



**SEXUAL SELECTION AND PERSONALITY IN ZEBRA FINCHES,
*TAENIOPYGIA GUTTATA***

VOL 1 OF 1

SUBMITTED BY

WIEBKE SCHUETT

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ABSTRACT

Despite recent increasing interest in the existence of animal personality, i.e. intra-individual consistency and inter-individual variation in the level of a behavioural trait, the evolutionary (and ecological) consequences of these consistent behavioural differences remain poorly understood. Some recent studies have revealed that variation in animal personalities might be linked to competitive interactions, resulting from natural selection. However, since personalities might similarly affect mate acquisition and reproductive success, it seems crucial to also explore their evolution under the framework of sexual selection theory. In this thesis I investigate the influence of personality on mate choice, reproductive success, female-male and male-male interactions, using zebra finches, *Taeniopygia guttata*, as a model species. After (I) I review the few existing studies assessing the link between sexual selection and personality, I propose a framework on the relationship between sexual selection and personality. Subsequently, (II) I show with different experimental approaches for the first time that (a) females choose males on the basis of their behaviour *per se* (male behaviour was experimentally disentangled from any appearance effects) whilst considering their own personality in their choice: less exploratory females did not distinguish between exploratory and non-exploratory appearing males, whereas moderately and highly exploratory females preferred similar males. (b) These preferences have an adaptive value to the exploratory females: exploratory females which had a behaviourally similar partner raised chicks in best condition but chicks in worst condition if they had a dissimilar partner. Low exploration females always raised chicks in intermediate condition, which may explain why they did not choose males on the basis of their exploratory behaviour. (c) I provide evidence that the combination of personalities in a pair, not only in terms of the level of the behaviour but also in terms of the behavioural consistency, influence reproductive success. However, this was only true for foster but not genetic parents, suggesting that behavioural rather than genetic compatibility (for the measured personality traits) is important for reproduction. (d) Moreover, some male behavioural characteristics appear to be a signal of male quality: highly exploratory foster males raised chicks (both males and females) in best condition, which themselves raised foster chicks of increased conditions. (e) Furthermore, a number of sex differences in personality traits (both level and consistency) are identified, including different responses to social interactions. (f) Additionally, I show how females with different exploratory tendencies differ in their movement patterns during mate choice. (g) Finally, I demonstrate that in competitive male-male situations, a measurement of condition, the fat score, and aggressive behaviour are positively correlated. These findings are set into sexual selection context (but other evolutionary processes are also considered) and both their ecological and evolutionary consequences are discussed. I outline how these results make a valuable contribution to the research field and discuss their potential to indicate new directions for future studies.

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LIST OF CONTENTS

Title Page	1
Abstract	2
Acknowledgements	3
List of Contents	5
List of Tables and Figures	6
Author's Declaration	10
Introduction	11
Chapter 1:	
Sexual selection and animal personality	
WIEBKE SCHUETT, TOM TREGENZA & SASHA R.X. DALL	18
Chapter 2:	
Sex differences, social context and personality in zebra finches, <i>Taeniopygia guttata</i>	
WIEBKE SCHUETT & SASHA R.X. DALL (in Press in <i>Animal Behaviour</i>)	57
Chapter 3:	
Female zebra finches choose males for their "personality"	
WIEBKE SCHUETT, JEAN-GUY J. GODIN & SASHA R.X. DALL	81
Chapter 4:	
Pairs of zebra finches with similar "personalities" make better parents	
WIEBKE SCHUETT, SASHA R.X. DALL & NICK J. ROYLE	94
Chapter 5:	
Appearance, "state" and behaviour in male zebra finches, <i>Taeniopygia guttata</i>	
WIEBKE SCHUETT & SASHA R.X. DALL	116
Chapter 6:	
Conclusions and prospects: sexual selection and personality	138
Bibliography	146

LIST OF TABLES AND FIGURES

INTRODUCTION

Figure 1. Time line of experiments conducted during my PhD project. The arrows indicate how different experimental parts were followed on from previous findings.

CHAPTER 1: SEXUAL SELECTION AND ANIMAL PERSONALITY

Table 1. Selected studies investigating (a) sex differences, (b) inter-individual agreement and (c) variation in mate choice, (d) influences of partners' personality and assortative mate choice in/on the level (I) and consistency of behaviour (II, only (a) and (b)).

Figure 1. Suggested framework for understanding sexual selection on personality, both behavioural consistency and variation in the level of behaviour. ¹ = selection via mate choice; ² = selection via male-male competition. For more details see text.

CHAPTER 2: SEX DIFFERENCES, SOCIAL CONTEXT AND PERSONALITY IN ZEBRA FINCHES, *TAENIOPYGIA GUTTATA*

Table 1. Terms included in the maximal mixed effect models applied to the data collected (a) in novel environment tests prior to pairing and (b) when individuals were tested in feeding contexts after being grouped with an individual of the opposite sex, matched or unmatched, respectively, for their exploratory tendency.

Table 2. Repeatabilities and standard errors ($R \pm SE$) of individuals' behaviours in a feeding context.

Figure 1. Distribution of the mean number of features visited by (a) females and (b) males in the novel environment over four test series.

Figure 2. Distribution of the difference between the maximum and minimum number of features visited by (a) individual females and (b) individual males in the novel environment over four test series.

Figure 3. Influence of a companion's exploration (number of features visited) on exploration by the focal individual (number of features visited in social context – mean number of features visited in non-social context) in a novel environment.

Figure 4. The relationship between the number of features visited by males and females in a social and an asocial context in different orders (back transformed). Black lines: female

responses; grey lines: male responses; solid lines: tested in a social context first; dashed lines: tested in an asocial context first. Dots represent fitted values.

Figure 5. The mean proportion of time (\pm SE) at the feeder that males and females spent with their opposite sex companion depending (a) on the kind of grouping conducted (matched or unmatched for exploratory tendency) and (b) on their exploratory tendency (low, medium, high) in the novel environment (Part I). F: female; M: male.

Figure 6. The mean proportion of time (\pm SE) at the feeder that matched (Mat.) and unmatched (Unm.) individuals spent with their companion depending on their exploratory tendency (Part I).

CHAPTER 3: FEMALE ZEBRA FINCHES CHOOSE MALES FOR THEIR “PERSONALITY”

Figure 1. Mean (\pm SE) proportion of time females with different exploratory tendencies (low, medium and high) spent near the apparently adventurous male relative to the male which appeared to be unadventurous in a novel environment (UA-A trials). The females’ exploratory tendencies were categorised based on the mean number of features in a novel environment they had visited over two pre-experimental novel-environment tests (as equally distributed around the median of 3 as possible): low exploration (N = 16), mean < 2.5; medium exploration (N = 23), mean = 2.5-3.5; high exploration (N = 13), mean > 3.5. The figure is based on estimates from a GLM, with “female exploratory tendency” as fixed effect. Estimates have been back-transformed to the original scale for display. The stippled horizontal line denotes random choice. *: significant difference; n.s.: non-significant difference.

Figure S1: Overhead plan view of the cage set-up for the pre-choice observation period. A focal female (f) observed two brothers (m), each in one novel-environment cage containing 10 features (features not shown). Each male was allowed to either explore the environment (released from box; “adventurous”) or not (kept in a box; “unadventurous”). The males in the two environmental cages could not see each other. The cage of the female was covered on 3 sides and the top (dashed lines) and lights in front of the female cage were directed towards the males to create a light gradient towards the males’ cages. Both males and females had access to food (not shown). Dotted line denotes mesh wire.

CHAPTER 4: PAIRS OF ZEBRA FINCHES WITH SIMILAR “PERSONALITIES” MAKE BETTER PARENTS

Figure 1. Influence of foster parents’ exploratory tendencies on mean brood condition (mass/head-bill length in g/mm) of cross-fostered nestlings at independence. Exploratory

tendency was measured as the mean number of features visited in two novel environment tests prior to breeding.

Figure 2. Combined effect of foster parents' behavioural consistency in exploration on mean brood (a) condition and (b) mass of cross-fostered nestlings at independence. Consistency in exploration was measured as the coefficient of variation (CV) for the latency to approach the first feature in two novel environment tests prior to breeding. The P-values show if partners' consistency has an effect on each extreme for foster mothers' and fathers' CV, respectively (e.g. highly consistent foster mothers raise chicks in better condition with a similarly consistent male than with a dissimilar male ($P = 0.03$)). Significant P-values are shown in bold.

Figure 3. Relation between foster fathers' mean tendency to approach the first feature in a novel environment (pre-breeding) and mean brood (a) condition (mass/head-bill length in g/mm) and (b) mass (in g) of their cross-foster nestlings at independence.

Figure 4. Influence of males' exploratory tendency (2007) on the condition (mass/head-bill length in g/mm) of their second generation foster-offspring at independence (offspring in 2008). Exploratory tendency was measured as the mean number of features visited in two novel environment tests prior to breeding in 2007.

Table S1. Reproductive success of zebra finch pairs.

Figure S1. Plan view of the cage set-up for the mirror test. For more details see text. Grey bar: perch; striped bar: mirror. F: feeder placed under the mirror.

Figure S2. The relationship between the mean latency to approach the first feature in two novel environment tests pre-breeding and the CV for these approach latencies for (a) females and (b) males.

Figure S3. Influence of foster parents' tendencies to interact with a mirror on brood mean (a) condition (mass/head-bill length in g/mm) and (b) mass (in g) of cross-fostered nestlings at independence. This tendency was measured as the mean number of interactions (sum of all interactions shown but song, as song only occurs in males) in two mirror tests after breeding. Two outlier data points are excluded for scaling reasons (but not from the analyses).

CHAPTER 5: APPEARANCE, "STATE" AND BEHAVIOUR IN MALE ZEBRA FINCHES, *TAENIOPYGIA GUTTATA*

Table 1. Experimental design: the three males in each cage were randomly assigned to one of three treatments each, consisting of different leg band colour combinations (number of replicates: 10). Each of the ten groups was videoed six times per each phase, resulting in 180 trials.

Table 2. Component loadings (varimax rotated) of behavioural and morphological measurements as quantified by principal component analysis.

Table 3. Component loadings (varimax rotated) of aggressive interactions as quantified by principal component analysis.

Table 4. Summary of minimal linear mixed effect models for (a) scan sampled behaviour, weight, size and fat measurements^a, (b) all interactions occurred (all-occurrence sampling)^b, and (c) PCA component “aggression”^c.

Table 5. Summary of studies on effects of coloured leg bands in zebra finches.

Figure 1. Mean (\pm SE) weights of the different treatment groups (“red”, “orange”, “green”) over the three experimental phases. The graph is based on the raw data and not on the model output. For more details see text and Table 4a. P: phase.

Figure 2. Relation between the principle component “aggression” and fat score.

CHAPTER 6: CONCLUSIONS AND PROSPECTS: SEXUAL SELECTION AND PERSONALITY

Figure 1. Standardised repeatabilities (\pm 95% confidence intervals, CIs) of males’ (m) and females’ (f) exploration. C2, C3, C4: standardised repeatabilities (\pm 95% CIs) for data from Chapter 2, Chapter 3 and Chapter 4, respectively. MA: overall estimates from meta-analysis. 95% CIs were calculated as standardised repeatability \pm 1.96 SE for data from Chapter 2-4; whereas a t-distribution with appropriate d.f.s, rather than 1.96, was used for the estimates from the meta-analysis due to the small sample size (see Nakagawa & Cuthill 2007 for discussion).

