The Role of Learned Foraging Behaviour in Mate Interactions and Mate Choice Decisions in Birds

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To my parents Kees and Michalien
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Preface

This is a manuscript-based thesis, consisting of a collection of papers of which I am the primary author. Chapters 1 and 4 have been published; Chapter 6 is in press; Chapter 3 is submitted; and Chapter 5 is being prepared for submission. All chapters have been formatted in the style of the scientific journal Behavioral Ecology. The manuscripts and associated journals are as follows:

**Chapter 1**

**Chapter 2**
Boogert NJ. Do zebra finch mates forage together in their natural habitat in Australia? Not intended for publication.

**Chapter 3**

**Chapter 4**

**Chapter 5**

**Chapter 6**
Contributions of Authors

I am the primary author of all of the studies included in this thesis. I formulated the hypotheses, designed the experiments, collected all the data (sometimes in collaboration with others; see below), analyzed the data and wrote the manuscripts. Louis Lefebvre supervised the conceptual framework, experimental design, interpretation of results and writing of all manuscripts in this thesis, except for Chapter 5, which was supervised by William Searcy (University of Miami) and Stephen Nowicki (Duke University).

For Chapter 1, Karine Monceau performed the molecular sexing of tested birds and provided comments on the manuscript.

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For Chapter 6, Tim Fawcett wrote the sections on human and state-dependent mate choice. He also provided extensive comments that greatly improved the manuscript. Louis Lefebvre wrote the section on trade-offs and variation in cognition across species.
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Thesis Abstract

Successful foraging is essential for survival and reproductive success. Although many components of foraging are hard-wired, learning can affect the efficiency, techniques and food types chosen during searching, handling and feeding. It should therefore pay to choose and/or forage with a mate who has learned to be an efficient forager and can quickly exploit novel food sources. However, few studies have investigated whether learned foraging behaviour guides mate choice decisions, and whether mates actually profit from each other’s foraging success. I addressed these questions using a combination of field and captive experiments in birds. I presented a novel foraging apparatus to territorial pairs of Zenaida doves (Zenaida aurita) in Barbados, and found that the same individual of a pair was always first to solve learning tests. Mates benefited by scrounging from each other’s food discoveries and learned to exploit the novel food source as a result. When I presented food dispensers to flocks of wild zebra finches (Taeniopygia guttata) in Australia, mates visited the dispensers together more often than with other flock members. I then investigated whether learned foraging behaviour guides mate choice in zebra finches in captivity. Domesticated female zebra finches did not prefer the more efficient forager of two candidate mates, nor did they preferentially associate with males performing the same foraging technique as they had acquired as juveniles. When I released flocks of these birds into an aviary containing food patches that required different foraging techniques to exploit, they did not preferentially associate or form pair bonds with others exploiting the same patch. However, mates with different foraging techniques scrounged more from each other and thus benefitted from each other’s skills more than did mates with the same technique. Overall, I found no evidence that foraging behaviour guides mate choice directly. However, in two further studies, one on zebra finches and one on song sparrows (Melospiza melodia), I demonstrated a positive correlation between song complexity and learning performance in a foraging context. These findings suggest that song complexity might indicate a male’s learning abilities. Foraging behaviour is therefore a cognitive trait that may guide avian mate choice indirectly.
Résumé

S’approvisionner en nourriture est essentiel à la survie et au succès reproducteur. Même si plusieurs aspects des comportements d’approvisionnement sont innés, l’apprentissage influence souvent l’efficacité, les techniques et les choix alimentaires durant la recherche, la manipulation et l’ingestion des aliments. On peut donc s’attendre à ce qu’il soit avantageux de choisir et/ou de s’approvisionner avec un partenaire qui a appris à s’approvisionner efficacement et qui peut utiliser rapidement de nouvelles ressources. Cependant, peu d’études ont examiné si les comportements d’approvisionnement appris peuvent guider les décisions quant au choix de partenaire, et si les individus profitent du succès d’approvisionnement de leur partenaire. J’ai examiné ces questions en utilisant une combinaison d’expériences menées sur le terrain et en captivité. J’ai présenté une nouvelle tâche d’approvisionnement à des couples territoriaux de tourterelles à queue carrée (Zenaida aurita) à la Barbade, et découvert que le même membre d’un couple était toujours le premier à résoudre les tests d’apprentissage. Les partenaires chapardaient les aliments découverts et apprenaient ainsi à exploiter la nouvelle ressource alimentaire. Lorsque j’ai présenté des mangeoires à des volées de diamants mandarins (Taeniopygia guttata) sauvages en Australie, les partenaires ont visité les mangeoires ensemble plus souvent qu’avec d’autres membres du groupe. J’ai ensuite examiné si les comportements d’approvisionnement appris pouvaient guider le choix de partenaire chez le diamant mandarin en captivité. Les femelles diamants mandarin domestiquées n’ont pas préféré le plus efficace de deux partenaires potentiels, et n’ont pas choisi de s’associer à des mâles utilisant la même technique d’approvisionnement qu’elles avaient acquise comme juvéniles. Lorsque j’ai utilisé ces individus pour former des groupes dans des volières contenant des parcelles alimentaires qui devaient être exploitées avec différentes techniques, les individus n’ont pas préféré s’associer ou former des liens de couple avec d’autres individus utilisant le même type de parcelles. Cependant, les partenaires utilisant différentes techniques ont chapardé plus l’un de l’autre et ont ainsi davantage bénéficié d’aptitudes complémentaires que les partenaires utilisant tous deux la même technique. En résumé, le comportement d’approvisionnement ne semblait pas guider le choix de partenaire directement. Cependant, dans deux études conduites ultérieurement, une sur les
diamants mandarins et une sur les bruants chanteurs (*Melospiza melodia*), j’ai démontré une corrélation positive entre la complexité du chant et certains aspects de la performance d’approvisionnement. Ces découvertes suggèrent que la complexité du chant pourrait indiquer la capacité d’apprentissage des mâles. Les comportements d’approvisionnement sont donc des processus cognitifs qui peuvent guider le choix du partenaire indirectement chez les oiseaux.
**General Introduction**

Foraging theory and sexual selection are at the heart of behavioural ecology (Krebs and Davies 1997). However, these topics have rarely been integrated. Although successful foraging is essential for survival and reproductive success, as famously shown by Peter and Rosemary Grant’s work on Darwin’s finches (Grant and Grant 2008), very few studies have tested whether foraging behaviour guides mate choice directly. Instead, indirect traits favoured in mates, such as higher courtship feeding rate (Helfenstein et al. 2003) or brighter carotenoid-based plumage colouration (Hill et al. 2002), are assumed to be indicators of foraging ability in birds, even though there have been few studies testing the association between these traits and foraging success. Yet there is reason to think that foraging behaviour should influence mate choice, as supported by a recent study on red crossbills (*Loxia curvirostra*) in which females preferred the more efficient of two males extracting conifer seeds at different speeds (Snowberg and Benkman 2009). Is this result generalizable to other species? What aspects of foraging behaviour are important for mate choice? And if foraging techniques and efficiency are improved by learning, can successful foraging act as an indicator of cognitive skills, another trait that might prove useful in mate choice?

The aim of this thesis is to explore the role of foraging behaviour, in particular learned foraging, in mate interactions and mate choice decisions in birds. For foraging behaviour to be relevant for mating decisions, there should be 1) inter-individual differences in learning and foraging behaviour that 2) affect reproductive success, and 3) are heritable if they are to provide indirect fitness benefits. In the following sections I briefly review the literature that supports these requirements.

**Juvenile foraging behaviour and survival**

Juvenile birds provide a good example of the relationship between foraging skill and survival. In Wunderle’s (1991) comprehensive review of age-specific foraging proficiency in birds, he concluded that in all species examined up to then, juveniles were less efficient than adults in some aspect of foraging behaviour, such as selection of foraging sites, search patterns, recognition and selection of food, and/or capture and
handling techniques. Maturation has an effect on this temporal change, but learning has also been shown to be crucial.

There is interspecific variation in how long it takes juveniles to reach adult levels of foraging efficiency. In some species, such as white-winged choughs (*Corcorax melanorhamphos*), this can take up to four years (Heinsohn 1991), whereas the process is faster in other species: juvenile white-throated magpie-jays (*Calocitta formosa*), for example, reach adult levels of foraging proficiency within one year of fledging (Langen 1996). Langen (1996) argued that, apart from increases in magpie beak length within the first four months post-fledging, learning rather than physical development is the mechanism underlying foraging skill acquisition in juvenile magpies, and some skills, such as exploitation of wasp nests, take even longer to acquire.

Wunderle suggested that the lack of food-handling proficiency of young birds can have major implications for survival (Wunderle 1991). Indeed, death rates of birds in their first year of life are 70-90%, especially in small passerines, where high mortality can be attributed partially to nest predation, but also to starvation of recently independent juveniles due to lack of foraging skills (Sullivan 1989; Weather and Sullivan 1989). A similar conclusion was reached by Daunt et al. (2007) who found that juvenile European shags (*Phalacrocorax aristotelis*) compensated for their poor foraging skills by increasing the proportion of daylight hours they spent foraging. However, as winter days grew shorter, juveniles did not have sufficient hours of daylight available for foraging, and come mid-winter juvenile mortality was five times that of adults. There thus appears to be a high level of variance in the extent to which learning improves foraging, as well as high levels of differential mortality, which both lead to strong effects of learned foraging on fitness.

**Adult differences in foraging behaviour and effects on fitness**

Given that juvenile foraging efficiency is linked to survival, one might expect the same to be true for adults, with an added effect on the number and quality of offspring produced. Adult birds have been shown to differ in their feeding preferences and feeding efficiency in species such as great tits (*Parus major*; Partridge 1976), pigeons (*Columba livia*; Giraldeau and Lefebvre 1986), spice finches (*Longura punctulata*; Beauchamp et al.}

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1997), and starlings (Sturnus vulgaris; Boogert et al. 2008) in captivity. Although foraging behaviour is often assumed to have significant consequences for their longevity and lifetime reproductive success, few studies have directly tested the fitness effects of adults’ foraging behaviour.

Interestingly, one of the main model systems for studies of sexual selection and mate choice, the zebra finch (Taeniopygia guttata), has been used to study the fitness effects of foraging rates, but never in association with its possible relevance for mate choice decisions. For example, Lemon (1991) presented captive zebra finch populations with a standard amount of seed mixed with increasing proportions of husk, thus manipulating their net rate of energy gain. He found that birds with fewer husks in their diet, and thus higher rates of energy gain, lived longer and produced more offspring than birds that had to forage longer to obtain the same amount of food (Lemon 1991).

Wiersma and Verhulst (2005) manipulated intake rates according to Lemon (1991) and found that daily energy expenditure decreased with decreased foraging efficiency (i.e. increased proportions of husk). In addition, reduced intake rate hampered somatic repair in terms of the length of re-grown feathers, and delayed the onset of breeding (Wiersma and Verhulst 2005). A delayed onset of breeding was also found in zebra finches that had to perform increased hopping activity to get a food reward as compared to zebra finches that had to work less for their food (Deerenberg and Overkamp 1999).

Field studies have mostly looked at the fitness effects of foraging indirectly, by measuring variation in presumed correlates of foraging ability. For example, a study on Gould’s petrels (Pterodroma leucoptera) showed that the average body condition and provisioning rate of a breeding pair correlated positively with their chick’s growth rate and body condition (O’Dwyer et al. 2007). A study on the common guillemot (Uria aalge) found positive correlations between chick provisioning rate and breeding success (Lewis et al. 2006). The latter study also found a trend towards successful females making shorter foraging trips, which the authors suggested could imply they were more efficient foragers. A recent study on Adélie Penguins (Pygoscelis adeliae; Lescroël et al. 2010) is one of the first field studies to measure individual variation in foraging efficiency directly and relate it to breeding success in the field. In the study, the authors showed that more successful breeders were able to find sufficient food during shorter foraging trips.
than were poorer breeders, and were therefore more efficient foragers. The relationship between breeding quality and foraging efficiency was most apparent under harsh environmental conditions towards the end of the breeding season, when chicks’ needs were greater and food availability was lower, and in years when giant icebergs restricted access to foraging areas and forced the penguins to make longer foraging trips.

Adult diet choice has also been shown to have significant fitness effects in the wild. Western gulls (Larus occidentalis) that fed mostly on fish had longer breeding lifespans, higher reproductive success and recruited more offspring to the breeding population than birds that fed mostly on human refuse (Annett and Pierotti 1999). In addition, male offspring of fish-feeding parents also tended to feed mainly on fish, which the authors suggested was because sons learned to forage for fish from their parents. In pigeon guillemots (Cepphus columba), pairs that primarily fed their chicks fish with a high lipid content fledged more chicks (and their chicks also grew faster) than did generalist parents or parents who fed their chicks a lower quality diet (Golet et al. 2000).

The ability to flexibly adjust foraging behaviour when environmental conditions change can also increase individuals’ likelihood of survival. For example, young cactus finches (Geospiza conirostris) that acquired the foraging skills necessary to exploit unfamiliar food sources in a time of severe drought were more likely to survive than juveniles that stuck with typical wet-season foraging behaviour (Grant and Grant 1989). The application of existing foraging skills to novel food sources can also broaden the diet, as in the case of birds opening milk bottles, a behavioural innovation first observed in tits in 1921 in southern England and then seen to spread over the British Isles (Fisher and Hinde 1949) and the European continent (Hinde and Fisher 1951). Another example of foraging flexibility is provided by New Zealand keas (Nestor notabilis), who started to open the lids of rubbish bins with their bills to obtain anthropogenic food scraps (Gajdon et al. 2006). Comparative analyses using frequency counts of such foraging innovations in the wild (following Lefebvre et al. 1997) suggest that more innovative bird species are better able to cope with seasonal environments and can stay sedentary, whereas less flexible species are forced to become migratory (Sol et al. 2005a). In addition, species with more foraging innovations are more successful at establishing themselves after having been introduced by humans to novel environments (Sol et al. 2005b).
Heritability of foraging behaviour

For a trait to have a role in the evolution of species by providing indirect fitness benefits, it must be heritable. The few studies that have addressed this issue suggest that at least some aspects of foraging behaviour are inherited. The rate at which parents feed their offspring has received most attention. This measure of parental effort has a heritable component in Savannah sparrows (*Passerculus sandwichensis*; Freeman-Gallant and Rothstein 1999) and long-tailed tits (*Aegithalos caudatus*; MacColl and Hatchwell 2003), although it should be noted that these field studies did not adopt a cross-fostering design, so that genetic effects cannot be distinguished from, for example, parental effects and parent-offspring interactions. A recent study on four generations of house sparrows (*Passer domesticus*) was the first to adopt a cross-fostering design and showed that parental food delivery rate was heritable, especially in sons (Dor and Lotem 2010).

When foraging in groups, animals can search for food themselves (“producer” tactic) or they can search for opportunities to exploit the food discoveries of others (“scrounger” tactic). Mathot and Giraldeau (2010) found significant family differences in the use of producer versus scrounger tactics in zebra finches, in that individuals from some families tended to mostly scrounge in flocks composed of non-relatives, whereas other families could be characterized by using mainly the producer tactic.

Whether learning ability is heritable has not been addressed in field studies. However, several studies on captive animals suggest that learning abilities are significantly correlated between family members (Galsworthy et al. 2005; Karino et al. 2005), and affected by large-scale genetic modifications caused by inbreeding and domestication (Harker and Wishaw 2002; Stuermer and Wetzel 2006; Lewejohann et al. 2010; Smith and Litchfield 2010). Even though diverse learning paradigms are used by psychologists, the majority involve food rewards and could potentially be extended to tests of learned foraging in the field.
The role of foraging behaviour in mate interactions and mate choice decisions in birds

The previous sections suggest that learned foraging behaviour can be an important determinant of birds’ longevity and reproductive success, and that flexibility in foraging behaviour may allow birds to cope with changing environmental conditions. It should thus be profitable to choose and forage with a mate who is an efficient forager or who can quickly learn novel foraging techniques.

In the five experimental chapters of this thesis, I assess the relationship between foraging behaviour, mate interactions, mate choice and a sexually selected trait (bird song) in the field and in captivity. In Chapter 1, I develop a learning experiment on a well-studied, territorial bird species, the Zenaida dove (Zenaida aurita) of Barbados, to verify the feasibility of novel feeding tests in the field. I also investigate whether mates obtain benefits from each other’s foraging skills. Even though mates forage together in many territorial bird species (e.g. pileated woodpeckers Dryocopus pileatus: Kilham 1976; magpies Pica pica: Birkhead 1979; hazel grouse Bonasa bonasia: Swenson 1993), it is not clear whether they profit from each other’s skills in the field.

In Chapter 2, I move to a more challenging field site in the Australian outback and explore whether mates in a colonial species, the zebra finch, forage together in the wild. The zebra finch is the model system for studies of mate choice. Once mated, individuals in captivity have been shown to scrounge from each other outside a flock context (Beauchamp and Kacelnik 1991), to lead each other to novel food sources (Schuett and Dall 2009), and to cooperate more with each other to obtain food than they do in dyads with non-mates (St-Pierre et al. 2009). However, no one has verified that zebra finch mates stay in close proximity to each other in the natural context of foraging flocks in Australia.

As reviewed above, foraging efficiency correlates positively with survival and reproductive success in zebra finches in captivity. In Chapter 3, I present domesticated zebra finch females with candidate mates that differ in foraging technique and foraging efficiency, and test whether either aspect of foraging behaviour affects their mate preferences. I then release all test subjects in aviaries to explore the role of foraging habitat choice in pair bond formation and social foraging tactic use.
Since Chapter 3 suggests that foraging behaviour per se does not directly affect the mate preferences of zebra finch females, in Chapter 4 I test whether a male trait known to be under sexual selection, song complexity, correlates with learning efficiency in a foraging context. If this is the case, then females may indirectly favour good foragers by choosing males with more complex songs. In Chapter 5 I test whether the same association between song complexity and learning exists in a wild bird species for which song repertoire size has been shown to correlate with longevity and reproductive success, the song sparrow (Melospiza melodia). Finally, in Chapter 6 I review the literature on the role of cognitive traits, such as learned foraging behaviour and song complexity, in mate choice in non-human vertebrates. This chapter integrates the previous five chapters and points to new avenues to explore the link between foraging behaviour and mate choice.

References
Freeman-Gallant CR, Rothstein MD. 1999. Apparent heritability of parental care in
Gajdon GK, Fijn N, Huber L. 2006. Limited spread of innovation in a wild parrot, the kea
cognitive ability in a battery of cognitive tasks for laboratory mice. Behav Genet.
35: 675-692.
Giraldeau LA, Lefebvre L. 1986. Exchangeable producer and scrounger roles in a captive
flock of feral pigeons: a case for the skill pool effect. Anim Behav. 34: 797-803.
and reproductive success in pigeon guillemots. Auk. 117: 82-91.
Nat. 133: 377-393.
Grant PR, Grant BR. 2008. How and why species multiply: the radiation of Darwin's
Harker KT, Whishaw IQ. 2002. Place and matching-to-place spatial learning
affected by rat inbreeding (Dark-Agouti, Fischer 344) and albinism (Wistar,
Sprague-Dawley) but not domestication (wild rat vs. Long-Evans, Fischer-
Heinsohn RG. 1991. Slow learning of foraging skills and extended parental care in
Helfenstein F, Wagner RH, Danchin E, Rossi JM. 2003. Functions of courtship feeding in
black-legged kitiwakes: natural and sexual selection. Anim Behav. 65: 1027-
1033.
Hinde RA, Fisher J. 1951. Further observations on the opening of milk bottles by
Karino K, Utagawa T, Shinjo S. 2005. Heritability of the algal-foraging ability: an


Contributions to Knowledge

Chapter 1 describes the first test of reversal learning in the natural habitat of a species. Although reversal learning is commonly used in psychology and neuroscience to measure individuals’ behavioural flexibility, field measures of flexibility have centered on novel problem-solving tasks and frequency counts of innovative feeding in the wild. In this chapter, I show that reversal learning tests can be conducted in the field to quantify individuals’ behavioural flexibility. In Zenaida doves, repeated responses of the same individuals to the test were favoured by tameness, site fidelity and exclusive defense of territories. This study is also the first to describe the benefits that mates of a territorial species can obtain from each other’s foraging skills when encountering a novel food source, by scrounging from each other’s food exploitations and learning to exploit the novel food source as a result. Finally, this study shows that territorial defence does not hamper test subjects’ learning performance, but tameness does.

Chapter 2 is the first study to show that zebra finch mates visit feeders together in their natural habitat in Australia, where they always forage in flocks. This finding validates previous captive studies that used pairs as the units of study in a foraging context, and raises the question whether zebra finches may use foraging behaviour as a mate choice criterion. Chapter 3 is the first study to investigate whether foraging technique and/or efficiency guide domesticated zebra finch mate choice decisions in a newly designed two-level mate choice apparatus. I followed this with a more naturalistic assessment of pair bond formation in aviaries with different foraging habitats. This study is also the first to show that zebra finches can be trained to become foraging specialists, and maintain their foraging specialisations even when encountering specialists and food sources of the alternate technique. The study convincingly shows that neither foraging technique, nor efficiency or habitat choice, guides mate choice decisions or pair formation in captive zebra finches. However, pairs composed of birds with different techniques scrounged more from each other than did pairs in which both birds used the same foraging technique, suggesting that mates can profit from each other’s foraging skills in a colonial species, as was shown in Chapter 1 for a territorial bird species.
Since Chapter 3 showed that zebra finch foraging behaviour does not guide mate choice decisions directly, Chapter 4 explores whether it might do so indirectly through its association with song complexity. This is the first study to suggest that domesticated zebra finch females may use a male’s song complexity, a sexually selected trait, as an indicator of his general cognitive abilities, such as the ability to learn to exploit a novel food source. Chapter 5 extends this finding to a wild bird species with a more complex song system, the song sparrow. I find that song sparrow performance on a cognitive test correlates with song repertoire size, a trait that has also been shown to correlate with longevity and reproductive success in this species. This study is also the first to explore whether individual birds’ scores on a series of learning tests correlate with each other, which would point to the existence of a general cognitive ability in a wild bird species. Chapter 6 provides the first literature review assessing the evidence for a role of cognition in non-human vertebrate mate choice, and proposes new avenues of research to advance our understanding of sexual selection and cognition.
Linking statement 1

In Chapter 2, I use a field test of foraging to assess the relationship between mate interactions and novel food source exploitation in the zebra finch (*Taenopygia guttata*), an avian species used as a model system for mate choice. However, in the outback of Australia, field conditions are unpredictable and the feasibility of a foraging test in the wild is unknown. In Chapter 1, I develop a learning test for a species in field conditions that are much more accessible. The Zenaida dove has been studied by our research group at McGill’s Bellairs Research Institute for many years. The birds are very tame, show high site fidelity and low neophobia towards an artificial feeding apparatus. Mated pairs show a high probability of feeding together and defend food from both conspecics and heterospecifics, making repeated testing of the same individuals in the field feasible.
Chapter 1:

A field test of behavioural flexibility in 
Zenaida doves (*Zenaida aurita*)

Abstract

Animals’ ability to adjust their behaviour when environmental conditions change can increase their likelihood of survival. Although such behavioural flexibility is regularly observed in the field, it has proven difficult to systematically quantify and predict inter-individual differences in free-living animals. We presented 24 Zenaida doves (*Zenaida aurita*) on 12 territories with two learning tests in their natural habitat in Barbados. The dove pairs showed high site fidelity and territoriality, allowing us to test individuals repeatedly while accounting for the effects of territorial chases and pair bonds on our learning measures. We used a foraging apparatus that enabled Zenaida doves to access seed, yet excluded other species, and measured doves' performance on colour discrimination and reversal learning tests. We found that 1) doves on all 12 territories passed the two tests; 2) mates within a pair were consistently solvers or scroungers; 3) sex, body condition and territorial chases did not consistently affect learning rates; 4) tameness was a significant negative predictor of learning to feed from the foraging apparatus and 5) scrounging within pairs seemed to facilitate learning. Our study presents a method to quantify intraspecific differences in behavioural flexibility in the field and relate these to individuals’ physical and social traits.
Introduction

The ability to adjust behaviour when environmental conditions change can increase an individual's likelihood of survival. For example, young cactus finches (*Geospiza conirostris*) that acquired the foraging skills necessary to exploit unfamiliar food sources in a time of severe drought were more likely to survive than juveniles that stuck with typical wet-season foraging behaviour (Grant and Grant 1989). Apart from a few illustrative cases, however, intraspecific differences in behavioural flexibility have proven difficult to quantify in the field, as no systematic measures existed until relatively recently.

In contrast, behavioural flexibility has long been a standard term in psychology and neuroscience, where it is often quantified using a subject's performance on tests of reversal learning (e.g. Fellows and Farah 2003; Izquierdo et al. 2007; Haluk and Floresco 2009). In the traditional reversal learning paradigm, an animal is presented with two stimuli simultaneously, where one is associated with a reward and the other is not. After the animal has achieved a certain learning criterion, or after it has experienced a predetermined number of trials, the reinforcement value of the two stimuli is reversed. Animals often make several errors in the first reversal trials (a phenomenon known as negative transfer), but improve over successive reversals until performance asymptotes. Despite its usefulness as a measure of flexibility, reversal learning has never, to our knowledge, been assessed in the field. Instead, field measures of flexibility have centered on novel problem-solving tasks (Webster and Lefebvre 2001) and frequency counts of innovative feeding in the wild (Lefebvre et al. 1997; Overington et al. 2009). One drawback of the latter approach is that foraging innovations in less cognitively advanced species might be too rare to be practically used as a quantitative measure of inter-individual differences in behavioural flexibility (Overington et al. 2009). In addition, organisms may not need to deviate from established behavioural routines to solve novel problems or to acquire new stimulus-response associations in stable environmental conditions and times of plenty (Tebbich et al. 2010).

A difficulty associated with presenting a novel foraging task to measure behavioural flexibility in the field is that dominant individuals may monopolize the task and prevent conspecifics from accessing it. This is what happened in the New Zealand wild mountain
parrot, or kea (*Nestor notabilis*), when presented with butter inside a tube attached to a pole, a food reward requiring innovative behaviour to access (Gajdon et al. 2004). In free-living Florida scrub-jays (*Aphelocoma coerulescens*), the presence of dominant breeding males inhibited task performance by subordinate helpers at the nest, who would only perform when the dominant adults had left the vicinity of the task (Midford et al. 2000). Social dominance did not prevent keas from attempting to open the lids of rubbish bins, but this mechanical task appeared to be too challenging to solve for most keas (Gajdon et al. 2006). When a foraging task is too difficult to solve, or the food reward too large for the solving conspecific to monopolize, individuals in gregarious species may opt to scrounge from the solvers’ food rewards instead of attempting to solve the task themselves (Giraldeau and Lefebvre 1987; Gajdon et al. 2006). A final problem with measuring behavioural flexibility is that it ideally involves measures of individuals’ performance on more than one trial (Deaner et al. 2006; Tebbich et al. 2010). Although it is easy to measure animals repeatedly in captivity, free-living subjects come and go as they wish. Following a cohort of focal individuals over a controlled series of repeated trials may thus be difficult because some of them may be absent on given trials.

