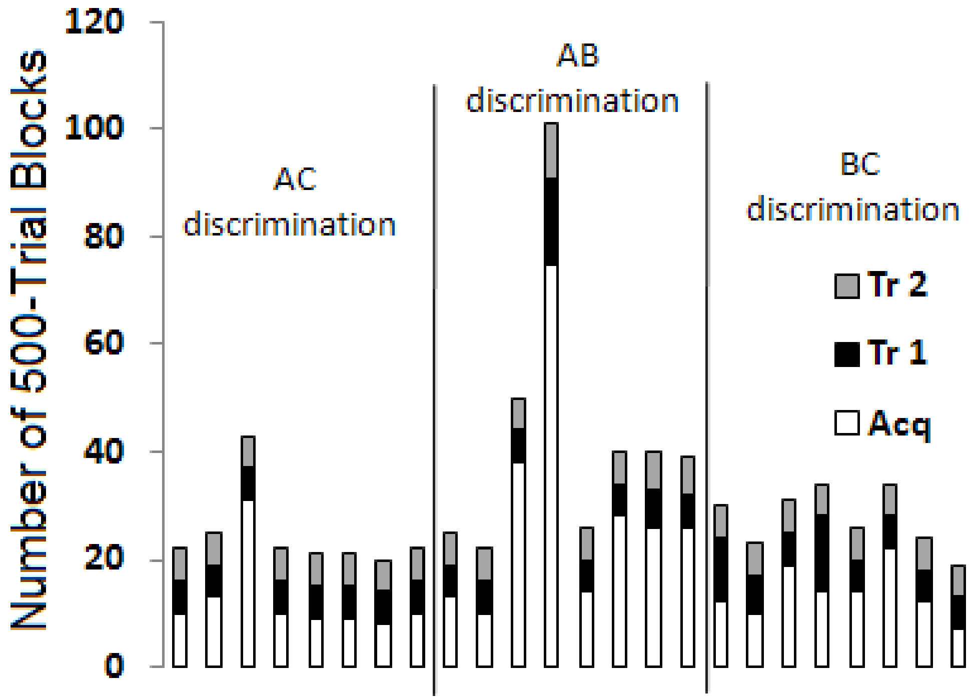
Number of 500-Trial Blocks
120
100
80
60
40
20
0
AC discrimination
AB discrimination
BC discrimination
Tr 2
Tr 1
Acq

Figure 2-1.

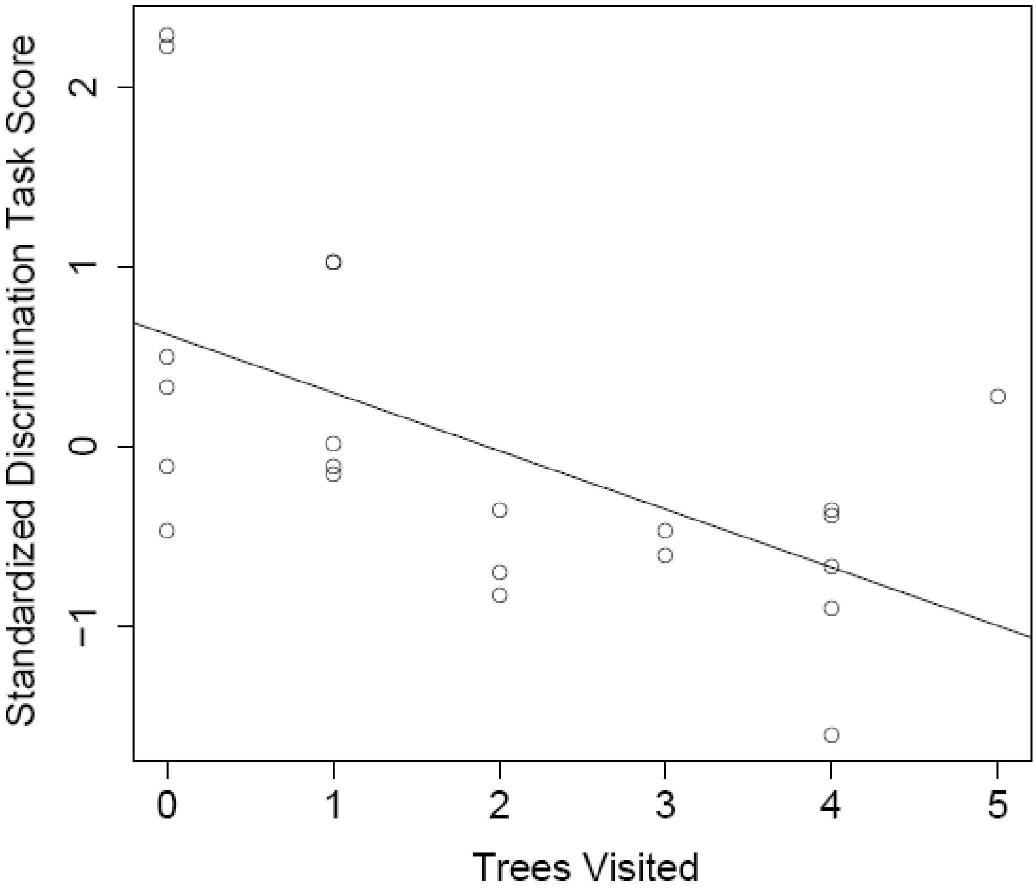
Standardized Discrimination Task Score
2
1
0
−1
0
1
2
3
4
5
Trees Visited

Figure 2-2.

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Chapter 3 Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task [2]

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[2] *A version of this chapter has been published. Guillette, L. M., Reddon, A. R., Hoeschele, M. & Sturdy, C. B. 2011. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proceedings of the Royal Society B: Biological Sciences, 278(1706), 767-773.*

Introduction

The study of animal personality (also known as temperament, Réale, Reader, Sol & McDougall 2007; behavioural syndromes, Shi & Bell 2008; and coping styles Koolhaas et al. 1999) is concerned with how behavioural characteristics are related across contexts and over time within a species. A survey of personality-related research by Gosling (2004) showed that such studies included 66 species spanning a diverse array of taxa. As species are added to this list (e.g., Pruitt, Riechert & Jones 2008; Guillette, Reddon, Hurd & Sturdy 2009; Kurvers et al. 2009; see Stamps & Groothuis 2010; Schuett, Tregenza & Dall 2010, for recent reviews), so too are new behavioural characteristics being linked to existing suites of correlated traits (e.g. boldness correlates with aggressiveness, Sih, Bell, Johnson & Ziemba 2004).

The field of animal personality has begun to pose questions about how individual differences in behaviour develop, evolve and how these differences are maintained within a species or a population (Stamps & Groothuis 2010; Schuett, Tregenza & Dall 2010; Bell 2007). Individuals can differ in their overall personality (or behavioural profile) associated with differing life-history strategies (Stamps 2007; Wolf; Van Doorn, Leimar & Weissing 2007; Wolf; Van Doorn & Weissing 2008). For instance, some individuals may focus on current reproduction and thus behave in a more risk-prone manner, whereas other individuals may focus on future reproduction and behave in a more risk-averse manner (Wolf, Van Doorn, Leimar & Weissing 2007; Wolf, Van Doorn & Weissing 2008; Wolf, Van Doorn, Leimar & Weissing, In Press). Variation in the personality of animals within a species may be maintained when one personality phenotype is rare and has higher fitness compared with alternate personality phenotype(s) (negative frequency-dependent selection, Wolf et al. 2007; Wolf et al. In Press; Wilson, Clark, Coleman & Dearstyne 1994) or is more effective in different local habitats (habitat-dependent selection, Réale et al. 2007; Wolf et al. In Press).

While individual variation in exploratory behaviour represents one of the best-studied personality characteristics (e.g., Réale et al. 2007; Sih et al. 2004; Verbeek, Drent & Wiepkema 1994; Verbeek, Boon & Drent 2006; Sih, Bell & Johnson 2004), individual variation in learning ability has received less attention (Sih & Bell 2008; Koolhaas et al. 1999; Moreira, Pulman & Pottinger 2004). Previous work has suggested that individual variation in discrimination learning is related to how black-capped chickadees (*Poecile atricapillus*) explore a novel environment (Guilette et al. 2009). Guillette et al. (2009) showed that chickadees which are quicker to explore a novel environment are also quicker to learn an acoustic operant discrimination task. The notion that, in general, fast explorers are fast learners is further supported by evidence from a study with wild-caught male starlings (*Sturnus vulgaris*, Boogert, Reader & Laland 2006) Boogert et al. (2006) found that starlings which were faster to feed in a novel environment solved a learning task faster than starlings that were slower to feed in a novel environment.

Here, we test the idea that fast explorers may perform better in a stable (predictable) environment where it is adaptive to learn new tasks quickly and commit them to a routine (Verbeek et al. 1994; Dall, Houston & McNamara

2004), while slower exploring animals may benefit in unstable (unpredictable) environments where behavioural flexibility is favoured (Nussey, Wilson & Brommer 2007; Groothuis & Carere 2005). The notion that personality spans a behavioural continuum (e.g. bold, exploratory → shy, non-exploratory) and that the type of personality that is favoured changes with habitat variation across space or time is supported by studies in several species (e.g., Dingemanse, Both, Drent & Tinbergen 2004). For example, during range expansions in western blue birds (*Sialia mexicana*), aggressive individuals are initially favoured when colonizing new areas. The number of aggressive individuals declines rapidly following colonization, presumably because aggressive males tend to provide lower levels of parental care (Duckworth & Badyaev 2007). However, the link between exploration and learning has not yet been thoroughly examined.

Birds that are faster to act when faced with novelty (black-capped chickadees' exploration in a novel environment, Guillette et al. 2009; starlings' latency to feed in a novel environment, Boogert et al. 2006) are also faster to learn a cognitive task; however, the cognitive task used in these particular experiments may have inadvertently favoured individuals with bold, exploratory personality types because the task demands were stable, and forming a routine would have been advantageous. Experiments that might favour shyer, less exploratory individuals have yet to be examined. This could be accomplished through testing learning in a dynamic, rather than a stable, environment. If slow-exploring birds perform better in a testing environment where task demands are altered, this suggests that they may have an advantage over fast-exploring birds in certain micro-habitats (in line with the habitat-dependent selection hypothesis).

We trained black-capped chickadees in an instrumental discrimination paradigm that required each bird to respond to rewarded (S+) stimuli, but not respond to non-rewarded (S−) stimuli belonging to different note-type categories (e.g. A notes, B notes) from their namesake *chick-a-dee* call. Once a bird had learned this task, the reward contingencies associated with each category were reversed. This represents an environmental change that birds need to adapt to in order to maximize their reward (food). Only the reward contingency (i.e. rewarded or non-rewarded) associated with each category changed, so previous learning (discrimination training on categories) will aid birds in the reversal if they are able to exhibit flexibility in their learned behaviour. The number of trials it took each bird to learn the discrimination task served as a baseline for learning with which the number of trials needed to learn the reversal was compared. All birds were first run in a novel environment exploration task, and then run in the operant discrimination task.

Methods

Subjects

Thirty birds (second year or after the second year, determined by the shape and colouring of outer tail retrices, Pyle 1997) were captured between 19 December 2008 and 28 January 2009. Seventeen birds (nine males, eight females) originated from the North Saskatchewan River Valley in Edmonton, Alberta, Canada (538340 N, 1138310 W), and the remaining 13 birds (seven males, six females) originated from Stony Plain Alberta, Canada (538310 N, 1148000 W), 36 km west of Edmonton. Prior to and between testing phases, each bird was housed individually at the University of Alberta in Jupiter Parakeet cages (30 × 40 × 40 cm; Rolf C. Hagen, Inc., Montreal, Canada), which allowed for auditory and visual, but not physical contact among birds. Birds had free access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St Louis, MO, USA), water (vitamin supplemented on alternating days; Prime vitamin supplement, Hagen, Inc., Montreal, Canada), grit and cuttlebone. Birds were given three to five sunflower seeds daily. Birds also received one mealworm (*Tenebrio molitor*) or superworm (*Zophobas morio*) three times a week and a mixture of greens and eggs twice a week. Birds were maintained on a light/dark cycle that mimicked the natural light cycle for Edmonton, Alberta, Canada.

Apparatus

Novel environment room

The novel environment room (2.03 × 1.52 × 2.44 m) housed five artificial trees. The artificial trees consisted of a 5 × 5 cm unfinished, wooden ‘trunk’ that was 1.4 m high. There were four, 1 cm diameter unfinished wooden dowel ‘branches’ that extended 20 cm from the trunk. Two upper branches were 5 cm from the top of the trunk, and the other two branches were 20 cm lower and perpendicular to the top branches (following Verbeek et al. 1994). In one end of the room there was a 35 × 24 cm opening behind which the bird was placed in its home cage (30 × 40 × 40 cm). Each session was recorded with a JVC Everio camcorder, fit with a wide angle lens, so behavioural data could be scored at a later date.

Operant conditioning chamber

A detailed description of the instrumental discrimination apparatus can be found in Sturdy & Weisman (2006). In brief, each bird was placed in a modified budgerigar cage (30 × 40 × 40 cm) that had several perches, a grit cup, cuttlebone, water tube, an opening on one side to allow access to the food hopper and a plastic mesh suspended from the bottom so that birds could not eat spilled food. A request perch with an infra-red beam was situated approximately 5 cm from the opening to the food hopper; another infra-red beam spanned the entrance to the food hopper. A speaker that broadcast stimuli was at perch height next to the food hopper on the outside of the cage. This apparatus was housed in a ventilated sound attenuating chamber.

Stimulus preparation

The stimuli for the acoustic operant discrimination were exemplars of ‘B’ and ‘C’ notes from the namesake *chick-a-dee* call of the black-capped chickadee. The chick-a-dee call is composed of four note types; A, B, C and D, produced in a fixed order, but each note type may be omitted or repeated (Haliman, Ficken & Ficken 1985). These note types are perceived as belonging to natural, open-ended categories by black-capped chickadees (Charrier, Lee, Bloomfield & Sturdy 2005; Sturdy, Phillmore & Weisman 2000). That is, birds can continue to classify notes as belonging to a natural category when they are tested with novel exemplars. A detailed description of stimulus preparation can be found in Charrier et al. (2005). Briefly, notes were taken from high-quality recordings of black-capped chickadee *chick-a-dee* calls. Twenty exemplars each of two note types (i.e. 20 B, 20 C, 40 total) were recorded, one note per track, to a recordable compact disc for discriminative stimuli in the instrumental discrimination task.

Novel environment task

Birds were tested for exploratory behaviour in the novel environment task before initiation of the instrumental discrimination task. Individual birds in their home cages were placed with their cage against the opening to the novel environment room. A clear barrier controlled birds' physical, but not visual, access to the novel environment room. We allowed visual access to the novel environment room because pilot tests for previous experiments (i.e., Guillette et al. 2009) revealed that birds rarely left their home cage within 30 min if the barrier to the novel environment was opaque. One hour later the barrier was removed, allowing the bird access to the room. Each bird was recorded via the JVC camcorder suspended from the ceiling for 10 min. All trials were conducted between 11.00 and 15.00 h. Birds were returned to the colony room after testing, and the length of the left tarsus was measured as an index of body size. All birds visited the novel environment between 27 April and 25 May 2009.