AUTHOR'S DECLARATION

CHAPTER 1: SEXUAL SELECTION AND ANIMAL PERSONALITY

The review presented reflects my own survey and interpretation of the relevant literature and was guided and improved by Dr Sasha Dall and Dr Tom Tregenza. I was lead author on the manuscript.

CHAPTER 2: SEX DIFFERENCES, SOCIAL CONTEXT AND PERSONALITY IN ZEBRA FINCHES, *TAENIOPYGIA GUTTATA*

I planned the experiment, collected and analysed all data while Dr Sasha Dall provided guidance. I am first author on the manuscript.

CHAPTER 3: FEMALE ZEBRA FINCHES CHOOSE MALES FOR THEIR "PERSONALITY"

I planned the experiment together with Prof Jean-Guy Godin and Dr Sasha Dall both of which provided guidance throughout. I conducted the experiment, collected and analysed all data and I am lead author on the manuscript.

CHAPTER 4: PAIRS OF ZEBRA FINCHES WITH SIMILAR "PERSONALITIES" MAKE BETTER PARENTS

Dr Nick Royle and Dr Sasha Dall provided guidance throughout. I collaborated with Dr Nick Royle to collect the data. I analysed all data and am leading author on the manuscript.

CHAPTER 5: APPEARANCE, "STATE" AND BEHAVIOUR IN MALE ZEBRA FINCHES, *TAENIOPYGIA GUTTATA*

I planned the experiment, collected and analysed all data while Dr Sasha Dall provided guidance. I am first author on the manuscript.

CHAPTER 6: CONCLUSIONS AND PROSPECTS: THE ROLE OF SEXUAL SELECTION ON PERSONALITY

The chapter represents my interpretation of the data outlined and conclusions drawn from these. The chapter was commented on by Dr Sasha Dall.

INTRODUCTION

Since Darwin proposed his theories of natural and sexual selection (Darwin 1859; Darwin 1871), evolutionary biologists have attempted to understand the competitive causes and evolutionary consequences of adaptive variation at different levels of biological organisation, starting from broad scales gradually moving to finer scales, i.e. from variation between genera over variation between species to adaptations at the population level (van Valen 1965; Wilson 1998; Dall et al. 2004). Indeed, over the last few decades, intraspecific variation in behavioural traits has started to attract considerable attention. Remarkably, recent studies have revealed substantial consistent behavioural variation between individuals within the same populations (animal “personality”) in numerous taxa (reviewed in Benus et al. 1991; Boissy 1995; Gosling & John 1999; Koolhaas et al. 1999; Gosling 2001; Groothuis & Carere 2005; Réale et al. 2007). This means, individuals are consistent in their behaviour over time, contexts (i.e. functional behavioural categories like feeding or mating) and/or situations (i.e. set of conditions at a given point in time like the degree of predation risk in the surrounding environment) but vary from each other in the level of their behavioural expression (Sih et al. 2004b). Since the identification of these consistent individual differences in behaviour, interest in animal personality is burgeoning, with the research field expanding rapidly. Yet, most empirical personality research (both on humans and non-human animals) lack distinct research questions and hypotheses which might explain the still persistent opposition to the notion that consistent variation in individual behaviour, an even finer scale of variation, is adaptive (Wilson 1998; Buss & Greiling 1999; Dall et al. 2004). However, thanks to an increasing number of studies investigating links between personality and natural selection, evidence is accumulating that the expression of a given personality trait can increase individual fitness (reviewed in Dingemanse & Réale 2005; Smith & Blumstein 2008). Hence, these personality traits are unlikely to reflect random variation around adaptive population means (Wilson 1998; Buss & Greiling 1999; Dall et al. 2004). Despite this improvement in the field, the possibility that animal personalities are also subject to sexual selection has hardly ever been considered (Dingemanse & Réale 2005, see also Chapter 1). But only by exploring both the role of natural selection and sexual selection in the evolution and maintenance of personality will a complete understanding of the evolutionary origin and consequences of personality be achieved. Therefore, this thesis aims to investigate and shed further light on the poorly understood link between personality differences and sexual selection, whilst also considering alternative processes. The second aim of this thesis is to study some of the ecological consequences of personality in more detail; ecological aspects that might help to understand the relationship between personality and social interactions, like behavioural interactions within mated pairs, which in turn may also help to understand mate choice, access to mates, and reproductive success in relation to personality.

Results from the few existing animal personality studies considering aspects of sexual selection already give hints that personality is subject to sexual selection. However, virtually all studies thus far consider only one aspect of personality, the inter-individual variation in the level of behaviour, but neglect the second aspect, the intra-individual consistency. Secondly, available studies mostly do not assess the role of sexual selection on personality experimentally, thus observed links could simply arise due to correlations between personality traits and other traits under selection. Thirdly, the existing studies have not assessed the mechanisms underlying the observed patterns (e.g. genetic and behavioural compatibility).

In this thesis I employ diverse behavioural observations and experimental manipulations to tackle the role of sexual selection on personality traits in more detail using zebra finches, *Taeniopygia guttata* (Vieillot 1817), as model organisms. Zebra finches are an ideal study species in this context because (a) their biology both in the wild and in captivity has been widely studied (see e.g. Zann 1996) and (b) some consistent behavioural traits have already been identified (e.g. Beauchamp 2000; Forstmeier et al. 2004; Forstmeier & Birkhead 2004). Furthermore, (c) zebra finches are socially monogamous and both parents provide parental care, so behavioural coordination in a pair during breeding may be crucial and therefore mate choice on the basis of personality could be adaptive. Finally, (d) zebra finches breed easily in captivity, hence are suitable for breeding experiments, and (e) as for other bird species, the use of zebra finches for breeding experiments is advantageous since cross-fostering of eggs provides opportunities to disentangle genetic from environmental effects (Roff 2002), like the influence of parental care.

Personality traits investigated in my thesis include mainly exploratory tendencies (mostly in a novel environment) and aggression, but also affiliative behaviour and behaviour in a (potentially) risky foraging situation. These behavioural traits were chosen for several reasons: both aggression and affiliation might have influences on different aspects of social life, particularly in a highly gregarious species like the zebra finch (see below). For instance, aggression and affiliation are likely to influence the strength of the bond, coordination and cooperation between partners and consequently their reproductive performance (see Spoon et al. 2006). Furthermore, aggression is often a costly trait and could therefore serve as an honest signal of quality. Exploratory behaviour on the other hand is likely to be crucial for exploring habitats, for finding high quality breeding sites and food patches (e.g. for offspring provision) or for approaching conspecifics (e.g. to copy their foraging decisions). Furthermore, exploratory behaviour has been shown to correlate with a number of other ecological relevant traits such as natal dispersal (Dingemanse et al. 2003), risk-taking (van Oers et al. 2004a), aggression (Verbeek et al. 1996) and dominance (Verbeek et al. 1996; Dingemanse & de Goede 2004) in

great tits, *Parus major*, and other species (reviewed in Sih et al. 2004b; Dingemanse & Réale 2005; Groothuis & Carere 2005; Réale et al. 2007; Smith & Blumstein 2008).

Besides these general (potential) implications of the behavioural traits measured, some species-specific relevant aspects may apply as well, related to the biology of the zebra finch. Zebra finches are extensively distributed in eastern Indonesia and Australia and share many adaptations to arid environments with other estrildine species in terms of their physiology (e.g. low metabolic rate), morphology (e.g. small size) and life-history (e.g. life long pair bond, short lifespan, Zann 1996). Zebra finches have relatively simple habitat requirements, which include accessible sites for drinking, grass seeds for food and bushes/shrubs for roosting and nesting (Zann 1996). These resources are often distributed in patches in arid environments (Zann 1996) thus that exploration might be a particularly important behaviour for locating these required elements. Furthermore, male zebra finches present their female partner potential nest sites, fetch nest material, and lead their female through the colony (during most of the year, Zann 1996). Consequently, (a) exploration is likely to be a particularly important behaviour for male zebra finches and (b) a female may be expected to consider a male's exploratory behaviour in her mate choice. This does not necessarily have to apply just to a male's level of exploration but also to the degree of consistency with which he performs this behaviour: a female may benefit from choosing a male whose exploration and leading behaviour is predictable so as to gain access to foraging sites in a consistent manner (see Chapter 2 for detailed discussion). Additionally, the combination of both exploratory tendencies and risk-taking behaviour (in a foraging context) in a zebra finch pair (or in social contexts in general) may be crucial, for instance for providing food for offspring or for decreasing predation risk (e.g. via risk dilution when foraging/moving together in groups) and therefore influence partner choice. This seems particularly likely for two reasons: firstly, the risk of predation has been shown to be high for zebra finches, especially around waterholes (Zann 1996). Secondly, pairs of zebra finches are inseparable and synchronise their behaviours both during non-breeding and breeding (except for incubation and brooding, Zann 1996). Finally, most zebra finches breed within a colony, where they maintain a roosting and a breeding nest. These nests, especially the breeding nest, are defended intensely against conspecifics. Fights also occur over food, nest material or against same-sex rivals. In all these cases a pair fights together against the opponent (Zann 1996), making the tendency to be aggressive another trait potentially important during mate choice.

Chapter 1 reviews the studies available on sexual selection and personality differences (both from human and non-human animal research) and introduces possible underlying mechanisms in detail. A framework on the role of sexual selection on personality is developed, along with a framework on how to study these relationships. A number of novel hypotheses and predictions are postulated. No review has been published yet dealing with the link between non-

human personality and sexual selection and no attempt has been made to integrate available findings into a broad, species-comprehensive theoretical framework. Therefore, I feel this review would make a valuable contribution to the scientific literature and has the potential to open new directions for future research on this topic by delivering clear guidelines.

Subsequent chapters employ a number of empirical approaches suggested in Chapter 1 to test predictions made for the link between personality and sexual selection.

Chapter 2 investigates sex differences in personality traits, both in behavioural consistency and in the mean level of behaviour, and assesses how social interactions affect individuals of different sexes and personalities. The possibility that the sexes differ in the degree to which they exhibit personality in both social and non-social contexts and implications of social performance has not yet received serious attention, despite the fact that the sexes are usually subject to differing selection pressures. The scope of this chapter is broadened and also includes other mechanisms and factors beside sexual selection that may explain sex differences in behavioural traits. I show that males were more consistent in several traits linked to exploration than females and behaved more consistently across social and asocial contexts than females, although individuals of both sexes similarly influenced each other's exploratory behaviour in a social context: the more exploratory its companion, the more exploratory a focal individual became. An individual's exploration and sex also affected its performance in a social foraging context. These results stress the importance of looking for sex differences in personality and of considering the influence of social context in animal personality studies. Understanding how sexes differ in their personality and how they interact in social situations seems crucial for identifying selection pressures acting on male and female behaviour and any patterns observed (e.g. behavioural compatibility in a pair in relationship to their personality combination) as well as ecological consequences of personality. I derive both (a) some specific explanations as to why male and female zebra finches differ in the personality traits measured given their biology and (b) some general expectations as to which personality traits seem likely to show sex differences in biparental species. These predictions along with the findings presented could be helpful for future research on ecological and evolutionary implications of personality.