In this paper, we bridge the gap between measures of behavioural flexibility in the field and in captivity by conducting tests of discrimination and reversal learning in free-living birds. To circumvent the aforementioned problems, we conducted our learning tests on a tame territorial animal with high site fidelity, the Zenaida dove (*Zenaida aurita*) of Barbados. The Zenaida dove is a monogamous columbid species endemic to the Caribbean islands. In most areas of Barbados, Zenaida doves defend stable year-round territories, feed on the ground, are very tame around humans and readily approach provisioned feeding sites that contain a novel apparatus (Webster and Lefebvre 2001). In addition, the doves form stable pair bonds and both members of the pair aggressively chase intruders attempting to feed on the territory (Lefebvre 1996; Sol et al. 2005). Zenaida doves are thus very likely to interact with a learning apparatus in conditions that are easy to observe, as well as to provide repeated measures on their territory. We trained free-living Zenaida doves to feed from a novel apparatus that was subsequently used for a discrimination test (where a colour cue identifies the apparatus with accessible seed) and
a reversal test (changing the colour cue that identifies which apparatus has accessible seed).

We first describe the conditions under which learning in Zenaida doves occurred, with particular reference to the roles of pair bonds and territorial aggression. We then test whether sex, aggression, scrounging, body condition or tameness can predict individuals’ performance during training and the two learning tests. Previous studies on free-living birds have suggested that males may be more inclined to solve a foraging task than females (e.g. in keas: Gajdon et al. 2006; and in New Caledonian crows *Corvus monedula*: Bluff et al. 2010) and to aggressively exclude mates from experimental food sources (e.g. in New Zealand robins *Petroica australis*: Steer and Burns 2008). We therefore expected that in Zenaida doves, males would be the first within each pair to interact with the apparatus during training trials and to choose the correct apparatus consistently in both of the learning tests presented on the pair’s territory. The role scrounging may play in acquiring a task solution is difficult to predict: while captive experiments on feral pigeons showed that scrounging prevented learning of a foraging task solution (Giraldeau and Lefebvre 1987), recent avian field studies suggest that scrounging might facilitate learning (e.g. Midford et al. 2000; Gajdon et al. 2006). Whether scrounging from mates within free-living pairs facilitates or inhibits learning has not yet been tested. Finally, tolerance of human proximity, or tameness, predicted differences in latency to feed from an experimental food source in the field when comparing different species: tamer feral pigeons (*Columba livia*) were faster to feed than less tame Zenaida doves (Seftert et al. 2001). However, individual differences in tameness have, to our knowledge, not been related to learning performance in the field. We predicted that tamer Zenaida doves would be faster at solving our learning tasks than individuals less tolerant of human proximity.

**Materials and methods**

**Zenaida doves**

We studied adult male and female Zenaida doves at the Bellairs Research Institute of McGill University and the adjacent grounds of Folkestone Park and St-James Church (Holetown, Saint James Parish, 13.19° N; -59.64° W). Between March 1st and June 20th
2006, we caught 85 doves in walk-in traps baited with seed, and banded each individual with a unique colour combination of four plastic leg bands (A.C. Hughes, Hampton Hill, U.K.). For each bird, we measured left and right tarsus and wing length, tail length, bill length and width. Tarsus and bill measurements were conducted with a digital calliper (precision: ± 0.01 cm) and wings and tail with a ruler (precision: ± 0.05 cm). Heavily damaged tails were excluded. Individuals were weighed with a digital pocket scale (precision: ± 0.1 g). A small blood sample (40 µl twice) was also collected by puncturing the brachial vein for molecular sex identification (Monceau 2009). Once morphological measurements and blood samples were taken, doves were released at their site of capture. Many of the doves we banded were not resighted again, possibly because they were floaters in search of a territory (Sol et al. 2005). Two pairs of territorial doves were used for pilot studies and tests of another six pairs were aborted as the doves did not interact with the task apparatus regularly enough. This left us with 24 birds making up 12 pairs. For all 24 test subjects, molecular sex assignment confirmed behavioural sexing from field observations.

**Learning tests**

Each pair of doves on the 12 territories was allowed to habituate to the test apparatus before learning tests were started, to prevent individuals’ object neophobia from interfering with learning test performance (Boogert et al. 2008). The same test apparatus was used for all learning phases presented to each pair in the same order: a) training phase, b) colour discrimination test, and c) colour reversal test.

**Test apparatus**

The test apparatus consisted of the top 10 cm of a plastic bottle placed upside-down in a glass bowl and secured to the bowl with a metal wire. The bottle was filled with mixed bird seed and covered with a plug to prevent other bird species from eating the seed. Doves could access the seed by pecking at a small triangular gap cut in the rim of the bottle opening. This apparatus was positioned in an open wooden box (i.e. missing top and front; see Figure 1).
**Habituation, training, and learning test procedure**

All observations were made at a distance of 15 m from the task apparatus. If no territory owners appeared within 20 min of task presentation, the trial was aborted and another trial attempted at the same territory circa four hours later on the same day, or the next day. A dove was considered to have habituated or to have passed a training or test level if it fed from the apparatus for three consecutive minutes. The experimenter then slowly approached the task in a straight line at a constant pace. At the moment the dove fled, the experimenter dropped a marker and measured the distance to the task apparatus to quantify the dove’s tolerance to human proximity or ‘tameness’. A dove failed a habituation, training or test level when it left the apparatus without having fed from it and did not return to the apparatus within the next 10 min. Habituation, training and test levels progressed according to the fastest learner in each dove pair, but all task interactions of both members were recorded.

**Habituation phase**

Before starting the training phase, each test subject was habituated to the test apparatus by allowing it to feed on mixed bird seed presented progressively more like the food presentation in the actual task apparatus: 1) mixed bird seed on a 30 x 10 x 2 cm wooden shelf; 2) seed in a glass bowl on the shelf; 3) the bowl with seed on top of the wooden apparatus box; 4) the bowl with seed inside the box. Once the test subject had passed these four levels, it was presented with the actual task apparatus and trained to gain access to the seed within.

**Training phase**

To raise doves’ interest in the task apparatus, we preceded each trial of the training phase by presenting the bowl with seed inside the open box (habituation level 4). Once the test subject had fed for 3 min, we replaced the bowl with the task apparatus. As none of the test subjects discovered how to extract the seed from the bottle top when there was no seed available in the bowl holding the apparatus, we shaped the doves towards pecking the bottle rim gap by providing seed in front of it. Once the test subject learned to peck the gap without seed in the bowl, we turned the apparatus such that the gap was oriented...
towards the back of the box. In this way, the dove could only inspect the gap by entering
the box and putting its head in between the bottle and the back of the box. This procedure
was necessary for the colour discrimination and reversal learning tests (see below). For
each task apparatus visit, we recorded the time at which the test subject entered and left
the box, and duration of pecking the bottle top. We also recorded the durations of all
territorial chases. Each dove’s latency to learn to feed from the foraging apparatus was
calculated by summing time spent in the box up to the moment it had pecked the gap
oriented towards the back of the box, without seed presentation in the bowl, for 3 min.

Colour discrimination test
Before starting the colour discrimination test, we conducted a pre-test to establish test
subjects’ inherent colour preferences: we presented two copies of the learning task
apparatus in two boxes, one green and the other white, positioned next to each other with
15 cm in between, and recorded the colour of the box entered first. We then started the
actual discrimination test by presenting each test subject with four boxes simultaneously,
two of each colour. Boxes of the colour entered first during the pre-test contained task
apparatuses with sealed gaps, making them unrewarded, whereas boxes of the non-
preferred colour contained the rewarded apparatuses (i.e. with open gaps). We recorded
the time at which the test subject entered and exited each of the boxes and measured the
latency to access seed in one of the rewarded task apparatuses and the number and
duration of visits to unrewarded task apparatuses if any such errors were made before the
test subject made the correct choice. We also noted the trials in which the subject reached
a criterion of immediate exploitation of the correct box, without errors or time delays
(latency < 5 sec). After the test subject had fed from a rewarded box for 3 min, we
approached the boxes, measured flight initiation distance, and presented the four boxes
again, but in a different order. The four boxes were thus presented next to each other five
times in a row, each time in a different colour order (e.g. for trial 1, from left to right:
green-white-white-green, trial 2: white-green-white-green, etc.). Colour orders were
determined beforehand and held constant across all test subjects.
Reversal test

The rewarded colour was reversed for each dove pair, and the test was conducted in the same way as the colour discrimination test. However, in this test the four boxes were presented ten times in a row on each territory, because two subjects who had acquired the learning criterion during the discrimination test (i.e. immediate exploitation of the correct box) had not reached this learning criterion by the 5th trial of the reversal test.

Depending on the pair tested, the total test procedure from habituation to reversal learning took between 8 and 32 days (mean ± SD = 21.33 ± 7.22 days). All habituation, training and learning trials were conducted between 6:00 and 18:00 hours and were recorded with a Panasonic 3CCD camera to check data recorded manually during direct observations.

Analyses and Results

We conducted our analyses in R version 2.8.1 using the functions ‘glm.nb’ (MASS library) and ‘lme’ (nlme library; R Development Core Team 2008), and SPSS version 15.

General observations

Territorial Zenaida doves reliably visited our task apparatus and defended it against conspecifics. At least one member of the 12 targeted pairs interacted with the apparatus on 96% of all test days, while both members of these pairs appeared on 69% of all test days. Bullfinches tended to visit the apparatus before Zenaida doves, attracting territory owners to the food (Webster and Lefebvre 2001), and were generally tolerated. Seed exploitation during the habituation and training phases by ground doves and neighbouring Zenaida doves or floaters was met with aggressive territorial chases. On average, territorial doves spent 9.77 ± 8.11% of their trial time chasing away conspecifics and ground dove intruders and 47.94 ± 15.56% interacting with the apparatus, with a mean of 0.86 ± 1.22 aggressive interruptions of foraging per trial.
Do Zenaida doves learn in the field?

At least one member of each territorial pair learned to feed from the apparatus and completed all trials for the two learning tests on each of the 12 territories, with the number of individuals that learned to feed from the apparatus and that participated in the learning tests increasing over tests (Table 1).

To assess whether doves required less time to extract seed across trials, which would suggest they learned to enter the correct colour box in the discrimination and reversal tests, we modeled ‘latency to extract seed’ as a function of ‘trial number’ and ‘bird’, using a negative binomial generalized linear model to accommodate the non-normal error structure of the data. ‘Bird’ was a fixed effect instead of a random effect because there is as yet no mixed-effects version of the glm.nb function available in R (R Development Core Team 2008). Inclusion of ‘bird’ as a fixed effect is more conservative than it would be as a random effect by using up more degrees of freedom. We ran glm.nb models on the five trials of the colour discrimination test and on only the first five trials of the reversal test to compare the effect of trial number in these two tests.

Individuals may become faster at accessing food from a rewarded box across trials by learning to switch more quickly from unrewarded to rewarded boxes, rather than by acquiring the intended colour-reward association. To assess this possibility, we transformed the abovementioned latencies into binomial scores where individuals that chose the rewarded box immediately were assigned a ‘1’, and individuals that entered and/or pecked at an unrewarded apparatus during a trial before exploiting the rewarded box for three consecutive minutes were assigned a ‘0’. We then plotted the proportion of all doves that immediately chose the correct box for each discrimination and reversal learning trial. Doves were expected to perform below chance levels during the first few trials of the discrimination test, as the box of the colour that was not preferred by the test subject during a pre-test was rewarded first (see methods). However, if individuals acquired the colour-reward association, the proportion of doves choosing the correct box should increase to above-chance levels across trials.

We found trial number to be a significant negative predictor of birds’ latencies to extract seed in both the discrimination and reversal learning tests, for all solvers as well as the first solvers within each pair only (Table 2). This significant decrease in doves’
latency to access seed from the correct box, together with an obvious increase in the proportion of birds choosing the correct box immediately (i.e. without entering an unrewarded box first) across both discrimination (linear regression slope estimate ± SE = 0.192 ± 0.077, $t_5 = 2.475$, $R^2 = 0.819$, $P = 0.090$; Figure 2A) and reversal learning trials (linear regression slope estimate ± SE = 0.047 ± 0.019, $t_9 = 2.466$, $R^2 = 0.657$, $P= 0.039$; Figure 2B) suggests that individuals acquired the colour-reward association.

**Predictors of learning performance**

*Body condition:* We operationally defined a bird’s body condition as its residual on a regression of body mass against body size (Jakob et al. 1996). We expressed body size as the first two factors on a Principal Components Analysis that included log$_{10}$-transformed and standardized measures of wing length (mean of left and right wings), tail length, tarsus length (mean of left and right tarsus), bill length and bill width. We used the residuals of the regression of log$_{10}$-transformed and standardized body weight against each bird’s factor scores on body size Principal Components 1 and 2 as an index of body condition.

*Tameness:* We used a one-way ANOVA to test whether mean distance to flee from the experimenter differed significantly between individuals. We calculated the repeatability r of individuals’ fleeing distance according to Lessells and Boag (1987). We used a linear mixed effects model to test whether birds’ distance to flee changed across trials, including ‘bird’ as a random effect, ‘test number’ as a fixed effect and ‘distance’ as the response variable.

*Territory disturbance:* We gave each territory a score between 1 and 3 according to the intensity of human disturbance in the area, with ‘1’ indicating hardly any disturbance and ‘3’ indicating frequent disturbance. Our scores were confirmed by four independent observers familiar with the study area. We used Spearman rank correlation tests to explore whether intensity of human territory disturbance was correlated with mean experimenter approach distance at which birds fled or with learning performance.

*Analysis:* Effects of sex, body condition, time spent on territorial chases (excluding individuals with zero chase time), and tameness on latency to learn to feed from the apparatus during the training phase, and to extract seed during each of the two learning...
tests, were tested with multiple regressions. We used backward selection to obtain the
minimally adequate model with a selection criterion of \( \alpha = 0.05 \). We included only the
individual that was first to acquire seed from the apparatus on each territory (‘first
solver’), as on territories where both mates solved, data from the two individuals cannot
be considered independent.

Neither sex nor body condition significantly predicted performance during the
training phase and learning tests. In six of the 12 dove pairs that we tested, the first bird to
finish training and to choose the correct box immediately in the discrimination and
reversal tests was always the male of the pair, whereas in the remaining six pairs a female
was the first to do so. Interestingly, both body condition and tameness of mates in each
pair were strongly and positively correlated (body condition: \( r = 0.783, N = 8, P = 0.022; \)
tameness: \( r = 0.776, N = 11, P = 0.005 \)), so we used only the data for first solvers in our
multiple regressions to avoid co-linearity problems. Body condition did not predict first
solvers’ latency to learn to feed from the apparatus  (estimate ± SE = -0.0715 ± 0.049, \( t_7 =
-1.466, R^2 = 0.235, P = 0.186 \)) nor total time spent in unrewarded boxes during the colour
discrimination (estimate ± SE = -0.026 ± 0.096, \( t_7 = -0.269, R^2 = 0.010; P = 0.795 \)) or
reversal tests (estimate ± SE = -0.140 ± 0.157, \( t_7 = -0.891, R^2 = 0.102; P = 0.402 \)).
However, tameness significantly predicted performance during the training phase: the
bolder the dove was towards experimenter approach, the longer it took to learn to feed
from the foraging apparatus (estimate ± SE = -311.316 ± 85.862, \( t_{10} = -3.626, R^2 = 0.754,
P = 0.005 \); Figure 3).

Tameness was not significantly correlated with the usual level of human
disturbance on the territory (\( r_s = -0.492, N = 12, P = 0.104 \)). However, doves on territories
with higher human disturbance tended to be slower at learning to feed from the apparatus
than doves on less disturbed territories (\( r_s = 0.577, N = 12, P = 0.049 \)). Individuals
differed significantly and consistently in tameness (repeatability \( r \) of mean tolerated
approach distance = 0.77, \( F_{10,143} = 47.504, P < 0.001 \)), although our linear mixed effects
model showed that experimenter approach distance decreased significantly as the number
of times a bird was tested increased (estimate ± SE = -0.098 ± 0.036, \( t_{42} = -2.719, P =
0.007 \)). Mean tolerated approach distance, in turn, was significantly predicted by dove
body weight (estimate ± SE = 0.137 ± 0.049, \( t_7 = 2.777, R^2 = 0.524, P = 0.027 \)), but not by dove body condition (estimate ± SE = 2.320 ± 1.350, \( t_7 = 1.718, R^2 = 0.297, P = 0.129 \)).

Time spent on territorial chases did not predict the latency to learn to feed from the apparatus (estimate ± SE = 0.012 ± 0.150, \( t_{10} = 0.077, R^2 < 0.001, P = 0.94 \)), nor total time spent in unrewarded tasks in the reversal learning test (estimate ± SE = 0.423 ± 0.328, \( t_{10} = 1.287, R^2 = 0.142, P = 0.227 \)). However, time spent chasing intruders did significantly and negatively predict the time that territory owners spent in unrewarded tasks across the five trials of the colour discrimination test (estimate ± SE = -0.403 ± 0.150, \( t_{10} = -2.683, R^2 = 0.419, P = 0.023 \)): individuals that displayed more aggression towards intruders spent less time in unrewarded tasks.

**Learning performance across the three learning phases**

Negative transfer from the discrimination to the reversal learning test would be suggested by individuals performing below chance levels in the first trials of the reversal learning test. In the first reversal learning trial, 8 out of 12 doves chose the incorrect box first (Chi-Square test \( X^2_1 = 1.333, P = 0.248 \)), while in the second reversal learning trial, 10 out of 12 doves chose the incorrect box first (\( X^2_1 = 5.333, P = 0.021 \); see Figure 2B), perhaps suggesting that the colour-reward association acquired during the previous day hampered doves in learning the reversed association.

The ranks of individuals’ latencies to learn to feed from the apparatus and the slopes of their discrimination and reversal learning curves showed no significant correlation (Kendall’s coefficient of concordance \( W = 0.012, N = 12, X^2_2 = 0.298, P = 0.862 \)).

**The effect of scrounging**

Scrounging from the successful mate occurred on 9 of the 12 territories in the training phase, but decreased over the discrimination and reversal tests. Table 1 shows that mates scrounged without solving on 7 of the 12 territories in the training phase, but on only 1 of the 12 territories in the reversal test. In contrast, both mates learned to feed from the apparatus during the training phase on only 3 of the 12 territories, but this number
increased to 7 pairs in the reversal test. The difference between the training phase and reversal learning test in solving without scrounging and scrounging without solving is significant ($X^2_{1} = 19.8, P < 0.001$). Some of the mates that scrounged in the early trials of the training phase or a learning test eventually learned to feed from the apparatus in later trials. This occurred on 2 territories in the training phase, 2 territories in the discrimination test and 1 territory in the reversal test (Table 1). The mates that learned to feed from the apparatus after scrounging spent significantly more time interacting with the task apparatus and scrounging from their solving partners than mates that scrounged without ever learning to feed from the apparatus (time spent interacting with task: $t_{8} = 2.654, P = 0.029$; scrounging: $t_{8} = 2.467, P = 0.039$).

**Discussion**

Our study shows that inter-individual differences in behavioural flexibility can be quantified in the field in a species where site fidelity and territorial defence allow repeated testing of focal individuals and exclusion of non-focal ones. At least one member of each targeted Zenaida dove pair was present in 96% of all test days, and both learning tests were completed on all territories. Thus, Zenaida doves, despite the fact that they are the slowest problem-solvers in the mixed species aggregation that feeds together in urbanized areas of Barbados (Webster and Lefebvre 2001), yielded repeated measures on tests of discrimination and reversal learning in the field.

Latency to pass each of the learning phases was not predicted by sex, body condition, the number of territorial chases performed by the solver’s mate or the time the latter spent scrounging, but it should be noted that our sample size was small and our negative findings on these points should thus be taken with caution. However, tameness towards humans was a significant predictor of performance during the training phase: tamer doves required more time to learn to feed from the foraging apparatus than did doves that were more inclined to flee upon experimenter approach. Our finding might be explained by the fact that doves are often fed by visitors of our field sites. Bolder individuals may be habituated to feed on easily accessible food provided by humans and may have focussed on the experimenter instead of the apparatus to gain a food reward, whereas individuals more fearful of human proximity may tend to look for food in other
places, and performed better during the training phase as a result. In support of this explanation, we found that slower learners owned territories that were more often subject to human disturbance than the territories of faster learners.

Møller (2008) reported that urban bird populations have shorter flight distances when approached by humans than do rural populations, and that an urban population’s flight distance decreases as the number of generations since urbanization increases. Our research on a semi-urbanized bird population shows that tameness is a highly repeatable and individual-specific trait. While comparative studies suggest that inter-specific differences in flight initiation distance may have important consequences for the distribution and abundance of species (Blumstein 2006), our study suggests that within species, individuals’ degree of tolerance to human proximity may be an important determinant of their tendency to exploit novel food sources.

While the territoriality of Zenaida doves offered advantages for this study, the fact that subjects often interrupted their interactions with the task to chase away intruders could have posed some problems. Overall, however, territory defence did not have a strong, systematic effect on individual differences in performance. Time spent on territorial chases did not predict the latency to learn to feed from the apparatus, nor total time spent in unrewarded tasks in the reversal learning test. The only significant effect we found was in the colour discrimination test, but in the opposite direction to the one we would have predicted: individuals that displayed more aggression towards intruders spent less time in unrewarded tasks, and were more efficient in solving the task as a result. Territorial aggression was thus not traded-off against learning performance in our study, as two of the three learning phases showed no significant relationship between the two variables and one test showed an effect in the opposite direction. However, the latter result should be treated with caution as, with our small sample size, it could have been found by chance.

Scrounging by the mate was frequent in the training phase, but decreased over successive tests. An indication that scrounging had a positive effect on learning performance lies in the difference between scroungers that later passed tests on their own and scroungers that did not: mates that learned to feed from the apparatus after scrouning spent significantly more time interacting with the apparatus and scrounging
from their solving partners than mates that scrounged but never learned. As observed in Florida scrub-jays (Midford et al. 2000), keas (Gajdon et al. 2006), and wild meerkats (Suricata suricatta; Thornton and Malapert 2009), scrounging might thus have facilitated learning to feed from the apparatus, by encouraging mates to spend more time interacting with the task. With regards to the non-solvers in this study, however, it should be noted that only a separate test of the scrounger in the absence of its successful mate can establish whether or not the scrounger has learned the task by observation, but never shown it when the producer was present (Giraldeau and Lefebvre 1986, 1987; Lefebvre and Helder 1997). This was not possible here, as our goal was to examine learning under normal field conditions. Had we removed producers, neighbouring doves would likely have moved in, as a previous study involving territory owners has suggested (Sol et al. 2005).

Experimenters who adopt the reversal learning paradigm in captivity usually present their animals with tens to hundreds of reversals (Macphail 1982). However, authors of such papers have pointed out that interspecific differences in error rates are most pronounced in the first test session following each reversal (Warren 1966; Gossette 1968; Bond et al. 2007). In addition, Day et al. (1999) and Tebbich et al. (2010) showed that a predicted species difference in performance was achieved after a single reversal. Given these findings and the fact that in the field, opportunities to conduct learning tests are constrained by environmental conditions, test subject availability and feeding motivation, as well as experimental time constraints, we subjected the Zenaida doves to a single reversal test.

One surprising result of our study is the lack of correlations between learning rates in the three phases of the study. It would be profitable for future studies of reversal learning in the field to conduct enough trials in the discrimination test to ascertain that all individuals reached the same learning criterion of choosing above chance levels multiple times in a row, before allowing them to proceed to the reversal test. Perhaps not doing so caused the predicted negative transfer effect from the discrimination to the reversal learning phase to be relatively weak. Even so, individuals that performed well in the training phase did not necessarily do as well on the colour discrimination and reversal tests. This finding was unexpected because comparative studies have reported positive
correlations between a variety of learning-associated behaviours, such as innovation, tool use, problem-solving and reversal learning across bird species (Lefebvre and Bolhuis 2003). Within species, individual learning correlates positively with social learning in wild-caught, captive pigeons (Columba livia; Bouchard et al. 2007). However, a recent study on male satin bowerbirds (Ptilonorhynchus violaceus; Keagy et al. 2009) reported that birds’ scores on two problem-solving tests conducted in the field were not correlated. The number of individuals available for testing can be limited in field studies such as Keagy et al.’s and ours, and our relatively small sample sizes may present part of the reason that we failed to find a significant correlation between test performances. In addition, perhaps significant correlations between performances on different tests are more likely to be found when individuals are tested in isolation in captivity, where one can influence motivation (e.g. through food deprivation) and control other factors. When conducted in the field, tests of behavioural flexibility provide data that may be more ‘noisy’, but render important insights into the effect of ecological and social factors on the performance of the studied species as well.

Acknowledgements

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References


Giraldeau L-A, Lefebvre L. 1987. Scrounging prevents cultural transmission of
food-finding behaviour in pigeons. Anim Behav. 35: 387-394.
Møller AP. 2008. Flight distance of urban birds, predation, and selection for urban...


**Table 1.** Total number of birds across the 12 targeted territories that finished each of the three learning phases, and the number of pairs in which birds learned to feed from the apparatus while scrounging from their mates’ seed extractions.

<table>
<thead>
<tr>
<th>Test</th>
<th># of birds solving without scrounging</th>
<th># pairs in which mate scrounges without solving</th>
<th># pairs in which mate learns to solve after scrounging</th>
<th># pairs in which mate does not participate</th>
<th># pairs in which both mates solve / total # pairs tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>Training phase</td>
<td>13</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>3/12</td>
</tr>
<tr>
<td>Colour discrimination</td>
<td>15</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>5/12</td>
</tr>
<tr>
<td>Reversal</td>
<td>18</td>
<td>0</td>
<td>1</td>
<td>5</td>
<td>7/12</td>
</tr>
</tbody>
</table>
Table 2. Results of negative binomial generalized linear models in R used to test whether trial number was a significant predictor of latency to extract seed in the discrimination test and first five trials of the reversal test, including ‘bird’ as a fixed effect to accommodate the repeated measures-structure of the data. Analyses were conducted on all solvers as well as first solvers only for both learning tests. Negative estimate values indicate that latencies to extract seed decreased across trials, suggesting that doves learned the colour-reward association.