Instrumental discrimination task

Preliminary training. Once a bird learned to use the request perch and food hopper to obtain food, preliminary training began. To start a trial, a bird had to wait on the request perch, thus breaking an infra-red beam, for a randomly selected interval of between 900 and 1100 ms. Following this, a note from the pool of 40 notes (20 of each note type) was randomly selected and played (between approx. 70 and 80 dB SPL as measured by a Radio Shack Sound Level Meter (fast setting, A weighting)). If the bird left the request perch before the note had finished playing, the trial terminated and a 30 s inter-trial interval (ITI) with the houselights off ensued (termed a zap). This was to train birds to remain on the perch and attend to each stimulus in its entirety before making a response. If the bird remained on the perch until the note finished playing and then flew to the feeder within 1 s from the termination of the stimulus, it was given 1 s access to food followed by a 30 s ITI, with the houselights on. If the bird listened to the entire note, left the request perch within 1 s of stimulus termination but did not enter the feeder, the trial ended after 1 s. If the bird listened to the entire note and remained on the request perch, the trial ended after 1 s and a 60 s ITI followed, with the houselights on. If the bird left the perch during the 60 s ITI for 1 s, the 60 s ITI was terminated and a new trial initiated. We used preliminary training to train birds to create high, uniform, responses to all training stimuli that would be used in the discrimination phase of the experiment, and to train the birds to listen to each stimulus in its entirety, while also training them to leave the request perch after each stimulus was played (see Charrier et al. 2005 for details). This step ensured that birds readily approached all stimuli prior to discrimination training, thus eliminating any inherent bias resulting from individual differences in neophobia that might be present among the birds and that could affect discrimination performance. The criteria to complete preliminary training was six blocks (one block = 500 trials) with over 60 per cent responding to all stimuli, and no more than 3 per cent difference in response to all note types to ensure no initial preferences for note types biased the discrimination. Exemplars were presented equally and in a random order within blocks, and randomized for each block, for each subject.

Discrimination acquisition. Charrier et al. (2005) describes the acoustic discrimination and transfer training procedures in great detail. In this phase, breaking the infra-red beam in the food hopper after food-rewarded (S+) notes resulted in 1 s access to food, whereas visits to the feeder following non-rewarded (S−) notes resulted in a 30 s ITI with the house lights extinguished and no food access. All other procedures from preliminary training (e.g., random selection of notes, remaining on the perch until stimulus completion etc.) remained in effect during discrimination training.

Discrimination training was initiated immediately following preliminary training. All 30 birds learned to discriminate the notes (B notes were S+, and C notes were S−). Birds were initially trained to discriminate between 10 S+ and 10 S− stimuli. Next, the birds were presented with the remaining 10 S+ and 10 S− stimuli, referred to as the first set, and second set, respectively, hereafter. Finally, the birds were presented with all 20 S+ and 20 S− stimuli. The criterion to complete each of the phases of the discrimination task was six blocks with a discrimination ratio (DR; calculated by dividing the average percentage of response to S+ notes by the average percentage of response to all (both the S+ and S−) notes, excluding zap trials) of 0.8 or greater with the last two blocks of 0.8 or greater occurring consecutively.

Reversal training. Following completion of discrimination training, all birds were placed on reversal. In reversal, reward contingencies were modified such that C notes were now rewarded (S+) and B notes were now unrewarded (S−); opposite to that of discrimination training. The stages of training and the criterion to complete each of the phases of reversal task were the same as during the discrimination task. All birds were tested in the instrumental discrimination task between 30 April and 18 December 2009.

Scoring

We scored the number of trees (out of five) visited by each bird in the novel environment room from the recording of each 10 min trial. A score of zero was awarded to a bird that failed to leave the home cage. In the instrumental discrimination task, the number of blocks needed to reach criteria served as the learning scores. The reversal speed score is the learning score for set 1 reversal minus the learning score for set 1 discrimination. The longer (more blocks) it took a bird to learn the reversal task, compared with the initial task, the higher the reversal speed score, reflecting that the bird was slow at reversing relative to a bird with a lower score.

Statistical analysis

One-sample t-tests were conducted to test whether the DRs were different from chance (chance = 0.5) during various blocks of learning stages. Linear regressions, using residuals from the number of trees perched on (0, 1, 2, 3, 4 or 5) in the novel environment after controlling for sex and tarsus length (as a proxy for estimating body size), were used to predict learning scores. We controlled for sex and body size (both permanent between-individual sources of variation) because males and females may show differences in predictability of some behaviours (Schuett et al. 2010; Nakagawa, Gillespie, Hatchwell & Burke 2007; Guillette, Bailey, Reddon, Hurd & Sturdy 2010a) and boldness is related to body size in at least some species (Réale et al. 2007; Exnerová, Svádová, Fucíková, Drent & Stys 2010). All analyses were conducted in PSAW Statistics v. 18.

Results

Owing to equipment failure during operant testing, the data for three birds were discarded; leaving 27 individuals (12 from Stony Plain: six male, six female; and 15 from River Valley: seven male, eight female). All numbers reported are mean ± s.e.m. Responding was not different from chance at the start of training (DR first block of first set of discrimination = 0.51 ± 0.01, t26 = 0.86, p = 0.40). When birds were transferred to the second set of stimuli, the DR was significantly higher than chance (DR = 0.78 ± 0.01; t26 = 26.31, p < 0.001; Fig. 3-1), demonstrating significant savings as birds moved through the various stages of acquisition (see Fig. 3-2 for the number of blocks required to complete each training stage).

A linear regression predicting the reversal speed score from the number of trees on which a bird perched during the novel environment test showed a significant effect ($r^2 = 0.20$, $F_{1,25} = 6.16$, $p = 0.02$; Fig. 3-3). Birds that visited fewer trees learned the reversal task more quickly, compared with baseline scores, than birds that visited more trees. However, there was no relationship between the birds' baseline (discrimination) learning scores and the number of trees on which a bird perched during the novel environment test ($r^2 = 0.003$, $F_{1,25} = 0.006$, $p = 0.799$).

Discussion

Black-capped chickadees that visited more trees during a 10 min exploration trial took longer to reverse their acoustic discrimination task compared with conspecifics that did not readily enter and explore a novel environment. That is, slower exploring individuals required fewer trials, relative to their baseline, to learn to respond to C notes (C+, from their namesake *chick-a-dee* call) and withhold responding to B notes (B−) following initial discrimination training on a B+ C− discrimination, compared with faster exploring individuals with the same training. This finding cannot be explained by neophobic tendencies related to exploration because each individual was pre-trained with all discriminative stimuli until they were equally familiar with, and responding to, all stimuli (Guillette et al. 2009).

Our findings support predictions derived from the habitat-dependent hypothesis for maintenance of different personality types within a species (Réale et al. 2007). This hypothesis posits that different personality types may fare better in different local habitats. Following this, it has been further hypothesized that fast explorers may fare better in a stable, predictable environment, where they can form stable behavioural routines, while slower exploring birds may fare better in an unpredictable, changing environment because they are more sensitive (and thus adaptable) to changes in the environment. Verbeek et al. (1994) found that male great tits that were more likely to explore a novel environment, or approach a novel object, were also more likely to return to a location where food had previously been available. By contrast, birds that were slower to explore a novel environment and approach a novel object altered their foraging habits more rapidly when food locations varied. In another study with great tits, slower exploring birds out-performed faster exploring birds in an avoidance learning task (Exnerová et al. 2010). Once slow birds began to attack aposematic prey, they learned to avoid this prey more rapidly than the fast-exploring birds. The result suggests an underlying difference in learning between slow- and fast-exploring great tits. Exnerová et al. (2010) put forth two hypotheses to account for their findings. The first hypothesis was that their results were specific to the avoidance learning task (i.e. the use of aversive stimuli) and that tests which use positive stimuli could yield different results. Our results suggest that, in addition to avoidance learning tasks, tasks using positive reinforcement also yield results in support of the idea that slow-exploring birds are faster to learn some cognitive tasks. Our results also support the second hypothesis put forth by Exnerová et al., that slow birds are generally more flexible. These assertions are in line with characteristics of birds with proactive and reactive personalities that were proposed by Cockrem (2007). Specifically, it was proposed that birds with reactive personalities are likely to be slow explorers, more flexible and sensitive to environmental stimuli.

We expected to find that chickadees which were faster to explore the novel environment would learn the discrimination task (B+ C−) faster than slow-exploring birds, in accordance with Guillette et al. (2009). Interestingly, this finding was not replicated in the current study. A possible explanation may relate to subtle differences in methodology between the two studies. Guillette et al. (2009) used three different note-type pairs in the operant discrimination (AB, BC and AC), we only used one note-type pair (BC). Previous work with note-type discriminations and black-capped chickadees has shown that the amount of perceptual similarity between note types mediates the number of trials needed to learn the discrimination (Guillette et al. 2010b). That is, it takes chickadees more trials to discriminate between A and B notes, compared with A and C notes. Perhaps using the B/C note pair was not sufficiently perceptually demanding to uncover differences in learning speed when the task demand was held constant.

We believe that differences in the speed of learning an acoustic discrimination may have fitness consequences for individuals. This is especially true for chickadees because they rely on acoustic communication for survival. Learning to discriminate between these acoustic cues and respond appropriately could potentially have fitness advantages such as being able to discriminate between dominant and subordinate males (e.g., Hoeschele et al. 2010) during mate selection or between territory neighbours, thus avoiding unnecessary aggressive responses (dear enemies *sensu* Wilson 1975), thereby increasing fitness (Stoddard 1996).

Although our laboratory task can be considered highly artificial relative to the demands of a natural environment, a recent study by Herborn et al. (Herborn, Macleod, Miles, Schofield & Arnold 2010) suggests there may be a strong link between an animal's behaviour on a personality test in the laboratory and behaviour in the wild. Herborn et al. demonstrated that, for blue tits (*Cyanistes caeruleus*), performance in novel environment exploration tasks in the laboratory and an analogous test in the wild yielded similar results. This result lends support to the validity of examining animal personality in the laboratory. The next step will be to carry out analogous experiments in the wild, to test for the fitness advantages of birds of varying degrees of exploratory tendency, in different micro-habitats.

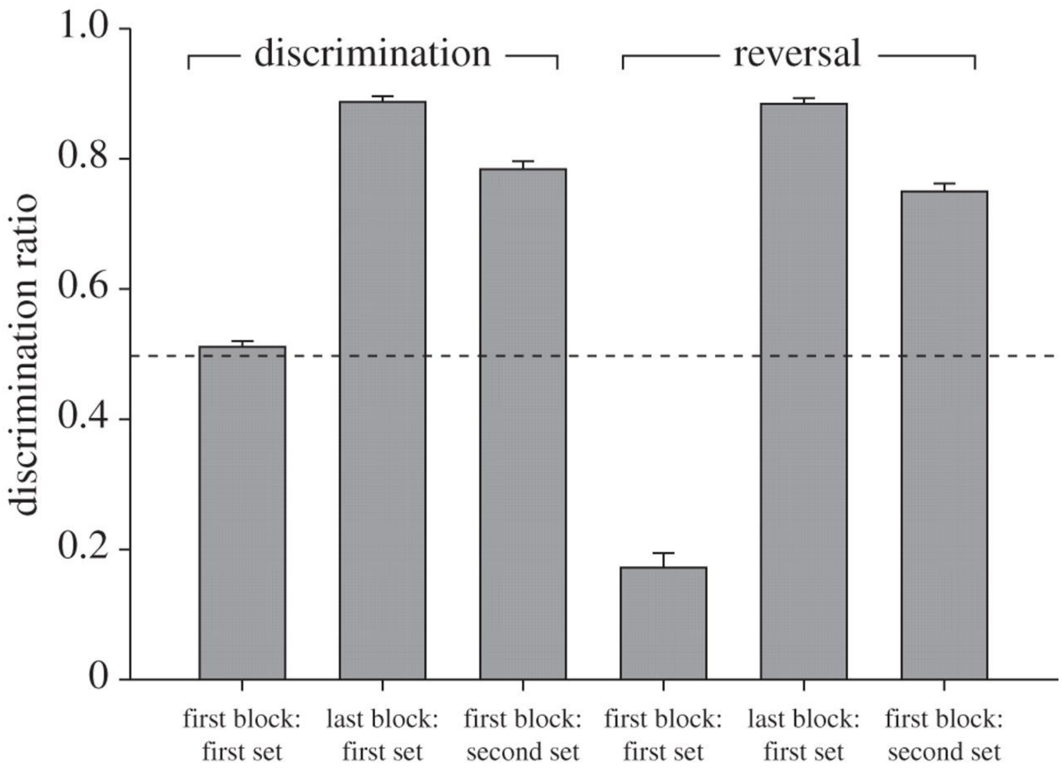

1.0
0.8
0.6
0.4
0.2
0
discrimination ratio
discrimination
reversal
first block: first set
last block: first set
first block: second set
first block: first set
last block: first set
first block: second set

Figure 3-1.

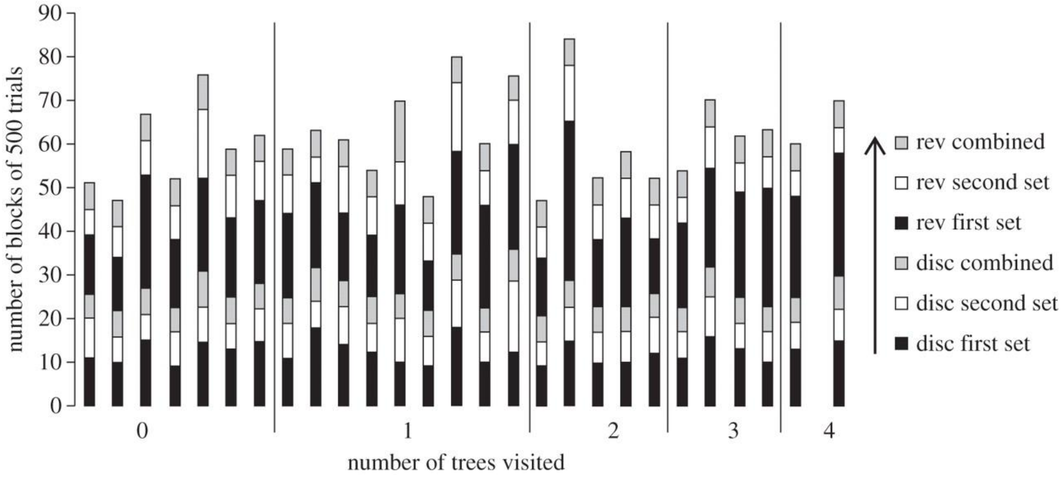
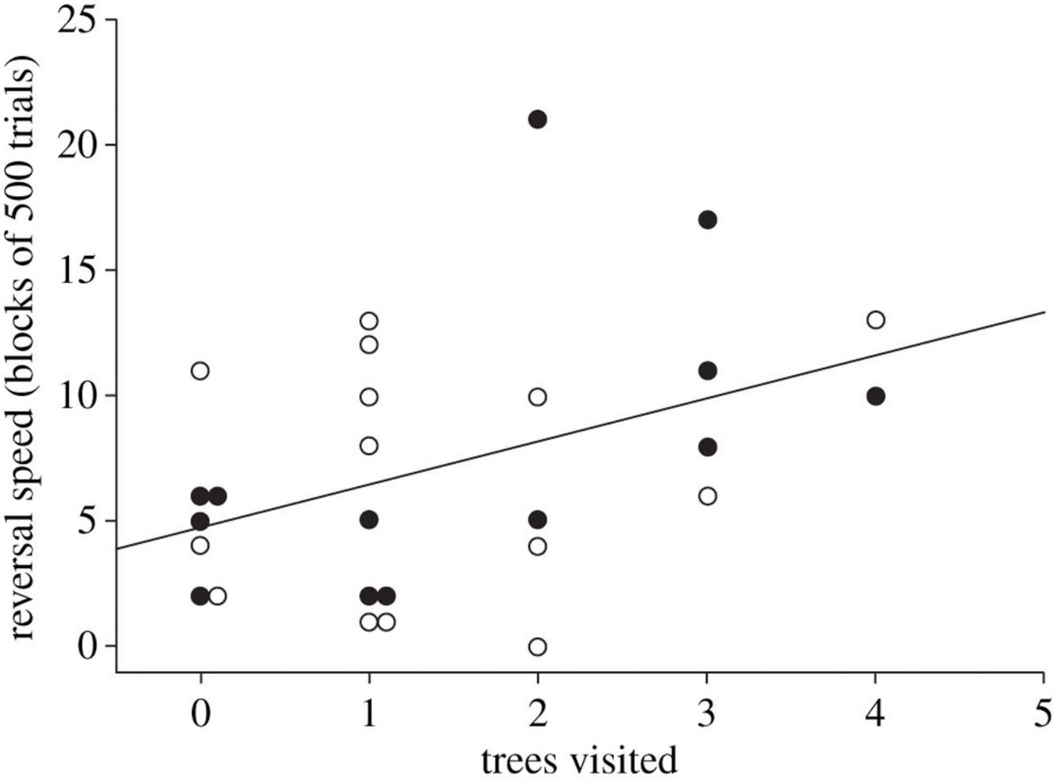

90
80
70
60
50
40
30
20
10
0
number of blocks of 500 trials
0
1
2
3
4
number of trees visited
rev combined
rev second set
rev first set
disc combined
disc second set
disc first set

Figure 3-2.