The experiment and findings described in Chapter 2 - i.e. that novel environment tests are suitable to assess personalities in zebra finches, that social interactions affect individual males and females differently and depending on their personalities, and that males and females generally differ in their personality traits - provided the basis for further investigations on the potential links between personality and sexual selection (e.g. sex differences can often indicate sexual selection, see discussion in Chapter 1). Following this line of enquiry, I conducted two

further experiments (see Figure 1), one assessing the role of personality traits in mate choice (Chapter 3) and the other testing for potential effects of personality, and their combination in a pair, on reproductive performance (Chapter 4). The latter experiment consisted of two breeding rounds, one in 2007 and one in 2008, during which break the mate choice experiment was conducted on a different captive zebra finch population.

Chapter 3 is the first study to test experimentally if (non-sexual) personality traits are important for female mate choice by disentangling male behavioural from appearance effects whilst considering female personality. I experimentally altered the perceived personality of the males available for choice and could show that females chose males purely on the basis of their behaviour: less exploratory (“unadventurous”) females did not distinguish between unadventurous and adventurous appearing males, whereas more exploratory females preferred similar over dissimilar males. Also, this chapter provides detailed data on how different personality traits correlate with each other in male and female zebra finches. For instance, females that were exploratory in a novel environment followed different movement patterns during mate choice than less exploratory females which could have important implications for mate searching strategies. This chapter provides a substantial advance in our understanding of the role of personality during mate choice as it is the first contribution showing that females choose male on the basis of their behaviour and consider their own personality in their choice. This provides an important basis for subsequent studies.

Chapter 4 presents the first study that quantifies both effects of genetic parents’ personality on the onset of reproduction/their reproductive success and effects of foster parents’ personality on their parental performance. In a cross-fostering breeding experiment I show that genetic parents’ personality (aggression and exploration) does not influence whether a pair starts reproducing and how well it reproduces. However, the combined personalities of foster parents influenced their parenting qualities: highly exploratory or aggressive individuals which had a similar partner raised heaviest and best conditioned chicks but did worst if they had a dissimilar partner. For less exploratory females the personality of the partner did not influence the condition of the chicks raised. Furthermore, the first evidence for increased raising success of foster parents matched for their behavioural consistency is provided. Finally, the first data for an intergenerational effect of the exploratory tendency of “foster-grand-fathers” on “foster-grand-chicks” condition could be shown. The implications of these results are manifold: the results provide the first evidence that (a) behavioural compatibility but not genetic compatibility for the level of a behavioural trait can be crucial for reproduction and that (b) the combination of behavioural consistency influences parental care. Also, the intergenerational effect suggests that male personality traits may sometimes be a signal of quality with long-lasting consequences.

The experiment outlined in Chapter 5 was the first experiment I conducted during my project. It was originally not designed to assess the link between personality and sexual selection but to investigate if an individual's state (a characterisation of an individual at a given point in time, representing features of this individual such as its energy reserves, size or environmental aspects, see Houston & McNamara 1999; Dall et al. 2004) can "lock" the organism into distinct personality differences, i.e. if positive feedbacks between state and behaviour could generate consistent behavioural differences (Rands et al. 2003; Dall et al. 2004). Contrary to a number of published studies, the manipulation of appearance using different coloured leg bands failed and hence the experimental hypothesis could not be tested. As the study was carried out on male groups which had repeatedly temporary access to single females, results from this experiment may also be important in the light of sexual selection. A positive correlation between male fat score and aggression was found: males which stored more fat were more likely to initiate and win aggressive interactions and were less likely to be recipients of aggression. This could suggest that aggression is an honest signal of quality (condition), information potentially important during male-male competition over access to females (or resources in general) or information used by females during mate choice. The chapter finishes off with a review on leg band studies in zebra finches which is not evident in the published literature as yet, despite numerous studies in that area.

Chapter 6 summarises the implications of the findings of preceding chapters and puts them into broad ecological and evolutionary context. Finally, questions arising from the findings are derived for future research.

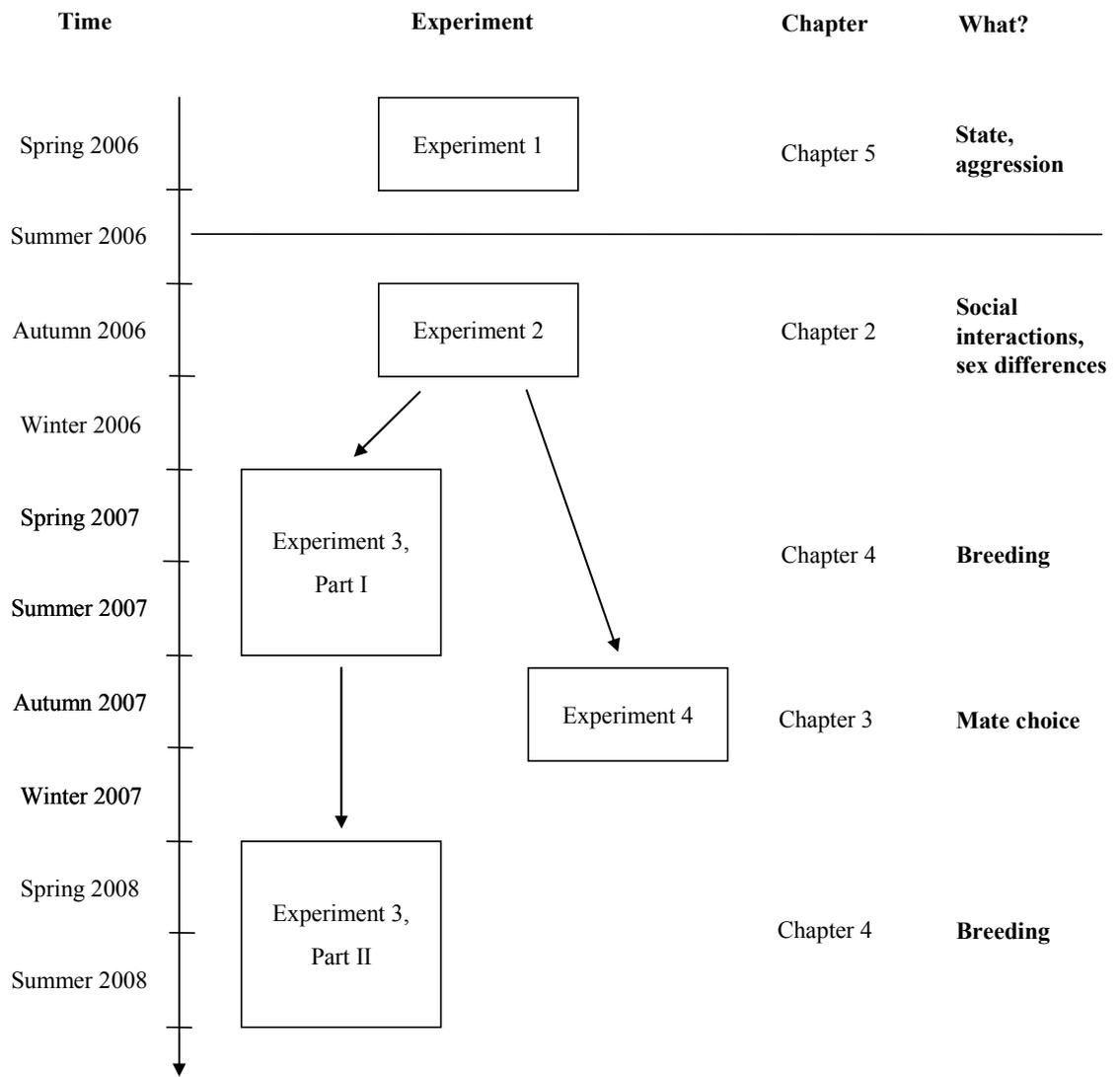


Figure 1. Time line of experiments conducted during my PhD project. The arrows indicate how different experimental parts were followed on from previous findings.

Chapter 1

Sexual selection and animal personality

ABSTRACT

Consistent individual behavioural tendencies, termed “personalities”, have been identified in a wide range of animals. Functional explanations for personality have been proposed, but as yet, very little consideration has been given to a possible role for sexual selection in maintaining differences in personality and its stability within individuals. We provide an overview of the available literature on the role of personality traits in intrasexual competition and mate choice in both human and non-human animals and integrate this into a framework for considering how sexual selection can generate and maintain personality. For this, we consider the evolution and maintenance of both main aspects of animal personality: inter-individual variation and intra-individual consistency.

Keywords: sexual selection; behavioural syndrome; sex differences; individual differences; consistency; repeatability; behavioural synchronisation; mate choice; competition

CONTENTS

I. Introduction	22
(1) Background	22
(2) Objectives	23
(3) Sexual selection	23
(4) Is personality subject to sexual selection?.....	23
II. Selection for level of behavioural expression.....	24
(1) Sex differences in the level of behaviour in animals and humans	24
(a) General rationale	24
(b) Empirical support	24
(c) Frameworks suggested	25
(2) Mate choice and personality traits	26
(a) General mechanisms of mate choice	26
(3) Female preference for male behavioural traits – inter-individual agreement	26
(a) General rationale: behavioural traits as indicators of quality	26
(b) Empirical support	27
(4) Female preference for male behavioural traits – inter-individual variation	28
(a) Empirical support and interpretation	28
(5) Combination of personality traits in a pair and reproductive success – advantages of choosing a mate who behaves similarly or dissimilarly	30
(a) General rationale: genetic and behavioural compatibility	30
(b) Rationale of disassortative mate choice for behaviour	30
(c) Empirical support	31
(d) Rationale of positive assortative mate choice for behaviour	31
(e) Empirical support	32
(f) Further notes on assortative mating	33
(g) Assortative versus disassortative mating – role of environmental conditions?	33
(h) Summary of rationales for assortative and disassortative mating	33
III. Selection for behavioural consistency – advantages of being predictable or a quality indicator?	34
(1) Sex differences in consistencies	34
(a) General rationale: advantages of predictability	34

(b) Empirical support	36
(2) Mate choice and behavioural consistency	36
(a) General rationale: consistency as a signal of quality	36
(b) Empirical support	37
IV. Framework for understanding sexual selection on personality differences	37
V. Future directions	39
VI. Conclusions	40
VII. Acknowledgements	40

I. INTRODUCTION

(1) BACKGROUND

In behavioural ecology, individual behaviour is normally presumed to be plastic, so that an organism can adapt its behaviour in every situation in order to behave in the best way possible in a given set of circumstances (e.g. Sih et al. 2004a; Sih et al. 2004b). Nevertheless, individuals often show very limited behavioural plasticity which can be manifest in consistent individual differences in behaviour (e.g. Benus et al. 1991; Boissy 1995; Gosling & John 1999; Koolhaas et al. 1999; Gosling 2001; Groothuis & Carere 2005; Réale et al. 2007), also known as personality differences (Eysenck & Eysenck 1985; Gosling 2001; Dall et al. 2004), behavioural syndromes (e.g. Sih et al. 2004a; Sih et al. 2004b), coping styles (Benus et al. 1991; Koolhaas et al. 1999) or temperaments (Boissy 1995). These behavioural differences between individuals are still sometimes considered to be non-adaptive variation around a potentially adaptive population mean (Wilson 1998; Buss & Greiling 1999; Dall et al. 2004). However, they (a) often occur in a non-random fashion, in that individuals differ consistently in suites of correlated traits and along a subset of potential axes of behavioural variation (Sih et al. 2004a; Sih et al. 2004b) and (b) have fitness consequences (Dingemanse & Réale 2005; Smith & Blumstein 2008).