<table>
<thead>
<tr>
<th>Learning test</th>
<th>N</th>
<th>Estimate ± SE</th>
<th>Statistics</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Discrimination: 5 trials</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All solvers</td>
<td>15</td>
<td>-1.077 ± 0.164</td>
<td>$z_{1,72} = -6.566$</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>First solvers only</td>
<td>12</td>
<td>-0.971 ± 0.117</td>
<td>$z_{1,58} = -8.275$</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td><strong>Reversal: first 5 trials</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All solvers</td>
<td>18</td>
<td>-0.530 ± 0.102</td>
<td>$z_{1,80} = -5.181$</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>First solvers only</td>
<td>12</td>
<td>-0.596 ± 0.171</td>
<td>$z_{1,58} = -3.478$</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Figure 1. Task apparatus. The gap was oriented towards the back of the box during the final part of the training phase and the colour discrimination and reversal tests. The apparatus was designed to exclude the four other avian species (Carib grackles, *Quiscalus lugubris*; Lesser-Antillean bullfinches, *Loxigilla noctis*; Common ground doves, *Columbina passerina*; Shiny cowbirds, *Molothrus bonariensis*) that normally compete with Zenaida doves for food in mixed species aggregations (Dolman et al. 1996). Dimensions: glass bowl: 11.8 cm diameter, 7.0 cm high; plug: 5.0 cm diameter, 1.4 cm high; wooden box: 34.2 x 15.2 x 11.8 cm high.
Figure 2. Proportion of doves ($N=12$) choosing the rewarded box immediately in A) the discrimination test and B) the reversal test.
Figure 3. The relationship between the mean distance of experimenter approach at which each of the twelve doves fled, and the time they took to learn to feed from the foraging apparatus.
Linking statement 2

In Chapter 1, I developed a field test of learning for a species, *Zenaida aurita*, that has been extensively studied in our lab, and that, due its year-round territoriality, shows very high site fidelity and can defend exclusive access to an experimental feeder. I showed that mates in territorial *Z. aurita* pairs gain benefits from foraging together by scrounging from each other's food discoveries and learning to exploit a novel food source on the territory as a result. In the next three chapters, I examine the relationship between learned foraging behaviour, interactions between mates and mate choice in the species most often used for mate choice studies in captivity, the zebra finch *Taenopygia guttata*. Chapters 3 and 4 feature experiments on domesticated zebra finches, while Chapter 2 looks at foraging in mated pairs of zebra finches in the wild. The chapter tests a necessary assumption for Chapters 3 and 4 to be ecologically valid, namely that mated pairs of zebra finches feed together in natural conditions. This would allow mates to benefit from each other's foraging behaviour and would suggest that foraging behaviour could be an important mate choice criterion.
Do zebra finch mates forage together in their natural habitat in Australia?

Status: Boogert NJ. Do zebra finch mates forage together in their natural habitat in Australia? Not intended for publication.
Abstract

The zebra finch is the avian model system for studies of mate choice and sexual selection. Wild zebra finches breed opportunistically when irregular rainfall allows seeds to ripen, making them available to feed young. Captive studies show that reduced foraging rates have significant negative effects on longevity and reproductive output. Zebra finches in the wild would thus benefit from choosing and foraging with a mate that can locate and efficiently exploit the unpredictable and ephemeral patches of food. We studied two wild zebra finch colonies in a semi-arid zone of Australia to address the hypothesis that mates maintain a tight pair bond while foraging. We banded birds and tracked all their feeder entrances and exits for five consecutive days. We then determined, for every possible combination of bird pairs (regardless of sex), the number of times the two birds visited the feeder together within a short time window. We found that mates visited the feeder together more frequently than they did with any other tracked individual on average, but exited the feeder together only as often as they did with non-mates. The latter finding can be explained by the observation that all birds would immediately leave as soon as a threat approached the feeder. Our observations that zebra finches always forage in flocks, and that mates maintain a tight association even when foraging in flocks, raise the question whether zebra finches may use foraging behaviour as a mate choice criterion. We address this question in Chapter 3.
Introduction

The zebra finch (*Taeniopygia guttata*) is a small (12-13 g) passerine endemic to Australia, and has become one of the classic model systems for studies of sexual selection and mate choice. Zebra finches are both socially (Zann 1996) and genetically (Griffith et al. 2010) monogamous in the wild, where they form pair bonds for life (Zann 1996). Zebra finches breed in loose colonies and both parents contribute to nest construction, incubation and chick provisioning. However, natural nests are hard to find and individuals are difficult to track due to their nomadic life history (Zann 1996), which is why most work on zebra finch mate choice has been done on domesticated zebra finches in Europe (e.g. Clayton 1990; Ten Cate and Vos 1999; Forstmeier 2004; Forstmeier and Birkhead 2004; Forstmeier et al. 2009; Witte and Sawka 2003; Riebel 2009) and North America (e.g. Burley et al. 1982; Burley 1986; Burley 2006; Burley and Foster 2006) as they are easy to keep and breed in captivity.

In flocks of domesticated zebra finches in captivity, pair formation can start within minutes of unfamiliar birds being introduced to each other (Silcox and Evans 1982). Within the first two days of observations of captive flocks, newly paired birds tend to clump (i.e. perch in bodily contact) significantly more often, show less aggression to each other, court and copulate, stay in closer proximity to each other and behave in synchrony significantly more often than do non-mates (Silcox and Evans 1982). Perhaps this rapid pair formation has been selected for by conditions in the wild; in arid central Australia, zebra finches need to breed opportunistically as soon as flushes of ripening grass seeds are available to feed young, which depends entirely on irregular rainfall (Zann et al. 1995; Perfito et al. 2007). Any delay in reproduction, for example due to new pair formation (Delesalle 1986; Adkins-Regan and Tomaszyci 2007), is expected to be tightly and negatively linked to lifetime reproductive success, as suitable breeding conditions are so brief and unpredictable in the wild.

The ability to find and exploit these short-lived, superabundant patches of food is thus essential for zebra finch survival and reproduction. In captivity, foraging efficiency has been shown to have significant fitness consequences in domesticated zebra finches. Lemon and colleagues (1991) mixed empty seed husks into a standard amount of grass seeds provided to captive flocks of zebra finches, thus reducing their foraging rate and
maximum rate of energy intake. This, in turn, increased mortality and reduced reproductive success by decreasing brood size and increasing the time intervals between subsequent broods (Lemon 1991; Lemon and Barth 1992). Similar results were reported by Wiersma and Verhulst (2005), who manipulated energy intake rates following Lemon (1991) and reported that both somatic repair and reproductive rate were hampered. Others subjected domesticated zebra finches to a high workload to access food and found that their reproduction was delayed by almost a week as compared to that of zebra finches subjected to a lower workload (Deerenberg and Overkamp 1999).

This close association between zebra finch foraging behaviour and reproductive success suggests that birds may benefit from choosing and foraging with a mate that has the ability to rapidly locate profitable food patches and exploit them efficiently. Pair bonds in the wild have been observed to remain tight throughout the breeding and non-breeding seasons (Zann 1994), and new mates forage together more than they do with other flock members in captivity (Silcox and Evans 1982). However, whether zebra finch mates in the wild forage with each other significantly more than they do with other colony members is unknown. We studied two wild zebra finch colonies in a semi-arid zone of Australia to determine whether mates would maintain a tight pair bond even during foraging in flocks on a novel food source presented near the colony.

**Methods**

This study was conducted in October and November 2009 at the University of New South Wales Arid Zone Research Station at Fowlers Gap, 112 km north of Broken Hill in the far west of New South Wales, Australia (31°05’S, 142°42’E). The research station is located in Australia’s semi-arid zone with an average annual rainfall of 240 mm (as compared to 980 mm in Montreal). We studied two of the four zebra finch nest-box breeding colonies established in the area in 2005 (Griffith et al. 2008), called ‘Saloon’ (31°03’90”S, 141°50’60”E) and ‘Gap Hills’ (30°57’S, 141°46’E). Both of our study colonies are located in areas of acacia shrub land associated with open clay water tanks that are part of a watering infrastructure to support sheep on the station (Griffith et al. 2008).

To distinguish individuals, we caught zebra finches in the morning during the weeks preceding observations either at the nest with a nest trap when chicks were 4-8 days old,
or at seed-baited traps. All birds caught were immediately removed from the traps and fitted with a unique combination of three coloured leg bands and a numbered metal ring (provided by the Australian Bird and Bat Banding Scheme). In addition, one of the three coloured leg bands contained a Passive Identification Transponder (PIT) tag (Trovan ID100, The Netherlands). These transponders are small (11 mm long, 2 mm wide, 0.1 g) passive devices that emit a unique identification code when in close proximity to powered antennae. Birds typically returned to their nest or to the seed-baited trap on the day of capture.

We placed two feeders ca. 500 m from the centre of each colony. Each feeder consisted of a wire finch holding cage (70 x 40 x 50 cm) containing a tray (30 x 35 x 9 cm) with mixed bird seed, buried partly into the ground to avoid displacement by wind, sheep or kangaroos. Birds entered the feeder by walking through an 11 x 11 cm opening on the long side of the cage to which we fixed a powered antenna (11 cm diameter) attached to a PIT-tag detection system (Trovan LID-650 decoder, The Netherlands) that automatically recorded the unique identification code of any tagged bird going through the feeder entrance. The lower 15 cm of the cage and the top were covered with green cloth to provide shade and make the entrance more conspicuous.

Starting at sunrise, we filmed each feeder for five consecutive hours from Oct 27th – 31st in Saloon, and from Nov 7th – 11th in Gap Hills. The PIT tag detection system cannot register all PIT tags when many birds enter or exit the feeder simultaneously, and may register a PIT tag multiple times when a bird sits in the entrance or very close to it. We therefore used PIT tag records to locate the general time period during which focal individuals were active in/around the feeder. We then located the same time period on the video recordings, and from these we scored whether focal individuals had entered or exited the feeder and the durations of their feeder visits.

Nest boxes in both colonies were equipped with the same PIT tag detection system. Focal individuals were pairs that had been caught and PIT tagged, recorded to visit the same nest box (using the PIT tag detection system) and observed to build a nest together, as well as to visit the colony feeders in the period that we filmed those. Observations were conducted only after the pairs had finished incubating eggs, as during incubation mates take turns feeding (Zann 1996) and synchronous foraging cannot be expected to
occur. We compared the time intervals between entries and exits of pair mates to those between non-pair mates, and tested the prediction that pair mates entered and exited the feeder within one minute of each other significantly more often than they did with non-mate flock members.

This work conformed to Australian laws, and was approved by the Macquarie University Animal Ethics Committee, a Scientific Research Permit from the New South Wales Parks and Wildlife Service and under authority of the Australian Bird and Bat Banding Scheme.

Results
Because there was very little rainfall in our study area in the summer of 2009, many of the birds we had caught and PIT tagged left our nest-box breeding colonies, presumably in search of better habitat, and breeding rates were very low. As a result, we had little data on nest box visits to confirm that birds were paired. In addition, we were not always successful at catching and banding both mates of a pair. These factors caused our sample size to be small; we obtained data for five mated pairs and an additional seven females and nine males in the Saloon colony. In the Gap Hills colony, a bird of prey (brown goshawk Accipiter fasciatus) had detected the most popular feeder and guarded it for two days in the middle of our observation period, decreasing zebra finch visit rates to the feeder and thus our sample size. We managed to collect data for six pairs and an additional seven males and three females in the Gap Hills colony, but feeder visit numbers in this colony were significantly lower than in Saloon (independent samples t test comparing number of pair-wise visits in Saloon versus Gap Hills: entries: $t_9 = 2.638, P = 0.027$; exits: $t_9 = 2.500, P = 0.034$). As all subsequent analyses compare visit numbers within colonies, we pooled the data across colonies to increase our sample size.

The absolute number of feeder entries and exits pair mates made within one minute of each other was significantly larger than the average numbers of entries and exits they made with other flock members (paired samples t tests: entries: $t_{10} = 4.331, P = 0.001$; exits: $t_{10} = 3.370, P = 0.007$; Figure 1). For each mate, we then selected the non-mate flock member it most often entered and exited the feeder with (i.e. within 1 minute). There seemed to be a trend towards mates entering the feeder together more often than
either of the mates did with their non-mate associate (paired samples t tests: female mate entries with non-mate associates: \( t_9 = 2.248, P = 0.051 \); male mate entries with non-mate associates: \( t_{10}=1.698, P = 0.120 \); Figure 1). However, birds exited the feeder as often with their non-mate associates as with their mates (female mate exits with non-mate associates: \( t_9 = 0.829, P = 0.428 \); male mate exits with non-mate associates: \( t_{10} = 1.354, P = 0.206 \); Figure 1).

Across the 11 pairs for which we collected data, most mated males had male rather than female associates with whom they visited the feeder often (9 males versus 2 females; Chi-Square test: \( \chi^2 = 4.455, P = 0.035 \)). Mated females also had a higher number of male associates, but this difference was not significant (7 males versus 3 females; Chi-Square test: \( \chi^2 = 1.600, P = 0.206 \)). It should be noted, however, that we were able to track more males than females, so these findings should be interpreted with caution.

In the Saloon colony, seven of the 10 associates of our 10 mated focal birds nested in PIT tag-monitored nest boxes. Four of these seven associates used nest boxes adjacent to the nest boxes of our focal birds. Indeed, colony observations suggested that the birds nesting in this cluster of neighbouring boxes tended to leave and return to the colony together. Our feeder visit data do not show any sign of Gap Hills neighbours visiting the feeder together, but the feeder visit numbers for this colony are too small to draw any conclusions from these negative findings.

**Discussion**

We found that zebra finch mates in Australian colonies tended to visit feeders together significantly more often than they did with any other tracked colony members. When we compared the mates’ pair-wise visit frequency to that of either mate with its most synchronous non-mate colony member, we found that mates entered the feeder more often together, but exited the feeder just as often with non-mates as they did together.

Males may have foraged in close proximity to their mates to guard them against potential rivals. Zebra finch males are known to guard their females during nest construction in the wild, but mate guarding has been observed to end two days after the first egg is laid (Birkhead et al. 1988). However, Birkhead et al. did not study mate guarding between breeding attempts, the period during which we conducted our study.
Pair-wise foraging may offer various benefits in addition to securing one’s paternity. Experiments on domesticated zebra finch pairs (i.e. outside a flock context), for example, suggest that ignorant mates can benefit from their knowledgeable partners by scrounging from the latter’s food exploitations of a novel foraging task (Beauchamp and Kacelnik 1991), that more exploratory birds can lead their less exploratory mates to novel food sources (Schuett and Dall 2009) and that zebra finch mates cooperate more with each other to obtain food rewards than they do with non-mates (St-Pierre et al. 2009). Unfortunately, our attempts at establishing whether similar benefits were obtained when mates foraged together in the field failed due to overcrowding in the feeders, which obscured mate interactions. The highly nomadic behaviour of these wild birds in times of drought also cut our foraging experiments short, as feeder visit numbers suddenly dropped dramatically. However, even without additional experimental data, our observations provide us with a better understanding of the dynamics of zebra finch colonies in their natural habitat.

One of the most striking features of zebra finches in the wild is their extremely social nature. One will rarely, if ever, see a zebra finch by itself, whether it is resting, flying, or foraging. For example, before the zebra finches entered our feeders, they would cluster together in small flocks in adjacent trees. Once one of them had entered the feeder, others would follow one by one, which often resulted in over twenty birds foraging in the feeder at the same time. In the colonies, the birds also grouped together in trees before taking off in small flocks in the direction of the feeders. This gregarious behaviour is likely to provide significant survival advantages: many eyes may allow for timelier predator detection, while flocks may confuse predators and reduce the risk of any one individual getting caught (the confusion effect; Miller 1922; Krause and Ruxton 2002). In a foraging context, increased group size allows a decline in individuals’ vigilance rate coupled with an increased foraging rate (the group size effect; Lima 1995). Indeed, we observed on multiple occasions that upon detecting an aerial predator, one of the zebra finches in the colony would give an alarm call and all colony members would rush to hide in the centre of the closest shrubs, and would stay there for up to an hour. Whenever one of our feeders was approached by a threat (such as an experimenter or a bird of prey), all birds attempted to exit the feeder immediately and simultaneously. These flock-wise exits
might explain our finding that pairs exited the feeder as often with their mate as they did with others.

The fact that zebra finch mates were found to enter the feeder more often together than they did with any of the other tracked birds may be surprising, given that they always travelled to and visited the feeders in small flocks. However, despite their gregariousness, individuals differed in the latency with which they first found the feeders, and not all birds visited all feeders (PIT tag data, not shown). Thus, zebra finches differed in the flocks they joined, and our results show that mates tended to join the same flocks and followed each other in entering the feeders. Interestingly, zebra finches from one of the two colonies we studied seemed to visit feeders in flocks composed of birds that bred in directly neighbouring nest boxes, even though distances between non-neighbouring nest boxes were never larger than 175 m, with most being less than 125 m apart. It may be that zebra finch colonies break up into smaller flocks with stable group memberships. Alternatively, our observations could be due to chance given our small sample size.

Whether zebra finch colonies contain social networks (Krause et al. 2009), and what their functional significance would be, are interesting questions for future research to address.

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References


guarding in wild zebra finches *Taeniopygia guttata*. Anim Behav. 36: 1853-1855.
Burley N, Krantzberg G, Radman P. 1982. Influence of colour-banding on the
conspecific preferences of zebra finches. Anim Behav. 30: 444-455.
Burley N. 1986. Sexual selection for aesthetic traits in species with biparental
Evolution. 60: 1076-1085.
Burley NT, Foster VS. 2006. Variation in female choice of mates: condition
influences selectivity. Anim Behav. 72: 713-719.
Clayton NS. 1990. Assortative mating in zebra finch subspecies, *Taeniopygia
Deerenberg C, Overkamp GJF. 1999. Hard work impinges on fitness: an
experimental study with zebra finches. Anim Behav. 58: 173-179.
Delesalle VA. 1986. Division of parental care and reproductive success in the
Forstmeier W. 2004. Female resistance to male seduction in zebra finches. Anim
Behav. 68: 1005-1015.
Forstmeier W, Birkhead TR. 2004. Repeatability of mate choice in the zebra
finch: consistency within and between females. Anim Behav. 68: 1017-1028.
Forstmeier W, Burger C, Temnow K, Derégnaucourt S. 2009. The genetic basis of
Griffith SC, Pryke SR, Mariette M. 2008. Use of nest-boxes by the zebra finch
(*Taeniopygia guttata*): implications for reproductive success and research.
Griffith SC, Holleley CE, Mariette MM, Pryke SR, Svedin N. 2010. Low level of
extrapair parentage in wild zebra finches. Anim Behav. 79: 261-264.
Behav Ecol Sociobiol. 63: 967-973.
Schuett W, Dall SRX. 2009. Sex differences, social context and personality in zebra finches, Taeniopygia guttata. Anim Behav. 77: 1041-1050.
Silcox AP, Evans SM. 1982. Factors affecting the formation and maintenance of pair bonds in the zebra finch, Taeniopygia guttata. Anim Behav. 30: 1237-1243.
**Figure 1.** The number of feeder visits made by mated zebra finches within one minute of their mate (grey bar), the average of all tracked non-mates (black bar), or the most closely associated non-mate (white bar). The left three bars indicate feeder entries, whereas the right three bars indicate feeder exits.
Linking statement 3

In Chapter 2 I studied zebra finches in their natural habitat in Australia. I observed that zebra finches are extremely social birds that always travel and forage in flocks. Even so, mates were found to stay in close proximity to each other and visited our feeders together. In Chapter 3 I investigate whether foraging behaviour may be used as a mate choice criterion by domesticated zebra finches in captivity.
Chapter 3:

Does foraging behaviour affect female mate preferences and pair formation in captive zebra finches?

Abstract

Many studies on avian mate choice investigate females’ use of indicator traits, such as song or plumage, to assess male quality. However, females may be able to evaluate male quality more reliably using traits directly related to fitness, such as foraging behaviour. Previous studies suggest that proficient foragers may provide females with both direct and indirect fitness benefits, while positive assortative mating for alternative foraging techniques would support assumptions of sympatric speciation models. We first tested whether female zebra finches (*Taeniopygia guttata*) taught one of two foraging techniques showed a preference for males with the same technique or for the most efficient foragers regardless of technique. Neither a male's foraging technique nor his foraging performance affected the time females spent in his proximity in the mate choice apparatus. We then released flocks of these finches into an aviary to investigate whether assortative pairing would be facilitated by birds taught the same technique exploiting the same habitat. Zebra finches trained as juveniles in a specific foraging technique maintained their foraging specialisation in the aviary as adults. However, pair formation and nest location were random with regard to foraging technique. Our findings show that zebra finches can be successfully trained to be foraging specialists, but suggest that foraging behaviour does not affect mate choice in our experimental context.
Introduction
In species with mate choice, the choosy sex is assumed to prefer mates of high quality in terms of the direct (resource-based) or indirect (genetic) benefits they can provide (Andersson 1994). In many birds, females evaluate male quality indirectly by using indicator traits such as song or plumage characteristics. These indicator traits are assumed to correlate with male quality and therefore may enable females to identify superior males (Zahavi 1975). Indeed, males with larger song repertoires have been shown to be in better body condition, have more robust immune systems, defend higher-quality territories, live longer and raise more chicks to independence than males with smaller song repertoires (Boogert et al. 2008; Catchpole and Slater 2008), while brighter red, orange or yellow plumage indicates superior health through the antioxidant and immune-stimulant properties of the dietary carotenoids that colour the feathers (McGraw and Ardia 2003; McGraw 2005).

As male quality is often thought to be difficult or impossible to evaluate directly, many avian mate choice studies focus on these and other indicator traits (Candolin 2003). However, some aspects of male quality, such as foraging technique and performance, may be observed and evaluated directly. Previous studies have shown that a male’s foraging proficiency may provide considerable direct (Belovsky et al. 1996; Helfenstein et al. 2003) and indirect benefits (Gibbons et al. 2005; Karino et al. 2005) to the choosing female. However, to our knowledge, only one previous study has assessed whether direct observation of foraging behaviour can guide avian mate choice. Snowberg and Benkman (2009) reported that female red crossbills (*Loxia curvirostra*) associated preferentially with males who were more efficient in extracting seeds from conifer cones.

In this study, we test whether direct observation of foraging technique and efficiency can affect mate preferences in captive domesticated zebra finches (*Taeniopygia guttata*) that have been trained as juveniles to obtain their food through one of two foraging techniques. In the wild, juvenile and adult zebra finches forage together in flocks (Zann 1996; personal observation). Males and females should thus have ample opportunity to evaluate each other’s foraging abilities. Furthermore, foraging rate has been shown to correlate positively with longevity and reproductive output in captive zebra finches (Lemon 1991). In addition, the extent to which zebra finches make
profitable foraging patch choices seems to be heritable (Lemon 1993). Thus, female zebra finches may obtain both direct and indirect benefits from preferring good foragers as mates.

If zebra finches choose mates on the basis of foraging skills, this would not only add to our understanding of avian mate choice, but would also be relevant to models of evolutionary divergence. The potential of behaviour to favour evolutionary change has long been recognized (Baldwin 1896; Miller 1956; Mayr 1963; Bateson 1988; West-Eberhard 1989; Futuyma 1998). A recent theoretical model by Van Doorn and colleagues suggests that speciation in the face of gene flow may be facilitated by females preferring males on the basis of traits that indicate adaptation to the local environment (Van Doorn et al. 2009). Foraging behaviour is an obvious candidate for such a trait, suggesting that female preferences for males with the appropriate foraging skills to exploit local food sources could ultimately lead to sympatric speciation.

The model by Van Doorn et al. (2009) predicts that female preferences for locally adapted males would lead to positive assortative mating for the locally adaptive trait. Positive assortative mating, when combined with disruptive selection against intermediate phenotypes, plays a key role in this and other models of sympatric speciation (e.g. Artzy-Randrup and Kondrashov 2006; Bürger et al. 2006; Doebeli et al. 2007). In birds, positive assortative mating has been established for a variety of morphological traits, such as plumage characteristics (Jawor et al. 2003; MacDougall and Montgomerie 2003; Komdeur et al. 2005; Pryke and Griffith 2007; Bitton et al. 2008; Bortolottia et al. 2008), bill characteristics (Jawor et al. 2003; Christensen and Kleindorfer 2007; Huber et al. 2007) and body size (Grant and Grant 2008), as well as age (Cézilly et al. 1997; Komdeur et al. 2005; Ludwig and Becker 2008) and developmental quality (Holbeck and Riebel 2010), while disassortative mating may be based on MHC diversity (Bonneaud et al. 2006) and phenotype mismatching for inbreeding avoidance (although see Schielzeth et al. 2008). Disassortative mating might also allow pair-bonded individuals to reciprocally profit from each other's foraging specializations without having to learn the other's technique, forming a skill pool based on mutual producing and scrounging (Giraldeau 1984; Beauchamp and Kacelnik 1991). However, few avian studies have focused on assortative and disassortative pairing based on behaviour, except for explorativeness.
Whether direct observation of foraging behaviour can guide (dis)assortative mate choice has never been tested.

In the first of two experiments reported here, we tested whether female zebra finches taught one of two foraging techniques would show a preference for males with the same or the alternative technique, or for males that were most efficient at extracting seed from the foraging apparatus (Snowberg and Benkman 2009) whatever the technique. As mating preferences in zebra finches are substantially influenced by early learning about visual (Ten Cate and Vos 1999) and acoustic traits (Riebel 2009), we taught zebra finches their respective foraging techniques while they were still juveniles, and tested them for mate preferences once they had reached sexual maturity. To remove any confounding effects of other sexually selected traits, we matched candidate mates for morphology and masked their songs.

In the second experiment, we released these zebra finches in mixed-sex and mixed-foraging technique flocks into aviaries wherein one side contained foraging patches that required one of the foraging techniques to exploit, while the other aviary side contained foraging patches that required the alternate foraging technique. We then investigated whether pair formation and nest location were assortative with regards to foraging technique, which could be due to males and females with the same foraging specialization exploiting the same food patches. This assumes that zebra finches, when interacting with conspecifics performing the alternate foraging technique in aviary flocks, would continue to perform only the technique they were trained on as juveniles, an assumption that we tested first.

Methods

Test subjects and housing

We bred ten adult pairs from the zebra finch colony at the Université du Québec à Montréal to obtain 51 chicks to participate in our experiments. Chicks were separated from their parents when 6 weeks of age and housed with 1-2 other birds of the same sex and similar age, but from a different family, in housing cages (57 x 29 x 42 cm) containing two perches, a tree branch and two reed nest baskets. Males and females were
kept in separate rooms, illuminated with standard 40 W and wide spectrum Gro-Lux®
fluorescent tubes on a 12:12 h light:dark cycle (lights on at 0600, off at 1800 hours) and
kept at 24±2 ºC ambient temperature. The regular diet of vitamin-supplemented mixed
millet seed, fresh water, cuttlefish bone and crushed oyster shells was supplemented once
per week with fruits, vegetables and protein paste.