25
20
15
10
5
0
reversal speed (blocks of 500 trials)
0
1
2
3
4
5
trees visited

Figure 3-3.

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Chapter 4 Individual differences and repeatability in vocal production: stress-induced calling exposes a songbirds' personality[3]

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[3] *A version of this chapter has been published. Guillette, L.M. & Sturdy, C.B. 2011. Individual differences and repeatability in vocal production: stress-induced calling exposes a songbirds' personality. Naturwissenschaften, 98, 977-981.*

Introduction

One aspect of animal personality is that individuals behave in a consistent manner over time or across different contexts. A second aspect of animal personality is that behavior of an individual in one context is correlated with their behavior in a second context (Stamps & Groothuis 2010). A study conducted by Naguib et al. (2010) demonstrates both aspects of animal personality. Naguib et al. (2010) found that not only were male great tits consistent in the number of overall songs produced and the time of day during which they sang, but also that males that sang more songs also tended to have higher exploration scores in a novel environment. Amy et al. (2010) found similar results; fast-exploring male great tits sang longer, more complex songs than slow explorers. While learned song production is almost exclusive to male songbirds, both sexes produce species-typical calls that rely less on learning and are not sexually selected traits to the same degree as are songs. Although yet untested, bird calls may also show consistent individual differences and be related to other aspects of personality, such as exploratory behavior. We hypothesized that bird calls which are biologically relevant signals produced and used by both sexes in a variety of functional roles (e.g., flock cohesion, foraging, and mobbing) across the diurnal and annual cycles would be related to individual differences in exploratory behavior. Clearly, call production and perception are critical to survival in black-capped chickadees (Smith 1991). Similarly, exploratory behavior has been demonstrated to be linked to fitness in other avian species (Smith & Blumstein 2008). Here we tested if vocal output (songs and calls) of a songbird can be viewed as a behavioral personality trait, that is, whether they are repeatable and covary with other behavioral traits. We examined whether the vocal output of black-capped chickadees (*Poecile atricapillus*) was: (1) consistent (repeatable) within an individual over time within two different contexts (control and playback), (2) consistent (repeatable) within an individual across contexts, and (3) related to how an individual explores a novel environment. We predicted that fast-exploring birds would produce more mobbing and alarm calls in response to the playback compared to slow-exploring birds and that the number and type of vocalizations (both calls and songs) will be repeatable. We also predicted that the number of and types of calls and songs produced in each context to be related to novel environment score.

Methods

Subjects

We captured 24 black-capped chickadees between 19 December 2008 and 28 January 2009 with 14 (seven of each sex) from the North Saskatchewan River Valley in Edmonton, AB, Canada and 10 (five of each sex) from Stony Plain, AB, Canada, 36 km west of Edmonton. The sex of each bird was determined by DNA analysis (Griffiths et al. 1998). For details of housing and bird care please refer to Guillette et al. (2009 [Chapter 2]; 2011 [Chapter 3]).

Apparatus

Novel environment task

We scored the number of novel trees visited (0 to 5) by each bird in the novel environment room from the video recording of each 10-min trial (see Guillette et al. 2011 [Chapter 3] for details of the novel environment room, task, and exploration score methodology).

Playback apparatus

Each bird was moved to an experimental cage (30×40×40 cm) that contained perches, food cups, and water tubes arranged symmetrically, along with one cardboard “mouse house” on the cage floor. Each cage also contained grit and a cuttlebone. Individual cages were placed into a sound-attenuating chamber (Industrial Acoustics Co. Inc.; inner dimensions 58×168×83 cm) during the playback experiment. Each chamber had a video camera connected to a laptop computer. A condenser microphone (AKG C 1000s) located 40 cm above the top of the cage connected to a Marantz PMD 670 digital recorder recorded all vocalizations that were analyzed with SIGNAL 5 (Engineering Design, Berkeley, CA, USA). Videos were viewed using a RealPlayer v1.1.5.

Playback stimuli

The experimental stimuli were *chick-a-dee* mobbing calls produced by a single male black-capped chickadee that was captured in Edmonton, AB, Canada in December of 2007. The stimulus was 60 s in duration (first 15 s mobbing calls with the remaining 45 s silence) played on an MP3 player (creative ZEN MX) through a Cambridge A300 Integrated Amplifier and broadcast through a Fostex FE108 Sigma speaker (Fostex Corp., Japan) ~10 cm from the outside of the experimental cage.

Playback procedure

Each playback lasted 10 min, during which time each bird was audio and video recorded 5 min prior to playback (control context) and during the entire 5 min playback (stressful context). Each experimental cycle lasted 4 days: day 1, subject moved to the sound-attenuating chamber; day 2, playback no. 1 between 60 and 120 min post-light onset; day 3, bird remained in the chamber; and day 4, playback no. 2 between 60 and 120 min post-light onset, then returned to a colony room. All playbacks contained the same stimuli and were performed between 05 May and 27 May, 2010.

Vocal and video scoring

From the vocal recordings taken, we counted the number of times each bird gave the following calls: (1) *tseet*, (2) *chick- a-dee*, (3) *gargle*, (4) *alarm*, and songs: (1) *fee-bee* and (2) *fee* only. For representative spectrograms of the vocalizations scored see Fig. 4-1. From the video recordings, we counted the number of hops by each bird as a measure of general activity. A hop is defined as jumping or flying between perches or another part of the cage. We also recorded the amount of time (in seconds) that each bird performed a wing display (Smith 1973).

Statistical analysis

The repeatability (intraclass correlation coefficient) for individual vocalizations and behaviors was calculated using the formula $r = s^2_A/s^2+s^2_A$, where s^2_A is the variance among individuals and s^2 is the variance within individuals over time (Bell et al. 2009; Lessells & Boag 1987; Stamps & Groothuis 2010).The standardized scores (z scores) were calculated separately for each vocalization type, behavior, and context. Linear regressions, predicting the number of trees perched upon in the novel environment, after controlling for sex and tarsus length, from the standardized score for vocalizations and behaviors performed during either the control or playback period, were conducted. The data from one female was discarded due to equipment failure during playback, resulting in data from a total of 12 males and 11 females. All analyses were conducted in PASW statistics v18.

Results

Please refer to Table 4-1 for descriptive statistics for vocalizations and behaviors produced during the control and playback periods. Across the two control periods, *tseet* calls, *fee-bee* songs, and hops were significantly positively correlated (all Ps<0.01) and no wing displays were given. Across the two playback periods, tseet calls and *fee-bee* songs remained significantly correlated, as they were in the control context. In addition, *gargle* calls, *alarm* calls, and wing displays were significantly correlated (all Ps<0.001, see Table 4-2). Across both contexts, *tseet* calls (P<0.001) and hops (P=0.007) were significantly correlated. There was no relationship between the total vocal and motor behavior of birds during the control periods and the number of trees visited in the novel environment, R^2=0.32, $F_{6, 16}$= 1.27, P=0.32. During the playback periods, all vocal and motor behaviors entered together significantly predicted the number of trees visited in the novel environment, R^2=0.65, $F_{8, 14}$=3.29, P=0.025. Therefore, a stepwise regression was conducted to eliminate nonsignificant variables. This regression (R^2=0.44, $F_{2, 20}$=7.80, P=0.003) showed that the more *chick-a-dee* calls (β=0.62) and *alarm* calls (β= 0.36) given during playback, the more trees an individual visited in the novel environment, see Fig. 4-2.

Discussion

We found an individual's vocal output, including calls in addition to songs, is consistent within given contexts and over time in black-capped chickadees. This finding is important because previous personality research on songbird vocal behavior has mainly focused on birdsong (e.g., Garamszegi et al. 2008; Naguib et al. 2010; Amy et al. 2010; but see Hollander et al. 2008). We also found that the production of *tseet* calls was consistent across contexts. This is important because *tseet* calls function to keep members of a flock in contact with one another and therefore is the most frequently produced vocalization by black-capped chickadees (Odum 1942). Recent bioacoustic analyses have also suggested that the *tseet* call contains species, sex, and individual identity features (Guillette et al. 2010). Hops, a measure of activity, considered one of the five main trait categories in animal personality research, were significantly correlated within the control context and across both contexts.

We suggest that underlying physiological mechanisms, such as sympathetic nervous system arousal, may contribute to consistent vocal production while motivational and state variables were held constant, as they were within each of the contexts in the current experiment. Similar results, suggesting that birds' overall behavior (i.e., factors that described aggressive behavior, nonaggressive vocalizations, eating/drinking, and being supplanted) is consistent across time, have been reported in Carolina chickadees (*Poecile carolinensis*; Harvey & Freeberg 2007).

Results from the current study show that vocal output in response to playback of conspecific mobbing calls is related to exploratory behavior, while vocal output under control conditions is not. There was a positive relationship between *chick-a-dee* and *alarm* calls and exploratory behavior. While the number of *chick-a-dee* calls was a better predictor of exploratory behavior than *alarm* calls, it should be noted that for the latter call, this relationship is likely driven by a subset of bird that neither gave *alarm* calls nor left their home cage in the novel environment task. We did not find a relationship between song output and explorations in either context, as we had predicted based on results from recent work in great tits (Naguib et al. 2010; Amy et al. 2010). However, a previous study with great tits reported the number of alarm calls produced in response to the presence of a human observer standing near a nest with 13-day-old hatchlings was positively related to the exploration scores (Hollander et al. 2008). Garamszegi et al. (2008) reported that, in collard flycatchers, high-exploring risk-taking males sang at lower post-heights compared to shy males. The link between singing and other behavioral traits here might be due to the nature of songs, namely, there are trade-offs between sexual advertisement and risk taking that are not at play with calling behavior. Establishing a link between vocal output and exploration is important because exploration is one of the best-studied personality axes (Réale et al. 2007). This convergent evidence supports the theory of reactive and proactive avian personalities outlined by Cockrem (2007). Birds with a proactive personality, for instance fast-exploring songbirds, give more *alarm* calls during a stressful event. This higher rate of calling, compared to Parids with reactive personalities, may be partially mediated by or covary with (due to a common regulatory mechanism) high sympathetic nervous system reactivity and/or low corticosterone response (Cockrem 2007).

Table 4-1. Percentage of individuals producing vocalizations and behaviors during the control and playback periods, sorted by vocalization/behavior type.

	Condition			
Vocalization/	Baseline		Playback	
Behaviour	Males	Females	Males	Females
Tseet call	83	73	83	100
Chick-a-dee call	42	18	75	100
Gargle call	8	--	50	27
*Fee-bee*song	17	9	42	55
Fee song	8	18	25	73
Alarm call	--	--	58	27
Hops	83	73	83	91
Wing display	--	--	58	27

Table 4-2. Control context and playback context show within context repeatability of vocalizations and behaviors. Across context shows repeatability across contexts. Control context and playback context repeatability scores were calculated across five 1-min bins in each session. The scores in the All column were calculated across the sessions on days 2 and 4, for a total of ten 1-min bins. The Pearson's r and corresponding P values were calculated for the total vocalizations/behaviors given between days 2 and 4. Bold values under the P column are significant when the Bonferroni correction ($P < 0.01$ for control context, $P < 0.006$ for playback context) for multiple tests was applied. Across contexts repeatability scores were calculated across 20, 1-min bins. The Pearson's r and corresponding P values were calculated for the total vocalizations/behaviors between the control and playback context. Bold values under the P column are significant when the Bonferroni correction for multiple tests was applied ($P < 0.008$). 1st is the session on day 2, 2nd is the session on day 4.

Vocalization/ Behaviour	Control context				
	1st	2nd	All	Pearson *r*	*p*
Tseet call	0.78	0.72	0.68	0.91	**< 0.001**
Chick-a-dee call	0.20	0.57	0.18	-0.09	0.699
Gargle call	--	--	--	--	--
Fee-bee song	0.19	0.53	0.30	0.79	**< 0.001**
Fee song	0.00	0.25	0.05	-0.09	0.673
Alarm call	--	--	--	--	--
Hops	0.82	0.88	0.70	0.65	**0.001**
Wing display	--	--	--	--	--
	Playback context				
	1st	2nd	All	Pearson *r*	*p*
Tseet call	0.59	0.73	0.62	0.82	**< 0.001**
Chick-a-dee call	0.24	0.49	0.25	0.29	0.188
Gargle call	0.60	0.14	0.33	0.69	**< 0.001**
Fee-bee song	0.35	0.51	0.39	0.70	**< 0.001**
Fee song	0.39	0.62	0.25	0.06	0.774
Alarm call	0.59	0.38	0.42	0.71	**< 0.001**
Hops	0.54	0.67	0.42	0.52	0.012
Wing display	0.41	0.36	0.35	0.75	**< 0.001**

	Across contexts		
	r	Pearson *r*	*p*
Tseet call	0.43	0.64	**< 0.001**
Chick-a-dee call	0.13	0.19	0.394
Gargle call	0.17	0.36	0.090
Fee-bee song	0.21	0.23	0.298
*Fee*s Song	0.12	-0.15	0.504
Alarm call	--	--	--
Hops	0.45	0.55	**0.007**
Wing display	--	--	--

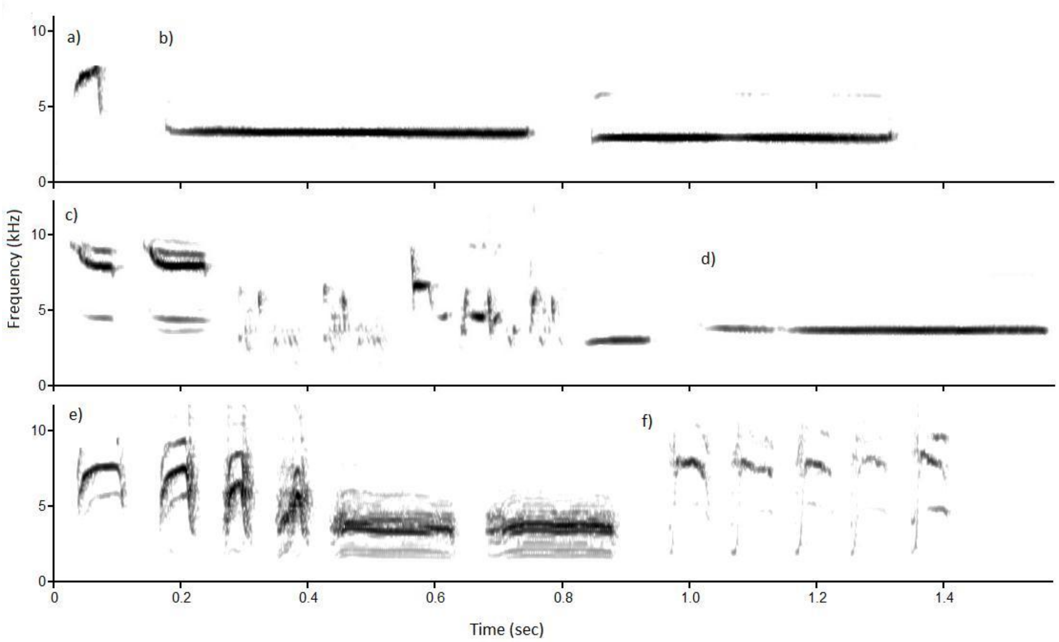

Figure 4-1.