If an individual is consistent in its behaviour, over time, over different functional behavioural categories (contexts) and/or situations, it will appear to behave “maladaptively” in many situations. Consequently, the question arises why these personality differences exist; i.e. what is their evolutionary origin, and how are they maintained? More specifically: (1) Why do individuals in the same population differ in their behavioural responses, even under the same environmental conditions and (2) why are individuals consistent in their behaviour over time or space, even when ecological significant factors change (Stamps 2007)? The first question focuses on the reasons for the evolution of different levels of expression of a behavioural trait, i.e. inter-individual variation, whereas the second one concentrates on reasons for the evolution of behavioural consistency, i.e. intra-individual stability (Stamps 2007). As discussed further by Stamps (2007), one would either expect a combination of both low inter- and intra-individual variation in a population (if one behavioural pattern results in highest fitness) or a combination of both high inter- and intra-individual variation (if more than one behavioural pattern results in equal fitness); but instead high inter- *and* low intra-individual variation are often observed (e.g. Dall et al. 2004; Sih et al. 2004b; Dingemanse & Réale 2005).

A number of hypotheses, which are not necessary mutually exclusive, have been postulated recently to explain the observed patterns from a functional perspective (Mangel

1991; Dall et al. 2004; Sih et al. 2004b; McElreath & Strimling 2006; McElreath et al. 2007; Stamps 2007; Wolf et al. 2007; Wolf et al. 2008; McNamara et al. in press). Another possibility, which has not received much attention, is a role of sexual selection in the evolution and maintenance of personality differences, potentially acting together with some of the other evolutionary processes hypothesised.

(2) OBJECTIVES

Our aims are to draw attention to the potential role of sexual selection in the evolution and maintenance of personality differences and to develop a framework to study such a role. It seems important to raise awareness of the potential role of sexual selection in this context because (a) sex is ubiquitous in multicellular organisms (e.g. Barton & Charlesworth 1998) and (b) it is highly underrepresented by researchers at the moment (Dingemanse & Réale 2005). This under-representation of the topic is also clear from a conducted search of the ISI Web of Knowledge v.4.2 for “sexual selection” in combination with “personality”, “behavio(u)ral syndrome”. Only 35 publications matched these search terms (in October 2008). Just 5 of these studies were based on non-human animals, while the rest were based on humans. We provide an overview of how sexual selection could generate and maintain personality traits, how this theory has been tested in the literature and how sexual selection has been used in psychology to explain sex differences in human behaviour.

(3) SEXUAL SELECTION

Sexual selection is caused by variation in reproductive success amongst individuals (Darwin 1871; Andersson 1994). Females typically produce far fewer but invest more in each gamete than males. The greater the investment of one sex into gametes and post fertilisation care than the other (parental investment, see Trivers 1972), the more selective such individuals should be in whom they mate with, and hence the greater the competition for matings in the less investing sex (nearly always males, Darwin 1871; Trivers 1972; Andersson 1994). The resulting competition for access to females leads usually to greater variance in reproductive success of males than of females.

(4) IS PERSONALITY SUBJECT TO SEXUAL SELECTION?

As pointed out above, there are two main components of animal personality differences: behavioural consistency and variation in the level of behavioural expression, both of which are likely to have heritable components. Consequently, sexual selection acting on these aspects is expected to result in evolution. Sexual selection has the potential to both generate and maintain

individual consistency in behaviour arising from non-random mate choice and/or male-male competition. In the following we outline these processes, starting with inter-individual variation in the level of behavioural expression as this is the component of personality differences to which nearly all attention from a sexual selection perspective has been paid. An overview of the studies discussed is provided in Table 1. In this review, we will not consider alternative mating tactics of individuals within one sex (i.e. discrete differences in mating behaviour, e.g. sneaker versus fighter males) and how they are influenced by sexual selection. This is for two reasons. Firstly, several excellent reviews on these alternative reproductive strategies exist already (e.g. Andersson 1994; Gross 1996; Brockmann 2001), highlighting that different tactics are often associated with certain behavioural features (e.g. for sneaker males it is not adaptive to be aggressive, whereas for territorial males it can be). Secondly, alternative reproductive tactics are often also associated with different morphological, physiological or life-history traits. These phenotypic constraints in themselves frequently explain why males following varying tactics differ consistently in their behaviour (e.g. sneaker males are often much smaller than territorial males and would therefore be unlikely to be successful in an escalating fight over access to a mate and hence are expected to be consistently less aggressive).

II. SELECTION FOR LEVEL OF BEHAVIOURAL EXPRESSION

(1) SEX DIFFERENCES IN THE LEVEL OF BEHAVIOUR IN ANIMALS AND HUMANS

(a) General rationale

Because sexual selection results in different selection pressures acting on males and females that manifest in sex differences for those traits under selection for instance in body size or visual ornaments (Andersson 1994), a first indication of a role of sexual selection on behavioural traits could be sex differences in behavioural expression.

(b) Empirical support

There is evidence from numerous studies that males and females can differ in the mean level of their behavioural expression, for instance in aggression (Holder et al. 1991; Whoriskey 1991; Budaev et al. 1999; Bales & Carter 2003), parental responsiveness (Lonstein & De Vries 2000), fearfulness (Johnston & File 1991; Aguilar et al. 2003), risk-taking (Rangeley & Godin 1992) or foraging (Pérez-Barbería et al. 2004). Sexual dimorphism in many behavioural traits is also found in humans (e.g. Buss 1995), e.g. with respect to relational and overt aggression (Crick & Grotpeter 1995), risk-taking (Fetchenhauer & Rohde 2002), humour (McGhee 1979),

vulnerability to social stress (reviewed in Troisi 2001), some aspects of theory of mind (e.g. Knickmeyer et al. 2006) and behavioural responses to partner's infidelity (Shackelford et al. 2002). In more comprehensive meta-analyses, women score for instance higher on measures of Neuroticism, like anxiety, and Agreeableness, but are less assertive and excitement seeking (Extraversion) than men (e.g. Feingold 1994; Costa et al. 2001). Neuroticism, Agreeableness and Extraversion are three of five personality dimensions categorised for humans in the Five-Factor Model (i.e. Openness, Conscientiousness, Extraversion, Agreeableness, Neuroticism, see McCrae & Costa 1999). How can these sex differences in the level of behaviours be explained and is there any evidence that these patterns are the result of sexual selection?

(c) Frameworks suggested

Troisi (2001) provides a framework for how sexual selection can explain the origin of sex differences in vulnerability to stress in humans: due to the different reproductive investment of men and women, women should only reproduce when the best resources are available and males should engage in additional mating. Therefore, men and women are expected to differ in their psychological responses to stressful events related to reproduction, like pregnancy loss – with females being more prone to distress or depression – which is in accordance to empirical evidence (Troisi 2001).

Similar approaches have been used to explain other sex differences in human behaviour (e.g. sex differences in psychological domains in general: Buss 1995; sex differences in social cognition: Geary 2002), including differences in aspects of the theory of mind: Knickmeyer et al. (2006) suggest competition between women may explain ultimate differences in social cognition (see also Geary 2002; Geary 2006). Female-female competition can occur over men because of their potential to provide parental care. There is evidence that in ancestral humans, women dispersed, whereas males stayed in their natal groups (Seielstad et al. 1998) where they formed kin-based coalitions. When women entered their mate's groups, they competed with the other, non-kin women of their polygynous partner; the resulting social networks and alliances among women were likely to be based on reciprocal altruism and more dependent on aspects of theory of mind than the competition among the bigger, hierarchically structured, male groups (for more detailed discussion see e.g. Geary 2002; Geary 2006; Knickmeyer et al. 2006). These relationships are supported by the finding that men are more physically aggressive than women, whereas women are more relationally aggressive, employing lies, betrayals or bullying to compete (social aggression, e.g. Crick & Grotpeter 1995; Campbell 1999). Relational aggression in female groups was probably used to destroy the existing networks of support and to exclude competing women from the group (Geary 2002). Also, women show a higher preference for a socially dominant partner (Botwin et al. 1997) and are generally more choosy

than men (Botwin et al. 1997; Woodward & Richards 2005), supporting the idea that women should choose a partner who is able and willing to invest resources (like parental care, Buss 1995), which is often linked to a man's dominance rank (Botwin et al. 1997). This suggests other ideas about why we find sex differences in human behaviour which involve female mate choice.

(2) MATE CHOICE AND PERSONALITY TRAITS

(a) General mechanisms of mate choice

A number of mechanisms that could drive the evolution of mate choice have been discussed (e.g. Andersson 1994; Kokko et al. 2003; Andersson & Simmons 2006). Proposed mechanisms of mate choice involve either direct benefits (females prefer male traits reflecting his ability to supply material benefits, like food or paternal care, e.g. Møller & Jennions 2001), or indirect benefits (females prefer males that have genes that increase fitness of offspring). Indirect benefits may occur because sons are more attractive (Fisher 1930) or because offspring are more viable in general (Zahavi 1975). Higher offspring fitness may occur either because some males have genes that code for intrinsically superior phenotype offspring, or because some male genomes are more compatible with particular female genomes (genetic compatibility, e.g. Tregenza & Wedell 2000). Hence, sexual selection can generate similar mate preferences across females or preferences that differ among females according to their compatibility with particular males. For the purpose of this review we will refer to male (behavioural) traits that lead to direct or indirect benefits for females collectively as indicators of quality and will consider them separately from traits that are beneficial for just particular females (due to some sort of compatibility).

(3) FEMALE PREFERENCE FOR MALE BEHAVIOURAL TRAITS – INTER-INDIVIDUAL AGREEMENT

(a) General rationale: behavioural traits as indicators of quality

If some male behavioural traits signal their quality – for instance their parental abilities or genetic quality – we expect consistent female preferences for these traits (assuming that all females have the same ability to assess benefits gained by choosing a certain male), resulting in inter-individual agreement in choice, and selection for these behaviours, or levels of behavioural expression. If these behavioural expressions are costly to produce (which is normally assumed if a trait signals quality reliably, Zahavi & Zahavi 1997), then we also expect variation in males' expression of these behavioural traits, as not all males can afford to display the signal due to quality differences.

Miller (2007) expands previous researchers' ideas (e.g. Darwin 1871) that many human moral virtues have been sexually selected for as costly signals. According to this argument, moral virtues are predicted to signal either genetic quality in that genes that are associated with generally higher fitness might be required for showing moral virtues like a 'sophisticated, empathetic social intelligence'; or signal good parental abilities, which are predicted to be indicated by empathic personality traits, as they could help for caring for offspring; or signal good partner skills, which lead to mutual benefits and effective coordination in long lasting partnerships (Miller 2007).

(b) Empirical support

Miller's idea is supported by empirical studies demonstrating that many moral traits are sexually attractive and could be indicators of mental fitness as well as genetic quality and parental qualities (reviewed in Miller 2007). Hawkes & Bliege Bird (2002) argue that there is evidence that men hunt to display their own quality and not because of intrinsic rewards of this behaviour. As a number of studies have been published with regard to humour and mate choice in humans and humour has been shown to be correlated to health (Thorson et al. 1997; Celso et al. 2003; Boyle & Joss-Reid 2004), we can use their findings to apply Miller's ideas (2007): if humour indicates quality, and women are the choosier sex, we not only expect males to invest more into showing humour but also females to respond more to humour, for instance with laughter (Kaufman et al. 2008). Furthermore, females should prefer males showing a higher level of humour as partners. As we predict, males use humour more often than females (McGhee 1979; Myers et al. 1997; Robinson & Smith-Lovin 2001), and females appreciate humour more by laughing more than men do (Kaufman et al. 2008). Also, males prefer females who are receptive to their own humour, whereas females prefer a partner that produces humour (Bressler et al. 2006). Similarly, in a study, in which humour of males was experimentally manipulated, Bressler & Balshine (2006) demonstrated that only females but not males preferred humorous appearing persons as partners for relationships.