Training on foraging tasks
We transferred juvenile males and females when 65±5 days old (i.e. once males had
acquired their songs; Williams 2004) to visually isolated, same-sex experimental rooms
where they were trained for 45 days to obtain their food by solving either a lid-flipping or
a stalk-pulling task (see Figure 1). Same-sex siblings were assigned to different tasks.
Birds were housed with 1-2 unrelated same-sex birds trained on the same task in white
corrugated plastic cages (24.5 x 55 x 28 cm) with wire mesh fronts and tops and four
perches. Water, cuttlefish bone and crushed oyster shells were available ad libitum
throughout the training phase. Birds were trained each day from 0800 to 1500 hours,
during which time they had access to the food provided in the foraging tasks only. From
1500 hours onwards birds could feed on mixed millet seed ad libitum until the lights were
turned off at 2000 hours.

Birds in the same training cage were separated by a wire mesh partition just before
training started each day to prevent them from scrounging from solving cage companions
and to ensure that each bird learned the task. We used a systematic shaping procedure
(Carlier and Lefebvre 1996) to get the birds to learn the foraging task. All birds learned
their respective task within 10 days of training. Nevertheless, all birds were exposed to
foraging tasks, refilled with seeds every 60 min, as the only means to acquire food
between 0800 and 1500 hours for a total of 45 days to ensure that they would memorize
their task.

After this 45-day training phase, males were trained to perform their task in the
mate choice apparatus while facing a task-solving cage companion on the other side of a
wire-mesh partition. Each male was trained in the mate choice apparatus until it had
solved at least 8 of the 12 tasks within 10 min. To familiarize females with the apparatus,
they spent the day before preference tests started in the apparatus with their cage companions.

**Female preferences for male foraging behaviour**

We used a two-level mate choice apparatus to test for female preferences for male foraging technique and efficiency, as well as for the influence of male-female interactions on female preferences for male foraging behaviour. When the female was positioned in the upper compartment (Figure 2A), she could observe the males performing their respective foraging techniques but could not interact with them (‘No-Interaction tests’) because they could not see her, whereas she could both observe and interact with the candidate mates when she was in the lower compartment (‘Interaction tests’; Figure 2B). To test for repeatability in female preferences, each female was presented with the same two candidate mates eight times: four times while she was in the upper compartment of the mate choice apparatus (i.e. four No-Interaction test trials), and four times while she was in the lower compartment (i.e. four Interaction test trials).

Each No-Interaction trial started with a 10-min observation phase in which the female was free to move about her upper observation compartment while the males at the lower apparatus level were solving either 12 lid tasks or 12 stalk tasks, which gave access to one millet seed per task. After 10 min we scored ‘male foraging performance’ as the number of tasks each male had solved. This observation phase was followed by a 10-min test phase. For this phase, we introduced an opaque divider in the upper female compartment that prevented the female from looking into the right male compartment when she was sitting on the perch in front of the left male compartment and vice versa (Figure 2A). During these No-Interaction tests, the candidate mates in the lower compartment were facing cage companions positioned underneath the female observation compartment. These companions provided company to the candidate mates and kept them from being distracted by the female above. As an additional measure to prevent distraction, we placed two natural-spectrum 60 W light bulbs directly above each candidate mate’s compartment, making it hard for the males in their brightly lit environment to see the female in her shaded compartment above them.
Thus, in the 20-min No-Interaction tests, female-male interactions were excluded. Throughout this phase, we never observed any male displaying to the female in the compartment above him.

To check whether females had a preference for one of the foraging task apparatuses, the day before each No-Interaction test trial we conducted control trials that were identical to test trials except that no males were placed in the lower compartment.

A week after a female zebra finch had gone through the series of four control and four No-Interaction test trials she was introduced to the Interaction test. During this test she was placed in the lower compartment of the apparatus (Figure 2B) and so could interact with the candidate mates. To ensure males would continue to solve their tasks rather than courting the observing female during the first 10 min of the Interaction test, the female was confined to the rear of the observation compartment by an extra wire mesh partition that allowed her to observe but not approach the males performing their foraging tasks. At the end of this first 10-min observation phase we recorded the number of tasks solved by each male. We then removed this extra wire mesh partition so that the female could now approach and interact with the males through the remaining wire mesh partition for another 10-min bout. Before the final 10 min of the Interaction test trials, we inserted an opaque barrier into the female’s compartment so that she could only observe one of the males at a time. We determined the proportion of time that a female spent on each male’s side of the compartment during this final 10-min period for our analyses of female preferences in the Interaction tests. Each female was subjected to four consecutive Interaction test trials, using the same pair of males as in the No-Interaction test, with five days in between trials. All birds used in the mate choice apparatus were sexually naive at the time of testing.

To control for differences in the candidate males’ songs, we masked their songs during all tests by playing a zebra finch male chorus through two Logitech R10 speakers that were attached to the sides of the two male compartments. The male chorus was composed of song recordings of the ten fathers of the birds in this study. These fathers were among the test subjects recorded in Boogert et al. (2008, Chapter 4). Detailed recording methods are described therein. The male chorus was created by assigning 3-min song recordings (containing natural silences between songs) of the ten fathers to three
tracks in Adobe Premiere Pro CS3. We formed a single 30-min sound file by overlaying these three tracks. The result was the sound of three songs from varying combinations of males singing continuously. The chorus was played through the speakers at a mean volume of 68 dB (min: 54 dB, max: 70 dB) at 20 cm from the speaker. As the chorus males were fathers of the test subjects, the test subjects had already been exposed to these songs in the breeding room during the first 65 days of their lives.

To control for morphological differences, we took a picture of each male against a white background with a Panasonic 3CCD camera and visually matched the candidate mates in each female preference test as closely as possible in terms of size, plumage, morphology and beak colour. In this way we selected eight pairs of candidate males who differed in their foraging techniques but were otherwise similar. We presented sisters with the same unrelated male pair to control for the influence of shared genotype and developmental conditions on female mate preferences (N = 31 females from 10 families). To ensure female mate preference was not guided by hunger, the female compartment was equipped with a filled food bowl. Within each pair of candidate mates, one of the males was banded with a white leg band and the other was banded with a dark blue leg band (A.C. Hughes, Hampton Hill, U.K.). These leg band colours were chosen to be neutral in terms of attractiveness to female zebra finches (Burley et al. 1982). The leg band colour assigned to the lid versus the stalk male in each pair was randomized. To control for female side bias, we changed the sides where males performed their respective foraging techniques between each consecutive mate choice trial.

We recorded all trials from above with a Panasonic 3CCD mini-DV recorder. To measure female preferences we used the video recordings to determine the time that the female spent sitting on the perch closest to each male compartment (Witte 2006) while facing that male compartment (Rutstein et al. 2007), a measure that has been shown to predict later pair formation (Clayton 1990a). Time spent on the front perch but facing backwards and time spent on other perches were excluded from analyses.

**Assortative pair formation based on shared foraging habitats**

A week after the tests of female preferences for male foraging behaviour were completed, we released the same birds in mixed-sex flocks of four males and four females in indoor
aviaries containing two foraging habitats. The aim of these aviary tests was to investigate whether assortative pairs could result from same-skilled males and females foraging in the same habitats. We created a lid habitat at one side of the aviary and a stalk habitat at the other. Four nest baskets, nest material dispensers and water bottles were available on the walls next to each foraging habitat (Figure 3). We tested eight flocks of eight birds each, consisting of two stalk-pulling males, two stalk-pulling females, two lid-flipping males and two lid-flipping females. Wherever possible we allocated stalk/lid sisters to the same group, together with the male pairs they had been presented with in the female preference tests. As we only had eight stalk/lid male pairs during the preference tests and we used the same males for the aviary tests, some male pairs were used in multiple aviary groups, but never in two groups tested consecutively. Across the eight aviary groups, we tested 18 male and 32 female zebra finches.

Each group was released into the aviary and video recorded for three consecutive days from 0800 to 1600 hours. Each of the 100 wells in the foraging habitats (50 stalk wells, 50 lid wells) was refilled with two millet seeds every two hours (at 0800, 1000, 1200 and 1400 hours). At 1600 hours, mixed millet seed was provided ad libitum until 0800 the next morning. Lights were switched off at 2000 and switched on again the next morning at 0800 hours.

For the third and final day of observations for each aviary group, we noted the foraging habitat (stalk or lid) and the identity of the solver for each occurrence of task solving. When an individual was not seen to solve at least 10 tasks during the third day, we reviewed earlier video recordings and included task solutions on previous days until the focal individual had been observed to solve a task at least 10 times. In addition, we recorded all occurrences of scrounging, along with the identity of the individual solving the task (i.e. producer) and the identity of the scrounger.

Finally, we recorded all pair formations. We determined that a pair had been formed when a male and female were repeatedly observed to be sitting together making physical contact and to be preening each other (Silcox and Evans 1982). For each nest, we recorded whether it was constructed on the stalk side or the lid side of the aviary (Figure 3).
The experiments described in this study were approved by the Animal Care Committee of the Université du Québec à Montréal, protocol #0807-592-0708 and conformed to all guidelines of the Canadian Council on Animal Care.

**Analyses**

*Female preferences for male foraging behaviour*

To analyze a female’s mate preferences, we calculated the proportion of time that she spent facing the stalk male’s compartment as compared to the total time spent facing either compartment in the mate choice apparatus. We arcsine-square-root transformed the resulting proportions to normalize their distribution. We used this measure of female preference as a response variable in a linear mixed-effects model that contained the following fixed effects: training treatment, test trial number, lid male’s identity, colour of lid male’s leg bands, lid male’s performance during observation phase and stalk male’s performance during observation phase. Random effects were female test subject’s identity nested within family. Lid and stalk males were matched for morphology and always presented in the same combination to female test subjects. Thus, lid and stalk male identities were perfectly correlated and only the lid male’s identity was included in the model to avoid co-linearity problems. Likewise, only the colour of the lid male’s leg bands was included, as it always complemented the stalk male’s leg band colour: dark blue or white.

The linear mixed-effects model of female preferences was run first on data collected during the No-Interaction tests conducted in the upper compartment of the mate choice apparatus and second using the Interaction test data from the lower compartment. We used backward selection to obtain the minimal adequate model with a selection criterion of $\alpha=0.05$.

We used a similar linear mixed-effects model to analyze female preferences in the task control tests conducted when the female was in the upper compartment of the mate choice apparatus, facing the male compartments that contained foraging tasks but no candidate mates. Fixed effects were training treatment and test number, while random effects were female identity nested within family.
We calculated the repeatability, $r$ (Lessells and Boag 1987), of females’ preferences and males’ task performances across the four No-Interaction test trials and across the four Interaction test trials. We checked whether the performance of lid males differed significantly from that of stalk males in the No-Interaction and Interaction tests using paired $t$-tests. In addition, we tested for significant differences between the two males’ task performances during the observation phase of each female preference test trial by assigning the number of tasks each male solved to a ‘better’ or ‘worse’ category, depending on the performance of the other candidate mate in that trial. We conducted paired $t$-tests to explore whether the difference between the ‘better’ and ‘worse’ performer was significant for each of the four No-Interaction and Interaction test trials.

To test whether the time females spent facing the compartment of the better performer depended on the difference in the males’ task performances, we ran another linear mixed-effects model. The response variable was the arcsine-square-root-transformed proportion of time females spent facing the compartment of the better performer, while fixed effects were test trial number, treatment, and the difference in the number of tasks performed by the ‘better’ and ‘worse’ performer (‘better’ minus ‘worse’). Random effects were female identity nested within family. We ran the model for both No-Interaction and Interaction test trials.

**Assortative pair formation based on shared foraging habitats**

We used Chi-Square tests to determine whether pairing was more assortative than expected by chance, and whether technique-matched pairs were more likely to construct their nests on the side of the aviary containing their foraging task, pooling data across groups. As the formation of second and subsequent pairs in the aviary flocks is not independent of previous pair formations (the set of available mates reduces with each subsequent pair formed), we also tested whether the first pair in each aviary flock was technique-matched more often than expected by chance. We used a paired Wilcoxon signed-ranks test to assess whether, in birds that started to solve both tasks, the latency to solve the trained task differed from the latency to solve the task on which they had not been trained. Finally, we tested whether scrounging occurred more frequently in disassortative than in assortative pairs using a generalized mixed-effects model with the
number of scrounging occurrences within a pair (Poisson-distributed) as the response variable and assortativeness of the pair as the predictor variable. We included male identity as a random effect to correct for the fact that some pairs in different aviary flocks contained the same male.

We used R version 2.8.1 (R Development Core Team 2008) for all of our analyses.

Results

Female preferences for male foraging behaviour

Task control tests revealed that females, in the absence of males, were indifferent and uninterested in the foraging tasks available in the mate choice apparatus. They spent no time facing either task compartment in 29 of the 122 task control tests (= 23.8%), and neither training treatment nor test trial number predicted the proportion of time they spent in front of the stalk compartment (linear mixed-effects model, treatment: estimate ± SE = 0.033±0.071, \( t_{20} = 0.462, P = 0.649 \); test: 0.024±0.028, \( t_{90} = 0.842, P = 0.402 \)). In contrast, in No-Interaction test trials all females showed interest in the task compartments. However, the foraging task that a female was familiar with had no influence on the mean proportion of time she spent facing one male or the other (Figure 4A) and the same was true for Interaction tests (Figure 4B). Females’ behaviour from one trial to another was not repeatable (Table 1) and could not be predicted by any of the variables included in the model.

The lack of female preferences for males that had either the same or a different foraging technique from theirs was not due to poor performance or lack of differences in foraging behaviour between males. There was a significant difference in the number of tasks solved in each test trial between the better and worse task performers, in the No-Interaction tests (test trial 1: \( t_{19} = 5.072, P < 0.001 \); test trial 2: \( t_{19} = 6.419, P < 0.001 \); test trial 3: \( t_{18} = 5.471, P < 0.001 \); test trial 4: \( t_{18} = 4.558, P < 0.001 \)) as well as in the Interaction tests (test trial 1: \( t_{28} = 6.733, P < 0.001 \); test trial 2: \( t_{29} = 6.099, P < 0.001 \); test trial 3: \( t_{29} = 7.997, P < 0.001 \); test trial 4: \( t_{29} = 7.378, P < 0.001 \)). However, the proportion of time females spent facing the better performer was not predicted by the magnitude of difference in performance between the better and worse task performer in the No-
Interaction tests (linear mixed-effects model, difference in performance: 0.009±0.023, $t_{46} = 0.397, P = 0.693$), nor in the Interaction tests (0.004±0.015, $t_{85} = 0.236, P = 0.814$). Lid males were consistent in their lid task performance (Table 2), both when they were facing their cage companions (No-Interaction tests), and when they were facing the female test subject (Interaction tests). Lid males did not differ significantly from stalk males in their task performance (paired $t$-test: $t_{77} = 0.556, P = 0.580$) across the four No-Interaction test trials. However, across the four Interaction test trials, stalk males performed significantly better than did lid males (paired $t$-test: $t_{118} = 4.108, P < 0.001$), despite the fact that individual stalk males’ performances were less repeatable across trials (Table 2).

**Assortative pair formation based on shared foraging habitats**

Assortative pair formation facilitated by exploitation of the same foraging habitats could occur only if flock members maintained their foraging specializations, which was the case in our birds: subjects solved only the foraging tasks on which they had been trained as juveniles. In total (i.e. including birds from all groups), 44 birds performed 1263 task solutions according to their taught foraging technique, while six birds (four males and two females, representing 12% of our captive population) were observed to solve both tasks during the third day of observation. Three of these birds had been trained on the stalk task and three on the lid task. Solving the task these birds were not trained on was still very rare: it occurred in only 23 of the 2222 task solutions scored across all aviary groups, representing 1% of all well-openings. The latency between contacting a task and solving it was significantly lower for the task these birds had been trained on ($\bar{X}±SE = 1.61±0.30$ s) than it was for the alternative task ($4.93±1.13$ s; paired Wilcoxon signed-ranks test: $Z = -2.201, N = 6, P = 0.028$). The birds were thus more efficient in solving the task of their specialisation than they were in solving the alternative task.

Across the eight aviary groups, 23 pairs were formed ($\bar{X}±SE = 2.88 ± 0.64$ per group). Of these, 11 were mated assortatively with regard to foraging technique (five lid male – lid female pairs, six stalk male – stalk female pairs), while the remaining 12 pairs were mated disassortatively with regard to foraging technique (seven lid female – stalk male pairs, five stalk female – lid male pairs). Thus, pair formation was random with regard to foraging technique (Chi-Square test: $X^2 = 0.044, P = 0.835$). This was still the
case when we considered only the first pair formed in each of the eight aviary flocks (assortative: three lid male – lid female pairs, one stalk male – stalk female pair; disassortative: three lid female – stalk male pairs; one stalk female – lid male pair; i.e. four assortative vs. four disassortative pairs). Of the seven nest locations we recorded for the assortative pairs (not all pairs had started to built nests), four nests were constructed on the side of the aviary containing tasks of the pair’s foraging specialization, and three nests were located on the other side. There was therefore no evidence that nest location was related to assortative pairs’ foraging specialisations.

Scrounging occurred significantly more often in disassortative than in assortative pairs (generalized mixed-effects model, assortativeness: estimate ± SE = -1.392±0.392, \( z_{20} = -3.547, P < 0.001 \); Figure 5). However, total food consumption did not differ between pair types (independent samples t-test: \( t_{19} = -0.192, P = 0.850 \).

Discussion

In this study, we used a mate choice apparatus to test whether female zebra finches would choose mates based on the specific foraging technique used or based on the males’ foraging efficiency regardless of technique. In a second experiment, we tested whether males and females trained on the same foraging technique would be more likely to form assortative pairs by exploiting the same foraging habitats in an aviary set-up. We found no indication of preference based on foraging technique or foraging efficiency in the mate choice apparatus. In the mixed-sex and mixed-technique flocks in the aviary, adults retained the foraging techniques they had acquired as juveniles. Although males and females trained on the same foraging technique thus shared the same foraging habitats in the aviary, pair formation was random with regards to foraging technique, and nest location was not associated with the habitat type most often exploited by the partners. The sample size of our study is similar to that of other zebra finch mate choice studies reporting significant effects of morphological and developmental traits on female preferences (Witte and Sawka 2003; Witte and Caspers 2006; Holveck and Riebel 2010). It is also comparable to Snowberg and Benkman’s study (2009) showing that female red crossbills prefer males with better foraging performance. Considering that female preferences in the mate choice apparatus and pair formation in the aviaries were
completely random with regards to foraging behaviour, we argue that the effect of foraging behaviour on mate choice in zebra finches is unlikely to be biologically relevant.

In our mate choice apparatus, females showed clear interest in the foraging males, but no interest in the foraging tasks when males were not present. Despite this interest in foraging males, females did not prefer males that shared their foraging specialisation either when the males could court them (Interaction condition), or when they could not (No-Interaction condition). Consistent differences in males’ foraging performance also did not significantly affect female preferences, in contrast to Snowberg and Benkman’s finding in red crossbills (2009). In fact, females showed low repeatability in their mate preferences across the four trials conducted both in the upper and lower compartments of the mate choice apparatus. Our results suggest that we successfully controlled for male differences in both morphology and song and show that females did not use male foraging behaviour to form a preference in the mate choice apparatus.

Even though females used neither foraging technique nor foraging efficiency to guide their mate preferences in our mate choice apparatus tests, outside our experimental context they may still choose mates that are more efficient in learning a novel foraging technique by assessing the males’ songs. In a previous paper on the fathers of the birds in this study (Boogert et al. 2008, Chapter 4), we found that males with songs composed of a larger number of song elements were faster at learning to solve an extractive foraging task analogous to the lid-flipping task in this paper. Furthermore, previous studies have shown that female zebra finches prefer songs with a larger number of syllables (Neubauer 1999; Holveck and Riebel 2007). Although females may not assess foraging efficiency through direct observation, they may be choosing efficient foragers as mates indirectly by selecting males with more complex songs. Foraging behaviour may not be suitable as a mate choice criterion because it can vary depending on the availability of food in the environment, the social foraging context, hunger levels and other confounding factors that make a short sampling of this behaviour less reliable as an honest indicator of male quality than traits such as song complexity and plumage brightness, which reflect a male’s developmental quality or condition over a more extended period of time (Birkhead et al. 1998; Nowicki et al. 2002).
While female zebra finches did not show repeatable mate preferences using the males’ foraging behaviour in the choice tests, they formed pairs within hours of release into the aviary, where they could assess male differences in song and morphology and share foraging habitats with males trained on the same foraging technique. The great majority (88%) of individuals in our zebra finch population exploited only the foraging habitat they had been trained on as juveniles. The six birds that exploited both habitat types exploited their non-trained habitat type only rarely and were significantly more efficient at exploiting the foraging tasks they had been trained on initially. Thus, foraging specialisations were by and large maintained during the three-day aviary tests in populations where half of all individuals performed an alternative behaviour to access food, and where the two food sources were not separated by any barrier. Similarly, Beauchamp et al. (1997) found that nutmeg mannikins (*Lonchura punctulata*) maintained their foraging specialisations for 10 consecutive days in flocks of four birds trained on two different foraging tasks, although pair formation was not considered in that study. Contrary to our prediction that pairs would form assortatively for foraging technique through exploitation of the same foraging habitat, both pair formation and nest location were random with regards to foraging specialisation.

Considering that the majority of birds maintained their foraging specialization, it would be interesting to explore how spatial scale and variation in food availability may affect pair formation and nest location. In our study the alternative foraging habitats were located less than a metre apart. In a significantly larger aviary where individuals would need to invest more time and effort to reach the alternative foraging habitat, foraging techniques may play a role in predicting social interactions and result in more positive assortative pair formation and nest location than expected by chance. Even though zebra finches are long-distance dispersers (Zann 1996), once settled in a colony in the wild individuals seem to differ in the food patches they prefer to exploit, and tend to arrive and leave food patches in small groups of the same individuals (Chapter 2; personal observations). When we first released the zebra finches into our aviary, they tended to fly to the side that contained the familiar foraging habitat. However, they then spent the first hour interacting with their aviary companions before showing interest in the foraging habitats, despite this time in the morning being their usual foraging peak. If the habitats
and associated nest sites had been spatially more segregated, birds may have spent more time in the side of the aviary containing the foraging habitat they were familiar with. Indeed, recent theoretical papers suggest that sympatric speciation might be possible through learned habitat preferences (Beltman and Metz 2005) and tradeoffs between adaptations to different habitats (Artzy-Randrup and Kondrashov 2006). On the other hand, if in our experiment we had provided food in only one habitat type at a time, hunger may have driven more exchange between the aviary sides and one might predict that disassortative pair formation would have prevailed. Even in the current set-up, scrounging occurred more frequently in disassortative than in assortative pairs, suggesting that disassortative mate choice with regards to foraging technique could be advantageous.

Previous work has reported assortative mating based on morphological and behavioural differences between zebra finch subspecies from the Australian mainland and Timor (Clayton 1990b), between domesticated and wild populations (Rutstein et al. 2007), and between birds from small versus large broods (Holveck and Riebel 2010). In those studies, birds were raised from birth by parents and/or with siblings of the type they later preferred as mates. Thus, another interesting avenue to explore would be to have parents exploit different types of foraging patches in the nesting environment without any period of ad libitum food availability, and test whether sexual imprinting on the parental foraging type would occur and result in assortative mate choice.

Acknowledgements

We would like to thank Kimberley Mathot for the idea of testing sisters and her help with breeding the zebra finches, Kimberly-Ann Côté and Dominique Drullion for their introduction to mate choice apparatuses and Julie Morand-Ferron for her help during experiments. We are grateful to Jeremy Schwartzentruber, Tim Fawcett, Sarah Overington, Kimberley Mathot, Mylene Mariette, Andrew Hendry and Katharina Riebel for extremely helpful comments on the manuscript.
References


Silcox AP, Evans SM. 1982. Factors affecting the formation and maintenance of pair bonds in the zebra finch, Taeniopygia guttata. Anim Behav. 30: 1237-1243.


Table 1: Repeatabilities ($r$) of female preferences for stalk male’s compartment

<table>
<thead>
<tr>
<th>Female training</th>
<th>Mean proportion of time facing stalk male (Min-Max)</th>
<th>Repeatability $r$</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
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<tr>
<td><strong>No-Interaction tests</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Lid</td>
<td>0.592 (0.00-1.00)</td>
<td>-0.082</td>
<td>16, 47</td>
<td>0.708</td>
<td>0.772</td>
</tr>
<tr>
<td>Stalk</td>
<td>0.559 (0.00-1.00)</td>
<td>-0.162</td>
<td>14, 43</td>
<td>0.463</td>
<td>0.941</td>
</tr>
<tr>
<td><strong>Interaction tests</strong></td>
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<td></td>
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<tr>
<td>Lid</td>
<td>0.527 (0.00-1.00)</td>
<td>0.084</td>
<td>15, 47</td>
<td>1.363</td>
<td>0.205</td>
</tr>
<tr>
<td>Stalk</td>
<td>0.494 (0.00-1.00)</td>
<td>0.016</td>
<td>13, 42</td>
<td>1.065</td>
<td>0.413</td>
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Table 2: Repeatabilities ($r$) of male task performance

<table>
<thead>
<tr>
<th>Male training</th>
<th>Mean # of tasks solved (Min-Max)</th>
<th>Repeatability $r$</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
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<td><strong>No-Interaction tests</strong></td>
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<tr>
<td>Lid</td>
<td>7.33 (0–12)</td>
<td>0.354</td>
<td>5, 72</td>
<td>7.758</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Stalk</td>
<td>7.68 (1–12)</td>
<td>0.096</td>
<td>6, 71</td>
<td>2.130</td>
<td>0.060</td>
</tr>
<tr>
<td><strong>Interaction tests</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lid</td>
<td>7.12 (0–12)</td>
<td>0.318</td>
<td>7, 111</td>
<td>7.617</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Stalk</td>
<td>8.75 (0–12)</td>
<td>0.043</td>
<td>6, 112</td>
<td>1.735</td>
<td>0.119</td>
</tr>
</tbody>
</table>

Significant results are given in **bold**.
**Figure 1.** The lid and stalk tasks. The base of the apparatus for the lid task (A) consisted of a wooden grid (26 x 22 x 2 cm) surrounded by corrugated-plastic walls (28 cm high) on three sides. Wooden cubes wrapped in blue tape were attached to the walls 4.5 cm from the cage floor at 4.5 cm intervals. Each cube contained one well (0.8 cm deep, 1.5 cm wide) with 2 white millet seeds, covered with a blue circular cardboard lid. The cardboard lid was lined with blue tape and pierced with a 1 cm-long screw. The screw was wrapped in foam material so that it fitted snugly into the well. To solve the task, the bird had to grab the edge of the cardboard lid with its beak and flip it out of the well.