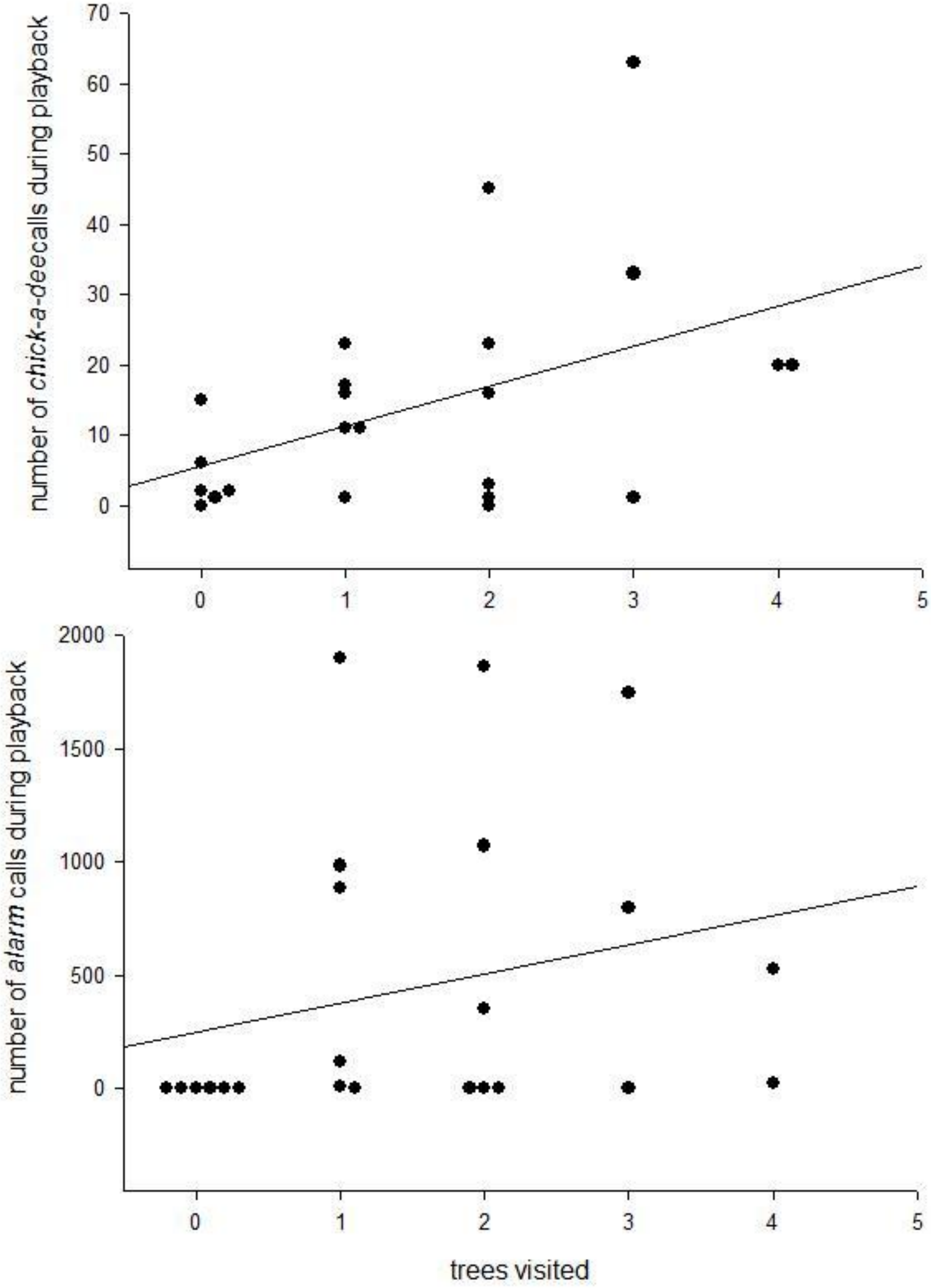
number of *chick-a-dee*calls during playback
70
60
50
40
30
20
10
0
0
1
2
3
4
5
number of *alarm* calls during playback
2000
1500
1000
500
0
0
1
2
3
4
5
trees visited

Figure 4-2.

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Chapter 5 Are slow-exploring birds more expert discriminators?[4]

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[4] A version of this chapter is currently under preparation to be submitted to the *Proceedings of the Royal Society B: Biological Sciences.* Authors: Guillette, L.M., Lubyk, D.M., MacDougall-Shakleton, S. A., Sturdy, C.B. & Spetch, M.L.

Introduction

Recent research in the field of animal personality has focused on two distinct styles of coping with stress: reactive and proactive (Carere, Caramaschi & Fawcett 2010; Koolhaas et al. 1999; Koolhaas, de Boer, Coppens & Buwalda 2010; Cockrem 2007, Carere & Locurto 2011). Although these two styles are characterized dichotomously, in nature, individual differences in behaviour and physiology fall along a continuum, and are usually measured as such. Animals characterized as falling near the proactive end of the continuum (hereafter referred to simply as *proactive*) tend to be aggressive toward male rivals, are fast and superficial explorers, and seek out novelty in their environment. In contrast, animals characterized as falling near the reactive end of the continuum (hereafter referred to as *reactive*) are less aggressive, are slow and careful explorers, and prefer the familiar (David, Cervantes, Trosky, Salinas & Delville 2004; Steimer & Driscoll 2005; for a review see Coppens, de Boer & Koolhaas 2010; Groothuis & Carere 2005, Cockrem 2007). These diverse personality types, also called behavioural profiles or coping strategies, such as proactive and reactive, coexist within the same population. To maintain the balance of the different personality types, one personality type must excel in one situation, while a second personality type must excel in another situation. The habitat-dependent selection hypothesis suggests that certain habitats may favour different behavioural types; for instance, slow versus fast explorers. Previous theoretical work (Cockrem 2007) hypothesized that fast-exploring birds may fare better in consistent environments because forming stable routines quickly is beneficial. Slow exploring birds may be more sensitive to environments that are constantly changing, and thus benefit in this environment. The results of several empirical studies using different songbird species as a model support Cockrem's hypothesis.

For instance, black-capped chickadees (*Poecile atricapillus*) that are fast-explorers in a novel environment also learn an acoustic discrimination task in fewer trials compared to slow-explorers (Guillette, Reddon, Hurd & Sturdy 2009). The cognitive task used in Guillette et al. 2009 was designed to favor individuals that formed routines quickly: there was only one rule to learn in the operant discrimination task, and that rule was: respond to exemplars that belong to one category (e.g., "B" notes from the *chick-a-dee* call of the black-capped chickadee) and withhold responding to exemplars that belong to a second category (e.g., "C" notes from the *chick-a-dee* call). In this task (Guillette et al. 2009), the proactive behavioural strategy (*sensu* Cockrem 2007) was advantageous because the environment was stable (i.e., only one rule). In a subsequent experiment Guillette et al. (2011) utilized the same operant discrimination paradigm but manipulated the task to favor individuals with reactive strategies by making the environment less-stable; this was accomplished by reversing the reward contingencies associated with responding to stimuli from different categories half-way through the task. As predicted, fast-exploring birds outperformed slow-exploring birds in the former experiment, while slow-exploring birds outperformed fast-exploring birds when the rules changed in the latter experiment (Guillette et al. 2009, 2011).

Similar results, in support of Cockrem's (2007) characterization of proactive and reactive avian personalities were observed in recent experiments conducted with great tits (*Parus major*), a European relative of the black-capped chickadees. Slow-exploring great tits out-performed fast-exploring great tits in an avoidance learning task (Exnerová, Svádová, Fucíková, Drent & Stys 2010). In another study using a dimension shift learning paradigm (color-location; Titulaer, van Oers & Naguib 2012) great tits exploratory behaviour was related to learning only in the most cognitively-demanding stages, but effects were opposite for males and females. In the reversal stage, fast-exploring males took fewer trials to acquire the task compared to slow-exploring males, whereas slow-exploring females outperformed fast-exploring females. The results obtained for females are in support of Cockrem's classification of proactive and reactive personality types, but the results for males are not, suggesting that there is a complex interaction between cognition, personality type, and sex. Previous work examining the role of personality type in adult survival in wild great tits has demonstrated this same complex interaction; in years of high beech masting fast-exploring males and slow-exploring females had higher survival, while the opposite was observed in years with low beech masting (Dingemanse, Both, Drent & Tinbergen 2004).

The studies outlined in the previous paragraphs demonstrate that operant conditioning, avoidance learning, and dimensional-shift learning paradigms are well-suited to examine variation in cognitive performance among individuals, and that differences in performance on cognitive tasks are related to differences in personality. However, the studies conducted with chickadees (Guillette et al. 2009, 2011) and great tits (Exnerová et al. 2010; Titulaer et al. 2012) only examined one aspect of learning, namely individual differences in learning rate.

The goal of the current study is not focused on differences in task acquisition (i.e., learning rate), but on whether different cognitive performance among individuals can be explained by differential sensitivity to slight manipulations in the environment (i.e., the test stimuli). In the current experiment, all animals were trained to the same level of expertise on a visual discrimination task, then tested under extinction (with no feedback [e.g., food reward as in Guillette et al. 2009, 2011; Titulaer et al. 2012; or internal feedback due to ingesting unpalatable, poisonous prey as in Exnerová et al. 2010]) for responses to a series of stimuli that lie on a continuum that vary in one dimension, from the trained stimuli (see methods section for details).

In the current experiment, homing pigeons (*Columba livia*) were used as a model species to examine if slow-exploring and fast-exploring birds differ in the way they generalize responses to novel visual line orientations after being trained on a binary line-discrimination task. Pigeons were first run in a novel environment task to assess exploratory behaviour. Each pigeon was then trained to discriminate between a reinforced (S+) and non-reinforced (S-) visual stimulus (two different line orientations). Upon successfully learning the discrimination, the responses of each pigeon to novel line orientations with varying degrees of similarity to the trained S+ and S- stimulus was tested. Our training and testing paradigm was based on a classic psychological testing paradigm similar to that of Honig, Boneau, Burstein, and Pennypacker (1963; see *Current Studies* in Chapter 1 for a more detailed description of this task). If fast-exploring birds do indeed have more superficial representations of environmental features (*sensu* Carere &

Locurto 2011), then we expect these individual to have broader response gradients (i.e., failure to discriminate novel stimuli that are similar to trained stimuli) compared to slow-exploring birds. In contrast, slow-exploring birds that are more sensitive to environmental stimuli (both the trained S+ and S-) should show steeper response gradients (i.e., are more expert discriminators).

In addition to behavioural and cognitive performance, many animals also exhibit consistent individual differences in physiology, such as in hypothalamic-pituitary-adrenal axis (HPA) reactivity (for reviews see Cockrem 2007; Carere, Caramaschi & Fawcette 2010; Koolhaas, de Boer, Coppens & Buwalda 2010). In birds, the hormone corticosterone is the major glucocorticoid secreted when a bird perceives a stressful situation, such as the presence of a predator (Silverin 1998; Cockrem & Silverin 2002). The presence of corticosterone causes an increase in the amount of glucose present in the blood stream and enhanced memory consolidation (for a review see Sapolsky, Romero & Munck 2000) and is considered to be an adaptive short term response to a stressful event (Levine 1971). Previous work examining the levels of plasma corticosterone in response to acute stress has been shown to be repeatable, and vary between individual great tits (Cockrem & Silverin 2002). Cockrem (2007) suggests that birds with different personality types (i.e., proactive or reactive) likely vary in their corticosterone response to stressors. As introduced earlier, fast-exploring, bold birds are less behaviourally flexible and are better suited to constant conditions. These fast-exploring birds are likely to display lower corticosterone response to stressors, compared to slow-exploring, shy birds that are more flexible and better suited to unpredictable conditions.

In addition to quantifying personality in the novel environment task and cognition in the operant discrimination task, we also measured plasma corticosterone levels for each bird after they explored a novel environment. Based on Cockrem's (2007) predictions regarding proactive and reactive personality types and corticosterone responses, we predict that birds that have a higher exploration score in a novel environment should have a lower stress response measured at the end of the novel environment assay, while birds that are slow explorers should have a higher corticosterone response.

Methods

Subjects

Twelve Homing pigeons (*Columba livia*; five male and seven female), were obtained from a local breeder (Vandermeer Farms, Sherwood Park, Alberta). Each pigeon was housed individually in a metal cage (42 × 47 × 42 cm) in a colony room that was maintained on a 12:12-hour light:dark cycle with light onset at 08:00 h. Pigeons had visual and vocal, but not physical, contact with one another. Standard poultry grit and vitamin-supplemented water (Vetoquinol, Poly-tonine A Complex) were available *ad libitum* and each pigeon was maintained at 85% of its free-feeding weight on a diet of Kee Tee pigeon pellets. No pigeons had prior open field (i.e., novel environment) experience. All pigeons had been subjects in either touch screen or touch key operant experiments but were naïve to current experimental stimuli.

Apparatus

Novel environment room

The novel environment (185 × 222 cm; see Fig. 5-1) consisted of a room surrounded by 92 cm high uniformly white walls constructed from plastic. Above the walls, white translucent curtains hung around the perimeter of the room, including the ceiling. The room was lit by four 40-watt fluorescent light bulbs located on the ceiling, which were hidden from view by the curtain. The floor was lined with approximately 4 cm of aspen chip bedding. A small transparent vertically-sliding door (38 × 61 cm) was located at the South end of the room, which connected to a start box (33.5 × 23 × 33.5 cm) , located on the outside of the room, that housed the bird at the start of each trial. Five uniformly gray 'walls' (30.5 × 30.5 ×11.5 cm), were positioned at equally-spaced intervals throughout the room. The gray walls served as visual barriers, so that the pigeon was unable to view the entire novel environment room from the start location, or any other location within the novel environment room.

Operant chamber

One operant chamber (74 × 31 × 40.5 cm) was used for both training and testing all pigeons. The custom-made chamber was composed of aluminum and stainless steel and had a 34 × 24.5 cm opening in the back wall for the flat-screen color computer monitor (IBM ThinkVision) with attached infrared touch frames

(CarrollTouch model no. D27566-001). The monitor screen was located 7 cm above the chamber floor and was covered with a thin sheet of Plexiglass that was located approximately 1.5 cm in front of the monitor. The touch frames had a resolution of 3 mm and detected individual peck responses. On the rear of the chamber, on either side of the monitor, was a food hopper, that when activated by a correct choice, provided the bird with a small amount of food. For the current experiment, both hoppers were activated each time reinforcement was provided, and the bird was able to choose which hopper to visit. A computer was located in the adjacent control room and controlled the stimulus presentation as well as recorded all data.

Stimulus preparation

Using EPrime, twelve stimuli at fifteen degree rotation intervals were created. The stimuli were created to be similar to those used by Honig, Boneau, Burstein, and Pennypacker (1963) and Bloomfield (1967). Each stimulus was a white circle (2.54 cm diameter) with a 1.60 mm wide black line through the center. Stimuli were always presented individually (dpi = 0.297) in the center of the monitor (IBM ThinkVision) on a black background.

Novel environment task

Each pigeon’s exploratory behaviour, activity, and boldness (defined below) were assessed in the novel environment prior to training and testing in the operant task. Individual birds were placed in the start box and the clear door separating the start box from the novel environment allowed the birds to visually assess the room without being able to move into it. Birds were allowed ten minutes to habituate to the holding box and visually inspect the novel environment room before the door was lifted and the bird was given 30 minutes to explore. Each bird's activity within the room was recorded by a JVC video camera suspended from the ceiling. Once 30 minutes had elapsed, the room lights were extinguished, the bird was immediately removed from the novel environment room, and approximately 50 microliters of blood was collected via hepranized capillary tube using a 27 g needle puncture of the femoral vein. Acquiring the blood sample took less than 60 seconds. Each blood sample was immediately centrifuged at 14,000 rpm for 10 minutes, and the plasma removed and frozen at -20°C until assays were performed. Plasma samples were used to measure circulating level of corticosterone. Thirty-five days after each bird's first session to the novel environment room, it participated in a second session, with all procedures carried out exactly as during the first session. A second blood sample was taken immediately after the second session in the novel environment. All novel environment trials were conducted between the hours of 10.00 and 14.00 between 16 Oct and 27 November 2011.