From animal studies there is indirect support for the hypothesis that personality traits can signal male quality to a female from a study of collared flycatchers, *Ficedula albicollis*, (Garamszegi et al. 2008). Risk-taking and exploratory male collared flycatchers have been shown to sing consistently from a lower song post when an observer was nearby than risk-averse or less exploratory males. These bold males singing from lower posts bonded relatively faster with a partner than individuals singing from higher posts. This could indicate (among other possibilities) that males on the lower posts were of superior quality or likely to commit more to raising offspring as risk-takers are likely to have lower prospects for future reproduction (Wolf et al. 2007).

More support for female mate choice on the basis of male behaviour comes from studies on Midas cichlid fish, *Cichlasoma citrinellum*: male Midas cichlids show a higher level of between-individual variation in aggressiveness than females (Holder et al. 1991). This variance in the level of male aggressiveness could be under sexual selection as females prefer aggressive over non-aggressive males (Barlow 1986). Males on the other hand do not discriminate among females based on their aggression (Barlow 1986). Furthermore, partnerships with aggressive males are more successful in establishing and maintaining a breeding territory and better in guarding their young (Rogers 1985). Contrary to males, females are all similarly aggressive when caring for the young and are all effective parents (discussed in Barlow 1986).

Finally, more evidence for mate choice based on non-sexual personality traits is provided by an elegant study by Godin & Dugatkin (1996): after showing that female Trinidadian guppies, *Poecilia reticulata*, prefer males that have conspicuous colour patterns and that behave boldly towards a predator (both traits were positively correlated), the authors demonstrated that when appearance and behavioural effects are disentangled experimentally, females show preferences for males behaving boldly towards a predator, regardless of their colour patterns. These results support the hypothesis that behaviour (here: boldness), can be an honest signal of quality – which is used in mate choice by females – particularly when considering that bold males feed at a higher rate (Murphy & Pitcher 1991; Godin & Crossman 1994) and are more likely to survive an approach by a predator than shy individuals (Godin & Davis 1995). Thus, it seems that only high quality males can pay the costs of approaching predators (e.g. costs related to the risk and energy demands, predator inspection is reviewed in Dugatkin & Godin 1992) and therefore advertise their quality to their mates by being bold (for more discussion see Dugatkin & Godin 1992; Godin & Davis 1995). This is underpinned by the fact that the level of risky predator inspection shows significant inter-individual variability in guppies (Dugatkin & Alfieri 1991).

(4) FEMALE PREFERENCE FOR MALE BEHAVIOURAL TRAITS – INTER-INDIVIDUAL VARIATION

(a) Empirical support and interpretation

Individual female guppies are consistent in their choice of male colouration but differ from one another in their preference, despite an overall preference for more conspicuous males (Godin & Dugatkin 1995). Similarly, Forstmeier & Birkhead (2004) demonstrate that captive female zebra finches, *Taeniopygia guttata*, are consistent in their preference for male behavioural traits, namely song rate and aggression. However, some females consistently prefer males with high song rates, others prefer males with low song rates, some prefer highly aggressive and others less aggressive males. Why do females differ consistently in their choice? If song rate or level

of aggression is a sign of quality, then we would expect all females to prefer the same expression of the trait, i.e. the quality reflecting trait expression. Only if females had different abilities to assess and identify the high quality signal or if they differed in their choosiness, would we predict individual females to differ in their preference. Indeed, there is some evidence that females vary consistently in their choosiness: individual females are consistent in their inclination to copulate with a male (Forstmeier 2004; Forstmeier 2007) as well as in their time allocation to the preferred male during mate choice trials (Forstmeier & Birkhead 2004). If some females are less accurate in their assessment abilities or if some females are less choosy, such females should not be consistent in their choice. Rather, what seems likely is that a female's personality plays a role choosing a mate. Indeed, Forstmeier & Birkhead (2004) found evidence that females that spent more time approaching available males during mate choice trials preferred males that sang at higher rates. It should be noted that both the female tendency to approach males (Forstmeier & Birkhead 2004) and male song rate (as well as male aggression, Forstmeier 2004; Forstmeier et al. 2004; Forstmeier 2007, see also Chapter 3 & Chapter 4) can be considered personality traits in zebra finches as they are highly repeatable within and differ amongst individuals.

To our knowledge, there is only one other study published on non-human animals that has considered the personality of not only the chosen but also the choosing individuals during mate choice (Groothuis & Carere 2005). In this study, male great tits, *Parus major*, from bi-directional selected lines for fast versus slow exploration (Drent et al. 2003) were assayed for their preference for females (also originating from these two selection lines). Males of the fast line expressed preference for similar females, whereas males of the slow line did not display preferences for females of either line (Groothuis & Carere 2005). Similarly, we found recently that female zebra finches that were moderately or highly exploratory preferred males that appeared to be exploratory (experimentally manipulated). Less exploratory females on the other hand showed no preference for males that were manipulated to appear shy or bold (see Chapter 3). These studies raise two questions: Why do some individuals mate assortatively, and why do not all individuals mate assortatively? Could it be that two processes are in play? (1) High exploration levels signal high quality in general (as discussed above for male risk-taking behaviour in female mate choice); therefore, all individuals should prefer fast explorers as mates. (2) At the same time mating with the same personality type has advantages (see below), resulting in a trade-off in choice for slow exploring individuals. Also, slow exploring individuals might need a longer time to assess a prospective mate's behavioural type accurately, or they could have a smaller time horizon for making a mate choice decision for instance due to being more easily distracted. This could be the case if slow exploring individuals, which have been shown to be also risk averse (in great tits: van Oers et al. 2004a), invest more time into information gathering to decrease the risk (see also Dall & Johnstone 2002), leaving less time to

invest into mate choice. Finally, it could be that highly exploratory behaviour is generally advantageous but less exploratory individuals mating with highly exploratory individuals may not be able to produce viable offspring that are moderately or highly exploratory. It has been shown that in great tits there is substantial additive genetic variation for exploration and boldness but also considerable genetic dominance, with low boldness and exploration being dominant over high boldness and exploration, respectively (van Oers et al. 2004b). Therefore, homozygous low exploration individuals would never produce medium or high exploration offspring and consequently might not show any preference for either low or high exploration partners. Clearly, more work is needed to shed further light into preference pattern shown. However, what is clear from these studies on great tits and zebra finches is that behavioural traits both of the choosy and the chosen sex have an impact on mate choice, and so sexual selection is likely to influence the maintenance of personality traits.

(5) COMBINATION OF PERSONALITY TRAITS IN A PAIR AND REPRODUCTIVE SUCCESS – ADVANTAGES OF CHOOSING A MATE WHO BEHAVES SIMILARLY OR DISSIMILARLY

(a) General rationale: genetic and behavioural compatibility

As outlined above, one proposed function of mate choice is that it allows females to choose genetically compatible males (e.g. Tregenza & Wedell 2000), which can either lead to assortative mating (Genetic similarity hypothesis, e.g. Rushton 1989) or disassortative mating (overdominance and heterozygote advantage). In support of this, male monogamous oldfield mice, *Peromyscus polionotus rhoadsi*, have higher lifetime reproductive success if paired with their preferred female, than males paired with an unpreferred female or males paired with a female which has been preferred by another male (Ryan & Altmann 2001) and female field crickets, *Gryllus bimaculatus*, preferentially fertilise eggs with sperm from unrelated males (Tregenza & Wedell 2002; Bretman et al. 2004). Similarly, behavioural compatibility or “complementarity”/“similarity” between partners could have an important role in mate choice (Trivers 1972; Burley 1983).

(b) Rationale of disassortative mate choice for behaviour

Some (Dingemanse et al. 2004; Both et al. 2005; van Oers et al. 2008) have argued that disassortative mating by personality could be adaptive, in that (a) partners of similarly extreme personalities could be behaviourally or genetically incompatible or (b) females produce offspring with intermediate personality that could be viable. Although in different years great tits at the different extremes of the exploratory trait distributions had highest survival rates – correlated to environmental conditions –, moderately exploratory individuals showed the lowest

variance in adult survival in the long term and therefore the highest life expectancy (Dingemanse et al. 2004). However, if disassortative mating by behavioural types is favoured by sexual selection, and personality effects are additive in expression, this would rapidly erode personality differences over time.

(c) Empirical support

In accordance with the disassortative mating hypothesis, van Oers and co-authors (2008) showed in a study of wild great tits that assortatively exploratory pairs (at both extremes of the trait distribution) have the highest extra-pair-paternity rates in their broods. If the above rationale holds, females in assortative partnerships should not only engage in more extra-pair matings but should also choose extra-pair males that are behaviourally dissimilar to themselves and to their social partner in order to produce offspring of intermediate personality. However, the extra-pair males and within-pair males in that study did not differ in how similar their personality was to that of the mother. Also, contrary to expectation, within-pair offspring had a higher probability of surviving to the next year than extra-pair offspring. On the other hand, males in assortative partnerships can be expected to have a fitness disadvantage from an increased likelihood of having extra-pair offspring in their nest (assuming that they do not offset this disadvantage by engaging in an increased number of extra-pair matings themselves). However, there may be a danger of placing too much interpretation on these data and further studies would be valuable to provide clarification.

(d) Rationale of positive assortative mate choice for behaviour

Alternatively, choosing a partner assortatively from a behavioural perspective could be adaptive and result in higher reproductive success than choosing a partner disassortatively (or at random). This assortative mating scenario might tend to maintain existing variation in the level of behavioural expressions. Females choosing males that behave similarly to themselves could be at an advantage if similar individuals are able to coordinate their behaviour to a greater extent than non-assortative pairs. Improved cooperation and coordination within a pair during parental care could increase reproductive success. For instance, synchronised behaviour may be important in a foraging context if predation risk decreases when partners are feeding closely together (e.g. via risk dilution: Krause & Ruxton 2002). Moreover, assortative pairs may provision their young more efficiently because, for instance, they can stagger their nest visits more reliably.

(e) Empirical support

Assortative pairs of extreme personalities (i.e. at the ends of the exploratory spectrum) in great tits have been shown to raise fledglings in best condition (measured as residual fledging mass, Both et al. 2005). Furthermore, we have found evidence in a cross-foster breeding experiment on zebra finches that highly exploratory or highly aggressive foster parents raised offspring in the best condition (Chapter 4). However, less exploratory females always reproduced chicks of intermediate condition, independent of the males' exploratory tendency (Chapter 4). Similarly, reproducing pairs in dumpling squid, *Euprymna tasmanica*, showed similar boldness levels in feeding tests: intermediate and bold females were more likely to reproduce successfully if paired with a similar male than if paired with a dissimilar male (Sinn et al. 2006). Shy females, on the other hand, tended to reproduce regardless of the boldness of the partner. Also, convict cichlids pairs, *Cichlasoma (Archocentrus) nigrofasciatum*, that reproduce successfully have been shown to have similar behavioural types (e.g. in terms of latency to explore a novel environment and interact with a mirror), whereas no interaction between male and female personality can be detected in non-spawning pairs (Budaev et al. 1999). That behavioural coordination could be one reason for a higher success of behaviourally assortative pairs is supported by Spoon et al. (2006): in cockatiels, *Nymphicus hollandicus*, highly behaviourally compatible partners had higher coordinated incubation and had higher reproductive success than individuals with lower behavioural compatibility. Compatibility in this study was measured as a composite of proximity, behavioural synchrony, allopreening, copulation frequency and aggression between partners. Also, individuals in a partnership with low behavioural compatibility were more likely to perform extra-pair copulations than highly compatible pairs (Spoon et al. 2007).