The base of the apparatus for the stalk task (B) consisted of a wooden grid (26 x 22 x 2 cm) with two rows of 5 wells (0.8 cm deep, 1.5 cm wide) spaced 4.5 cm apart (only one well shown). Each well opening was at the centre of a triangle of yellow tape. Each well contained 2 white millet seeds and was covered with a wooden stalk wrapped in yellow tape, to which a vinyl bumper was attached at the bottom with a pushpin. To extract the seed, the bird had to grab the stalk with its beak and pull it out of the well.
Figure 2. The mate choice apparatus contained two levels, an ‘upper compartment’ and a ‘lower compartment’ that had two adjacent male compartments. When the female was positioned in the upper compartment for the No-Interaction test trials, she could watch two candidate mates solving their respective foraging tasks in the male compartments below her (black male symbol in (A)) through a Plexiglas window (the white 11.5 x 50 cm surface in the female upper compartment in (A)). The candidate mates were accompanied by their cage companions, positioned in adjacent compartments underneath the female’s compartment (grey male symbol in (A)) and thus not visible to her.

To conduct the Interaction test trials, females were positioned in the lower compartment (B) after the upper compartment and the companion males of the lower compartment (A) had been removed. For the first 10 min of the test, the female was confined to a smaller observation chamber in the back of the lower compartment. After this 10 min observation period, the female was released into the main section of the lower compartment so that she could approach and interact with the males through the wire mesh separating her from the male compartments.

Throughout the mate choice tests, candidate mates were separated by opaque dividers.
Figure 2.
Figure 3. Plan view of the aviary test setup. The thick black bars indicate perches, the brown cylindrical objects are nest baskets, the small blue rectangles are nest-material dispensers and the small grey circular objects are water bottles. The left side of the aviary contained the stalk habitat and the right side the lid habitat. The four white rectangles with foraging task symbols represent the foraging patches. The two patches in the middle contained 16 stalk or 16 lid tasks each, whereas the patches next to the nest boxes contained 34 stalk or 34 lid tasks each.
Figure 4. Mean proportion of time (± SE) that females trained on the lid task ($N=16$, dark grey bars) and females trained on the stalk task ($N=15$, light grey bars) spent facing the stalk male’s compartment in each of the four (A) No-Interaction and (B) Interaction test trials. Chance proportion, indicating random choice, is 0.5.
Figure 5. Total number of seeds mates scrounged from each other in assortative pairs (mean ± SE, N=10, white bar) and disassortative pairs (N=11, black bar).
Linking statement 4

Chapter 3 showed that domesticated zebra finch females did not use male foraging technique or efficiency to form mate preferences in a mate choice apparatus. When I released mixed-sex, mixed-foraging technique flocks into aviaries containing food patches that required different foraging techniques to exploit, birds exploiting the same food patches were not more likely to form pair bonds with each other than they were to form pair bonds with birds performing the alternate foraging technique. However, male foraging performance could still guide female mate choice indirectly if it showed a positive correlation with a sexually selected trait, such as song complexity. In Chapter 4, I test the prediction that males’ performance on a novel foraging test correlates positively with their song complexity.
Chapter 4:

Song complexity correlates with learning ability in zebra finch males

Abstract

In species with mate choice, the choosy sex selects its mate based on traits that are thought to indicate the mate's quality. In several bird species, females prefer males that sing more complex songs but it is unclear which aspect of male quality is signalled by this trait. Here we test the hypothesis that a male’s song complexity conveys information about his learning capacity. We recorded the songs of 27 male zebra finches, *Taeniopygia guttata*, and quantified their complexity by measuring average song phrase duration, the total number of elements and the number of unique elements per song phrase. We then presented each male with a novel foraging task and recorded the number of trials he required to solve the task. We found a positive correlation between song complexity and learning proficiency: males with more song phrase elements required fewer learning trials to solve the novel foraging task. This result suggests that a male’s song complexity signals his learning ability, which may have contributed to the selective pressures driving females to choose males with more complex songs.
Introduction

A trait is under sexual selection when variation in its expression affects success in mating competition and reproduction (Andersson 1994). A prominent example of a sexually selected trait is bird song: females prefer males with specific song features that may involve the song’s structure, rate of output and quality of vocal performance (see reviews in Nowicki and Searcy 2004; Kipper et al. 2006; Byers 2007). A commonly studied structural trait is ‘song complexity’, which is related to the number of different songs, syllables or elements that a male produces (i.e., ‘song repertoire’; Neubauer 1999; Buchanan and Catchpole 2000; Pfaff et al. 2007), but can also include the total number of syllables or elements and song phrase duration (Airey and DeVoogd 2000; Spencer et al. 2005a; Zeng et al. 2007). Virtually all studies on mate choice and song complexity report that females prefer males that sing more complex songs (reviewed in Searcy 1992; Nowicki et al. 2002; Nowicki and Searcy 2004). This is true for species widely ranging in repertoire size, from the zebra finch (Taeniopygia guttata), in which each male sings a single song consisting of 3 to 14 different syllables (Clayton and Pröve 1989), to species such as the song sparrow (Melospiza melodia) with 4 to 13 distinct songs (Reid et al. 2004) and starlings (Sturnus vulgaris), whose repertoires can contain up to 68 different songs (Mountjoy and Lemon 1996).

Whereas there is a consensus, based on empirical evidence from many species, that song complexity is a sexually selected trait, there is no such agreement concerning the information this trait conveys about the quality of its bearer. The ‘developmental stress hypothesis’ (Nowicki and Searcy 2004) currently guides the majority of research efforts on this topic and revolves around the link between song complexity and the brain structures underlying song learning. These ‘song control nuclei’ develop most during the first few months after hatching, the life stage in which birds are also most vulnerable to developmental stresses (e.g. food scarcity, parasite infections, social stressors) that may negatively affect brain development. Because brain development is metabolically costly, the proper development of the song system would act as a phenotypic revealer of the animal’s ability to cope with environmental challenges (Nowicki and Searcy 2005). Chicks that can afford to develop better song control nuclei and associated neural structures should also be able to learn more complex songs (Nowicki and Searcy 2004).
Females choosing on the basis of song complexity would then be selecting males who demonstrate superior genotypic and/or phenotypic quality (Nowicki et al. 2002).

A series of recent experimental studies has confirmed the detrimental effects of developmental stress on song complexity and the brain structures underlying song learning (Buchanan et al. 2003, 2004; MacDonald et al. 2006; Spencer et al. 2003, 2004, 2005a,b; Soma et al. 2006; Zann and Cash 2008; but see Gil et al. 2006). Concurrently, various studies set out to determine which mate quality traits might be signalled by song complexity. Thus far, most empirical data support the hypothesis that a male’s song complexity indicates his body condition and fitness. For example, in great reed warblers (*Acrocephalus arundinaceus*), females obtained extra-pair fertilizations from neighbouring males with greater song repertoires than their social mates. Offspring resulting from these extra-pair fertilizations by complex singers had greater post-fledgling survival (Hasselquist et al. 1996). In sedge warblers (*A. schoenobaenus*), males infested with parasites had smaller song repertoires and weighed less than non-parasitized males (Buchanan et al. 1999). In pied flycatchers (*Ficedula hypoleuca*), males with more complex songs were in better body condition and defended higher quality territories (Lampe and Espmark 2003). In common nightingales (*Luscinia megarhynchos*), males with larger repertoires had longer wings, were heavier and arrived at their territories earlier (Kipper et al. 2006). In song sparrows, males with larger repertoires were in better body condition and had a more robust immune system than those with smaller song repertoires (Pfaff et al. 2007), and also lived longer, raised a greater proportion of chicks to independence and recruited more offspring as well as grand-offspring (Reid et al. 2005).

How can song complexity be an indicator of body condition and longevity? Several authors have suggested that a male’s cognitive capacity may provide a link between his song complexity and quality as a mate (Catchpole 1996; Nowicki et al. 2000; DeVoogd 2004). This hypothesis is tenable from a neuroanatomical perspective in view of three findings: first, song complexity (i.e. song element repertoire, total number of song phrase elements and song phrase duration) is strongly correlated with the volumes of the song control nuclei in the brain (Airey and DeVoogd 2000); second, these song control nuclei volumes are positively correlated with the volume of the telencephalon, a brain region
associated with complex learning; third, the volumes of both the song control nuclei and the telencephalon are heritable (Airey et al. 2000). Thus, females selecting males on the basis of song complexity may, in effect, be selecting for particular neuroanatomical qualities that underlie both song development and cognitive processing in general. Males with more complex songs might be more proficient in other cognitively demanding behaviours, such as learning when, where and how to feed and how to recognize and avoid predators (Nowicki 2000; DeVoogd 2004; Griffin 2004). Females choosing such mates might obtain direct fitness benefits such as more reliable food supplies, a high quality territory, or lowered risk of predation. Females may also gain indirect fitness benefits when they produce offspring bequeathed with the father’s cognitive capacity, which would increase the offspring’s fitness in turn (DeVoogd 2004).

The cognitive capacity hypothesis implies that song complexity correlates positively with learning performance, but this crucial prediction has never been addressed empirically. We tested this prediction in the zebra finch, the model system of birdsong and mate choice studies, by quantifying the song complexity of males and measuring their learning speed on a novel foraging task. Here, we present the first empirical evidence that zebra finch males with more complex songs are faster learners.

Methods

Subjects and housing conditions

Domesticated adult male and female zebra finches were obtained from a local breeder in 2005. Upon arrival in the lab, each individual was fitted with one numbered light blue leg band (A.C. Hughes, Hampton Hill, U.K.) and housed with 1-2 other birds of the same sex in wire-mesh housing cages (57 cm x 29 cm x 42 cm) containing two perches and two reed nest baskets. Males and females were kept in separate rooms. Except during experiments, birds had ad libitum access to mixed millet seed, fresh water, cuttlefish bone and crushed oyster shells. Laboratory rooms were illuminated with standard 40 W and wide spectrum Gro-Lux® fluorescent tubes (Osram Sylvania, Danvers, U.S.A.) on a 12:12 h light:dark cycle (lights on at 0600, off at 1800 hours) and kept at 24±2 °C ambient temperature. The experiments described in this study were approved by the
Animal Care Committee of the Université du Québec à Montréal, protocol #0807-592-0708 and conformed to all guidelines of the Canadian Council on Animal Care.

**Procedure**

We recorded the songs and learning performance of twenty-seven adult male zebra finches. We tested four birds at a time so that we could film all trials, for three consecutive days in a laboratory room that was isolated visually and acoustically from the housing rooms.

On test day 1, we stimulated each male to emit directed song (Zann 1996) by transferring it to a wire mesh cage (53 x 29 x 38 cm) adjacent to a similar cage containing a female zebra finch (see Brumm and Slater 2006). The two cages were surrounded by an echo-suppressing shell (92 x 70 x 42 cm) made of high-density fibreglass covered with cotton cloth, carton and plastic sheets, to reduce the background noise volume on the song recordings. We recorded males’ songs with an AT835b Shotgun condenser microphone and a Tascam DP-01FX/CD digital hard disk recorder. We presented the same stimulus female to the four males in a test group. When a male did not sing, we returned it to the housing room and made another attempt to record its song later that day. If the second song recording attempt failed, we replaced the female with another bird from the set of five stimulus females we used to elicit directed song. Zebra finch males are ‘critical period learners’ that sing the same stereotyped sequence of elements after their song has crystallized at around 90 days (Williams 2004). When males are courting females, their songs have a faster tempo, the sequence and fundamental frequency of the syllables are less variable and they are less likely to start in the middle of a phrase than when these males sing the same song but without a female audience (Williams 2004, Woolley and Doupe 2008). Although the calls of the stimulus female in response to the courting male may affect the probability that the male truncates or adds a note to his song phrase (Williams 2004), we analyzed complete song phrases only. Thus, we consider it unlikely that any small changes induced in the males’ song phrase structures affected our results. Song recordings were made between 0700 and 1500 hours.

At 1500 hours, we transferred each of the four birds to its own wire mesh cage (53 x 29 x 38 cm) containing four perches and water, mixed millet seeds and oyster shell ad
Cages were positioned next to each other but were separated by cardboard partitions so that males could hear but not see each other. Birds were food deprived from 1700 hours until 0730 hours the next day. The 2.5 light hours of food deprivation increased birds’ motivation to engage in solving the foraging task, while this amount of time not spent feeding is within the range observed in the wild (Zann and Straw 1984) and in captivity (Dall and Witter 1998).

We started the learning performance test at 0730 hours on test day 2 by presenting each bird with a foraging task containing 20 seeds. If the test subject did not solve the task during the 15-minute learning trial it was given free access to the 20 seeds at the end of the trial. We gave each bird one 15-minute trial per hour for a total of 17 trials: 9 trials on test day 2, and 8 trials on test day 3. After the final trial of a day, test subjects could feed *ad libitum* for two hours, after which they were food-deprived for another 2.5 light hours (and 12 night hours) until the next learning test day.

**Task apparatus and learning test protocol**

The base of the task apparatus consisted of a wooden foraging grid (26 x 22 x 2 cm) containing 10 wells (0.8 cm deep and 1.3 cm wide) with centre points 6 cm apart. Each well contained 2 white millet seeds and was covered with a lid. The lids consisted of blue cardboard circles (3.5 cm diameter) with small metal rings (1.2 cm diameter, 0.1 cm high) taped on top to weigh them down. We covered the upper sides of the lids and the metal rings on top with blue electrical tape, while the undersides had vinyl bumpers (1.3 cm diameter, 0.3 cm high) taped in the centre that fitted exactly in the wells of the foraging grid. Lids weighed 4.26 ± 0.1 g. To solve the task, a bird had to flip the lid off the well to gain access to the seeds. The difficulty of the task varied across four levels. At level 1, the lids were positioned next to the wells; at level 2, half of each well was covered by the lid; at level 3, the wells were fully hidden from view by the lids; and at level 4, the lids’ vinyl bumpers were fitted into the wells. Thus, in the final, most difficult level of the task, the test subject had to flip the lid up to lift the vinyl bumper out of the well to reach the millet seed reward.

We used a systematic shaping procedure (Seferta et al. 2001) to lead the subject progressively through the levels of the task. When the bird managed to reach the seeds in
2 of the 10 wells, it passed on to the next level of difficulty on the next trial, whereas failure to do so (i.e., when feeding from \( \leq 1 \) well) returned it to the previous difficulty level on the next trial. After a trial ended, we uncovered the wells that the test subject had not accessed during the trial, to provide the zebra finch with the 20 seeds per hour required to fulfill its energetic demands (Zann 1996). Just before the start of the next trial, we removed the foraging grids and lids from the individual cages, refilled the wells with seeds and covered them again with the lids. The next trial started with the presentation of the replenished foraging grids. We recorded all learning trials using a Panasonic 3 CCD mini DV recorder with a wide-angle lens.

Analyses
We analyzed the zebra finch song recordings with Avisoft-SASLab Pro 4.36 software (Avisoft Bioacoustics, Berlin, Germany). All song recordings were first high-pass-filtered (cut-off frequency: 0.4 kHz; Hamming window: 1024 coefficients) to remove low-frequency background noise (Brumm and Slater 2006). For each bird’s song, we analyzed 10 song phrases and averaged the results. We used the same song measures and methods as Airey and DeVoogd (2000) to estimate song complexity, recording the total number of elements per song phrase, the number of unique elements per song phrase, and song phrase duration in milliseconds. Introductory elements were not considered part of the song phrase and were excluded from analyses. The waveform amplitude was used to distinguish song elements: when it returned to baseline, we treated adjacent elements as separate. We used duration, the number and distribution of harmonics, and frequency modulation to categorize elements as ‘same’ or ‘different’ (Figure 1). Such classifications of complicated song structures are somewhat subjective and different researchers are likely to make slightly different judgments. To check if we had applied our criteria in accordance with the song analysis methods in Airey and DeVoogd (2000), we asked Prof. T. DeVoogd (TDV) to score our song recordings. We also asked an independent expert on zebra finch song, Prof. H. Williams (HW), to analyze our songs. Neither of these experts had information on the foraging task performance of individual birds. We estimated agreement between our scores and those of HW by computing intra-class correlation coefficients (ICCs) with a two-way random effects model (accommodating
variation due to raters as well as due to bird performance) that tested for absolute agreement. In this model, the expected correlation coefficient (‘test value’) with which the observed correlation coefficients were compared was 0.5. We also computed Cronbach’s $\alpha$, a measure that describes internal consistency based on the average inter-item correlation. Cronbach’s $\alpha$ increases with increasing correlations up to $\alpha = 1$, which indicates absolute agreement between the items under study.

Our measure of zebra finch learning performance was the cumulative number of trials required by each male to solve the final level of the lid flipping task. One male required 10 learning trials to feed from a well with the lid next to it (task level 1) and was excluded from all analyses. We considered this test subject to be too neophobic and/or unmotivated to participate in the test (Sanford and Clayton 2008) and its learning score might not have been representative of its learning capacity. Of the remaining 26 test subjects that fed next to the lid in <10 trials, males that did not solve the final level of the learning task within the 17 trials of the experiment were assigned a learning score of 18 trials (i.e., the maximum of 17 + 1). As the assigned value of 18 is arbitrary, we analyzed our learning data with and without non-solvers, and report both results below.

We used the Kolmogorov-Smirnov test to check whether the data conformed to a normal distribution and resolved non-normality with a natural log (‘ln’) transformation. We used Pearson correlations to explore the relationships between the three song measures, and tested for an association between these song measures and learning performance with linear regressions including ln(phrase duration), ln(total # of song phrase elements) and ln(# different song phrase elements) as predictors of ln(cumulative # learning trials required to solve the foraging task). Independent variable selection followed a stepwise procedure, where the statistical significance of F-tests determined whether the independent variables were included ($\alpha \leq 0.05$) or excluded from the model. We conducted all analyses in SPSS v. 15.0.

Results
Agreement between our song complexity analyses and those of TDV and HW was high. TDV found virtually the same total number of elements and number of unique elements (+/-1) for all birds but one that differed by 2 unique elements. The number of unique song
phrase elements assigned to this bird did not influence the results. Our element counts and those of HW differed by 1-2 elements for eighteen birds, by 3 elements for one bird and by 4 elements for two birds, due to our exclusion of introductory elements and our tendency to divide syllables into more elements. Cronbach’s $\alpha$ and the ICC’s (lower - upper bounds of 95% confidence intervals) between our song variable scores and those of HW were, for the total number of song phrase elements: $\alpha = 0.91$ and ICC = 0.91 (0.79-0.96), $F_{0.05, 25, 26} = 5.47$, $P < 0.001$; for the total number of different song phrase elements: $\alpha = 0.78$ and ICC = 0.78 (0.51-0.90), $F_{0.05, 25, 25} = 2.27$, $P = 0.022$; and for song phrase duration: $\alpha = 0.97$ and ICC = 0.97 (0.93-0.99), $F_{0.05, 25, 26} = 16.98$ and $P < 0.001$.

With regard to the relationships between our three song measures, we found that the total number of elements in a song phrase correlated positively with average song phrase duration (Pearson correlation test: $r = 0.70$, $N = 26$, $P < 0.001$) and with the number of different song phrase elements ($r = 0.41$, $N = 26$, $P = 0.037$). Song phrase duration did not correlate with the number of different song phrase elements ($r = 0.08$, $N = 26$, $P = 0.70$).

Six of the 26 males that required < 10 learning trials to feed next to the task’s lid at task level 1 did not solve the final level of the lid flipping task and were assigned a learning score of 18 trials. We found the same qualitative relationship between song complexity and learning performance whether we included or excluded non-solvers. Linear stepwise regressions showed that total number of song phrase elements was the only significant predictor of learning performance: males whose song phrases contained more elements required fewer trials to solve the final level of the lid flipping task ($R = 0.53$, $F_{1,24} = 9.50$, $P = 0.005$; Figure 2). When non-solvers were excluded, total number of song phrase elements still predicted learning performance ($R = 0.57$, $F_{1,18} = 8.63$, $P = 0.009$), and explained slightly more of the variance in the data ($R^2 = 0.32$, $N = 20$) than when the regression included both solvers and non-solvers ($R^2 = 0.28$, $N = 26$). Residuals of both regressions were normally distributed.

**Discussion**

We found that in domesticated zebra finches, males with more complex songs were faster to learn the solution to a novel foraging task. This finding supports the hypothesis that song complexity might be an honest indicator of learning capacity. Thus, females that
select males with more complex songs are effectively choosing mates that may learn more quickly than less complex singers where and when to find different food sources and how to exploit them efficiently.

In our study, the total number of song phrase elements was the only song measure that explained a significant proportion of the variance in learning performance. Number of song components is an important character in zebra finch mate choice, given that females prefer the songs of control males over songs of developmentally stressed males that contain fewer syllables (Spencer et al. 2005a), and given that, out of nine song measures, it is one of the best predictors of mate choice (Holveck and Riebel 2007).

It is unclear, however, whether female zebra finches’ preference for songs with more syllables (Spencer et al. 2005a; Holveck and Riebel 2007) extrapolates to songs with more elements, as operational definitions of syllables and elements vary between studies (Jones et al. 2001; Holveck and Riebel 2007). The fact that our song element counts were mostly consistent with those of two independent experts indicates that this song measure is robust. The lower agreement between our repertoire size estimates and those of Prof. H. Williams suggests that the procedure of categorizing elements as ‘same’ or ‘different’ is more susceptible to subjectivity. Even if all experimenters agreed on an exhaustive set of criteria to distinguish syllables or elements, however, the right set of criteria can only be obtained by asking the truly relevant raters, zebra finch females.

The number of song phrase elements explained 28-32% of the variance in learning performance in our experiment. It should be noted, however, that we tested zebra finches that were not experimentally stressed during development. Our finding suggests that even in captivity, where resource availability should meet developmental needs, individual differences in genetic constitution and/or social stimulation resulted in sufficient variation in cognitive development to detect a significant relationship between a sexual display and learning performance. Exposure to harsher environmental conditions and various stressors in the wild is likely to result in more individual variation in development, which could lead to more pronounced differences in learning performance.

The cognitive capacity to learn how to quickly adapt to variable foraging conditions might make the difference between life and death for individuals of many bird species. Although the hypothesis that greater learning capacity enhances fitness seems to be
widely accepted, it has been tested only with comparative analyses of brain sizes at the species level. Sol et al. (2007) showed that bird species with larger brains experience lower mortality in the wild than species with smaller brains. We are not aware of any long-term field study that has explored the relationship between individuals’ cognitive traits and their fitness, even though it would be feasible to incorporate a cognitive test in the series of ornithological measures commonly taken. A study by Both et al. (2005) on avian personality illustrates that simple and reliable tests can be developed to collect data on the explorativeness of hundreds of individuals from a wild bird population and relate this behavioural trait to birds’ fitness. Similarly, learning proficiency could be measured in wild bird populations, potentially using single tests that involve methods and tasks very similar to ours. Such tests have already been conducted on wild birds in short-term captivity and resulted in learning measures that correlated strongly with relevant traits in several species (e.g., in pigeons *Columba livia* and doves *Zenaida aurita*, learning performance vs. neophilia: $R^2 = 0.78$, Seferta et al. 2001; in starlings *Sturnus vulgaris*, learning vs. dominance: mean $R^2 \pm SD = 0.77 \pm 0.11$, Boogert et al. 2006, and learning vs. innovativeness: $R^2 = 0.55$, Boogert et al. 2008). We encourage those researchers working on long-term studies of bird populations to include measures of cognitive traits, so that these can be related to song complexity, body condition, mate choice and fitness and improve our understanding of the selective forces driving passerine evolution.

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References


Boogert NJ, Reader SM, Laland KN. 2006. The relation between social rank, neophobia and individual learning in starlings. Anim Behav. 72: 1229 -1239.


Spencer KA, Buchanan KL, Goldsmith AR, Catchpole CK. 2003. Song as an honest signal of developmental stress in the zebra finch (Taeniopygia guttata). Horm Behav. 44: 132–139.


**Figure 1.** Spectrograms of zebra finch male song phrases. The horizontal axis represents time in seconds, the vertical axis is the sound frequency in kHz. The transparent boxes cover introductory elements that were excluded from analyses. The brackets distinguish song elements, and letters indicate which elements were categorized as being unique (new letter) or the same (reused letter) within each bird’s song phrase. A) The characteristic song phrase of Bird 155 contained a total of 13 elements, but only 9 different elements as this male repeated its elements a, b, d and e. B) Bird 170’s characteristic song phrase contained a total of 8 song elements, with each element being different from the others as this male did not repeat any of its song elements.
**Figure 2.** The relationship between ln-transformed total number of song phrase elements in a zebra finch male’s song and ln-transformed cumulative number of learning trials it required to solve the final level of the foraging task. Each ● represents the data for one zebra finch male that solved the task, while each ▲ represents the data for one zebra finch male that did not solve the final level of the task and was assigned a maximum learning score of 18 trials. The enlarged symbols represent two datapoints lying on top of each other. The equation of the regression line (± SE) for all test subjects shown is ln(cumulative # trials required to solve task) = 4.868 (±0.832)–1.035 (±0.336) * ln(total # song phrase elements). When non-solvers are excluded, the intercept is 4.371 (±0.762) and the slope -0.892 (±0.304).
Linking statement 5

In Chapter 4, I showed that domesticated zebra finch males with the most complex songs were also the fastest learners. Males that required fewer learning trials to solve a novel foraging task sang songs with more song elements than did males that were slower to solve the task. Female zebra finch preferences for more complex songs might therefore lead them to choose males with a greater ability to learn to solve novel foraging problems.