Operant Task

Autoshaping. Each pigeon had previous experience with touch screen tasks but was naïve to current experimental stimuli. Each pigeon was given an initial *Autoshaping* phase to re-establish reliable pecking. *Autoshaping* paired the presentation of a white stimulus (2.54 cm diameter, see Fig. 5-2, left), with access to the food hoppers. Each trial started with a 10 s inter-trial-interval (ITI) with no stimulus presentation, followed by 45 s stimulus presentation with both hoppers activated. The trial ended 5 s after the infrared beams in one of the hoppers was broken or timed-out after 45 s if the beam in a hopper was not broken. Each daily session lasted until the bird received 30 food presentations (i.e., broken the hopper beam while the stimulus was presented), or until 45 minutes elapsed. The criterion to complete *Autoshaping* was entering a hopper on each of 30 opportunities per daily session for one day. After completing *Autoshaping*, pigeons moved onto *Peck Training I*.

Peck Training I. In *Peck Training I* the first peck on the stimulus (white circle, 1 cm diameter) was rewarded with a 2 s access to the food hoppers. Each trial began with a 10 s ITI with no stimulus presentation followed by a 60 s stimulus presentation. The first peck on the stimulus resulted in activation of both food hoppers. The opportunity for reinforcement remained available for 5 s, after the infrared beam in a hopper was broken a 2 s access to food was given, followed by a new trial. Failure to peck on the stimulus after 60 s elapsed ended the trial, and following a 10 s ITI, a new trial began. Each daily session continued until the pigeon received 60 reinforcement opportunities, or until 45 minutes had elapsed. The criterion to complete *Peck Training I* was one daily session where the pigeon responded to each stimulus presentation.

If a pigeon failed to peck during the stimulus presentation on two consecutive daily sessions it was moved to *Remedial Autoshaping* training. In *Remedial Autoshaping* training, all rules from *Autoshaping,* outlined above, remained in place, with the exception of the following: both food hoppers were activated 5 s after the stimulus was presented on each trial. The criterion to complete *Remedial Autoshaping* was entering a hopper on each of 30 opportunities per daily session for one day. Birds then moved back to *Peck Training I.* After completing *Peck Training I* pigeons moved onto *Peck Training II.*

Peck Training II. In *Peck Training II* the reinforced stimulus (S+) was introduced. To introduce the S+, the same white stimulus as was used in *Autoshaping*, *Remedial Autoshaping* and *Peck Training I* was displayed, but with the addition of a 90° (vertical) black line through the center (see Fig. 5-2, middle). The stimulus was fixed on the screen for the entire daily session (i.e., no ITI) and the bird was reinforced for each peck on the S+. Once the S+ was pecked, both hoppers were activated and the opportunity for reinforcement remained available for 5 s. As in the previous phase, once the infrared beam in a hopper was broken, the pigeon had 2 s access to food. Each daily session ended when the bird received 40 reinforcements or after 45 minutes elapsed, whichever came first. The criterion to complete *Peck Training II* was one daily session where the bird responded 40 times. After completing *Peck Training II* pigeons moved onto *Variable Interval S+ Training*.

Variable Interval S+Training. In this phase there were 55 trials per daily session. Each trial started with a 10 s ITI with no stimulus presentation followed by the S+ displayed on the centre of the screen. Each pigeon was reinforced on a variable interval (VI) 30 s schedule with 2 s access to food for its first peck on the S+ after a random amount of the time had elapsed from the start of the trial (range = 3-57 s). Each trial ended once the bird received reinforcement, or after 60 s elapsed with no response. The criterion to complete *Variable Interval S+ Training* was a no greater than a 10 % difference in response rate averaged over the last three days, after a minimum of 10 days of training. After completing *Variable Interval S+ Training* pigeons moved onto *Discrimination Training*.

Discrimination Training. The purpose of *Discrimination Training* was to train the birds to respond differentially to the reinforced (S+) and non-reinforced (S-; 135° line, see Fig. 5-2, right) stimuli. Each pigeon received 54 trials in each daily session (27 S+ and 27 S- presentations). Responses to the S+ were reinforced on a VI 30 schedule, with trials ending after the fixed 2 s access to the food hoppers. No reinforcement was provided for pecking on the S-. Trials were separated by a 10 s ITI. The presentation order of the S+ and S- were pseudo randomized so that there were never more than two consecutive presentations of any stimulus type. The lengths of the S- trials were yoked to the lengths of the S+ trials in a random order, so that the duration of daily experience with both the S+ and S- stimulus was equivalent. S+ trials timed out after 60 s with no response. The criterion to complete *Discrimination Training* was a discrimination ratio (DR) of 0.75 for three consecutive sessions where at least 19 of the 27 S+ presentations were rewarded. The DR was calculated by dividing the number of pecks on the S+ by the total pecks per session (the sum of the number of pecks on the S+ and the number of pecks on the S-). Discrimination is at chance (DR = 0.50) when the animal is responding equally to both stimulus types and perfect (DR = 1.00) when the animals is only responding to presentation of the S+. After completing *Discrimination Training* pigeons were moved onto Generalization Testing.

Some pigeons performed *Discrimination Training* with high DRs but did not receive the minimum number of reinforcements (19 per daily session). These pigeons were returned to *Variable Interval S+ Training*, and in some cases, to *Peck II Training*, and then were returned to *Discrimination Training*. If a bird still did not meet the minimum required number of reinforcements, it was moved onto *Generalization Testing* (described below) after 35 cumulative daily sessions of *Discrimination Training*.

Generalization Testing. Twelve stimuli of 15-degree increment line orientations, including the S+ and S- (see Fig. 5-3), were presented once per block, in six blocks, randomized for order in each daily session. Each trial began with a 5 s ITI with no stimulus presentation followed by a stimulus presentation where the stimulus remained fixed on the screen for 30 s. All stimuli were presented under extinction, including the S+. Testing continued for 10 daily sessions. All pigeons completed the stimulus generalization operant task between 10 January 2012 and 27 May 2012. Six pigeons were run in a squad; each pigeon was run seven days a week, at the same time each day, between 09 00 and 14 00 hr. After each daily session of training or testing, pigeons were returned to the colony room and fed each day at approximately 15 00 hr.

Hormonal Assay

Scoring

Plasma corticosterone levels were detected using a specific and sensitive ELISA kit that has previously been validated for use with a variety of bird species (Enzo Life Sciences [formerly Assay Designs] kit ADI-901-907; Wada et al. 2007). This kit uses a steroid displacement buffer (SDB) rather than a steroid extraction. To validate this kit for pigeons, serial dilutions of a pigeon plasma pool were assayed using 0%, 1% or 2% SDB. As in prior studies, use of 1% SDB yielded a plasma dilution curve that was parallel to the standard curve.

To assay the samples we followed the kit manufacturer's instructions, but used a 6 point standard curve ranging from 20,000 to 15.63 pg CORT per well run in triplicate. All samples were run in duplicate on a single plate. Plasma volumes used for each sample ranged from 10-20 μL and were individually measured using Hamilton syringe; final CORT concentration estimates were then individually corrected based on these dilutions. The sensitivity of the assay (2 s.d. from blank wells) was 32.6 pg/well (0.65 ng/mL) and samples that fell below this detection limit (n = 6) were assigned this value. Within-assay variation measured on replicates of a 250 pg/well standard was 10.1%.

Novel environment

The novel environment room was divided into thirty 37 × 37 cm squares, which were not visible to the pigeons, but were used by experimenters to quantify the amount of novel area explored, as well as the activity of each pigeon (see Fig 5-1). From the video recording of each pigeon's two novel environment sessions, we obtained three scores: (1) exploration, (2) activity, and (3) boldness. The exploration score was the sum of the novel boxes entered (out of 30 total) by each pigeon for the duration of each 30 minute trial. If a pigeon failed to leave the start box, it received an exploration score of zero. The activity score was the sum of boxes entered by a pigeon, regardless if it had been in that box previously. The activity score of the birds ranged from zero (did not leave start box) with no upward limit. The boldness score was the latency to emerge (in seconds) from the start box, into the novel environment room. To test for repeatability across the two novel environment sessions, the absolute scores for exploration, activity and boldness, and the amount of circulating corticosterone were converted to rank scores within each novel environment session. For statistical analyses examining the relationship between behaviour in the novel environment task and performance in the operant task, the sum of the exploration scores, activity scores, boldness scores and amount of circulating corticosterone were used. These sums provide more complete information about how each pigeon behaved across the 60 minutes it was allotted to explore the novel environment room.

Operant task

During *Generalization Testing* the number of pecks to each of the 12 stimuli were summed over the six presentations per daily session and a generalization gradient (stimuli on *x*-axis, number of pecks on *y*-axis) was constructed. The area under the curve between two points was calculated and scaled within each individual so that proportions could be compared across individuals. The area under the curve between the peak responding and the stimuli

15° to each side, 30° to each side, and 45° to each side were calculated. This measure explains what proportion of the responses of each individual fell around the peak response (i.e., lower proportion of area would indicate individuals with greater [more expert] discrimination ability). These area measures take into account the distribution of responses across the total range of test stimuli. This resulted in three area measurements for each generalization gradient. However, area measures may be misleading, even when comparing proportional data across subjects. For instance, if two individuals are responding at the same level to the trained S+, but one individual has an overall higher response rate (i.e., is a more active responder) compared to a second individual with overall lower response rate, the proportion of responses occurring around the trained S+ will be smaller for the former animal, compared to the latter. Because area under the generalization gradient can be confounded by response rate, even when two animals are responding similarly to the trained S+, we also measured the slope of the line between the responses to two stimuli. The slope measures the rate of change in response rate between two stimuli. Slope is considered to be the most sensitive measure of stimulus control (Honig & Urcuioli 1981). If the absolute value of the slope is large, then the animal is discrimination more expertly between two stimuli than when the slope is smaller, or close to zero. We calculated the slope between the stimulus where peak responding occurred for each individual and the stimuli at 15°, 30° and 45° angle rotations to each side. Stimuli rotated to the left are in the direction away from the trained S-, and stimuli rotated to the right are in the direction towards the trained S-. This resulted in six slope measurements for each generalization gradient. Lastly, we chose to use the stimulus that evoked the maximal responding for each individual, rather than the trained S+ (unless the maximal responding was to the S+) because of a phenomenon called the *Peak Shift Effect*. The peak shift effect is a product of the intradimensional discrimination procedure that we implemented for training and testing and is when maximal responding occurs not to the trained S+, but to another stimulus along the dimension is the direction away from the S- (Domjan 2009; Hanson 1959). Given our training procedure, it would be expected that individuals, during generalization testing, would respond more to the stimulus with the line orientation that is shifted 15° or possibly even 30 ° to the left of the trained S+.

Statistical Analyses

The novel environment assay measured three aspects of personality: (1) exploratory behaviour, the number of novel boxes entered, (2) activity, the number of lines crossed, and (3) boldness, the latency to emerge from the start box. The levels of circulating corticosterone were also measured immediately following each novel environment session. To test for repeatability of personality scores, and plasma corticosterone levels across time (the two sessions of the novel environment task), Spearman's Rank Correlation Coefficients were calculated on ranked scores. The total pecks given on the first day of generalization testing in the operant discrimination task can be taken as a measure of activity, therefore we tested for a correlation in activity, measured across different contexts (total lines crossed in the novel environment, and total pecks on the first day of generalization testing) using Pearson Correlation.

To examine if behaviour in a novel environment (i.e., exploration, activity, boldness, or plasma corticosterone levels) can be predicted by performance during generalization testing following intradimensional discrimination training, a series of linear regressions were conducted. Two stepwise linear regressions were conducted for each of the four traits measured in the novel environment, total boxes entered (out of 60 possible), total lines crossed (no upper limit), combined latency to emerge from the start box, total circulating plasma corticosterone levels as dependent variables. The first linear regression for each dependent variable used the three area measurements derived from each generalization gradient. The second linear regression for each dependent variable used the six slope measurements derived from each generalization gradient. The total pecks given on the first day of generalization testing in the operant discrimination task can be taken as a measure of activity, therefore we tested for a correlation in activity measured across different contexts (total lines crossed in the novel environment, and total pecks on the first day of generalization testing).

A series of Pearson's correlations examined if there was a relationship between the level of circulating plasma corticosterone during the novel environment task and each individual exploration, activity and boldness score.

Results

Repeatability of behaviour across time and context

Exploratory behaviour was not significantly repeatable; the rank order of the number of novel boxes entered was not significantly correlated across novel environment sessions, $r(12) = 0.330$, $p = 0.295$, see Panel a Fig. 5-4. Activity was repeatable; the rank score of total boxes entered was significant across novel environment sessions; $r(12) = 0.693$, $p = 0.025$, see Panel b Fig. 5-4. The rank score of activity per boxes entered (the number of total boxes entered, for each novel box entered) was significantly correlated across the novel environment sessions, $r(12) = 0.751$, $p = 0.005$, see Panel c Fig. 5-4. Boldness was not repeatable; the rank score of latency to emerge from the start box was not significant across novel environment sessions, $r(12) = 0.553$, $p = 0.062$, see Panel d Fig 5-4. The rank score of plasma corticosterone was not repeatable across novel environment sessions, $r(11) = 0.272$, $p = 0.419$, see Panel e Fig 5-4. The number of total pecks on first day of generalization testing was significantly correlated with the total number of boxes entered in the novel environment, $r(11) = 0.623$, $p = 0.041$. Pigeons that were more active in the novel environment also tended to more actively peck (respond) on the first day of generalization testing in operant task, see Fig. 5-5 Pigeons with higher exploration scores were more active[$r(12) = 0.643$, $p = 0.024$], and left the start box more quickly [$r(12) = -0.617$, $p = 0.033$]. However, there was no significant correlation between activity and boldness [$r(12) = -0.448$, $p = 0.144$].

Relationship between novel environment and operant discrimination task

The proportion of the responses under the generalization gradient in the area 15°, 30°, and 45° around the stimulus where peak responding occurred were not significantly related to any of the behaviours measured in the novel environment (exploration, activity, boldness or circulating levels of plasma corticosterone). In each of four stepwise regressions, no predictive variables entered into the equation. The slope of the line between the peak response and the stimulus rotated 15° to the right significantly predicted the total number of boxes entered in the novel environment, $F(1,9) = 8.903$, $R^2 = 0.441$, $p = .015$, $\beta = -0.705$. Pigeons with steeper slopes entered a greater number of novel boxes in the novel environment, see Fig. 5-6. Similarly, there was a significant relationship between the slope of the line between the peak response and the stimulus rotated 45° to the right and the total number of boxes entered, $F(1,9) = 9.089$, $R^2 = 0.447$, $p = .015$, $\beta = -0.709$. Pigeons with steeper slopes were more active in the novel environment, see Fig. 5-7. There was also a significant relationship between the slope of the line between the peak response and the stimulus rotated 15° to the right and the total latency to emerge from the start box, $F(1,9) = 24.896$, $R^2 = 0.705$, $p = .005$, $\beta = 0.857$, see Fig. 5-8 Pigeons with steeper slopes emerged from the start box more quickly. Total corticosterone was significantly related to the slope of the line between the peak response and the stimulus rotated 15° to the left, $F(1,8) = 18.220$, $R^2 = 0.657$, $p = .003$, $\beta = 0.834$. Pigeons with steeper slopes also had higher levels of circulating corticosterone, see Fig. 5-9.

Proximate control via circulating levels of plasma corticosterone

See Table 5-1 for the correlation coeffecients and *p* values associated with the circulating levels of corticosterone during the first and second session in the novel environment and the total exploration (novel boxes entered), activity (total boxes entered) and boldness (latency to leave start box). Notably, the corticosterone levels during the first session of the novel environment were marginally, although non-significantly, related to the exploration score, $r(11) = 0.594$, $p = 0.054$, suggesting that fast-exploring pigeons may have higher levels of circulating corticosterone, see Fig. 5-10. The corticosterone levels during the second session of the novel environment were significantly related to activity, $r(12) = 0.592$, $p = 0.042$. Pigeons that were more active had higher levels of corticosterone see Fig. 5-11.