There is also some evidence from humans for assortative partnerships in terms of personality; most of these are positive but sometimes also negative assortments (Vandenberg 1972; Thiessen & Gregg 1980; but see discussion in Penke et al. 2007). Negative correlations between personality traits of partners are not only rarer in human partnerships, but they are also more distinctive in unstable partnerships than in stable ones (Vandenberg 1972). Human partners have been shown to be behaviourally similar in numerous aspects of the five personality axes categorised for humans (i.e. Openness, Conscientiousness, Extraversion, Agreeableness, Neuroticism, see McCrae & Costa 1999): assortative human partnerships have been identified in antisocial behaviour (e.g. crime and any behaviour that is linked to negative results for the individual and the society, Rhule-Louie & McMahon 2007, factor Agreeableness), broad interests (Little et al. 2006, factor Openness), Extraversion (e.g. Little et al. 2006), Conscientiousness (e.g. Botwin et al. 1997; Little et al. 2006), Intellect-openness, Agreeableness (e.g. Botwin et al. 1997) and (overall) personality (Gonzaga et al. 2007). Both

Gonzaga et al.'s (2007) and Botwin et al.'s study (1997) also illustrate that humans actually prefer partners with personality traits that resemble themselves, instead of ending up with a similar partner just as a result of similar environmental and demographic backgrounds.

(f) Further notes on assortative mating

Unfortunately, most studies (both in humans and non-human animals) have not considered the personality of the focal individuals before mating (but see e.g. Buss 1984; Little et al. 2006: controlling for length of relationship), making it difficult to investigate whether individuals pair up assortatively in the first place or if they become more similar after pairing (Rhule-Louie & McMahon 2007). Only the first scenario would indicate a role of sexual selection on personality traits. Furthermore, it is unfortunate that human studies investigating the link between personality traits and fitness are rare (Dingemanse & Réale 2005; Penke et al. 2007) and human studies investigating the interaction between both parents' personalities on fitness seem absent altogether.

(g) Assortative versus disassortative mating – role of environmental conditions?

Although we have considered assortative and disassortative mating and their fitness consequences separately, these mating strategies do not need to occur mutually exclusive in the long term but could be both advantageous depending on environmental conditions. In a three-year study, Dingemanse et al. (2004) found that in one year, assortatively paired individuals at the extremes of the explorative spectrum had highest reproductive success (number of recruits), whereas in the other years assortative pairs with intermediate exploration seemed to be most successful in reproduction (although there were not enough data to analyse the interaction between father's and mother's personality on number of recruits statistically). These changes in selection pressures coincided with fluctuating environmental conditions (food availability). Surprisingly, great tits in this study mated either randomly (if the male was younger than a year), or disassortatively (if the male was older than a year).

(h) Summary of rationales for assortative and disassortative mating

In sum, there are a number of potential explanations for the occurrence of assortative and disassortative mating: genetic and/or behavioural incompatibility (disassortative mating), increased gene transmission (assortative mating), behavioural compatibility via behavioural coordination (assortative mating/disassortative mating), and production of viable behaviourally intermediate offspring (disassortative mating). Finally, both assortative and non-assortative mating could be favoured by selection, depending on environmental conditions. Far more

studies are needed to shed further light into the direction of mating and arising fitness consequences, also considering possible environmental influences. However, what has been shown to date is that positively and (less frequently) negatively assortative mating does occur and has fitness consequences (see also Table 1). Different environmental conditions might lead to advantages of different kinds of pairing, resulting in a stable mix of individuals showing different levels of behavioural expressions in a population.

However, this is only half the story. We have shown that different levels of behavioural expressions exist and presented explanations as to why this could be the case from a sexual selection perspective, but we still need to focus more on why individuals are consistently different from one another. We could argue that if an individual's quality is genetically determined and controls whether an individual expresses costly behavioural traits, this behavioural restriction (for low quality individuals) is not likely to change over its life and should therefore result in behavioural consistency. However, there is some evidence that behavioural traits are only partly heritable (van Oers et al. 2005a). Secondly, there may be direct selection on consistency.

III. SELECTION FOR BEHAVIOURAL CONSISTENCY – ADVANTAGES OF BEING PREDICTABLE FOR A QUALITY INDICATOR?

(1) SEX DIFFERENCES IN CONSISTENCIES

(a) General rationale: advantages of predictability

Dall et al. (2004) proposed that individuals that were consistent in their behaviour over time could acquire advantages from being predictable in competition over resources (if there is an audience around). This could be the case if behaving predictably influences competitors' future responses in a way that improves the focal individual's payoffs. This idea can be applied in a sexual selection context: males, who compete aggressively over the resource females, i.e. access for mates, could have an advantage in being predictable in their aggression if some individuals are "eavesdroppers" (*sensu* McGregor 2001; Bonnie & Earley 2007). These eavesdroppers can observe the outcome of fights between the contestants and adjust their behaviour depending on their opponents' previous behaviour (i.e. only escalate against previous losers). Consequently, individuals that are consistent in their level of aggression (low versus high) are favoured by selection, as their behaviour is predictable and eavesdroppers can therefore avoid costly fights with low prospect of winning. This way intra-sexual selection could *generate* consistency in male aggression. Similarly, consistency in males' behaviour could be selected for via female

mate choice if females have benefits from choosing a partner whose behaviour is predictable. We propose this is most likely to occur in species that form long-term pair bonds and/or in species in which both males and females engage in parental care. In these species, mate choice has long-term consequences and males and females are required to coordinate efficiently in order to maximise the number and condition of offspring raised, respectively. A female could gain not just benefits from choosing a male who shows a high level of paternal care or territorial defence (see above) but also from a male who cares in a predictable fashion. Females can compensate and adjust their parental effort according to a male's parental care level (Sanz et al. 2000). Johnstone & Hinde (2006) predict this is the case if there is an "informational asymmetry" between the sexes. Consequently, an estimate of male investment along with an estimate of the amount of parental effort needed to adapt to this male investment is likely to be more accurate and less costly if the male's parental effort is stable. If the level of caring is unstable, the female might either need to assess male's effort repeatedly – which could be costly in itself or the constant required adjustment could be costly – or she might accept an inaccurate initial estimate, resulting in over- or under-care by herself (depending on the initial estimate). The latter should lead to reduced efficiency in raising young as the female is unlikely to complement the male's parental care in the most effective way.

Other behaviours like preening/grooming of the partner might be more beneficial if expressed at a constant rate (but this should be equally true for both sexes, leading to no sex differences in consistency). Furthermore, taking the biology of the species of interest into account could help identify which behaviours are likely to be sexually selected for consistency. For instance, we found in one captive zebra finch population that male zebra finches are significantly more consistent in their exploration (but do not show a higher mean level of exploration) than females and that only males are consistent in their leading behaviour (Schuett & Dall in press, i.e. Chapter 2). This makes sense given the fact that male zebra finches lead their females around through the colony and through feeding sites (Zann 1996): a female should choose a male who explores the environment (while leading her around) in a predictable manner, as this is likely to result in a relatively predictable rate of finding feeding sites or high quality patches within a feeding site. Food in general is the limiting resource for females (Andersson 1994) and a predictable access rate to food should be in the interest of the female.

In sum, from this "predictability" perspective, we would expect males to be selected for consistency in their aggressive behaviour (intrasexual competition) and parental care (female choice). Both sexes should have an advantage of having a partner who is consistent in his allo-preening/grooming behaviour (no difference in consistency between sexes expected). Also at a species level, we expect further sex differences in the consistency of other behaviours, depending on the biology of the species.

(b) Empirical support

Unfortunately, hardly any studies have looked at sex differences in consistency (see Table 1) but rather assess repeatability of behaviours pooled for the sexes. To our knowledge, there are only two studies looking at sex differences in repeatability of exploratory behaviour (Dingemanse et al. 2002; Schuett & Dall in press, see above) and one other, looking at aggression (Holder et al. 1991). There are also a few studies estimating repeatability of parental care for the sexes separately (Budaev et al. 1999; Freeman-Gallant & Rothstein 1999; MacColl & Hatchwell 2003; Schwagmeyer & Mock 2003; Nakagawa et al. 2007a). However, from the latter, only Nakagawa et al. (2007a) tested for differences between the repeatabilities statistically and find that male house sparrows, *Passer domesticus*, are highly consistent in their feeding rates of offspring, both within and between years, whereas females are significantly less consistent in their parental care. This fits with prediction. The same effect is apparent in a long-tailed tit, *Aegithalos caudatus*, study (MacColl & Hatchwell 2003), a savannah sparrow, *Passerculus sandwichensis*, study (Freeman-Gallant & Rothstein 1999) and another house sparrow species study (Schwagmeyer & Mock 2003). However, in convict cichlids, *Cichlasoma (Archocentrus) nigrofasciatum*, males appear to be slightly (but probably not statistically) more unstable in terms of time spent with the brood than females (Budaev et al. 1999). Finally, Dingemanse et al. (2002) did not detect any sex differences in consistency for exploration in great tits, whereas Holder et al. (1991) found that only male Midas cichlids but not females are consistent in their tendency to behave aggressive over time.

(2) MATE CHOICE AND BEHAVIOURAL CONSISTENCY

(a) General rationale: consistency as a signal of quality

Consistency could be sexually selected for if the expression of behaviour in a consistent manner is costly and therefore an indicator of quality that could be used in mate choice by the choosy sex. Exhibiting consistency in behavioural expression could be particularly costly when environmental conditions change. For instance, imagine a male who shows a consistently high level of risk behaviour towards predators. This risk-taking behaviour is costly from an energetic point of view (see above). As long as food is abundant, we expect that a number of males can afford to show a high level of risk-behaviour (if we assume for illustrative purposes that there are no costs other than energetic ones associated with risk behaviour). However, the less food is available, the harder it is for an individual to find enough food for its energy demands. Therefore, we assume that only very high quality individuals can maintain their high level of risk-taking.

(b) Empirical support

We are only aware of one published study that tested for relationships between behavioural consistency and mate choice and/or reproductive success: Byers (2007) assessed links between male extra-pair reproductive success and consistency in song in wild chestnut-sided warblers, *Dendroica pensylvanica*. The study revealed that the degree of consistency in singing was positively correlated to a male's number of extra-pair offspring. Furthermore, support for the hypothesis that male behavioural consistency is beneficial for females comes from an unpublished study on wild lance-tailed manakins, *Chiroxiphia lanceolata*: in this lekking species, females that had male partners consistent in their display behaviour (among years) were more faithful than females that were paired to behaviourally inconsistent males (DuVal unpublished).