In Chapter 5, I test whether this finding is generalizable to a wild bird species with a larger song repertoire, the song sparrow (*Melospiza melodia*).
Chapter 5:

Song repertoire size correlates with learning test performance in song sparrow males

**Status:** Boogert NJ, Anderson RC, Peters S, Searcy WA, Nowicki S. Song repertoire size correlates with learning test performance in song sparrow males. *In preparation.*
Abstract

In many bird species, females prefer males with larger song repertoires or more complex songs. Song quality might be an indicator of developmental stress, as chicks subjected to fewer stressors develop larger neuronal structures and higher quality songs as adults than their more stressed counterparts. Developmental stress is also deleterious to the brain structures underlying more general cognitive processes that might be crucial for survival. We hypothesized that song quality might be used as an indicator of cognitive capacity by females when choosing a mate, and tested the prediction that song repertoire size correlates positively with performance on a range of learning tests in song sparrows. In this species, females prefer males with larger song repertoires, and song repertoire size correlates with various fitness measures. We tested song sparrow males on motor, colour discrimination, reversal learning and inhibitory control tests. We found that individuals’ performance on the colour discrimination test correlated positively with their performance on the reversal test, but performance did not correlate across any of the other learning tests. Males with larger song repertoires performed better on an inhibitory control test, but worse on a reversal learning test than males with smaller song repertoires. This is surprising as both tests are supposed to assess behavioural flexibility. Although our results suggest that song quality does correlate with some aspects of cognitive performance, more detailed song analyses and further cognitive tests are required to answer the questions raised by our findings.
**Introduction**

Bird song is a prominent example of a sexually selected trait (Andersson 1994): females in various species prefer males with larger song repertoires or more complex songs (reviewed in Searcy 1992; Nowicki et al. 2002a; Nowicki and Searcy 2004; Boogert et al. 2008; Catchpole and Slater 2008). However, this observation raises the question of what information is conveyed by a male’s song repertoire. If larger song repertoires are favoured by sexual selection and are honest indicators of male quality, they should be costly to produce and/or maintain (Zahavi 1975). But which aspects of song repertoire development or production are costly, and which qualities are indicated by a male’s song repertoire size?

With regards to the cost of this sexually selected signal, the developmental stress hypothesis (Nowicki et al. 1998; Buchanan et al. 2003; Nowicki and Searcy 2004) poses that the brain structures underlying song learning (the ‘song control nuclei’) develop most during a period in which chicks are also most susceptible to developmental stresses (e.g. food scarcity, parasite infections, sibling competition). Chicks subjected to more intense stresses and/or with less genetic resistance to these stresses should thus have poorer neuronal development. As a result, they may copy adult songs less accurately, and end up with lower quality, and therefore less attractive, songs as adults than their less stressed or genetically more robust counterparts. Most empirical tests of the developmental stress hypothesis confirm that some aspect of adult males’ song complexity or performance is negatively affected by exposure to experimental stressors during the first month of life (reviewed in Brumm 2009; Searcy and Nowicki 2009; Searcy et al. 2010; although see Gil et al. 2006; Bolund et al. 2010; Müller et al. 2010), or by large-scale genetic disruptions due to inbreeding (Reid et al. 2005a).

Why should females care about the developmental history of candidate mates? Are there any advantages to mating with a good singer, in addition to the potential indirect benefits of producing offspring with the genes to cope with developmental stresses and the ability to learn to sing attractive songs? Recent studies suggest that males’ song repertoire size also correlates with their body condition, territory quality, longevity and fitness (reviewed in Boogert et al. 2008; Catchpole and Slater 2008). One of the factors that may link a male’s song complexity with these qualities is his cognitive capacity (Catchpole
Developmental stresses not only negatively affect development of the song control nuclei (reviewed in Searcy and Nowicki 2009), but also the brain structures underlying more ‘general’ cognitive processing (e.g. telencephalon in swamp sparrows *Melospiza georgiana*: Nowicki et al. 2002a; hippocampus in western scrub jays *Aphelocoma californica*: Pravosudov et al. 2005, and in rats *Rattus norvegicus*: e.g. de Souza et al. 2008; McCormick et al. 2010). This translates to poorer performance on learning and memory tests in birds as well as mammals (e.g. in zebra finches *Taeniopygia guttata*: Fisher et al. 2006, Donaldson 2009; kitiwakes *Rissa tridactyla* and *R.* *brevirostris*: Kitaysky et al. 2003, 2006; rats: Castro et al. 1989, de Souza et al. 2008, McCormick et al. 2010; sheep *Ovis aries*: Erhard et al. 2004, and in humans: e.g. Levitsky and Strupp 1995; Lupien et al. 2009).

The fact that developmental stresses affect both song learning and more general cognitive processes suggests that females who prefer males with higher song quality may obtain mates that are more proficient in other cognitively demanding behaviours as well, such as learning when, where and how to feed (Nowicki et al. 2000; DeVoogd 2004). A recent test of this prediction in domesticated zebra finch males in captivity provided the first empirical evidence that males with more complex songs were faster at learning the solution to a novel foraging task (Boogert et al. 2008; Chapter 4). However, zebra finches are a domesticated species in which each male sings a single song, and males were tested on a single learning task. This result begs replication in a wild bird species with a larger song repertoire and using a greater variety of learning tests. The aim of this study is to investigate the relationship between song repertoire size and learning performance in song sparrow males (*Melospiza melodia*). The song sparrow is an excellent species to address this relationship, as it is already known that: 1) females prefer males with more accurately learned songs (Nowicki et al. 2002b) and larger song repertoires (Reid et al. 2004), 2) developmental stress negatively affects song control nucleus volume, telencephalon volume and song quality in the swamp sparrow (*Melospiza georgiana*), a close relative of the song sparrow (Nowicki et al. 2002a), 3) song sparrow males with larger repertoires are in better body condition, are more heterozygous and thus more outbred (Reid et al. 2005a) and have a more robust immune system than those with
smaller song repertoires (Pfaff et al. 2007), 4) males with larger repertoires live longer, raise a greater proportion of chicks to independence and recruit more offspring and grand-offspring (Reid et al. 2005b), and 5) song sparrows are diet and habitat generalists (Arcese et al. 2002) that show low neophobia (a correlate of learning, Boogert et al. 2006; Bouchard et al. 2007) in the field (Greenberg 1989) and in captivity (Greenberg 1990).

In this study, we predicted that male song sparrows with larger song repertoires would be more proficient at learning to solve novel foraging problems. We designed foraging problems that required song sparrows to adapt foraging behaviour from their normal repertoire to a novel context. We presented four tasks: A) a lid flipping task similar to Boogert et al. (2008); B) a colour discrimination test; C) a colour-reversal test, and D) an inhibitory control test that required birds to detour around a transparent obstacle to extract a mealworm inside. These tasks are based on foraging situations that song sparrows are known to encounter in the field, such as flipping obstacles to find food (the fronds of Laminaria spp. to find amphipods; Arcese et al. 2002) and cueing in on differently coloured plants to extract larvae (e.g. Nootka rose *Rosa nutkana* and common snowberry *Symphoricarpos albus*; Arcese et al. 2002).

**Materials and methods**

*Song recordings*

We recorded at least 300 songs for each of 52 song sparrow males in the vicinity of Linesville, Hartstown and Geneva, in Crawford County, PA, USA, between April 20th and June 1st 2009 (*N* = 24), and between May 3rd and June 2nd 2010 (*N* = 28). Playback of song sparrow song was used to locate territory owners and their territories’ boundaries, as well as to elicit song when a focal male had stopped singing. Depending on a male’s song rate and motivation to sing, the recording of ≥ 300 songs took between 1.5 and 6 hours. When the recordings for a male were made over two consecutive days, we cross-checked songs to ascertain we had recorded the same male on both days. For recordings, we used a Marantz PMD 670 digital recorder connected to a Realistic 33-1070B microphone in a Sony PBR-330 parabola.
Capture and housing

Males for which we had recorded \( \geq 300 \) songs were caught in mist nets and immediately transported to a laboratory where they were weighed, banded with a unique combination of three plastic colour bands and housed singly in holding cages (45.5 x 26 x 22.5 cm) that were inside sound attenuation chambers (AC-1, Industrial Acoustics, Bronx, NY, USA; 68.6 x 64.8 x 52.1 cm) on a 15:9 h light:dark cycle (lights on at 0600, off at 2100 hours). Birds had free access to mixed songbird seed (Canary Forti Diet) topped with mealworms (larvae of the beetle *Tenebrio molitor*) and water upon arrival until the next morning at 0545 hours, at which time the food dishes were removed and water and cage bedding refreshed. Upon finishing the cognitive test trials, between 1130 and 1200 hours, food dishes containing bird seed were returned, until 0545 hours the next day. Thus, the first day of captivity was the only time at which mealworms were freely accessible. From day 2 in captivity onwards, song sparrows could only obtain mealworms by participating in our cognitive tests.

Cognitive testing procedure

Cognitive test trials started each day at 945 hours, after the song sparrows had been deprived of food for 4 hours. Pilot trials indicated that this period of food deprivation was necessary to increase song sparrows’ feeding motivation to a sufficient extent to participate in our four cognitive tests: A) a motor test, B) a colour discrimination test, C) a reversal test, and D) an inhibitory control test.

Protocol for Tests A, B, and C

For each test, we presented each song sparrow male with two foraging grids (13.5 x 9 x 2.5 cm) of plastified wood, placed adjacent to each other, and containing 6 wells (1.3 cm diameter, 0.8 cm deep) each. The cage door was too small to fit one large foraging grid with 12 wells. During each test trial, four of the 12 wells contained one mealworm each. These cognitive tests required flipping blue and/or yellow circular plastic lids (2.2 cm diameter, 0.05 cm high) from the wells to access the mealworm reward underneath. Each lid was fitted with a vinyl bumper (1.3 cm diameter, 0.3 cm high) that fit exactly into the
wells. Each trial of tests A), B) and C) started with the presentation of the foraging grids and lasted 10 minutes, after which the foraging grids, lids and any uneaten mealworms were removed. The first trial started at 0945 hours and birds received trials every 30 minutes until six 10-min trials had been completed.

A) Motor test

We adopted a shaping procedure slightly modified from that described in Boogert et al. (2008, Chapter 4) to test each song sparrow’s speed of learning to flip lids off wells to obtain a mealworm reward. Test subjects learned this motor task in five stages. In stage 1, four mealworms were placed in four randomly selected wells; in stage 2, four lids (2 yellow, 2 blue) were positioned next to the four baited wells; in stage 3, the coloured lids were half-covering the baited wells; in stage 4, the lids were hinged/propped up in the wells, so that the lids were at an angle with the wells but the test subjects could not see the mealworms underneath the lids; and in stage 5, the vinyl bumpers of the lids were fit snugly into the wells, requiring the test subject to grab the lid with its beak to flip it off the well. We recorded the number of mealworms each bird had obtained after it was presented with the task for 10 min. For each task level, ‘success’ was defined as obtaining 3 or 4 mealworms, ‘failure’ was defined as obtaining 0 or 1 mealworm(s), and ‘neutral’ was defined as obtaining 2 mealworms. When a male failed during three consecutive trials, it regressed to the previous stage. When a male succeeded during three consecutive trials, it proceeded to the next stage. When a male obtained a neutral result, it stayed on the same task stage. To pass the final level of the motor test, stage 5, a bird had to obtain 3 or 4 mealworms in 6 out of 7 consecutive trials.

B) Colour discrimination test

Immediately after a test subject passed the motor test, we proceeded to the colour discrimination test. For each bird, we randomly chose one lid colour (yellow or blue) to be rewarded. In each trial, 8 of the 12 wells were used, four of which were covered by yellow lids and four by blue lids. Only wells covered by lids of the rewarded colour contained mealworms. For each trial, the positions of blue and yellow lids were determined randomly, using a customized randomization macro in Excel. Each trial was
observed through the screen door of the acoustic chamber in which the test subject was housed, and the order of the lid colours the test subject flipped was recorded. For each trial, a bird obtained ‘success’ if the first lid it flipped was of the rewarded colour and if it continued to flip all 4 rewarded lids before flipping any of the unrewarded lids. ‘Failure’ was defined as flipping the unrewarded colour during any of the first four flips. To pass the colour discrimination test, the test subject had to flip the rewarded colour for the first four flips in a trial during 6 out of 7 consecutive trials.

C) Reversal test
In the reversal test, we rewarded only the lid colour that had been unrewarded during the colour discrimination test. Otherwise, the test proceeded as B).

Protocol of the Inhibitory control test D)
In 2010 we added the inhibitory control test to our cognitive test battery and tested the final 22 birds of the sample (N=28) that season. The day after a song sparrow male had passed test C), we removed its food for 90 min before presenting it with the inhibitory control test: a dead mealworm was positioned in the centre of a horizontal plastic cylinder (5 cm length, 4 cm diameter) fashioned from plastic sheeting (0.1 cm thickness) and glued to a wood base (5 x 4 x 0.6 cm). During the habituation and training phases, the cylinder was opaque (wrapped in black window film), whereas it was transparent during the test phase. Each individual was presented with the opaque/transparent cylinder for a maximum of 20 trials per day.

D.1) Habituation phase
The goal of the habituation phase was to reduce test subjects’ fear of the novel object (or ‘neophobia’, Greenberg 1990). We presented the black opaque cylinder containing a dead mealworm in the right side of the cage, equidistant from, and with the openings facing, the front and back of the cage. Every 10 min we checked whether the test subject had consumed the worm. Each trial was followed by a 2 min time-out, during which the cylinder was left inside the cage. If the mealworm had been consumed, a different cylinder was baited and swapped with the empty cylinder at the start of the next trial. The
test subject passed the habituation phase and started the training phase if it consumed the mealworm in three consecutive 10 min trials.

**D.2) Training phase**

The goal of the training phase was for the test subjects to learn to detour to the side of the cylinder to obtain the food reward. The training phase was the same as the habituation phase except each trial was observed by the experimenter, who recorded 1) latency to retrieve the mealworm and 2) whether the test subject pecked at the opaque sides of the cylinder to remove the mealworm (incorrect) before retrieving it from one of the openings (correct). Test subjects moved on to the test phase once they had retrieved the mealworm from the opaque tube on their first attempt, without pecking the sides of the cylinder first, in 4 out of 5 consecutive trials.

**D.3) Test phase**

Once a test subject had learned to detour to the front or back of the opaque cylinder to obtain the mealworm, we presented it with a baited transparent cylinder. Because the test subjects could see the mealworm through the transparent sheeting, most of them were initially more inclined to peck the sides of the cylinder (incorrect) than they were to use the previously acquired detour movement to the front or back of the cylinder (correct) to retrieve the mealworm. The experimenter took the same two measures as during the training phase. However, test subjects had to retrieve the mealworm from the transparent tube on their first attempt (i.e. without pecking the sides of the cylinder first), in 6 out of 7 consecutive trials to pass the inhibitory control test.

Once a song sparrow male had passed all four cognitive tests, it was provided with seed and mealworms *ad libitum* for several hours, after which it was fitted with a U.S. Fish and Wildlife service aluminum band and released at its site of capture in the afternoon. All experiments were conducted under University of Pittsburgh IACUC protocols 090510107-A (2009) and 0904772A-1 (2010).
Analyses

All song recordings were digitized at 22050 points/s and 16-bit resolution, and examined spectrographically at 172.3 Hz frequency resolution and 5.8 ms time resolution using Syrinx-PC version 2.6h (John Burt 2006; www.syrinxpc.com). Two experimenters (NJB and RCA) scored the number of song types sung by each song sparrow male. These song repertoire size measures were made blind to the cognitive performance of the test subjects and checked by a third experimenter (SP).

For the motor test (A), we planned to use task stages 1, 2 and 3 as measures of habituation to captivity and neophobia. However, all test subjects passed these stages in the minimum number of trials, possibly because the mealworms were visible and could thus be easily obtained. As there was no inter-individual variation in scores for these first task stages, we omitted them from subsequent analyses. We summed the number of trials that each male required to pass task stages 4 (hinged lids) and 5 (snugly fitted lids), where the mealworms were no longer visible, and used this cumulative number of trials to learn to flip lids as the motor test score for each bird. For the colour discrimination tests, each male’s score was the total number of trials it required to flip the rewarded colour-lid for the first four flips in 6 out of 7 consecutive trials (i.e. including the final six successful trials). The same scoring method was used for the reversal test. A song sparrow’s score on the inhibitory control test was the number of trials it required to pass the test phase (i.e. obtain the reward from the transparent tube), and included the final six successful trials as well.

We performed a Principal Components Analysis to investigate whether the variance in the cognitive test performances could be explained by a single factor extracted from the data. If so, this would suggest the existence of a general cognitive ability (or ‘g’) underlying these behaviours (Galsworthy et al. 2002, 2005; Locurto et al. 2003; Matzel et al. 2006; Hermann et al. 2010).

As cognitive test scores and song repertoire sizes did not differ significantly between 2009 and 2010 (independent samples t-tests; motor test: \( t_{49} = -0.257, P = 0.799 \); colour discrimination: \( t_{50} = -0.499, P = 0.620 \); reversal: \( t_{49} = -1.663, P = 0.103 \); Mann-Whitney U test repertoire size: \( U = 284.5, N = 52, P = 0.335 \)) we pooled data from both years for our analyses.
Results

Males’ song repertoires contained 5 to 11 different song types ($N = 52$, mean ± SD: 7.94 ± 1.61). The cumulative number of trials they required to pass stages 4 (hinged lids) and 5 (lids fitted in wells) of the motor test ranged from 9 to 22 ($N = 51$, mean ± SD: 12.47 ± 3.07), the number of trials to pass the colour discrimination test ranged from 8 to 36 ($N = 52$, mean ± SD: 16.17 ± 6.17), and to pass the reversal test took between 13 and 40 trials ($N = 51$, mean ± SD: 23.67 ± 7.21). The inhibitory control test showed the largest variation in performance, with males requiring between 6 and 48 trials to pass this test ($N = 22$, mean ± SD: 21.27 ± 10.84).

Is learning test performance correlated with song type repertoire size?

Neither performance on the motor test nor performance on the colour discrimination test correlated significantly with song type repertoire size (Spearman correlations; motor vs. song: $r_s = -0.052$, $N = 51$, $P = 0.718$; colour discrimination vs. song: $r_s = 0.094$, $N = 52$, $P = 0.506$). We found a significant positive correlation between song type repertoire size and number of trials song sparrow males required to pass the reversal test ($r_s = 0.336$, $N = 51$, $P = 0.016$; Figure 1), meaning that males with larger song type repertoires were significantly slower at passing the reversal test. In contrast, performance on the inhibitory control test showed a significant negative correlation with song type repertoire size ($r_s = -0.621$, $N = 22$, $P = 0.002$; Figure 2). Thus, males with larger repertoires were faster at learning to inhibit their impulsive reaction to peck the side of the tube to obtain the food reward inside.

Is performance across learning tests correlated?

Males took significantly longer to pass the reversal test than to pass the colour discrimination test (paired t-test: $t_{50} = -6.773$, $P < 0.001$). Performance on the colour discrimination test was positively and significantly correlated with performance on the reversal test (Pearson correlation $r = 0.320$, $N = 51$, $P = 0.022$; Figure 3). However, none of the other learning test performances correlated with each other (all $P > 0.25$). Indeed, the unrotated solution of a Principal Components Analysis (PCA) of the four learning measures showed that both colour discrimination and reversal tests loaded positively on
the first principal component extracted. In contrast, performance on the inhibitory control
test loaded negatively on this first component that explained 36.65% of the variance in
the data (Table 1). Performance on the motor test loaded heavily on the second principal
component that explained an additional 25.64% of the variance in the learning test
performance data (Table 1).

As expected in view of the aforementioned findings, song repertoire size tended to
correlate positively with Principal Component 1 (Spearman correlation $r_s = 0.417$, $N = 22$,
$P = 0.054$) but not with Principal Component 2 ($r_s = 0.195$, $N = 22$, $P = 0.385$).

**Discussion**

Our study shows that song complexity in wild song sparrow males is associated with
some aspects of learned foraging performance during captive testing. It can therefore be
added to previous work (Boogert et al. 2008; Chapter 4) suggesting that females can
obtain information about a male's cognitive and foraging ability by listening to his song.
However, there are two paradoxical features of our results that set it apart from previous
studies. First, contrary to the results of Boogert et al. (2008) on domesticated zebra
finches, motor learning of an obstacle removal technique motivated by food was not
related to song complexity in our wild-caught song sparrows. It was the flexibility of
learned foraging behaviour (i.e. tests C and D) that correlated with song complexity here,
a feature that was not tested by Boogert et al. (2008). In the present study, behavioural
flexibility and associative learning were represented by a bipolar factor, Principal
Component 1, which included on one pole the latency to acquire a colour-reward
association and the number of reversal errors, and on the other pole the latency to learn to
detour away from visible but inaccessible food. Surprisingly, the two measures of
flexibility, latency to acquire the colour-reward reversal and to detour, correlated with
song complexity in opposite directions: song sparrow males with more complex songs
were faster at solving the detour problem, but made more errors in the colour reversal
task.

These results are difficult to reconcile with those from the literature. Comparative
studies of primate species’ learning performance by Deaner et al. (2006) and Amici et al.
(2008) report that reversal learning and inhibitory control test performance, respectively,
correlated with species’ performance on various other learning tests in the laboratory. In addition, a recent study by Banerjee and colleagues (2009) on ‘general intelligence’ in cotton-top tamarins (*Saguinus oedipus*) showed that performance on a reversal learning test and on an inhibitory control test (‘occluded reach’) both loaded positively on a general factor extracted, together with performance on a battery of other learning tests. Indeed, tests of reversal learning (Hauser et al. 2002; Boogert et al. 2010; Chapter 1; Tebbich et al. 2010) as well as of inhibitory control (Diamond 1990; Hauser 1999; Santos et al. 1999; Amici et al. 2008) should both represent behavioural flexibility, in the sense that they assess an individual’s ability to inhibit a predominant response: flipping the lid of the previously rewarded colour in our reversal test and reaching straight into the wall of the transparent tube to obtain the mealworm in our inhibitory control test. As the inhibitory control test has, to our knowledge, never been conducted with any other bird species, it is difficult to draw any general conclusions based on our finding that reversal learning performance appears to represent a different aspect of cognitive capacity from that represented by inhibitory control test performance in song sparrow males. One possibility that we can eliminate is that of sampling differences between years. The inhibitory control test was conducted on only a subsample ($N = 22$) of the birds tested in 2010, while the reversal test was done in both years on a total of 52 individuals. However, the positive relationship between reversal learning performance and song repertoire size is in the same range ($r = 0.329$ in 2009 and 0.339 in 2010) in both years.

The experiments and test subjects in Chapters 4 and 5 of this thesis differed in many ways and it is difficult to pinpoint which factors could have led to the difference in results. The zebra finches featured in Chapter 4 were domesticated and thus used to captive testing. The song sparrows featured in Chapter 5 were not. In addition, zebra finches are grass-seed specialists (Zann 1996), whereas song sparrows feed on insects, seeds and berries, a diet that requires a range of foraging techniques, including flipping over the fronds of plants in search of amphipods (Arcese et al. 2002). One can be confident that the domesticated zebra finches, born and raised in standardized conditions, had never experienced anything like the lid flipping task before, and were thus all equally naïve to this novel foraging task. It is conceivable, however, that the song sparrow males differed in the extent to which they had acquired relevant experiences in the wild before
tests started, obscuring a possible relationship between motor test performance and song repertoire size. Perhaps the lack of a correlation between colour discrimination test performance and song repertoire size can be explained along the same lines, with individuals differing in their experiences with colour cues. Only tests with hand-reared song sparrows can elucidate the role of previous experience on learning test performance (Kotschal and Taborsky 2010; Light et al. 2010).

One result that is consistent with the findings of other studies is the positive correlation between latency to learn the colour discrimination and performance on the reversal test. Reversal learning tests are most commonly adopted in comparative analyses of animal learning (e.g. Bitterman 1965, 1975; Day et al. 1999; Bond et al. 2007; Tebbich et al. 2010). As the focus has been on species differences rather than individual differences in performance on reversal tests, and the sample size per species tends to be quite small, it is difficult to put our results into a broader context. However, data kindly provided by Sabine Tebbich (Tebbich et al. 2010) for three species of Galapagos finches and Lainy Day (Day et al. 1999) for desert-dwelling lizards show that discrimination and reversal learning performance generally show positive correlations, even if significant only in one case (Cactospiza pallida; Spearman correlation $r_s=0.562$, $N=16$, $P=0.023$; Camarhynchus parvulus; $r_s=0.596$, $N=8$, $P=0.119$; Geospiza fortis; $r_s=0.180$, $N=8$, $P=0.671$; Acanthodactylus scutellatus: Pearson correlation $r=0.630$, $N=7$, $P=0.130$).

Our study represents a first step towards exploring the link between song quality and cognitive performance in song sparrows and suggests that song repertoire size correlates with some aspects of cognition. We used the relatively crude measure of song repertoire size as this seems to be a biologically meaningful variable in song sparrows (see introduction), but in the future we plan to look at more refined song measures such as within- and between-song type variation (as in Podos et al. 1992), syllable repertoire size, trill rate and frequency bandwidth (as in Podos 1997). Although some song parameters of song sparrow song are expected to correlate with each other (Podos et al. 1992; MacDougall-Shackleton et al. 2009), other song parameters may convey different types of information about the signaller, as has been found for the songs of male field crickets (Gryllus campestris; Scheuber et al. 2003), barn swallows (Hirundo rustica; Garamszegi

As Chapter 6 of this thesis will make clear, research addressing the hypothesis that sexually-selected traits can convey information about cognition is in its infancy. The mixed results reported in Chapters 4 and 5 of this thesis will hopefully be clarified by future work.

**Acknowledgements**

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**References**


Boogert NJ, Reader SM, Laland KN. 2006. The relation between social rank, neophobia and individual learning in starlings. Anim Behav. 72: 1229-1239.