Discussion

The results revealed that activity in the novel environment was consistent across both time, as measured in the two novel environment sessions, and context; pigeons that were more active in the novel environment also had a higher peck rate on the first day of testing in the cognitive task. Because exploration and activity scores were correlated, we tested for consistency in activity while controlling for exploratory behaviour and still found consistency in activity across both novel environment sessions. However, the exploration scores across both sessions of the novel environment were not consistent, perhaps suggesting that exploration is either; (1) not consistent in pigeons over a short time period, or (2) that the novel environment was not novel after the first session, and pigeons with different behaviour profiles attenuated (or habituated) to the novel environment at different rates. This latter explanation is likely true considering the variation in exploration and boldness scores as evidenced after the first session of the novel environment. That is to say, if one individual entered the novel environment and explored extensively during the first session, while a second individual did not, then the novelty during the second session of the novel environment room varied by individual.

The results reveal that how pigeons behave in a novel environment is related to their performance in a cognitive task. However, the direction of the relationship is opposite that of predictions derived from several empirical studies using songbirds as a model species (e.g., Guillette et al. 2009, 2011; Exnerová et al. 2010; Titulaer et al. 2012) and review papers (e.g., Cockrem 2007; Coppens et al. 2010). We predicted that slow-exploring pigeons would be more expert at discriminating among testing stimuli that were similar to trained stimuli. However, the results show that more active, exploratory pigeons that emerged from the start box more quickly discriminated among test stimuli to a greater degree than slow-exploring, less-active pigeons that took longer to emerge from the start box.

Alternative to our predictions, above, Cockrem's (2007) proposed characteristics of proactive and reactive avian personalities can also be interpreted in a manner that could account for the current results; that fast-exploring pigeons performed better on the line orientation generalization task. For instance, proactive birds do not alter their behaviour in reaction to environmental stimuli, rather they form routine and stick to it (e.g., Verbeek et al. 2004). If a proactive, fast-exploring pigeons learned the rule “peck to the S+ and only the S+” they could perform with a high discrimination ratio in the training phase. If these pigeons perseverated with the same response strategy during the test phase, “only respond to the S+” then they would have steep generalization gradients indicating behaviourally, that they are expert discriminators, even if they were not attending to all environmental stimuli (i.e., the lack or reinforcement or the presence of novel stimuli or the trained S-). Said another way, a fast-exploring pigeon need not have been sensitive or aware of anything in the environment with the exception of the S+ to achieve perfect discrimination. While this interpretation of Cockrem’s proposed characteristics of proactive and reactive birds seems plausible, it does not account for the complete pattern of results we obtained. For instance, if the fast-exploring, active pigeons were only responding according to the rule “only respond to the S+” then we would expect that the slope of lines between the S+ and the stimuli rotated in both directions (towards and away from the S-) to be predictive of behaviour. However, in regression equations that significantly predicted exploration, activity and boldness scores, only the slope of lines between the stimulus with peak responding and stimuli rotated towards the S- were predictive. Steeper slopes indicated more control (behavioural inhibition) by the S-, and fast-exploring, active pigeons had steep slopes on the side towards the S-. This indicates that fast-exploring, more-active pigeons were not likely relying on the strategy of “only respond to the S+”. This idea, that the fast-exploring, bold, active pigeons were more sensitive to the S- could be tested by training the pigeons with the same S+ (vertical line, 90°), and then training with two S-s, one at 135° as in the current experiment, and the other at 45°, the mirror image of 135°. With these methodological changes the prediction would be that the slope of the lines to both sides of the S+ would be steeper for fast-exploring, bold, active pigeons.

Another possible explanation for the discrepancy between the predicted and actual direction of the relationship between performance on a cognitive test and personality could be due to the training in the current cognitive test. Namely, the lack of an aversive stimulus. For instance, in the experiments with chickadees (Guillette et al. 2009, 2011) responses to the S- received a 30 second period with the house light turned off, an aversive event for a chickadee. In the current study, responses to the S- could have been viewed as neutral by the pigeons, rather than aversive.

Cockrem's (2007) characterization of proactive and reactive avian personalities was not only based on data from free living and bi-directionally selected lines of great tits (lines selected for fast or slow exploration scores) but also on data from domesticates species such as Japanese quail (e.g., Satterlee & Johnson 1988) and domestic Brown Hyline and Leghorn hens (e.g., Fraisse & Cockrem 2006). Due to the diversity of avian species used in constructing Cockrem's theory, we assumed our study species, the domestic pigeon, would behave in a similar manner. Therefore, we predicted that fast-exploring pigeons would have lower corticosterone response. However, our data suggest the opposite; higher levels of corticosterone are found in more-exploratory, active pigeons. Also opposite of our predictions, our data also suggest that higher levels of corticosterone are associated with individuals that are more sensitive to environmental stimuli (i.e., are better discriminators).

There is also evidence from zebra finches (*Taenopygia guttata*), a domesticated songbird species, that are in line with the current results (Martins, Roberts, Giblin, Huxham & Evans 2007). These zebra finches were from lines that had been artificially selected for high, average (control lines, no manipulation), and low plasma corticosterone responses to acute stress. Martins et al. (2007) found that increased corticosterone scores were associated with high scores for exploration. However, these results should be interpreted with caution because this effect was only seen in the line of zebra finches that was selected for low corticosterone response to acute stress.

It is possible that we did not see the relationship we predicted between corticosterone and exploratory behaviour because exposure to the novel environment was not an event that induced an acute response to stress in the pigeons. We collected blood samples after the pigeons had been in the novel environment for 40 minutes (10 minute habituation in the start box and 30 minutes with free access to the novel environment room). Pigeon were not forced to explore the room, therefore pigeons may have been self-moderating their stress responses because they were not required to perform any behaviour. This would have resulted in the corticosterone scores we measured to have represented baseline corticosterone scores. A similar case has been reported in a study that compared the behavioural and corticosterone responses of free-living great tits with that of great tits held in an aviary to presentations of a mounted predator (Cockrem & Silverin 2002). The free-living great tits responded to the mounted predator with alarm calls and decreased number of visits to a nearby feeder, while the great tits held in an aviary flew around more and spent less time feeding in the presence of the mounted predator. Only the latter group had an increase in the amount of corticosterone, suggesting that the ability to regulate ones' behaviour (i.e., move away from the mounted predator in wild but not in the aviary) alters the perception of threat, and thus the stress response. If the pigeons in our novel environment study were behaving in a way to mitigate the perceived stress, by moving around the environment as they wanted, then the samples collected in the current study may in fact represent baseline samples.

Although this possibility requires confirmation via a stress-induced corticosterone series, our current results are in line with several studies conducted on both wild and domestic avian species that found baseline corticosterone non-repeatable, but stress-induced corticosterone to be repeatable (e.g., American redstarts, *Setophaga ruticilla*, Angelier, Holberton & Marra 2009; zebra finches, Wada, Salvante, Stables, Wagner, Williams & Breuner 2008; house sparrows, *Passer domesticus*, Ouyang, Sharp, Dawson, Quetting & Hau 2011; Adelie penguins, *Pygoscelis adeliae*, Cockrem, Barrett, Candy & Potter 2009; and Brown Hyline hens, Littin & Cockrem 2001). However, results from one recent study found acute-stress corticosterone levels non-repeatable in wild great tits (Ouyanf, Hau & Bonier 2011). This same study found baseline corticosterone only to be repeatable during the breeding season, but not at other times during the yearly cycle in both male and female great tits and females tree swallows (*Tachycineta bicolour*), leading the authors to suggest that acute-stress corticosterone responses are highly plastic (Ouyang et al. 2011). We are currently running a stress series on each of the pigeons in the current study to determine if the acute stress response varies among individuals, is repeatable, and is related to personality and cognition scores.

In conclusion, we designed a novel environment test that can be used to examine exploratory behavior, activity, and boldness in a pigeon model. We also found that, contrary to our initial predication, fast-exploring pigeons were more sensitive to changes in environmental stimuli. Although further tests with either aversive stimuli, or the use of multiple unreinforced stimuli are needed to confirm current results. Last, we advocate for the use of pigeons as a model species to explore individual differences in cognition.

Table 5-1. The Pearson correlation and the associated *p* values between the corticosterone levels after the first and second session of the novel environment and the exploration (number of novel boxes entered), activity (total boxes entered) and boldness (latency to leave the start box) score from the novel environment

Corticosterone		Exploration	Activity	Boldness
1st NE session	Pearson correlation	0.594	0.355	-0.419
	p	0.054	0.284	0.199
2nd NE session	Pearson correlation	0.349	0.592	-0.398
	p	0.266	0.042*	0.200

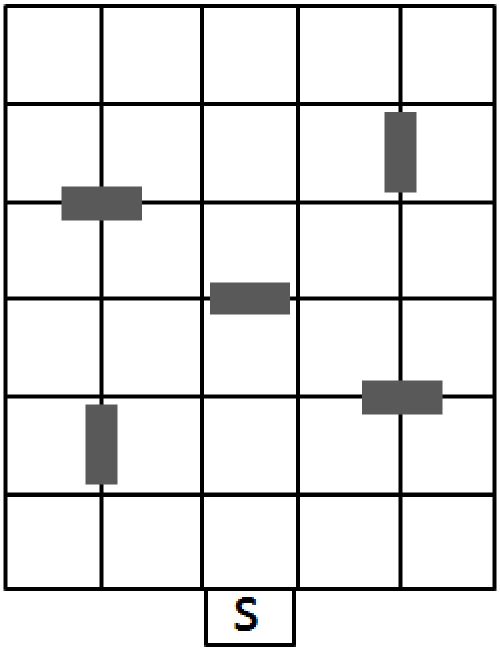

Figure 5-1.

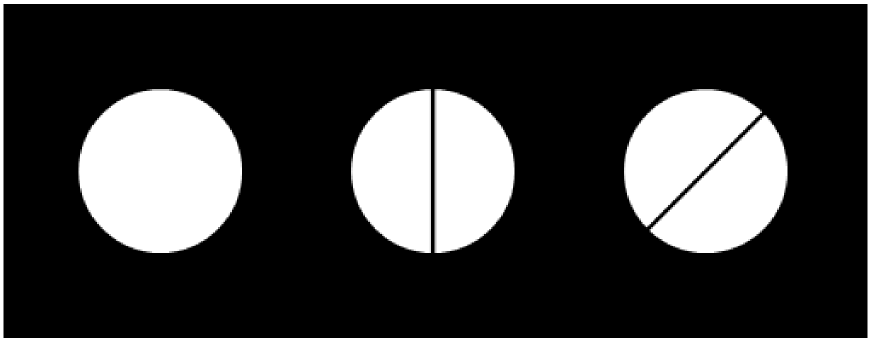

Figure 5-2.

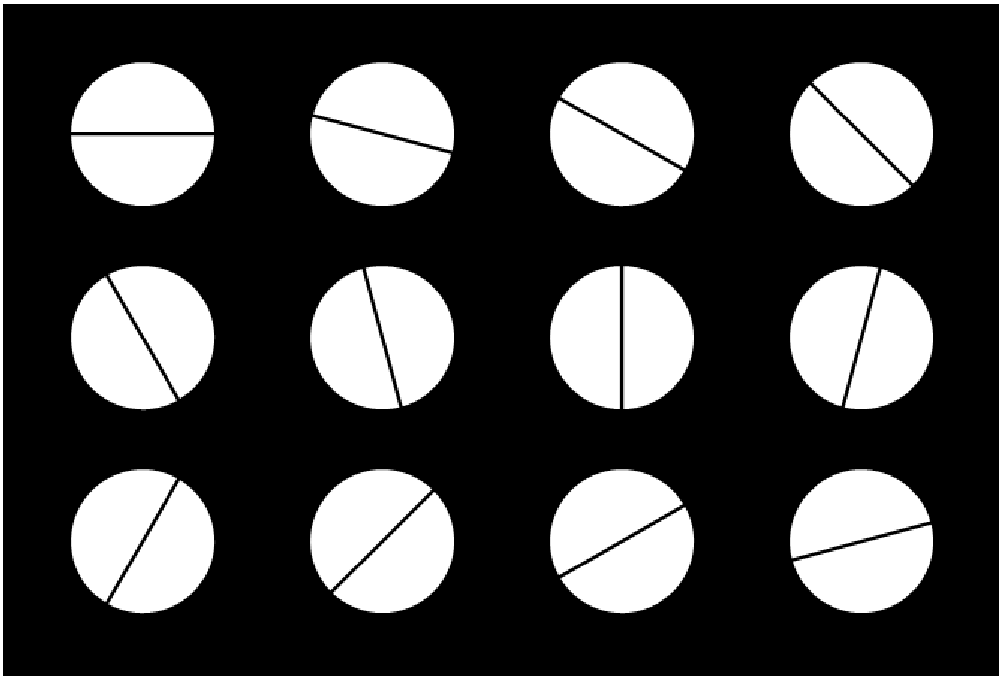

Figure 5-3.

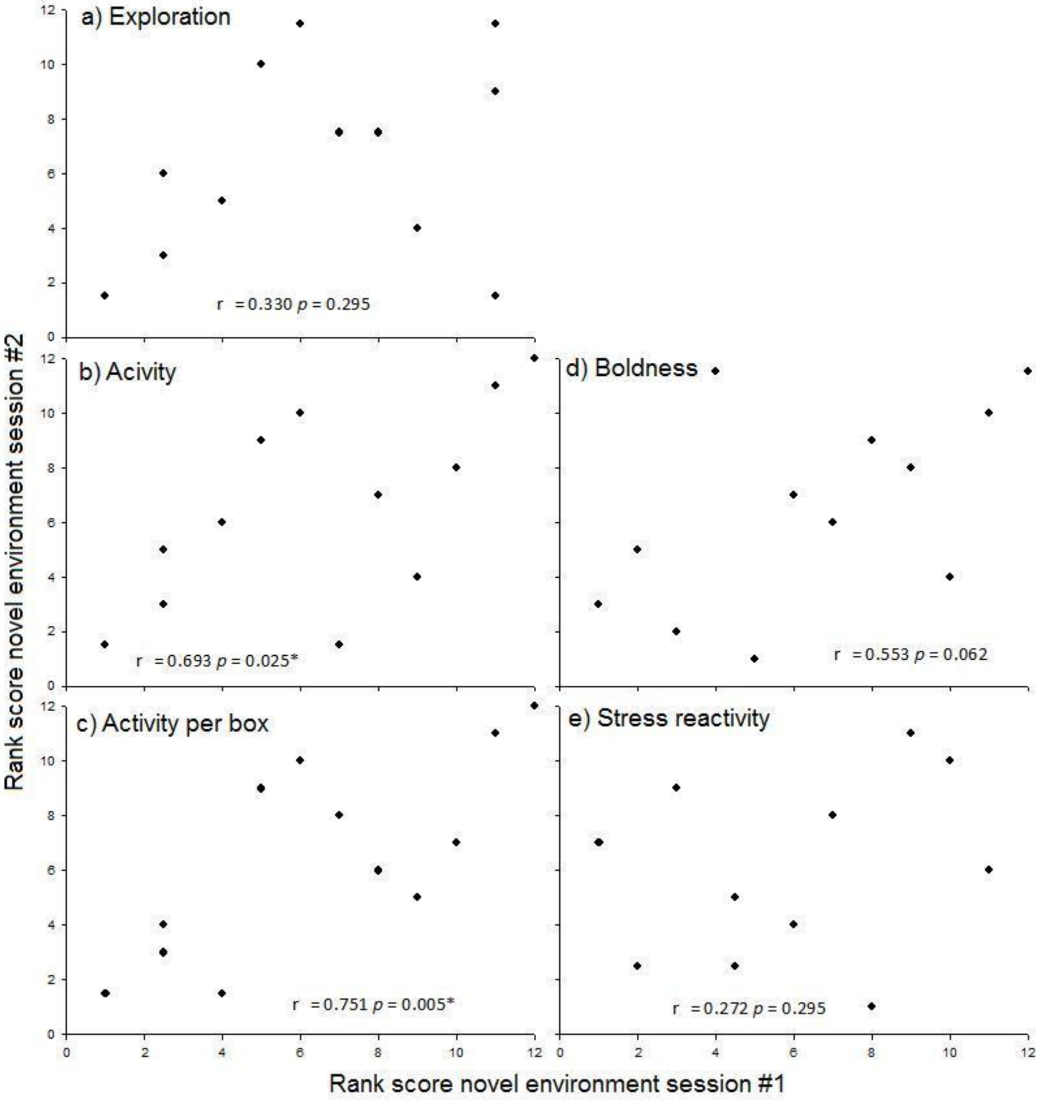
a) Exploration
r = 0.330 p = 0.295
b) Acivity
r = 0.693 p = 0.025*
c) Activity per box
r = 0.751 p = 0.005*
d) Boldness
r = 0.553 p = 0.062
e) Stress reactivity
r = 0.272 p = 0.295
Rank score novel environment session #2
Rank score novel environment session #1
0
2
4
6
8
10
12

Figure 5-4.