We provided two possible explanations as to why behavioural consistency could be sexually selected for: consistency could be a signal of quality and/or could be accompanied with advantages of being predictable. These ideas are not mutually exclusive: it could be that being consistent is in general costly, and therefore can only be displayed by high quality individuals, but is also beneficial in itself.

IV. FRAMEWORK FOR UNDERSTANDING SEXUAL SELECTION ON PERSONALITY DIFFERENCES

In general, for personality differences to be subject to sexual selection, we expect both selection on the variation in the level of behaviour expressed and on the consistency of behaviour expressed. Consistency could be generated by sexual selection, if females prefer consistent males or males do better in male-male competition when they are consistent (as discussed above). Incorporating predictions made by Miller (2007) for his 'sexual selection model for moral virtues' we can construct the following predictions for a personality based framework (Figure 1): firstly, sexual selection could act via female mate choice or via intrasexual competition for access to females. Both consistency and the level of behavioural expression could be an indication of quality (indirect or direct), information that can be used during mate choice and male-male competition. Consistency can also or alternatively indicate predictability (both in mate choice and male-male competition context), whereas the behavioural expression can alternatively signal compatibility (in mate choice context).

If the personality trait is an indicator of genetic quality, then this trait should exhibit some genetic variation and a positive genetic correlation with other fitness related traits.

However, if a personality trait predicts an individual's partner or parenting quality (in case of mate choice) or competitive ability (in case of male-male competition), this trait need not show genetic variation, heritability, or a positive genetic correlation to other fitness related traits but should be correlated to parenting, partner or competitive abilities. In both cases, the quality indicating personality traits should be expressed more often or more consistently by individuals in better phenotypic condition or quality, even under varying environmental conditions. Also, these traits should show a higher among-individual variance in the less investing sex, and should be preferred by all individuals of the choosy sex in a mate choice context (under the assumption that all individuals can assess the quality indicator in the same way). This should lead to positive assortative mating, if the same personality trait is a quality indicator in both sexes, with high quality individuals pairing up with one another, leaving the individuals with the low quality trait to mate with each other. Reproductive success is then expected to be increased for pairs of individuals bearing high quality personality traits, potentially resulting in an erosion of behavioural variation over time (Figure 1). An erosion of variation is also expected if the trait is only a quality signal in one sex.

If genetic or behavioural compatibility is important for mate choice, individuals of the choosy sex should vary in their preference for a personality trait and consider their own personality trait in their choice. This can also result in assortative or disassortative mating and increased reproductive success with increased compatibility (Figure 1). However, the preference pattern in a population will be different to the one based on overall quality indicating personality traits, because different individuals displaying different preferences, depending on their own personality. In the case of high behavioural compatibility, partners should display a high degree of coordination and cooperation, resulting in an increased reproductive success. We expect behavioural compatibility to only be crucial for the level of behavioural expression but not for behavioural consistency. Instead, consistency may always be expected to be beneficial (but see results in Chapter 4).

Consistency can signal predictability and predictability should be selected for via female mate choice as well as via male-male competition (Figure 1): females that choose a behaviourally consistent male should have advantages from their mates' predictability in many aspects of their social life (e.g. easier coordination of parental care, general synchronisation of behaviours in a pair). Behaviourally consistent males can also have fitness payoffs from being predictable in competitive male-male interaction, resulting in increased access to females.

V. FUTURE DIRECTIONS

For future work it would be desirable to apply more holistic approaches, looking at more than one aspect of sexual selection and personality differences in one species for more detailed understanding as well as accumulating studies across species. The first thing to do will be to look for sex difference in both the variation in the level and consistency of behaviour (the latter is neglected completely in most studies). A good place to start is likely to be behaviours that are generally expected to be subject to sexual selection like parental care or aggression, or behaviours that seem likely to be sexually selected for given the biology of the species. We can then ask: what are the different selective pressures likely to be and can we test them, for instance with mate choice trials: do females prefer a male which is more consistent in behaviour x? Or in case of no sex difference: is assortative mating favoured?

When conducting mate choice trials it will be important to consider both the personality of the choosing as well as the chosen sex. This will help to distinguish which behavioural traits (both in terms of consistency and level) are generally preferred (likely quality indicators) and which are preferred by some individuals but not by others. Also, it allows us to test why different individuals differ in their choice (e.g. due to disassortative or assortative choice). For mate choice tests it would also be favourable to allow the choosing sex first to actually observe the chosen sex displaying the behaviour of interest (e.g. approaching a predator) before conducting the mate choice trial. In combination with a manipulation of behaviour of the chosen sex, this would allow us to disentangle appearance effects from behavioural effects in mate choice and to identify direct correlations between preference and personality traits. Unfortunately, Godin & Dugatkin's study (1996) seems to be the only one which has done so thus far (but see also Chapter 3). With respect to breeding experiments for investigating the combined effect of father's and mother's personality on reproductive success, we suggest testing the personality of the parents before and after pairing. This allows investigating whether assortative/disassortative mating in itself is favoured by sexual selection, i.e. results in increased reproductive success or if partners become more similar/dissimilar after pairing due to shared experience (behaviour contagion, convergence, or socialisation, Rhule-Louie & McMahon 2007) which could then lead to increased reproductive success. Also, observations of interactions within pairs during breeding should give information about how the interaction between male and female personality is manifest in cooperation, behavioural synchronisation etc.

VI. CONCLUSIONS

(1) From our review two things become obvious: whereas human studies have a long history of explaining (mainly sex) differences in behaviour from a sexual selection perspective, hardly any animal studies have considered a possible role of sexual selection in the evolution and maintenance of personality differences.

(2) Secondly, from the available studies, a link between personality and sexual selection is already quite convincing: links between aspects of sexual selection, mate choice and intrasexual selection, and both aspects of personality differences, variation in the level of a behavioural expression and consistency in behavioural expression, were highlighted and an outline on how these findings might be explained was proposed.

(3) Many more studies are necessary to shed further light on the role of sexual selection acting on personality differences and to understand and test proposed underlying mechanisms in detail. We look forward to seeing more exciting results from this perspective.

VII. ACKNOWLEDGEMENTS

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Table 1. Selected studies investigating (a) sex differences, (b) inter-individual agreement and (c) variation in mate choice, (d) influences of partners' personality and assortative mate choice in/on the level (I) and consistency of behaviour (II, only (a) and (b)).

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
I. Level of behaviour								
(a) Sex differences								
Midas cichlid fish (<i>Cichlasoma citrinellum</i>)	aggression	m>f	130f, 132m	?, P<0.02	NR	KW		Holder et al. 1991
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	aggression	f>m	23f, 23m	F _{1,21} =6.72, P=0.017	NR	Rep- AOV		Budaev et al. 1999
three-spined stickleback (<i>Gasterosteus aculeatus</i>)	aggression (median per group)	f>m	24 groups (8 groups each: 12f; 12m; 6f+6m)	?, P<0.05	NR	KW		Whoriskey 1991
prairie vole (<i>Microtus ochrogaster</i>)	aggression (proportion of individuals)	m>f	22f, 20m	P=0.008, P=0.011 ^c	frequency: f: 1.71 \pm 1.15; m: 2.79 \pm 1.01; duration: f: 0.17 \pm 0.17; m: 1.65 \pm 0.07	FET		Bales & Carter 2003
hooded Lister rat (<i>Rattus norvegicus</i>)	fearfulness	m>f	16f, 16m	F _{1,14} =16.8, P<0.05	NR (can be read from graph in study)	AOV		Johnston & File 1999

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
Roman rat	fearfulness	m>f (for 14 variables)	394-455f,	for 33 variables	see study	AOV		Aguilar et al. 2003
(<i>Rattus norvegicus</i>)	(41 variables in different tests)	f>m (for 19 variables)	390-459m	P<0.05; (for 8 variables m=f, P>0.05)				
soay sheep (<i>Ovis aries</i>)	foraging (intake rate)	f>m	10f, 10m	$\chi^2=7.75$, df=1, P<0.001	f:0.14, m:0.11, SE of sex difference: 0.01	LMM		Pérez-Barbería et al. 2004
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	risk-taking	m>f	10f, 10m	P<0.05	NR	WT		Rangeley & Godin 1992
hooded Lister rat (<i>Rattus norvegicus</i>)	social behaviour (duration)	m>f	16f, 16m	$F_{1,14}=23.2$, P<0.001	NR (can be read from graph in study)	Sp-AOV		Johnston & File 1999
prairie vole (<i>Microtus ochrogaster</i>)	social behaviour (proportion of individuals)	f>m	20f, 22m	P=0.003, P=0.003 ^c	frequency: f: 0.71 \pm 0.23; m: 0.04 \pm 0.04; duration: f: 3.54 \pm 2.02; m: 0.04 \pm 0.04	FET		Bales & Carter 2003
rodent species	parental responsiveness			review				Lonstein & De Vries 2000

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human (<i>Homo sapiens</i>)	aggression (relational)	girls>boys	235f, 256m (4 age classes)	$F_{1,483}=7.8, P<0.01$	f: 0.42 ± 0.22 ; m: -0.4 ± 0.18	AOV	Crick & Grotpeter 1995	
human (<i>Homo sapiens</i>)	aggression (overt)	boys>girls	235f, 256m (4 age classes)	$F_{1,483}=68.1, P<0.001$	f: -1.09 ± 0.10 ; m: 0.77 ± 0.19	AOV	Crick & Grotpeter 1995	
human (<i>Homo sapiens</i>)	choosiness	f>m	334f, 134m	$F_{1,2329}=21.22, P<0.01$	NR	ACOV	Woodward & Richards 2004	
human (<i>Homo sapiens</i>)	emotional stability	m>f	dat: 59f?, 59m? mar: 106f, 105m	dat: $t=5.87, P<0.001$ mar: $t=8.80, P<0.001$	dat: $f: 4.08\pm0.08?$; m: $4.68\pm0.07?$ mar:	TT	Botwin et al. 1997	
human (<i>Homo sapiens</i>)	exacting & choosiness	f>m	dat: 57f, 53m; mar: 104f, 103m	dat: $t=-2.56, P<0.05$; mar: $t=-5.03, P<0.001$	dat: $f: 4.23\pm0.06$; m: 4.90 ± 0.05	TT	Botwin et al. 1997	
human (<i>Homo sapiens</i>)	humour (rate)	m>f	29 six-person groups (mixed & single-sexed)	$b=-1.41, P=0.01$	NR	GWM	Robinson & Smith- Lovin 2001	

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human (<i>Homo sapiens</i>)	humour	m>f	29 six-person groups (mixed & single-sexed)	b=-2.94, P=0.01	NR	GWM		Robinson & Smith- Lovin 2001
human (<i>Homo sapiens</i>)	intellect- openness	m>f	mar: 106f, 105m	t=2.32, P<0.05	f: 5.11 \pm 0.05;	TT		Botwin et al. 1997
human (<i>Homo sapiens</i>)	orientation (short-term)	m>f	133f, 131m	t=2.9, P<0.01	m: 5.24 \pm 0.05 f: 3.2 \pm 0.10;	TT		Fetchenhauer & Rohde 2002
human (<i>Homo sapiens</i>)	preference for surgency	f>m	dat: 57f, 53m; mar: 104f, 103m	dat: t=-2.33, P<0.05; mar: t=-3.68, P<0.001	m: 3.6 \pm 0.11 dat: f: 5.31 \pm 0.07; m: 5.09 \pm 0.06; mar:	TT		Botwin et al. 1997
human (<i>Homo sapiens</i>)	preference for intellect- openness	f>m	dat: 57f, 53m; mar: 104f, 103m	dat: t=-2.89, P<0.01; mar: t=-3.88, P<0.001	dat: f: 5.29 \pm 0.05; m: 5.02 \pm 0.06 dat: f: 5.89 \pm 0.07; m: 5.62 \pm 0.07; mar:	TT		Botwin et al. 1997
human (<i>Homo sapiens</i>)	preference for dominance	f>m	dat: 57f, 53m; mar: 104f, 103m	dat: t=-4.33, P<0.0001; mar: t=-3.46, P<0.001	NR f: 5.73 \pm 0.05; m: 5.47 \pm 0.05 NR	TT		Botwin et al. 1997