<table>
<thead>
<tr>
<th>Learning test</th>
<th>PC 1</th>
<th>PC 2</th>
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<tr>
<td>Motor</td>
<td>-0.104</td>
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<td>Colour discrimination</td>
<td>0.797</td>
<td>-0.019</td>
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<td>Reversal</td>
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<td>Inhibitory control</td>
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<td>Eigenvalue</td>
<td>1.466</td>
<td>1.026</td>
</tr>
<tr>
<td>% of total variance explained</td>
<td>36.646</td>
<td>25.644</td>
</tr>
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</table>

**Table 1.** Results of a Principal Components Analysis of the learning test scores of 22 song sparrow males: loadings on unrotated Principal Component 1 (PC1) and Principal Component 2 (PC2), eigenvalues, and percentage of total variance explained.
Figure 1. The relationship between song sparrow males’ (N=51) song repertoire size and their performance on the reversal test.
Figure 2. The relationship between song sparrow males’ (N=22) song repertoire size and their performance on the inhibitory control test.
Figure 3. The relationship between song sparrow males’ (\(N=51\)) performance on the colour discrimination test and their performance on the reversal test.
In Chapter 5, I found that wild song sparrow males with larger song repertoires performed better on an inhibitory control task but worse on a reversal learning test than did males with smaller song repertoires. To date, no other studies have subjected a bird species to the inhibitory control test or to such a range of different learning tests. It is therefore unclear whether song complexity can be used as an indicator of a male’s ‘general cognitive ability’ to guide mate choice in female passerines. In Chapter 6, I explore this issue further and review the evidence that male cognitive traits can guide female mate choice decisions in non-human vertebrates.
Chapter 6:

Mate choice for cognitive traits:
A review of the evidence in non-human vertebrates

Abstract

To what extent do individuals assess the cognitive abilities of the opposite sex when choosing a mate? With the exception of song learning in birds, the hypothesis that cognitive traits are under sexual selection has received attention only recently. Here we evaluate the evidence for this hypothesis in non-human vertebrates. We first briefly review the literature on brain development, which shows that cognition may be a sensitive indicator of early developmental conditions. We then consider the empirical evidence that females choose mates with better cognitive skills, which may be reflected in males’ courtship displays, foraging performance, courtship feeding or diet-dependent morphological traits. There is very little research that assesses whether females discriminate between males through direct observation of cognitively demanding behaviour. Instead, several studies support female choice on the basis of morphological traits correlated with cognitive abilities. We conclude by highlighting key questions for future research: (i) To what extent do cognitive skills determine foraging success, courtship feeding and the expression of diet-dependent morphological traits? (ii) Do behavioural courtship displays depend on motor development and physiological maturation, or learning through practice and experience? (iii) How do cognitive abilities affect survival and mating success? Studies on a range of vertebrate taxa, with their diverse mating systems and cognitive ecologies, offer great potential to tackle these questions and deepen our understanding of sexual selection on cognition.
1. Introduction

Cognition, defined as the neuronal processes concerned with the acquisition, processing, retention and use of information (Shettleworth 2001; Dukas 2004), allows animals to track changes in their habitat within their lifetime and solve novel problems, features that seem unequivocally advantageous (Johnston 1982). Yet animals differ widely in their cognitive abilities, both within and between species, and understanding this variation remains one of the key challenges in evolutionary biology (Dukas and Ratcliffe 2009; Shettleworth 2010). One idea, hinted at by Darwin (1871) and further developed by evolutionary psychologists (Miller and Todd 1998; Miller 2000, 2007; Kaufman et al. 2007), is that cognition or ‘intelligence’ is as much a product of sexual selection as it is of natural selection. Miller (2000) argued that humans evolved such large brains because the associated cognitive abilities were effective in attracting mates, thereby enhancing reproductive success. In line with this, studies of human mate choice suggest that intelligence is highly valued by both sexes (Buss 1989; Li et al. 2002; Prokosch et al. 2009).

A role of cognition in attracting mates could in principle be extended to other taxa, but biologists have been slow to explore this possibility. If enhanced cognitive skills enable males to acquire more resources, females may obtain direct benefits from choosing such males as mates; and to the extent that those skills are heritable, they may also benefit indirectly through their offspring. However, although cognitive specializations such as spatial learning and memory in mammals (Jones et al. 2003) and particularly song learning in birds (Catchpole and Slater 2008) have been relatively well studied in a mate choice context, the hypothesis that other cognitive abilities may play a role in mate choice seems to have received attention only very recently (Boogert et al. 2008; Keagy et al. 2009; Shohet and Watt 2009). We find this surprising for two reasons. First, we have a far better understanding of the adaptive basis of mate choice in non-human animals than we do in humans, thanks to decades of detailed field and laboratory studies of sexual selection (Andersson 1994) that would not be possible in our own species. Second, animal cognition is a burgeoning area of research and has demonstrated an impressive range of cognitive skills in a wide variety of different taxa (Shettleworth 2010),
questioning anthropocentric views of intelligence (Rogers and Kaplan 2004). We feel the time is ripe to unite these two fields of research.

In this paper we review the evidence that non-human vertebrates choose mates based on their cognitive ability. Other researchers have considered a role of cognition in non-human mate choice (Ryan et al. 2009), but their focus was on the cognitive processes used by choosing individuals to detect, evaluate and select a mate. Here we examine the other side of the interaction: we ask whether cognitive traits might be an important part of the display used to attract a partner. Although only a limited number of studies have addressed this topic directly, we will argue that several lines of evidence point to a potentially important role for cognition in mate attraction. We consider research on a range of non-human vertebrate taxa but focus mainly on birds, in which both mate choice (Andersson 1994) and cognition (Emery and Clayton 2004, 2005) are particularly well studied, though almost never together. Our aim is to identify major gaps in our current understanding and suggest ways in which future studies can address these gaps.

We start by briefly outlining the hypothesis that cognitive skills may be under sexual selection. We put this question into a brain-development framework and consider some of the factors affecting cognitive abilities, with a special focus on song learning and spatial learning, for which the underlying neuronal structures are well studied. Next, we discuss empirical evidence suggesting that females may choose mates that perform well on problem-solving tasks or that have accumulated the experience required for an effective courtship display. We then assess whether cognition influences mate choice indirectly through its effects on foraging performance, as revealed by diet-dependent morphological traits or courtship feeding. We conclude by highlighting some unresolved issues and by defining key areas for future work on this topic.

2. Mate choice for cognitive traits

Darwin (1871), in laying out his theory of sexual selection, was the first to suggest that cognitive traits might serve a mate-attracting function. In reviewing the ‘mental qualities’ of different taxa, he suggested that several distinctive features of human culture, including poetry, painting and music, evolved through sexual selection in a similar way to birdsong:
“musical notes and rhythm were first acquired by the male or female progenitors of mankind for the sake of charming the opposite sex” (Darwin 1871; p. 336, footnote 33).

Miller (2000) developed this into his influential ‘mating mind’ hypothesis, arguing that creative intelligence in humans is a costly indicator of genetic quality (‘good genes’). He proposed that intelligence stands out as a particularly good fitness indicator, because the growth and maintenance of the brain require so many genes and energetic resources that mutations or deficiencies in mate quality are easy to spot by assessing a person’s ‘mental fitness’ (Miller 2000). While the wider evolutionary claims are difficult to evaluate, evidence shows that humans are attracted to those who are creative or intelligent (reviewed by Miller 2000, 2007; Kaufman et al. 2007), which is at least consistent with Darwin’s (1871) original idea. Sexual selection on cognitive skills may in fact be easier to evaluate in non-human species, due to their greater experimental tractability. In addition, the multispecies comparative analyses that are routinely done on non-human cognition (e.g. Reader and Laland 2002; Byrne and Corp 2004) cannot be used on the monospecific Homo sapiens.

For cognition to play a role in attracting mates, there are three basic issues we need to consider:

(i) Is there enough variation in cognitive skills? There must be sufficient variation in cognitive ability between potential mates to allow choosers to discriminate between them. Such variation could arise from a range of genetic and environmental factors that affect brain development. We consider developmental and genetic influences on cognitive skills in the next section.

(ii) Are there benefits to be gained from choosing more cognitively skilled mates? Choosers should obtain some kind of fitness benefit from obtaining a mate with better cognitive skills. This benefit may directly enhance the chooser’s own fitness; for example, male spatial cognitive abilities have been suggested to have a strong impact on reproductive success in pinyon jays (Gymnorhinus cyanocephalus), as females rely on their mates for food from cache recovery during incubation, breeding, and feeding the offspring (Dunlap et al. 2006). Likewise, courtship feeding (see section 4C) provides direct benefits to females and may be influenced by the male’s cognitive ability. In addition, if cognitive traits are heritable, females might benefit indirectly through having
cognitively skilled offspring. It seems reasonable to assume that, to the extent that a male's cognitive skills affect his own survival and reproduction, they will also influence the direct and/or indirect benefits he offers to a female. However, we note that this has never been tested empirically. We encourage researchers to address this gap by measuring the reproductive success of females with males of varying cognitive ability.

(iii) Do choosers actually choose on the basis of cognitive traits? Even if sufficient variation in cognition exists and females could potentially benefit from assessing this, we need to show that they do so in practice. Assessing the evidence that females use male cognitive performance in choosing a mate forms the core of our review, in section 4.

3. Developmental and genetic influences on cognitive ability

Cognitive abilities might indicate mate quality by reflecting genetic and environmental influences on brain development. Evidence suggests that this is the case for at least some aspects of cognition. We start by considering developmental factors affecting song learning and spatial learning, two specialized forms of cognition which have been studied in detail, before moving on to other cognitive traits. We then turn to genetic influences on cognitive performance, as revealed through studies on inheritance, inbreeding and domestication. Finally we assess whether song learning, spatial learning and other cognitive traits are positively correlated, which would suggest the existence of a ‘general’ cognitive ability.

A) Developmental influences

Song learning

Birdsong, which has a clear role in mate attraction (Searcy and Andersson 1986), may be a sensitive indicator of brain development. Nowicki et al. (1998, 2002) argued that male songbirds in poor condition cannot sing high-quality songs to deceive females, as song learning in many passerines occurs in a restricted time window early in life during which individuals are most likely to experience developmental stress. According to the developmental stress hypothesis (Nowicki et al. 1998, 2002; Buchanan et al. 2003), birds
experiencing more stressors during development – for example restricted food, intense sibling competition or frequent immune challenges – or those with a genotype less able to cope with such stressors, are less likely to develop the high-quality brain structures required to learn and produce attractive song than birds with a more stable development or a better-adapted genotype. This hypothesis has received much empirical support: compared to control chicks that experienced a relatively stable development, chicks subjected to food deprivation, high sibling competition or parasite infection develop smaller brain control nuclei and acquire smaller song repertoires or songs that are poor copies of the tutor song (reviewed in Brumm et al. 2009; Podos et al. 2009; Riebel 2009). Males with more complex songs or larger song repertoires, in turn, tend to be in better body condition, live longer and produce more offspring than those with lower song quality (reviewed in Boogert et al. 2008; Catchpole and Slater 2008). These differences may also extend to other cognitive traits: two studies by Boogert et al. (2008, in prep; Chapters 4 and 5) found a positive correlation between song complexity and problem solving in a foraging context. It would be interesting to investigate whether similar relationships exist in other species and between other cognitive traits.

Spatial learning
Developmental stressors may have a similar impact on the brain areas involved in spatial learning. Stressors have been shown to reduce hippocampus volume, the total number of hippocampus neurons and spatial memory performance in adult western scrub jays (Aphelocoma californica; Pravosudov et al. 2005), and to reduce hippocampus and cerebellum fatty acid profiles, hippocampus cell proliferation, and spatial learning in rats (Rattus norvegicus; e.g. Fukuda et al. 2002; de Souza et al. 2008; McCormick et al. 2010).

There is also evidence that better spatial learners enjoy mating benefits. In meadow voles (Microtus pennsylvanicus), males with better spatial learning and memory abilities were not only found to have larger home ranges and to locate more females in the field (Spritzer et al. 2005a), but were also preferred by females in mate choice tests, even though the females did not observe males’ performance on spatial tests (Spritzer et al. 2005b). The authors suggested that female meadow voles might be able to distinguish
between males based on olfactory cues that are correlated with spatial ability, such as testosterone levels, but this hypothesis remains to be tested. Likewise, as mentioned above, reproductive success in pinyon jays may be strongly affected by the male’s spatial memory capacity (Dunlap et al. 2006). There is therefore a high incentive for females to select mates with better spatial skills, but whether they do so has never been tested. In guppies (*Poecilia reticulata*), males that learned faster to swim through mazes to gain a food reward were found to be more attractive to females (Shohet and Watt 2009). However, females were not able to see the males’ performance in the mazes. Although male learning ability was weakly correlated with saturation of the orange patches on his body (a sexually selected trait; see section on carotenoids), orange saturation surprisingly did not correlate with female preferences. Thus, the cues leading female guppies to prefer faster learners are unknown.

Whereas the links between developmental stability, song control nuclei development, song learning and mate choice have been particularly well studied, the ways in which hippocampus development affects mate choice through spatial learning skills remain to be investigated. The pinyon jay and meadow vole systems seem to be especially suitable to start addressing this question in more detail.

Other cognitive traits

The impact of developmental stress seems to extend to other types of cognition, even though for most of these cases we lack an understanding of the exact brain processes involved. Performance on general learning and memory tests is impaired by developmental stress in zebra finches (*Taeniopygia guttata*; Fisher et al. 2006; Donaldson 2009), in non-oscine birds such as black-legged kittiwakes (*Rissa tridactyla*; Kitaysky et al. 2003) and red-legged kittiwakes (*R. brevirostris*; Kitaysky et al. 2006), and in mammals including rats (Castro et al. 1989), sheep (*Ovis aries*; Erhard et al. 2004) and humans (reviewed in e.g. Levitsky and Strupp 1995; Lupien et al. 2009). In our own species, deviations from bilateral symmetry in morphological traits (e.g. dimensions of fingers, ankles, knees and eyes), which may reflect developmental perturbations, show negative correlations with individuals’ scores on commonly used intelligence tests (Cattell’s culture fair intelligence test (CFIT), Raven Standard/Advanced Progressive Matrices, and the WAIS III
and Shipley Vocabulary tests; Furlow et al. 1997; Prokosch et al. 2005; Bates 2007).
Furthermore, women prefer both more intelligent and more symmetric men (Buss 1989;
Gangestad et al. 1994; Thornhill and Gangestad 1999; Li et al. 2002; Brown et al. 2005;
Prokosch et al. 2009). Miller and Todd (1998) suggested that individuals may require
considerable to time to assess the intelligence of mate candidates, whereas symmetry
correlates positively with courtship displays such as dancing ability (Brown et al. 2005),
which can be evaluated within seconds.

Two recent laboratory studies illustrate the importance of environmental conditions
for the development of cognitive abilities. Kotrschal and Taborsky (2010) raised cichlids
of the African species Simochromis pleurospilus on either a stable or a changing food
supply. They found that fish in the latter group performed better on a learning task
involving visual discrimination and that this effect persisted into adulthood, long after the
feeding regime had ended. Similarly, Light et al. (2010) gave one group of outbred
laboratory mice (Mus musculus) 8 days of training in a radial arm maze, and found that
these mice performed better on a battery of cognitive tests (passive avoidance, odour
discrimination, associative fear conditioning, egocentric navigation in a Lashley maze,
and spatial navigation in a water maze) than mice given 8 days of experience of being
handled. Both these studies demonstrate that variation in cognitive ability can arise from
differences in the conditions experienced earlier in life.

B) Inheritance, inbreeding and domestication
The heritability of cognitive traits is critical for the consequences of mate choice based on
those traits. If cognitive traits are highly heritable, then choosers gain indirect benefits
through their offspring's inheritance of these ‘good genes’, whereas direct benefits might
result from choosing mates that are smart because of environmental factors during
development (Kotrschal and Taborsky 2010). There are many published estimates of the
heritability of general intelligence in humans, ranging from 30% in very young childhood
to 80% in adulthood (reviewed by Deary et al. 2009). In contrast, very little work seems
to have been conducted on the heritability of cognitive traits in non-human vertebrates. A
recent study on cognition in mice explored sibling correlations in performance on various
cognitive tasks, including spatial ones, and provided a heritability estimate of around
40%; but this estimate was an upper-limit because maternal and litter effects were not controlled for (Galsworthy et al. 2005). With regards to song learning, Forstmeier et al. (2009) showed that syllable repertoire size and motif duration, learned song traits that are thought to be sexually selected, have very low heritabilities in male zebra finches.

Inbreeding has been found to negatively affect IQ in various human populations (reviewed by Woodley 2009). In non-human vertebrates, the effect of inbreeding and domestication on learning performance differs depending on the species and particular tests used. In rats, inbred strains performed worse on tests of procedural and spatial learning than did outbred and wild rats. However, domestication did not significantly affect learning test performance (Harker and Whishaw 2002). In contrast, domesticated guinea pigs (*Cavia aperea f. porcellus*) outperformed their wild counterparts (*C. aperea*) on a spatial learning test (Lewejohann et al. 2010). Wild-type Mongolian gerbils (*Meriones unguiculatus*) raised in the wild took twice as long to succeed in an auditory discrimination learning test as wild-type gerbils raised in the laboratory and domesticated gerbils (Stuermer and Wetzel 2006). Domestic dogs (*Canis familiaris*) were less successful at solving a spatial task than wolves (*C. lupus*; Frank and Frank 1982) and captive-raised dingoes (*C. dingo*; Smith and Litchfield 2010).

Few studies have explored the effects of inbreeding and domestication on song learning. Song repertoire size decreased significantly with inbreeding in the small song sparrow (*Melospiza melodia*) population of Mandarte Island in British Columbia (Reid et al. 2005). In contrast, syllable repertoire size and motif duration are not affected by inbreeding in domesticated zebra finches (Bolund et al. 2010). The number of song elements per motif does not differ between domesticated and wild zebra finches, but wild birds have been found to sing more slowly, resulting in motifs of longer duration (Zann 1993).

**C) General intelligence?**

In the previous sections we treated song learning, spatial learning and other cognitive traits separately. In humans, multiple studies using thousands of test subjects show that individuals’ cognitive performance correlates positively across extensive batteries of learning tests, pointing to the existence of a general intelligence factor or ‘g’ (reviewed by
Deary et al. 2010). Few other vertebrate species have been subjected to such in-depth
cognitive testing to establish whether something equivalent to $g$ exists in those species
too. Although some recent studies on rats (Rajalakshmi and Jeeves 1968; Anderson
1993), mice (reviewed in Matzel and Kolata 2010), and cotton-top tamarins (Saguinus
oedipus; Banerjee et al. 2009) reported evidence for $g$, other studies on mice (Locurto et
al. 2003) and on primates and humans (Hermann et al. 2010) did not find the expected
positive correlations. The rat and mouse studies incorporated various spatial tests and
suggest that spatial learning performance might correlate with other cognitive abilities, at
least in these rodent species, but it is unknown whether the same holds true for non-
rodents. In birds, no studies have addressed whether song-learning ability correlates with
performance on other cognitive tests. Although the concept of $g$ has been developed at the
intraspecific level, positive correlations between cognitive abilities across species, genera
and parvorders have led several authors (Reader and Laland 2002; Lefebvre et al. 2004;
Deaner et al. 2006; Lefebvre 2010) to posit concerted evolution of general intelligence
differences at higher taxonomic levels.

Clearly, far more research is needed in non-human vertebrates to partition the
variance in cognitive performance between general and specific factors, as is currently
done in humans (Deary et al. 2009). It should be noted, however, that general and
modular perspectives are not mutually exclusive (Kolata et al. 2008).

In summary, the studies described in section A suggest that the brain structures
underlying song, spatial learning and other cognitive abilities are sensitive to the
conditions experienced during development. The extent to which these cognitive traits are
heritable and affected by large-scale genetic disruptions such as inbreeding is unclear and
requires more research. We also need more work on the precise way that genetic and
environmental factors interact to shape cognitive development. Overall, though, it seems
clear that differences in genetic make-up and external developmental factors, as well as
gene-environment interactions, are likely to result in substantial individual variation in
cognitive abilities. This cognitive variation may, in turn, affect the development of
attractive courtship displays and reproductive success.
4. Empirical evidence for mate choice based on cognitive traits

To what extent do females use male cognitive performance in choosing a mate? We first examine three types of male behaviour that females may assess directly: courtship display performance, foraging performance and courtship feeding. We then consider whether females assess male cognitive ability indirectly, via morphological traits that are affected by nutrient intake.

A) Courtship display performance

The most direct link between cognition and mate attraction is when the courtship display itself is cognitively demanding. Currently it is not known whether males with more effective courtship displays suffered less stress during development (due to favourable conditions or a genetic capacity to buffer stress), nor whether they excel in other cognitive tasks. However, in two bird genera with particularly elaborate courtship displays, the long process by which males develop the display has been studied in some detail.

Satin bowerbirds (Ptilonorhynchus violaceus) construct a bower of sticks woven into two walls, and decorate the surrounding display court with blue parrot feathers, blossoms, insect body parts and other natural and man-made objects (Borgia 1986). Females favour older, dominant males who build bowers of high quality decorated with scarce objects, and who are able to defend their bowers against theft and destruction by competitors (Borgia 1986). Juvenile males spend a lot of time observing the courtship displays of adult males and practicing bower building and display behaviours. Only during their fifth and sixth years of life do males go through a series of moults to finally obtain the adult blue plumage in their seventh year, and start building temporary bowers away from the permanent bower sites of adult conspecifics (Collis and Borgia 1993).

Collis and Borgia (1992, 1993) treated juvenile males with testosterone implants to experimentally advance the expression of adult characteristics and investigate how this would influence their social dominance and courtship displays. Even though the juveniles expressed more aggression, acquired dominance over control juveniles and molted into adult plumage the year following testosterone treatment, they remained subordinate to adult males and built bowers of lower quality with fewer decorations. The authors
suggested that delayed maturation allows young males to perfect their courtship behaviour through observing adult displays and practicing their own display, their juvenile plumage signaling subordinance and thereby affording some protection from chases by adult males (Collis and Borgia 1993). However, additional experiments are required to tease apart the effects of experience and maturation (Madden 2008).

Keagy et al. (2009) designed two problem-solving tests that took advantage of males’ strong aversion to red objects near their bowers, which the birds normally decorate with blue objects. One task involved removing a transparent cup covering red objects so as to allow their removal, whereas the other required them to cover up a red object that was fixed in front of the bower. Keagy et al. found that males who were more proficient at solving these tasks acquired more copulations than less capable problem solvers. However, given that females did not observe the males’ performance on these tasks, the authors suggest that females choose males on the basis of other correlated traits (e.g. quality of bower construction), or that better problem solvers are also better at convincing females to mate with them.

Comparative studies across bowerbird species have shown that relative brain size is larger in species that build bowers than in closely related non-building species (Madden 2001). In addition, relative brain size increases with the species-typical complexity of the bower (Madden 2001), and a comparative study on the relative size of specific brain regions showed that species with more complex bowers have a relatively larger cerebellum (Day et al. 2005). It remains to be determined whether similar patterns are also seen within species, that is whether individual males building more complex bowers have relatively larger brains (or specific regions of the brain) than conspecifics with less complex bowers (Madden 2008).

Two other aspects of the satin bowerbird’s courtship display seem good candidates for behaviours acquired through learning and perfected through experience: mimetic vocalizations and display intensity. Vocal mimicry is by definition learned, and females have been shown to prefer males that mimicked more species with greater accuracy during their courtship displays over males that showed less accurate learning of heterospecific calls (Coleman et al. 2007). In addition, males who were more responsive to an observing female’s reactions and adjusted the intensity of their dancing displays
accordingly were less likely to startle her and were consequently more successful in their courtship (Patricelli et al. 2002). Whether the latter behaviour is learned through experience or is a hard-wired neuronal response is unclear, however, and requires further experimentation (Madden 2008).

In long-tailed (Chiroxiphia linearis) and lance-tailed manakins (C. lanceolata), the great majority of courtship displays on leks are performed by the two top-ranking males (alpha and beta), who perform a joint song and dance to attract females. However, only the alpha male gets to mate with visiting females, and the subordinate beta male may wait up to 10 years to move up in rank. In long-tailed manakins, pairs of alpha and beta males whose songs are better matched in frequency receive more visits from females (Trainer and McDonald 1995). The beta male’s singing competence improves with age: the variability in his song structure decreases and the frequency matching with the alpha male’s call increases, thereby providing a more attractive courtship display. Trainer et al. (2002) suggested that the benefit to the beta male from deferring mating for so long is to increase his display competence through many years of practice, eventually leading to greater mating success when he finally attains alpha status. Similarly, beta males in the lance-tailed manakin rarely sire chicks and are not genetically related to their alpha courtship display partners (DuVal 2007), indicating that cooperation provides neither direct nor indirect benefits to the beta male. However, beta males are more likely to inherit alpha status than lower-ranked males, perhaps as a result of the display skills they have learnt through their interactions with the more experienced alpha male (DuVal 2007).

As with the evidence from bowerbirds, the key question that remains is whether learning is involved in the development of successful courtship displays, or whether neuronal, hormonal or motor maturation is all that is required.

B) Foraging performance
Foraging behaviour varies in cognitive complexity, ranging from simple, hard-wired responses, such as aquatic suction feeding in fire salamanders (Salamandra salamandra; Reilly 1995), to techniques that involve innovation (Overington et al. 2009), imitation (Byrne and Russon 1998; Fawcett et al. 2002), tool manufacture (Weir et al. 2002) and
extensive learning (Heinsohn 1991). Could females use differences in foraging
performance as a mate choice criterion via direct observation of candidate males?

Only one published study has directly addressed this question. A recent experiment
by Snowberg and Benkman (2009) using red crossbills (*Loxia curvirostra*) showed that,
after observing two males extracting seeds from conifer cones, females associated
preferentially with the more efficient forager of the two. The authors were able to exclude
female choice for correlated traits by experimentally manipulating foraging efficiency,
such that fewer seeds were available in the cones of one of the males. The males were
also swapped between treatments (i.e. slow versus fast forager) so that male identity
could not explain the females’ preferences for the most efficient forager.

In zebra finches, foraging ability is correlated with a sexually selected trait, namely
song complexity. Boogert et al. (2008, Chapter 4) recently found that males that sing
longer song motifs with a larger number of elements are better at solving a foraging
problem. Among the nine song-structure parameters investigated by Holveck and Riebel
(2007) in the same species, the number of song elements was found to be the song trait
that best predicted female preferences. Boogert et al. (2008) thus suggested that song
complexity might be used by females as an indicator of cognitive capacity. When females
directly observed males’ performance on a foraging task, however, neither problem-
solving efficiency nor foraging technique appeared to guide their mating preferences
(Chapter 3).

Whether females in other species use direct observation of foraging performance to
guide their mate choice decisions remains to be seen. It could be that other workers in the
field have conducted similar experiments but failed to find positive results, and did not
publish these due to the file-drawer problem or editorial bias against negative findings.
We urge researchers to address this gap and test for direct preferences for foraging
efficiency in other species.

C) Courtship feeding and allofeeding
In some species of birds, the male feeds the female during courtship and/or incubation
(Lack 1940). Courtship feeding plays a significant role in providing the female with
nutritional resources during egg laying and incubation (Lifjeld and Slagsvold 1986;
Neuman et al. 1998) and may advance laying date or increase clutch and egg size (Nisbet 1973; Green and Krebs 1995; Helfenstein 2003). In several species, there is a temporal correlation between courtship feeding events and copulations, suggesting that females may allow copulations in exchange for food (González-Solís et al. 2001; Mougeot et al. 2002, though see Green and Krebs 1995; Velando 2004; Tryjanowski and Hromada 2005). Females may assess the paternal investment of a male through his rate of courtship feedings and this variable has been found to correlate positively with chick-feeding rates (Niebuhr 1981; Wiggins and Morris 1986; Green and Krebs 1995).

Although courtship feeding seems to offer clear direct benefits to the female, it often commences after the pair bond has been formed, in which case it cannot be used as a mate choice criterion. Nevertheless, in some iteroparous species it may affect subsequent pairing success. Helfenstein et al. (2003) found that in black-legged kittiwakes, courtship feeding rate was related to the probability that a male re-paired in the following breeding season. Males’ courtship feeding rates were repeatable between years and correlated with arrival time at the breeding grounds, which, in turn, predicts reproductive success. These authors thus suggested that courtship feeding is a reliable indicator of male quality that may be used to choose mates in subsequent seasons, as “only males with high foraging ability and competitiveness for resources are likely to provide large amounts of food to satisfy both their mates’ and their own energetic needs” (p. 1032 in Helfenstein et al. 2003). However, in the absence of an experimental manipulation of courtship feeding, it is impossible to say whether the chances of re-pairing were directly related to this behaviour or to some other correlated trait.