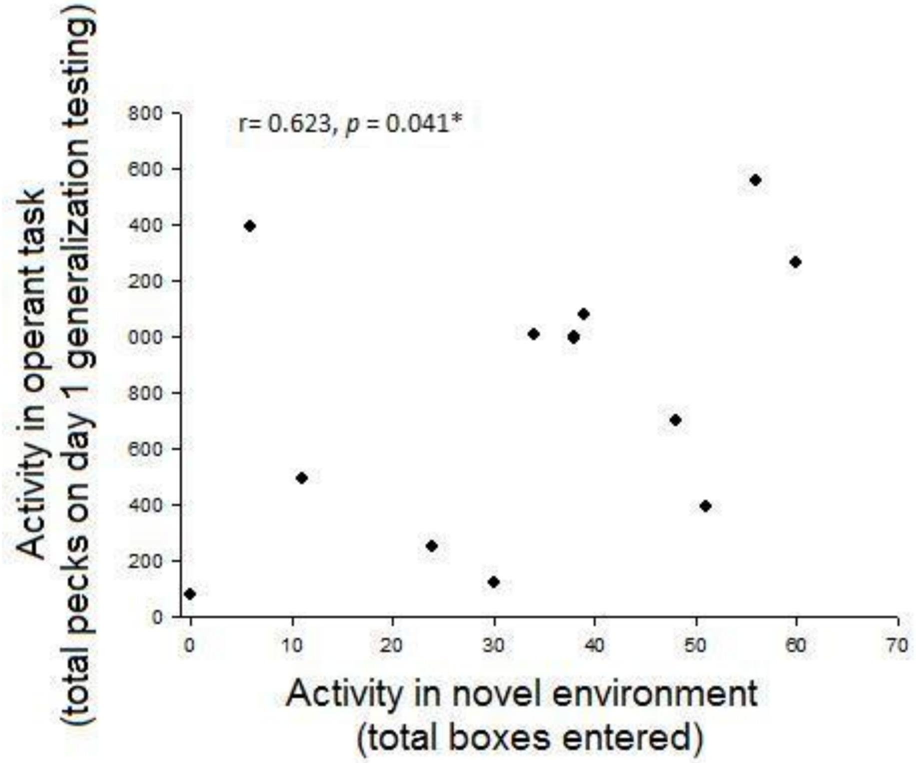
r= 0.623, p = 0.041*
Activity in operant task
(total pecks on day 1 generalization testing)
800
600
400
200
000
800
600
400
200
0
0
10
20
30
40
50
60
70
Activity in novel environment
(total boxes entered)

Fig. 5-5.

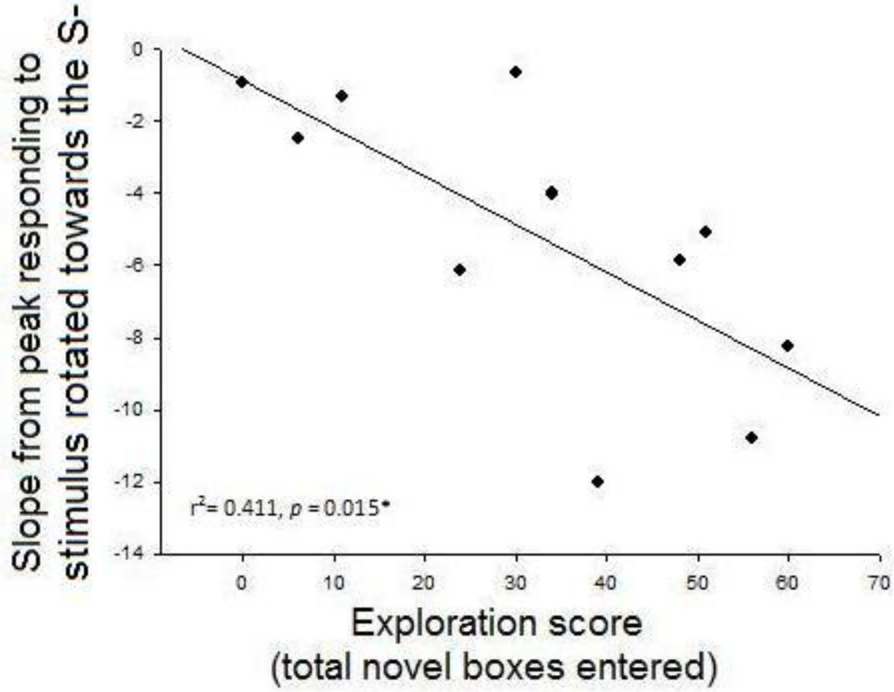
Slope from peak responding to stimulus rotated towards the S-
0
-2
-4
-6
-8
-10
-12
-14
0
10
20
30
40
50
60
70
Exploration score (total novel boxes entered)
r² = 0.411, p = 0.015*

Figure 5-6.

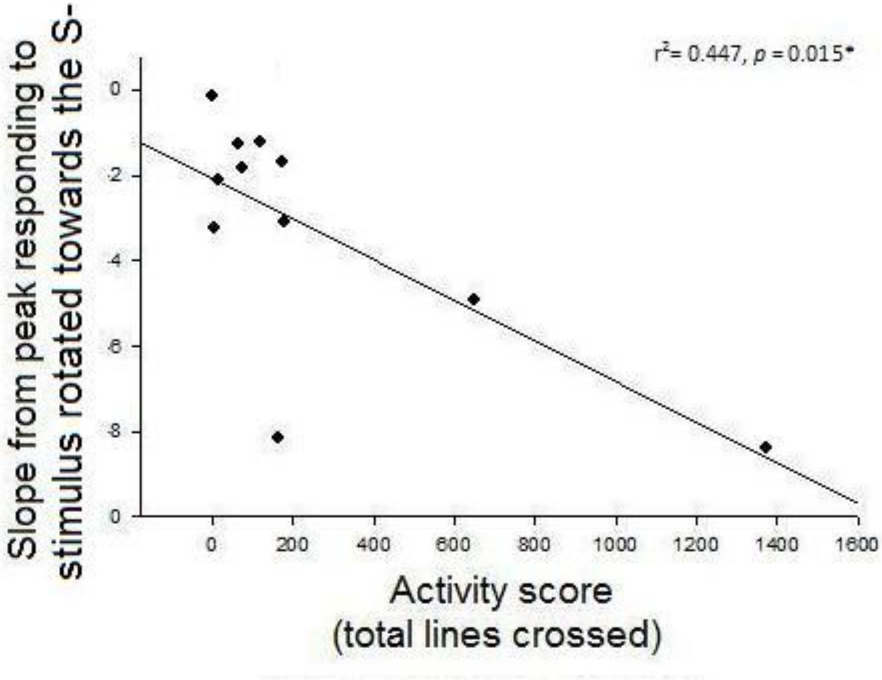
r^2= 0.447, *p* = 0.015*
Slope from peak responding to stimulus rotated towards the S-
0
-2
-4
-6
-8
0
0
200
400
600
800
1000
1200
1400
1600
Activity score
(total lines crossed)

Figure 5-7.

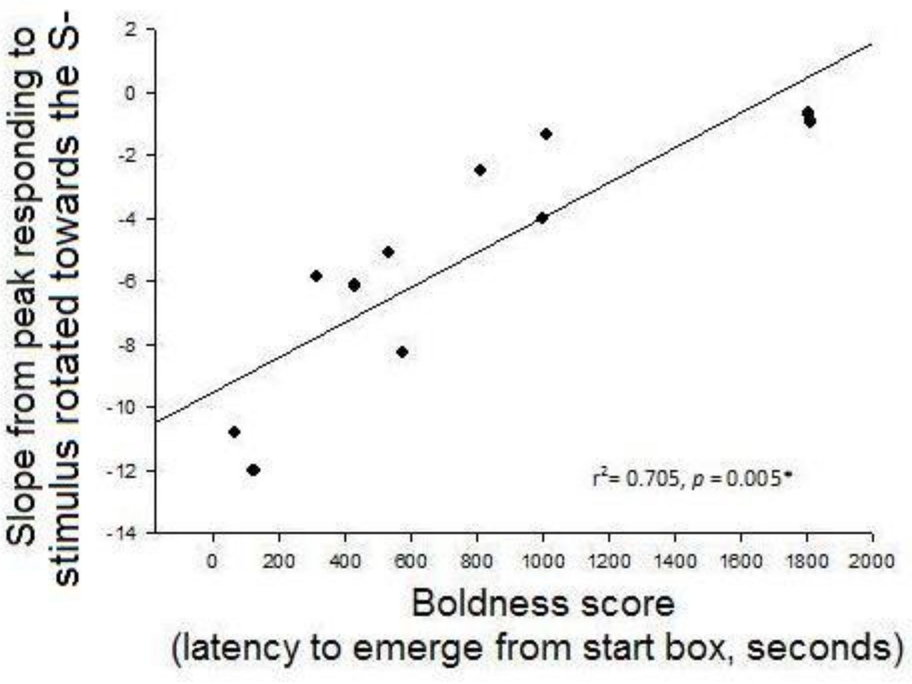
Slope from peak responding to stimulus rotated towards the S-
2
0
-2
-4
-6
-8
-10
-12
-14
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Boldness score
(latency to emerge from start box, seconds)
r²= 0.705, p = 0.005*

Figure 5-8.

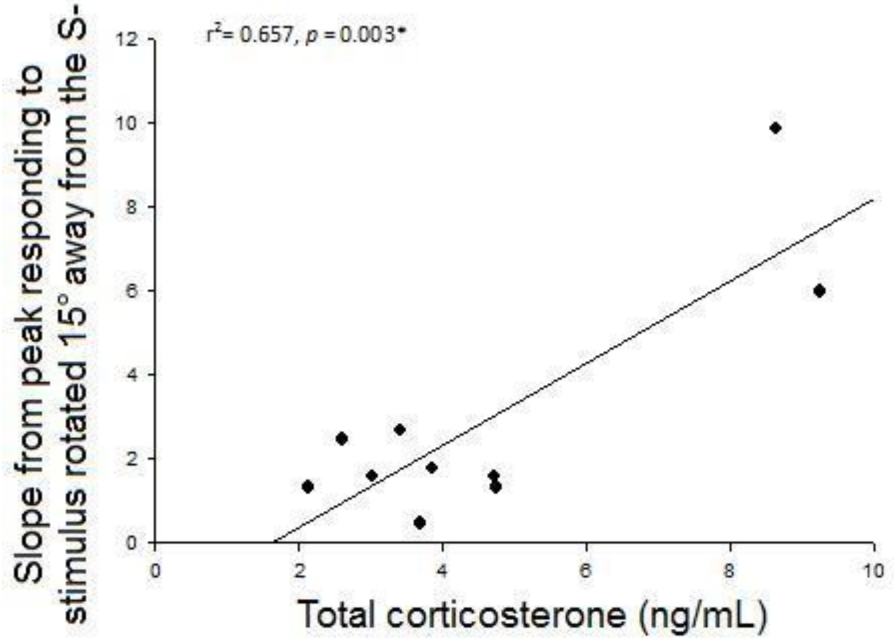
$r^2 = 0.657$, $p = 0.003$*
Slope from peak responding to stimulus rotated 15° away from the S-
Total corticosterone (ng/mL)
0
2
4
6
8
10
12
0
2
4
6
8
10

Figure 5-9.

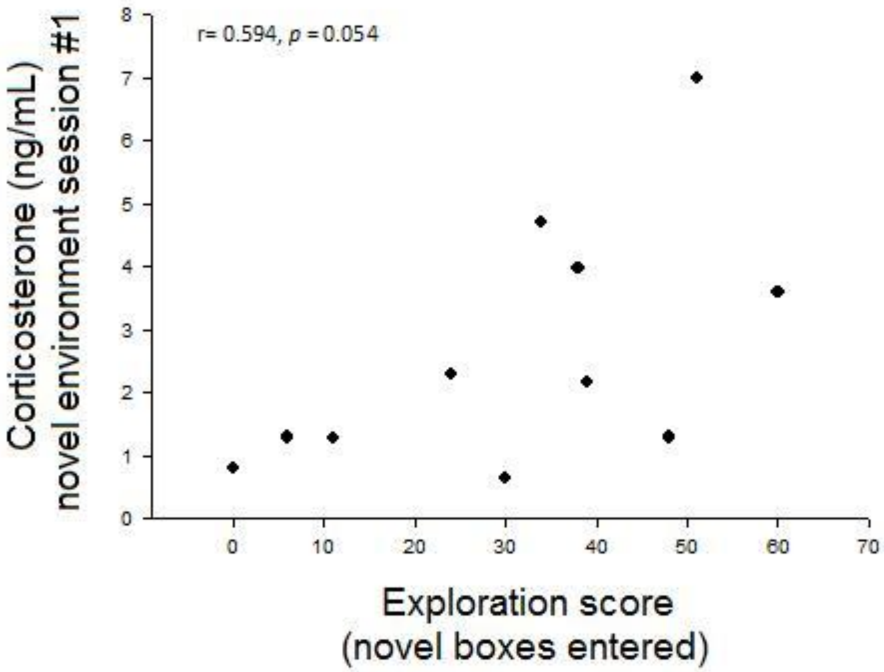
r= 0.594, p = 0.054
Corticosterone (ng/mL) novel environment session #1
0
1
2
3
4
5
6
7
8
0
10
20
30
40
50
60
70
Exploration score (novel boxes entered)

Fig. 5-10.

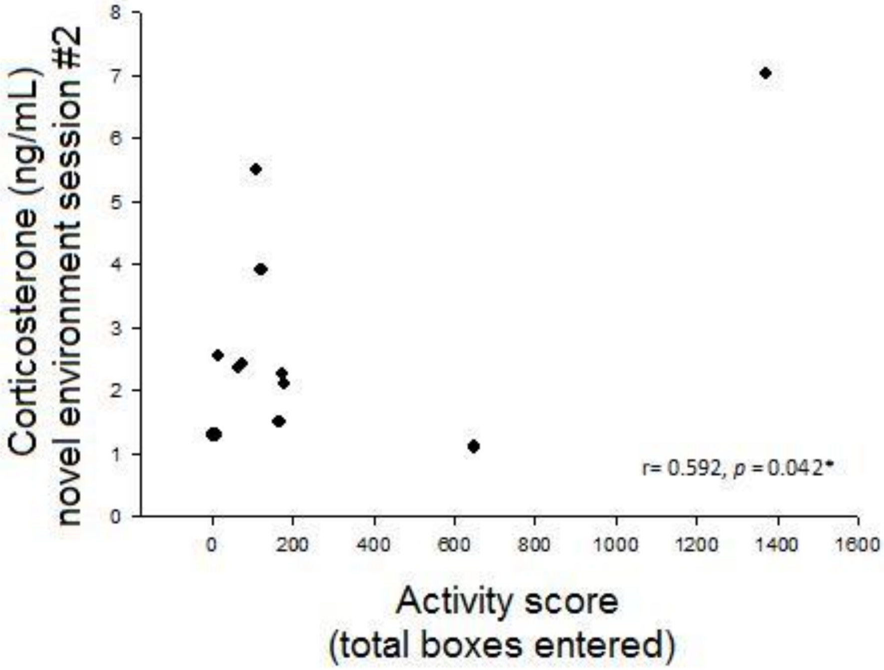
Corticosterone (ng/mL)
novel environment session #2
0
1
2
3
4
5
6
7
8
0
200
400
600
800
1000
1200
1400
1600
Activity score
(total boxes entered)
r= 0.592, p = 0.042*

Fig. 5-11.