Food offering, or ‘allofeeding’, has also been described between juveniles in both jackdaws (*Corvus monedula*, von Bayern et al. 2007) and rooks (*C. frugilegus*, Scheid et al. 2008), but this behaviour has been suggested to have different functions in the two species. Both of these corvid species form lifelong monogamous pair bonds and defend ‘micro-territories’ within large breeding colonies (Clayton and Emery 2007). In jackdaws, food offering is thought to facilitate the formation of social bonds and may serve to attract potential mates; juveniles eventually became more selective in the recipients of their food offerings until they offered food exclusively to the individual with whom they eventually mated (von Bayern et al. 2007). In contrast, no relationship between food offerings and
later pair formation was found in juvenile rooks (Scheid et al. 2008). Instead, social rank affected food offerings, with dominant males offering food significantly more often to subordinates than vice versa. Scheid et al. therefore suggested that juvenile rooks use food offerings to convey a message, for example concerning the donor’s quality, to the entire flock.

**D) Diet and mate choice**

If females do not assess male foraging performance directly, they might do so indirectly using morphological traits affected by nutritional intake, such as body size or colour brightness. Experiments have shown that appearance and body condition are affected by the dietary intake of nutrients such as proteins (Monaghan et al. 1996) and carotenoids (Hill 2006a), and this in turn can influence pairing success (Monaghan et al. 1996; Hill 2006b). We focus here on carotenoids, which are responsible for brightly coloured sexual ornaments in many vertebrates, notably birds and fish.

Vertebrates cannot synthesize carotenoids *de novo* and must obtain them through the diet; consequently, carotenoid colouration may act as an honest indicator of feeding success (Grether et al. 1999). For example, Hill et al. (2002) found that wild house finches (*Carpodacus mexicanus*) caught with a higher concentration of carotenoid pigments in the gut had brighter plumage. Individuals with more intense carotenoid-limited colouration are preferred as mates by females in house finches (Hill 1990), guppies (*Poecilia reticulata*; Kodric-Brown 1989) and three-spined sticklebacks (*Gasterosteus aculeatus*; Pike et al. 2007), and by both sexes in northern cardinals (*Cardinalis cardinalis*; Jawor et al. 2003) and American goldfinches (*Carduelis tristis*; MacDougall and Montgomerie 2003).

These findings are suggestive, but as yet there is little direct evidence that carotenoid colouration reflects foraging ability. Karino et al. (2007) found that wild-caught male guppies that had spots with higher colour saturation were better at finding algae (a natural source of carotenoids) in a maze in the laboratory than males with spots of lower colour saturation. It should be noted, however, that to determine whether foraging ability and colour saturation are causally related, one would have to manipulate foraging performance in the maze and measure the effect on colouration. Interestingly,
the same research group also established that male foraging ability for algae is heritable (Karino et al. 2005).

A recent study on male greenfinches (Carduelis chloris) found that individual differences in carotenoid colouration were consistent across different dietary conditions in captivity (Quesada and Senar 2009), perhaps reflecting genetic differences in foraging ability. However, the researchers did not measure actual foraging ability, so other factors could be responsible for the plumage differences. Senar and Escobar (2002) showed that siskins (C. spinus) with shorter yellow wing stripes called more when isolated and tended to approach decoy birds. They argued that this behaviour indicated a greater reliance on the foraging abilities of others, but this was not directly demonstrated. The links between social information use, distress calls and foraging skills have never been established empirically, which makes it problematic to interpret the positive correlation with wing-stripe length as evidence that this plumage trait is dependent on foraging ability.

5. Conclusions and directions for future research
Currently, Snowberg and Benkman’s (2009) study on crossbills provides the only evidence that females use direct observation of foraging efficiency as a mate choice criterion. While other studies have shown that female guppies, bowerbirds and zebra finches prefer males that perform well on problem-solving tasks, the actual cognitive performance of the candidate mates was not observed directly by the choosing females. More evidence exists for an indirect role of foraging performance in mate choice: for example, individuals who are better at obtaining scarce resources such as carotenoids from the environment seem to have morphological traits of higher quality that make them more attractive as a mate. Thus, females are perhaps more likely to choose on the basis of morphological traits correlated with cognitive abilities, rather than the cognitive behaviours themselves, but currently this is difficult to judge because so few studies have tested for a direct role (see Irschick et al. 2008 and Byers et al. 2010 for parallel discussions on the role of morphological versus performance traits). Identifying which traits are directly targeted by female preferences is in fact a common problem for studies of mate choice as multiple traits are associated with male attractiveness (Candolin 2003). However, although distinguishing direct from correlated effects would be interesting from
a mechanistic point of view, it is less important from an evolutionary perspective. Whether females assess cognitive performance directly or instead choose mates on the basis of a trait that is strongly correlated with cognition, heritable variance in male cognitive ability will be subject to sexual selection.

The study of mate choice based on cognitive traits is clearly in its infancy, but our review has highlighted several intriguing lines of evidence which deserve further investigation. While most recent work has focused on humans (Miller and Todd 1998; Miller 2000, 2007; Kaufman et al. 2007), we believe that other vertebrates offer great potential to deepen our understanding of sexual selection on cognition, due to their greater experimental tractability, diversity of mating systems and variation in cognitive ecology. We conclude by outlining some unsolved problems and key areas for future research.

A) Do foraging performance and courtship feeding rate indicate cognitive ability?

Although theory suggests that many forms of foraging behaviour involve a strong cognitive component (Shettleworth 2010), it remains to be established whether individuals that are more efficient at finding/handling resources, or that make better foraging decisions, also perform well on other cognitive tasks. Easily executable tests, such as those requiring individuals to learn the association between a stimulus and reward or the route through a maze, could be used in combination with tests of foraging performance to investigate whether these traits are correlated, and therefore indicative of general cognitive ability.

Ample evidence exists that juveniles are less proficient foragers than adults in many bird species (Sullivan 1989; Weathers and Sullivan 1989; Wunderle 1991; Yoerg 1998). However, it is unclear whether adult foraging skills are a result of motor development or are also mediated through learning experiences. This question could be addressed by comparing the foraging performance of birds that have had ample opportunities to practice in searching for, catching and/or extracting food, versus those with limited opportunities in captivity.
The recent study on red crossbills by Snowberg and Benkman (2009) provides the only evidence so far that females directly assess foraging efficiency in their mate choice decisions. We need more studies addressing this issue. Video playback could be a useful tool in exploring whether foraging efficiency can guide mate choice in other species. Video playback has been successfully employed in mate choice studies on guppies (e.g. Kodric-Brown and Nicoletto 2001; Sato and Karino 2006) and zebra finches (Swaddle et al. 2006; Drullion and Dubois 2008), as well as in social preference and foraging studies in rooks (Bird and Emery 2008) and nutmeg mannikins (Lonchura punctulata; Rieucau and Giraldeau 2009). To control for morphological and other individual differences that might confound a female’s preference, different video clips of the same candidate male could be used as choice stimuli, one in which he is foraging efficiently and the other in which he is foraging inefficiently. In this situation, female preferences would be guided by the male’s foraging behaviour alone, as any morphological or other inter-individual differences would be excluded. Systematic variation of the difference in foraging efficiency between the two clips could provide additional insights: if females only make a distinction when the difference in efficiency is large, the biological relevance of this behaviour for mate choice would be considered smaller than if even slight differences matter to the choosing female.

Researchers studying courtship feeding and allofeeding have suggested that these behaviours can be used by females to assess the male’s quality in terms of his foraging ability (Helfenstein et al. 2003; Scheid et al. 2008), but direct tests of the correlation between foraging ability and courtship feeding rate or food quality are lacking. We encourage future studies to address these questions.

**B) Do morphological traits indicate foraging ability?**

Experimental diet alterations, such as carotenoid or calcium supplementation, significantly affect the size, hue, saturation and brightness of coloured plumage patches in birds (reviewed in Griffith et al. 2006; McGraw 2007). However, the fact that artificial nutrient supplementation increases ornament quality does not demonstrate that males with brighter plumage are better foragers. Likewise, the study by Senar and Escobar (2002), often cited as evidence that carotenoid-derived plumage colouration is dependent on
foraging ability, did not measure individuals’ foraging skills directly. Karino et al.’s (2007) maze test with guppies seems to be the only study so far that has directly measured foraging behaviour in relation to nutrient-dependent traits. Even in this case, the results cannot be used to distinguish between cause and effect: males with more saturated orange spots might be of generally higher quality than less colourful males, as reflected in their greater ability to find food in the maze. To demonstrate a causal relationship between an individual’s foraging performance and his sexually selected nutrient-associated morphological traits, researchers need to measure foraging performance in a controlled setting and record subsequent changes in the nutrient-dependent traits. Such tests have yet to be conducted.

C) Learning versus maturation in the development of courtship displays
As discussed in section 4A, bowerbirds and manakins show an extended juvenile period that is thought to allow young males to practice and learn to perfect their courtship displays. Although the circumstantial evidence is intriguing, there has been no direct test of whether this involves learning instead of, for example, motor development and physiological or morphological maturation. It would be interesting to know whether the testosterone-implanted juvenile satin bowerbirds in Collis and Borgia’s (1993) study, which had fewer opportunities to watch adult displays as a result of their early adult plumage, ended up building lower-quality bowers at 7 years of age. Future studies on this species could manipulate practice opportunities by removing the materials required to build and decorate bowers in some areas, while supplementing the materials available in other areas (see e.g. Doerr 2010). If learning rather than maturation is involved in the development of courtship displays, juveniles provided with extra materials should end up building higher-quality bowers as adults than those with depleted materials.

D) Does cognition play a role in mate choice in corvids and parrots?
The evidence we have surveyed comes from diverse species of mammals, birds and fish, reflecting our contention that cognitive skills may be under sexual selection in a wide range of vertebrates. However, we suggest that researchers pay particular attention to two
avian taxa, the corvids (family Corvidae) and the parrots (Order Psittaciformes). Corvids and parrots are among the biggest-brained (relative to their body size) of all birds (Timmermans et al. 2000) and show the most technically advanced foraging behaviours (Weir et al. 2002; Kenward et al. 2005; Taylor et al. 2007; Bird and Emery 2009; Huber and Gajdon 2006; Schloegl et al. 2009; Schuck-Paim et al. 2009). Recent comparative studies have suggested that the quality and complexity of the alliances and pair bonds formed by corvids may also be associated with the evolution of their relatively large brains and cognitive capacities (Emery et al. 2007). Based on these observations, one would expect cognition to play a major role in mate choice in these taxa. Surprisingly, the traits that guide mate choice in the smartest birds of all are not well understood. Most of the little we do know about mate choice in corvids and parrots is inferred from observations of pair formation in nature, or mate choice experiments addressing one or two morphological or behavioural traits, including body, tail or plumage condition, testis length, age, dominance, and food offering/sharing (Johnson 1988a,b; Komers and Dhindsa 1989; Garnetzke-Stollmann and Franck 1991; Fitzpatrick and Price 1997; Pearn et al. 2001; Arnold et al. 2002; Masello and Quillfeldt 2003; Moravec et al. 2006; Spoon 2006; Emery et al. 2007; Schuck-Paim et al. 2008; Griggio et al. 2010). In contrast, a potential role of cognition has never been addressed.

It should be possible to adopt the series of measures listed by Herrmann et al. (2007, 2010), originally used to test for interspecific differences in social and technical intelligence across primates, to measure individual differences in cognition in corvids and parrots. Gaze following, behaviour thought to potentially signal one animal’s understanding of another’s intentions, has already been shown in ravens (Corvus corax; Bugnyar et al. 2004; Bugnyar 2007; Schloegl et al. 2007). In addition, ravens and jays show complex strategies of tactical deception when caching food or pilfering others’ caches (Grodzinski and Clayton 2010). Conducting a larger battery of cognitive tests in both the technical and social domains in corvid and parrot species, such as those described by Hermann et al. (2007, 2010) for primates, would allow us to assess whether social and technical intelligence correlate across individuals of the same species. One could then use these test scores, together with various morphological measures (e.g. age,
body condition, plumage and beak condition, colour and brightness, tail condition, parasite load, MHC composition) as predictor traits in mate choice tests.

Previous studies have suggested that male dominance may guide female mate preferences in these taxa (Johnson 1988a; Komers and Dhindsa 1989; Garnetzke-Stollmann and Franck 1991). In view of the important role that social intelligence seems to play in the life history of corvids, it would be interesting to test whether social intelligence is a predictor of social dominance, by putting males with known test scores for social intelligence together in a flock and seeing whether these scores can predict their social ranks. In addition, one could determine whether social intelligence has a genetic basis, and thus whether females gain not only direct benefits from mating with a dominant male, but also indirect benefits by producing potentially dominant offspring. Separate experiments could investigate whether females prefer males whom they observe to do well on social intelligence tests over males that seem to perform worse in the social domain. Finally, in corvid species that cache food items (Grodzinski and Clayton 2010), one could test whether females prefer males that have better skills in caching, pilfering others’ caches and protecting their own caches from pilfering.

E) Measuring cognition and its fitness consequences

Our review highlights how little is known about the fitness consequences of natural variation in cognition. Anecdotal and comparative studies provide some indirect evidence that increased cognitive capacity confers survival benefits. For example, during a dry year on the Galapagos island of Genovesa, Grant and Grant (1989) observed some juvenile cactus finches (Geospiza conirostris) using only traditional wet-season modes of foraging, and others using dry-season techniques; the only surviving juveniles that year came from the second group. In a study of 303 populations of 224 species of birds, Sol et al. (2007) found that yearly survival rate was positively correlated with residual brain size, all other factors being equal. However, we know of no studies that have directly tested whether cognitive abilities affect fitness, either through survival benefits or increased reproductive output. Likewise, there are no studies comparing the reproductive success of females mated to males of varying cognitive ability.
One major challenge is to define and quantify cognitive traits in a way that allows for ecologically relevant comparisons within a species. Researchers seem to agree that behavioural flexibility, the ability to deviate from established behavioural routines to solve novel problems or to acquire new stimulus-response associations, is an important component of animal cognition (Lefebvre et al. 1997; Roth and Dicke 2005; Amici et al. 2008). Behavioural flexibility can be quantified by measuring an individual’s innovativeness (Lefebvre et al. 1997), problem-solving ability (Webster and Lefebvre 2001) or performance on tests of reversal learning (Bitterman 1975), either in the laboratory (e.g. Weir et al. 2002; Tebbich et al. 2010) or in the species’ natural habitat (e.g. Midford et al. 2000; Webster and Lefebvre 2001; Reader and Laland 2002; Gajdon et al. 2006; Keagy et al. 2009; Chapter 1).

Unfortunately, individuals’ performance on cognitive tests can be confounded by several factors. For example, animals may refrain from the performance of certain behaviours based on informed decisions, such as to avoid retaliation or exploitation by dominant individuals in a group (e.g. Tebbich et al. 1996; Drea and Wallen 1999; Dally et al. 2005), or to adopt a more profitable behavioural strategy (e.g. scrounging; Barnard and Sibly 1981; Giraldeau and Lefebvre 1987; Beauchamp and Kacelnik 1991). Individuals may decide not to participate altogether due to lack of motivation (Sanford and Clayton 2008), although motivation can often be controlled for (see e.g. Keagy et al. 2009). In addition, performance on learning tests may be state-dependent, with mated or breeding females performing worse on spatial learning or memory tasks than non-mated females (Dunlap et al. 2006) or females in the non-breeding season (Galea et al. 1996). Finally, individuals may not need to perform cognitively demanding behaviours in stable conditions and times of plenty, while the incentive may be much higher when faced with novel and/or relatively harsh conditions (Tebbich et al. 2010).

In summary, there are a number of difficulties in measuring animal cognition, both in the laboratory and in the wild. It is important to bear these factors in mind when interpreting the performance of animals in cognitive tests. We urge researchers to examine natural variation in cognitive ability more closely, and measure the fitness consequences of this variation.
F) State-dependent choice for cognitive traits
Throughout this review we have implicitly assumed that individuals with enhanced cognitive abilities make better mates. In fact, this need not be the case: theoretical work on mate choice (McNamara et al. 1999; Todd and Miller 1999; Fawcett and Johnstone 2003; Härdling and Kokko 2005; Cotar et al. 2008; Fawcett and Bleay 2009; Venner et al. 2010) as well as empirical work (Little et al. 2001; Basolo 2004; Burley and Foster 2006; Bel-Venner et al. 2008; Holveck and Riebel 2010) has shown that often there will be no universally preferred mate, and that instead the best choice may vary depending on the chooser’s own state (reviewed in Jennions and Petrie 1997; Widemo and Sæther 1999; Cotton et al. 2006; Riebel et al. 2010). Market dynamics (Noë and Hammerstein 1995) are likely to affect mate choice for cognitive traits in much the same way as they will affect mate choice based on other traits. For example, individuals with poor cognitive skills may benefit from choosing a partner with similarly poor skills, because this represents a ‘safer’ option than a high-quality, intelligent partner: low-quality individuals are more likely to accept them in the first place (Todd and Miller 1999; Fawcett and Bleay 2009), and less likely to desert them for another mate (McNamara et al. 1999). There are no published studies examining whether preferences for a partner’s cognitive abilities might be state-dependent in this way. Human couples are positively assorted with respect to measures of intelligence (Vandenburg 1972), but this pattern could result from a uniform preference for the most intelligent partners (Kalick and Hamilton 1986; Riebel et al. 2010). For other animals, we do not know of any studies investigating whether mated pairs are matched for cognitive ability; this should be a priority for future research. Along the same lines, it would be interesting to test whether females achieve a higher reproductive output when paired with males of high cognitive ability, or with males whose cognitive ability closely matches their own.

G) Trade-offs and variation in cognition across species
Our review of the literature has revealed only a handful of studies examining sexual selection on cognitive abilities at the intraspecific level. There is, however, a small comparative literature on interspecific variation across mammals in cognitive traits related to sperm competition and mating systems. Because the brain is thought to be a
metabolically expensive organ (Aiello and Wheeler 1995; Isler and Van Schaik 2006a; see Isler and Van Schaik 2006b for birds), any increase in its size might be traded off against decreases in other physical traits. For example, Pitnick et al. (2006; confirmed by Lemaître et al. 2009) showed that bat species with stronger sperm competition had both larger testes and smaller brains. However, this does not seem to be the case in primates (Schillaci 2006) or in other mammals (Lemaître et al. 2009). Instead, a negative relationship between body size dimorphism and relative size of the whole brain (Schillaci 2006) and neocortex (Schillaci 2008) seems to be the trend in primates, as well as in mammals in general (Lemaître et al. 2009). Among birds, females have relatively larger brains than males in species with a higher degree of extra-pair paternity, while the reverse is true in species with lower rates of extra-pair paternity (Garamszegi et al. 2005).

Body size dimorphism typically covaries with mating system, because greater intrasexual variance in mating success generates stronger selection for traits that reduce competitor access to fertilizations. Body size dimorphism is associated with polygyny, while testes size is associated with sperm competition between males due to multiple matings by females (Harcourt et al. 1981). If large testes or large bodies are negatively associated with brain size, this might either constrain or favour female choice for male cognition depending on the mating system. In promiscuous or polygynous mating systems, the smaller brains of males might lead to low intra-specific variance in cognition, favouring female choice on resource-holding traits because these are the male qualities that have the strongest direct and indirect effects on her fitness. In contrast, monogamous systems with few extra-pair copulations by females would be associated with larger brains, smaller testes and low size dimorphism. It is in these species that male intelligence rather than male resource-holding potential might have the strongest effects on female fitness, leading to stronger female choice on male brains and cognition. These comparative predictions remain to be tested.
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References

Basolo AL. 2004. Variation between and within the sexes in body size preferences. Anim Behav. 68: 75–82.


cognitive ability in a battery of cognitive tasks for laboratory mice. Behav Genet. 35: 675-692.


Harker KT, Whishaw IQ. 2002. Place and matching-to-place spatial learning affected by rat inbreeding (Dark-Agouti, Fischer 344) and albinism (Wistar, Sprague-Dawley) but not domestication (wild rat vs. Long-Evans, Fischer-Norway). Behav Brain Res. 134: 467–477.


Prokosch MD, Yeo RA, Miller GF. 2005. Intelligence tests with higher g-loadings show higher correlations with body symmetry: evidence for a general fitness factor mediated by developmental stability. Intelligence. 33: 203–213.


Spritzer MD, Meikle DB, Solomon NG. 2005b. Female choice based on male spatial
ability and aggressiveness among meadow voles. Anim Behav. 69: 1121–1130.
Stuermer IW, Wetzel W. 2006. Early experience and domestication affect auditory
discrimination learning, open field behaviour and brain size in wild Mongolian
gerbils and domesticated laboratory gerbils (*Meriones unguiculatus* forma
Swaddle JP, McBride L, Malhotra S. 2006. Female zebra finches prefer unfamiliar males
but not when watching noninteractive video. Anim Behav. 72: 161–167.
Tebbich S, Sterelny K, Teschke I. 2010. The tale of the finch: adaptive radiation and
Tebbich S, Taborsky M, Winkler H. 1996. Social manipulation causes cooperation in
keas. Anim Behav. 52: 1–10.
Timmermans S, Lefebvre L, Boire D, Basu P. 2000. Relative size of the hyperstriatum
ventrale is the best predictor of feeding innovation rate in birds. Brain Behav Evol.
56: 196–203.
Todd PM, Miller GF. 1999. From pride and prejudice to persuasion: satisficing in mate
search. In: Gigerenzer G, Todd PM, ABC Research Group, editors. Simple
Trainer JM, McDonald DB. 1995. Singing performance, frequency matching and
courtship success of long-tailed manakins (*Chiroxiphia linearis*). Behav Ecol
Trainer JM, McDonald DB, Learn WA. 2002. The development of coordinated singing in
trade food for extrapair copulations? Anim Behav. 69: 529–533.


Final summary and conclusions

The possibility that animals can assess the cognitive and foraging abilities of potential mates and incorporate this information into mate choice decisions is an important but neglected question in behavioural ecology. In Chapters 1 and 2 of this thesis, I tested the assumption that mates forage together and can profit from each other's foraging skills in the territorial Zenaida dove and the colonial zebra finch in the field. In Chapter 3, I asked whether learned foraging skills were used as a direct cue for mate choice and showed that, in captive zebra finches at least, they were not. In Chapters 4 and 5, I demonstrated that some aspects of learned foraging behaviour correlated with male song complexity in zebra finches and song sparrows. In Chapter 6, I reviewed the available evidence for mate choice based on cognitive traits in non-human vertebrates and outlined some outstanding possibilities for research and theory. Taken together, the review, tests of assumptions and results from the experiments strongly support the possibility of indirect sexual selection for traits associated with learned foraging in songbirds.

Are there species differences in mate choice for foraging behaviour?

The results of Chapter 3 do not support those of Snowberg and Benkman (2009) who found a direct effect of foraging behaviour on mate choice. Although it is impossible to draw general conclusions from the findings of only two studies, we can speculate on the possible causes of this difference by considering the two species’ natural life histories. In red crossbills (Loxia curvirostra complex), individuals specialize on extracting the seeds from specific conifer species depending on their bill structure. This morphological differentiation in bills is associated with differentiation in non-song vocalizations (i.e. calls), based on which the red crossbills are divided into nine groups or ‘call types’. Females choose mates assortatively within their call type group, which should prevent their offspring from falling into a fitness valley of non-adaptive bill structure (Snowberg and Benkman 2007). Thus, crossbill females can use males’ calls to distinguish between individuals that specialize on different conifer species. However, within these call-type groups, inter-individual differences in feeding efficiency may be impossible to establish by using calls alone, and females may need to observe the males’ foraging behaviour.
directly. In contrast, if the finding that zebra finch males’ foraging performance correlates with their song complexity (Chapter 4) is robust, females may use candidate mates’ song rather than direct observation of their foraging behaviour to evaluate their relative quality as a mate; foraging behaviour might be more difficult to evaluate directly because of fluctuating external conditions, whereas zebra finch song does not change after circa 90 days of age (Williams 2004).

The literature reviewed in Chapter 6 seems to suggest that foraging behaviour may influence mate choice more often indirectly than directly; traits such as carotenoid-dependent plumage colouration/brightness and courtship feeding affect mate choice directly while foraging skills are assumed to underlie these traits. Many more studies are required to test whether differences in individuals’ foraging skills actually cause differences in these sexually selected traits. More work should also be done to establish whether foraging behaviour may guide mate choice directly in species other than red crossbills. However, whether females select males based on foraging behaviour directly or whether they do so indirectly through traits such as song complexity, plumage or courtship feeding, the evolutionary consequences are expected to be similar.

Does a general cognitive ability exist in birds?
Cognition involves all the mechanisms by which animals acquire, process, store and act on information (Shettleworth 2010). Song learning by juveniles is obviously a cognitive process, as it involves the acquisition of information (song templates) by listening to adult songs, storage of this information in the auditory memory, and usage of the stored information to shape the own song production through auditory feedback (Catchpole and Slater 2008). Similarly, many foraging skills are learned during the juvenile period (see General Introduction) and adult foraging behaviour involves acquiring and using information regarding, for example, the distribution of novel food sources or the techniques required to exploit them. Research conducted on rats, mice and primates shows that individual performance on various cognitive tests tends to correlate positively, pointing to the existence of a general cognitive ability or ‘g’ (see Chapter 6 section 3B). Chapters 4 and 5 showed that song complexity correlated with some aspects of cognitive performance in a foraging context in two songbird species. Unfortunately, cognitive test
batteries such as those commonly presented to mice (reviewed in Matzel and Kolata 2010) and primates (Amici et al. 2008; Banerjee et al. 2009; Hermann et al. 2007, 2010) have not yet been developed and presented to birds, even though this should be relatively straightforward (Chapter 6). The existence of g in birds is an important issue to address, as it would indicate to what extent males’ general cognitive capacity might be indicated by their song complexity. The proxies of song learning ability I used could also be refined further; whereas I used element (Chapter 4) and song repertoire size (Chapter 5), a more direct measure of song learning ability could be obtained by presenting all test subjects as juveniles with the same song tutor and comparing the quality of the learners’ songs with that of the song tutor. The results of Chapters 3, 4 and 5 thus form, with those of Keagy et al. (2009) and the suggestions for future studies in Chapter 6, the starting point for a new literature on indirect sexual selection of avian foraging and cognition.

References