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Chapter 6 General discussion

Summary of data chapters

This thesis integrates the field of animal personality with that of animal cognition by examining how individual differences in exploration are related to individual difference in learning. First, a well-known operant discrimination paradigm, used to examine acoustic perception in songbirds (e.g., Sturdy & Weisman 2006), was used to study individual differences in learning speed. Second, I adapted the novel environment test, previously used to assess personality traits in great-tits (e.g., Verbeek, Drent &Wiepkema 1994; Drent, van Oers & van Noordwijk, 2003) to test chickadees. Third, I used a classic reversal learning paradigm to test the hypothesis that slow-exploring birds are more sensitive to changes in the environment (e.g., Cockrem 2007; Verbeek et al. 1994). Fourth, I tested whether both learned (i.e., songs) and unlearned (i.e., calls) vocalization produced in two contexts (stress and control) were related to exploration behaviour. Last, in a pigeon model I utilized a classic experimental psychology paradigm, a visual intradimensional discrimination test (e.g., Hanson 1969), to test whether exploration behaviour was related to discrimination ability.

Establishing a learning/personality relationship

The experiments in Chapters 2 and 3 each followed the same basic design. Black-capped chickadees were first run in the novel environment, and then completed an acoustic operant discrimination task. The former task had not been previously used in our lab, or to assess exploratory behaviour in chickadees, rather, we adapted this test from a novel environment test that had previously been used extensively to test exploratory behaviour in great tits, a close European relative of chickadees (e.g., Verbeek et al. 1994; Verbeek, Boon & Drent 1996; Verbeek, de Goede, Drent & Wiepkema 1999; Drent et al. 2003). Our exploratory task differed in several ways from the paradigm used in great tits. First, we allowed the chickadees visual access to the room for one hour before allowing them to enter the novel environment room. We did this because extensive pilot testing of our novel environment task revealed that chickadees almost never entered the novel environment room within fifteen minutes if they were not allowed to first see the room. Furthermore, our chickadees were not food deprived prior to the novel environment test, as is sometimes done with great tits (e.g., Verbeek et al. 1994). We chose not to food deprive our birds because birds with different metabolic rates may be in different states after a standard food deprivation, and this could affect motivation to explore. In our novel environment test we did not turn out the lights in the rooms adjacent to the novel environment (i.e., where the birds were housed in their home cages) in an effort to facilitate movement into the novel environment room because we believed that altering the environment may differential affect chickadees of different personality types and thus interact with the exploration task. This allowed birds to self-regulate their behaviour, for instance, shy, non-exploratory chickadees may remain in their home cages and not explore the novel environment if they are not forced to exit their home cage. In personality studies conducted with great tits, the exploratory score is often a compilation of the scores for the novel environment and for two novel object tests. These two novel object tests consisted of placing a novel object (usually a pen light battery and a pink panther key chain) in the home cage and scoring how long it takes/whether or not the bird sits on the perch or comes in contact with the novel object. We chose not to use this test in constructing the exploratory score because the correlations between these tests (novel environment and novel object) have not been tested in black-capped chickadees. In fact, in mountain chickadees (*Poecile gambeli*), the sister species of black-capped chickadees, there is no relationship between novel object and novel environment scores (Fox, LaDage, Roth & Pravosudov 2009), similar results have been reported in the more distantly related songbird, domestic zebra finches (*Taeniopygia guttata*; Martins, Roberts, Giblin & Evans 2007). Taken together, these findings (Fox et al. 2009; Martins et al. 2007) suggest that the relationship between novel environment and novel object may be species-specific, even among songbirds.

After completing the novel environment task, chickadees were run in the acoustic operant discrimination task. This basic paradigm had been used previously in our laboratory for perceptual testing in chickadees (e.g., Charrier, Lee, Bloomfield & Sturdy 2005; Bloomfield, Sturdy, Phillmore & Weisman 2003; Guillette, Farrell, Hoeschele, Nickerson, Dawson & Sturdy 2010; Guillette, Farrell, Hoeschele & Sturdy 2010). We believe that our learning task was unique in controlling for the effects of neophobia, which may have driven many of the correlation between learning and personality in previous research (e.g., Sneddon 2002; Dugatkin & Alferi 2003; Coleman, Tully & McMillan 2005). We controlled for neophobia by pre-training the birds to respond to all stimuli (or in the case of Chapter 3, a sub-set of all stimuli, see discussion below), before beginning discrimination training.

In Chapter 2, the chickadees originated from two distinct populations, the first population from the Edmonton, Alberta area, and the second population originated from Kananaskis, Alberta, approximately 300 km to the south. Individuals were captured in different years, and were therefore tested in the novel environment after being held in captivity for differential amounts of time. Although we did find a distribution of exploration score (on a continuum from failure to leave the home cage to visiting five trees within the allotted time) we cannot rule out the fact that the birds behaviour could have been affected by (1) different ecological selection pressure in the different years they spent in the wild and (2) difference in behaviour due to different amount of time in captivity, both of which can affect behaviour. Field studies in great tits have shown that different personality types fare better (have better survival) in years of poor versus rich abundance of food, and that these effects are sex specific (Dingenamanse et al. 2004). Similarly, comparative neuroanatomical studies with mountain chickadees have shown that wild-caught birds have a larger hippocampal volume relative to the telencephalon compared to birds that had been housed in the lab (LaDage et al. 2009).

For the experiment in Chapter 3, I controlled differential ecological effect of location and time in captivity by capturing chickadees from two populations approximately 36 km away from each other. The first location was the Edmonton, Alberta North Saskatchewan River Valley, and the second location was located on an acreage in a small town to the southwest of Edmonton. Both sites had similar ecologies: they were located next to water and food supplements (sunflower seeds) were provided in feeders. All birds used in the experiment in Chapter 3 were caught within a 38 day span and were held in captivity for similar amounts of time (variable according to capture date) before being tested in the novel environment.

Speed/accuracy tradeoffs and cognitive syndromes

Taken together, the results of Chapter 2 and 3 provide support for the Cockrem's (2007) proposed characteristic for proactive and reactive avian personalities. These results show that fast-exploring chickadees (Chapter 2) learn an acoustic operant discrimination in fewer trials compared to slow-exploring chickadees. In Chapter 3, we found the slow-exploring chickadees learned the reversal stage of an acoustic operant discrimination in fewer trials compared to fast-exploring chickadees. However, in Chapter 3 we did not replicate the findings of Chapter 2. That is, in Chapter 3, fast-exploring birds did not learn the initial acquisition in fewer trials compared to slow-exploring birds. In the discussion for Chapter 3 we suggest that subtle differences in methodologies (i.e., using different discrimination pairs in the experiment in Chapter 2, and only one discrimination pair in the experiment in Chapter 3) could account for these different results. In addition, recent results from a learning study in great tits corroborate our findings from Chapter 3. Titulaer, van Oers and Naguib (2012) tested great tits in a dimensional-shift learning task. Birds were trained on a series of tests in which either the relevant dimension (e.g., color or location) switched, or the dimension stayed the same but new exemplars were rewarded (i.e., new colors or new locations), or the rules were reversed (for color only). The order of presentation was counterbalanced but across all great tits tested, the reversal learning stage took the greatest number of trials to complete, suggesting that it was the most difficult stage, although the authors had hypothesized that the inter-dimensional shift would be the most difficult. Interestingly, a relationship between learning and exploration was only observed in this most-difficult stage, but not the other stages. They suggest that the relationship between learning and exploration is context dependent, and only exists when the learning task is of a sufficient level of difficulty. Perhaps the initial discrimination task used in Chapter 3 was not sufficiently difficult to evoke any relationship between learning and exploration.

Another small, but important difference between the methodologies used in the acoustic operant discrimination task in the experiments in Chapters 2 and 3 was that all stimuli were used in pre-training in the latter experiment, but only half of the stimuli were used in pre-training in the former experiment. Therefore, the relationship between learning and exploration may have been observed in the experiment in Chapter 2 because the novel stimuli used in the transfer phase may have differentially-affected birds with different personality types. We are currently collecting data in another acoustic discrimination task that will allow us to examine the discrepancies in results between the experiments in Chapters 2 and 3. In the new experiment, birds were pre-trained with all stimuli that they would encounter throughout the experiment, as in Chapter 3. During initial acquisition training, birds were trained to discriminate between the two categories using only a sub-set of the stimuli, just as in the experiments in both Chapters 2 and 3. However, the next phase of our new experiment diverges from both previous experiments (Chapters 2 and 3). In the new experiment, the remaining stimuli (the stimuli not used in initial acquisition) were added to the stimulus pool as probe stimuli. Probe stimuli are neither punished nor reinforced. Analyzing the birds' responses to the first few exposures to these probe stimuli will allow us to assess if birds of different personality types respond differentially to the probes. That is, if not hearing the probe stimuli during initial acquisition caused the probe stimuli to become 'novel' again, then we might expect slow-exploring birds to respond less to probe stimuli. Alternatively, because previous studies have shown that fast-exploring great tits perseverate in responding (Verbeek et al. 1994) or retain previously learned information longer (Groothuis & Carere 2005) then we expect fast-exploring birds to have higher response rates, compared to slow-explorers, to the probe stimuli.

The results of Chapters 2 and 3 not only support Cockrem's (2007) characterization of proactive and reactive avian personalities, they also were cited as evidence for the theory of cognitive syndromes, specifically the notion that there is a cognitive speed-accuracy trade-off that is related to fast-slow behavioural types (Sih & del Giudice, 2012). This hypothesis is derived from data that show fast-exploring, bold, aggressive, active, proactive individuals are associated with speed, as opposed to accuracy in cognitive tasks and thus suggests that "factors (e.g., aspects of morphology, physiology, life history or condition) that lead animals to adopt a faster, more risk prone lifestyle might tend to produce both faster BTs [behavioural types; Biro & Stamps 2008; Reale, Garant, Humphries, Bergeron, Careau, & Montiglio 2010; Luttbeg & Sih 2010] and cognitive styles that emphasize speed over accuracy."

The idea that was proposed by Sin and Del Giudice (2012), and also mentioned in Carere and Locurto (2011), that is most intriguing to me is the idea that different types of cognition are likely differentially affected by (or affect, or interact with) different personality types. For instance, Carere and Locurto (2011) suggest that personality types might not interact with some forms of physical cognition, such as spatial navigation, but social cognition, such as cooperation and imitation, may be affected. While Sih and Del Guidice (2012) take the view that cognitive styles likely carryover across different aspects of cognition, that is, animal that exhibits a "fast" lifestyle will do so in all aspects of cognition. To take Carere and Locurto's example of navigation style and apply Sih and Del Giudice's framework, slow-exploring animals would be expected to have more information-rich, complex, integrated maps of their environments whereas fast-explorers may integrate little environmental information into their spatial maps. These ideas, of course, need to be empirically addressed.

In the new personality experiment we are currently conducting (mentioned above), designed to disentangle the results presented in Chapters 2 and 3, we are also running these same individuals through other cognitive tasks so we can do as Sih and Del Giudice (2012) and Carere and Locurto (2007) suggest: test multiple types of cognition. In addition to the novel environment test and the acoustic operant discrimination task used in Chapters 2 and 3, we are currently running the birds in a color association task that includes a reversal test and an intradimensional transfer (leaning the task with new colors) similar to the inter-dimensional shift tasked used by Titulaer et al. (2012) with great tits (discussed above). We are also running these same individuals through a motor-inhibitory task. In this task, individuals were first trained to retrieve food from an opaque cylinder. Once birds reliably perform this behaviour, the opaque cylinder is switched for a transparent cylinder. Although they have been trained to move the opening in the side of the cylinder to retrieve the food, the birds initially cannot inhibit pecking at the food through the transparent cylinder (e.g., Boogert, Anderson, Peters, Searcy & Nowicki 2011). In this task we are measuring how long it takes the birds to inhibit their pecking response and retrieve the food from the transparent cylinder. By testing the same individuals on this series of tests, we will gain a more comprehensive picture of whether or not there is carryover of cognitive styles (*sensu* Sih & Del Giudice, 2012) across the different cognitive domains each test measures.

Vocal behaviour and animal personality

The main goal of Chapter 4 was to not only test whether there was a relationship between vocal output and exploration, but also to further examine black-capped chickadees as a model species for studying animal personality. Chickadees are one of a small number of groups of animals that learn their vocalizations. Therefore, by exploring if vocal output is related to exploratory behaviour in chickadees, we are perhaps (indirectly) assessing another type of learning, in relation to personality. We found that vocal output was consistent within similar contexts over time, but not consistent across contexts. We found that certain call types were related to exploratory behaviour, but only in the stressful context. Interestingly, we did not find song production in either context to be related to exploratory behaviour as we had hypothesized. These results suggest that song production and exploratory behaviour do not co-vary in black-capped chickadees, as has been shown in great tits (e.g., Naguib, Kazek, Schaper, van Oers & Visser 2010; Amy, Sprau, de Goede & Naguib 2010). However, I think a more plausible explanation for the lack of relationship between songs in the stressful context and exploratory behaviour is because the bird's time was spent giving *alarm* calls and *chick-a-dee* calls at the exclusion of other vocalizations. I suggest that in other contexts, (i.e., intruder male song playback on focal male's territory), we might find that song production and exploratory behaviour co-vary in a positive direction. Other interesting studies that more directly examine vocal learning in relation to exploratory behaviour should be undertaken. For example, one possible question is: do males with different personalities learn their songs differently? One might predict that if slow-exploring males are more sensitive to not only the environmental, but also social stimuli than they might learn from different males tutors, or learn to copy certain song motifs over others, or copy more precisely. These theories would have to be tested in a species that has a more complex song than chickadees.

Measuring accuracy not speed with pigeons

The experiment in Chapter 5 followed the same design as the experiments in Chapters 2 and 3, however I used a different model species, domestic pigeons, and the learning test did not examine learning speed, but rather expertise of discrimination (i.e., accuracy, *sensu* Sih & Del Giudice, 2012). According to the speed/accuracy trade-off that likely co-vary with fast/slow behavioural types (Sih & Del Giudice, 2012) we predicted that slow-exploring pigeons would be better discriminators, but we found the reverse to be true. Fast-exploring pigeons were more sensitive to stimuli that were more similar to the S-. Moreover, there were some interesting findings linking high levels plasma corticosterone levels to high exploratory behaviour and high activity score, opposite to the predicted direction. However, one study in radio-tagged white-crowned sparrows (*Zonotrichia leucophrys gambelii*) found that birds that were implanted with corticosterone had increased activity levels compared to control birds that were not implanted with corticosterone (Breuner & Hahn 2003). Nonetheless, the coricosterone levels in the pigeons in the experiment in Chapter 5 were not repeatable across the two sessions of the novel environment. We are currently running an acute stress series on each of these pigeons to obtain a better understanding of the relationship between performance on a cognitive task, exploratory behaviour and hormonal responses to stress.

Sih and Del Giudice (2012) outline predictions for the relationship between different aspects of cognition and behavioural types. For instance, animals that have high speed/low accuracy likely have spatial maps with ‘shallow’ representations of environmental features. We advocate that pigeons would be a perfect model species with which to test this idea. Pigeons could also easily be tested on a variety of cognitive tasks, for example, reversal leaning or avoidance tasks, adding an important model species for deciphering mechanisms underlying differences in animal personality.

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