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human (<i>Homo sapiens</i>)	preference for sense of humour	f>m	74f, 55m	$t_{127}=4.2, P<0.001$	NR (can be read from graph in study)	TT		Bressler et al. 2006
human (<i>Homo sapiens</i>)	preference for humour production	f>m	74f, 55m	$t_{127}=5.14, P<0.001$	NR (can be read from graph in study)	TT		Bressler et al. 2006
human (<i>Homo sapiens</i>)	preference for humour production	f>m	61f, 59m	$t_{118}=3.23, P=0.002$	NR (can be read from graph in study)	TT		Bressler & Balshine 2006
human (<i>Homo sapiens</i>)	response to partner's infidelity (sexual or emotional)	m more responsive to sexual, f more to emotional	128f, 128m	$\chi^2_1=42.63, P<0.05$	NR	χ^2		Shackelford et al. 2002
human (<i>Homo sapiens</i>)	risk-taking	m>f	133f, 131m	$t=4.5, P<0.01$	f: 2.6 ± 0.10 ; m: 3.3 ± 0.14	TT		Fetchenhauer & Rohde 2002
human (<i>Homo sapiens</i>)	self-esteem, internal locus of control, anxiety, assertiveness	anxiety: f>m assertiven.: m>f	17729 (data from 68 studies, 105 samples; varying N for different behavioural traits); meta-analyses					Feingold 1994
human (<i>Homo sapiens</i>)	ToM (usage of affective state terms)	girls>boys	14f, 25m	$t_{19}=-2.17, P=0.04$	f: 0.09 ± 0.02 ; m: 0.04 ± 0.01	TT		Knickmeyer et al. 2006

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human (<i>Homo sapiens</i>)	ToM (usage of neutral propositions)	boys>girls	14f, 25m	$t_{33}=2.01, P=0.05$	f: 0.37 \pm 0.03; m: 0.45 \pm 0.03	TT		Knickmeyer et al. 2006
human (<i>Homo sapiens</i>)	aspects of FFM	anxiety: f>m assertiven.: m>f gregariousn.: f>m trust: f>m tendermind.: f>m	105742 (varying N for different behavioural traits); meta-analyses					Feingold 1994
human (<i>Homo sapiens</i>)	aspects of FFM		22642 (data from 29 human studies of 26 cultures); meta-analyses					Costa et al. 2001
human (<i>Homo sapiens</i>)	aggression (overt)	m>f		review				Campbell 1999
human (<i>Homo sapiens</i>)	aggression (relational)	f>m		review				Campbell 1999
human (<i>Homo sapiens</i>)	humour	f>m		review				Kaufman et al. 2008
human (<i>Homo sapiens</i>)	appreciation							
human (<i>Homo sapiens</i>)	vulnerability to stress	f>m		review				Troisi 2001
human (<i>Homo sapiens</i>)	social cognition			review				Geary 2002

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human	ToM, social							Geary 2006
(<i>Homo sapiens</i>)	cognition							
human	different							Buss 1995
(<i>Homo sapiens</i>)	behaviours							
(b) Inter-individual agreement in mate choice								
Trinidadian	boldness towards	h>l	20f	?, P<0.03		BT	f-MC	Godin & Dugatkin 1996
guppy (<i>Poecilia reticulata</i>)	predator (courtship inhibited)							
Trinidadian	boldness towards	h>l	20f	?, P<0.01		BT	f-MC	Godin & Dugatkin 1996
guppy (<i>Poecilia reticulata</i>)	predator (courtship possible)							
collared flycatcher	song post	h>l ^d	22m?	R ₀ =0.564, 95%CI=0.095/0.828		PP-COR	time to pair bond	Garamszegi et al. 2008
(<i>Ficedula albicollis</i>)	distance (relative to source of risk)							
human	humour	h>l	74f, 55m	f: t ₇₃ =11.1, P<0.001; m: t ₅₄ =6.56, P<0.001		TT	f-MC, m-MC	Bressler et al. 2006
(<i>Homo sapiens</i>)	appreciation (receptivity)							
human	humour	h>l	74f, 55m	f: t ₇₃ =8.40, P<0.001; m: t ₅₄ =0.70, P=1		TT	f-MC, not m-MC	Bressler et al. 2006
(<i>Homo sapiens</i>)	(production)							

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human (<i>Homo sapiens</i>)	humour	h>l	63f, 64m	f: $t_{60}=5.79$, $P<0.0001$; m: $t_{58}=0.36$, $P=0.72$		TT	f-MC, not m-MC	Bressler & Balshine 2006
human (<i>Homo sapiens</i>)	humour (sense of)	h>l	74f, 55m	f: $t_{73}=15.4$, $P<0.001$; m: $t_{54}=7.10$, $P<0.001$		TT	f-MC, m-MC	Bressler et al. 2006 Miller 2007
human (<i>Homo sapiens</i>)	moral virtues			review				
(c) Inter-individual variation in mate choice								
zebra finch (<i>Taeniopygia guttata</i>)	aggression		102f	$R=0.16$, $P=0.048$		REP1	f-MC	Forstmeier & Birkhead 2004
great tit (<i>Parus major</i>)	exploration		10FE, 8SE	?, $P=0.02$		WT	m-MC	Groothuis & Carere 2005
zebra finch (<i>Taeniopygia guttata</i>)	song rate		83f	$R=0.24$, $P=0.014$		REP1	f-MC1	Forstmeier & Birkhead 2004
(d) Partners' personality and reproductive success								
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	aggression (latency to approach mirror)	ass>nona**	23 pairs (sp: 13, n-sp: 10)	sp: $R_s=0.52$, $P=0.004$; n-sp: $R=?$, $P>0.44$		S-COR	RS (spawning: y/n)	Budaev et al. 1999
cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	h>l	21 pairs (5 w/o eggs, 16 w)	$U=2$, $P<0.002$		MWU	RS (egg laying: y/n)	Spoon et al. 2006

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	h>l	21 pairs	$R_s=0.91$, $P<0.001$		S-COR	RS (no. chicks reared to independ.)	Spoon et al. 2006
cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	h>l	14 pairs	$R_s=0.93$, $P<0.001$		S-COR	RS (hatchling success of fertile eggs)	Spoon et al. 2006
cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	l>h	21 pairs	$U=12$, $P=0.004$		MWU	EPC (y/n)	Spoon et al. 2007
dumpling squid (<i>Euprymna tasmanica</i>)	boldness (foraging test)	ass>nona (for intermediate & bold f)	92 mating attempts	$R_s=0.47$, $P=0.01$ (all individuals)		S-COR	RS (% successful reproduction)	Sinn et al. 2006
great tit (<i>Parus major</i>)	exploration	ass>nona	69 pairs	$\chi^2_1=14.85$, $P=0.0001$		GLM	EPP	van Oers et al. 2008
great tit (<i>Parus major</i>)	exploration	ass>nona	141 pairs?	$F_{1,135}=7.82$, $P=0.006$		GLM	RS (fledgling condition)	Both et al. 2005
great tit (<i>Parus major</i>)	exploration	ass>nona	44 pairs	$\chi^2_1=4.16$, $P=0.046$		GLM	RS (no. of recruits)	Dingemanse et al. 2004
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	exploration (latency to enter novel area)	ass>nona**	23 pairs (sp: 13, n-sp: 10)	sp: $W=456$, $P=0.004$; n-sp: $W=?$, $P>0.44$		KT	RS (spawning: y/n)	Budaev et al. 1999

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	response towards novel fish (PCA comp.)	ass>nona**	23 pairs (sp: 13 n-sp: 10)	sp: $R_s=0.57$, $P=0.029$; n-sp: $R_s=0.03$, $P=0.473$		S-COR	RS (spawning: y/n)	Budaev et al. 1999
(e) Behaviourally assortative partnerships								
human (<i>Homo sapiens</i>)	agreeableness	positive	dat: 59? pairs; mar: 107? pairs	dat: $r=0.27$, $P<0.05$; mar: $r=0.33$, $P<0.001$		COR		Botwin et al. 1997
human (<i>Homo sapiens</i>)	broad interests (openness)	positive	85 pairs	$r=0.28$, $P=0.01$; controlling for age & attractiveness: $r=0.24$, $P=0.033$ $r=0.33$, $P=0.007$		P-COR		Little et al. 2006
human (<i>Homo sapiens</i>)	conscientious.	positive	65 pairs	$r=0.33$, $P=0.007$		P-COR		Little et al. 2006
human (<i>Homo sapiens</i>)	conscientious.	positive	dat: 59? pairs; mar: 107? pairs	dat: $r=0.27$, $P<0.05$; mar: $r=0.22$, $P<0.05$ $r=0.25$, $P=0.049$		COR		Botwin et al. 1997
human (<i>Homo sapiens</i>)	extraversion	positive	65 pairs			P-COR		Little et al. 2006
human (<i>Homo sapiens</i>)	(intellect)- openness	positive	dat: 59? pairs; mar: 107? pairs	dat: $r=0.51$, $P<0.001$; mar: $r=0.38$, $P<0.001$		COR		Botwin et al. 1997
human (<i>Homo sapiens</i>)	problem behaviour (agreeableness)	positive	14 studies (out of 16) supported assortative mating b/w partners for measured problem behaviours (1 support for social homogamy, 1 no support for assort. mating)					Rhule-Louie & McMahon 2007

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
human (<i>Homo sapiens</i>)	multiple personality measures	positive, (negative)	mar: 93 pairs	32 (out of 93) correlations $P < 0.05$, (30 positive, 2 negative)		COR		Buss 1984
human (<i>Homo sapiens</i>)	personality (BFI)	positive	dat: 66 pairs	$r = 0.21$, $t_{65} = 6.08$, $P < 0.001$		TT, COR		Gonzaga et al. 2007
human (<i>Homo sapiens</i>)	personality (NEO)	positive	mar: 172 pairs	$r = 0.42$, $t_{171} = 24.46$, $P < 0.001$, $d = 3.74$		TT, COR		Gonzaga et al. 2007
human (<i>Homo sapiens</i>)			review					Vandenberg 1972
II. Consistency of behaviour								
(a) Sex differences								
Midas cichlid fish (<i>Cichlasoma citrinellum</i>)	aggression (y/n)	$m > f^{**}$	14f, 14m	f: $P < 0.05$ m: $P > 0.05$ ($P < 0.05$ indicates instability)		CQT		Holder et al. 1991
great tit (<i>Parus major</i>)	exploration	$f = m$	74f, 111m	f: $R \pm SE = 0.27 \pm 0.11$, $P = 0.01$; m: $R \pm SE = 0.48 \pm 0.07$, $P < 0.0001$; $F_{3,432} = 1.09$, $P = 0.35$		REP2		Dingemans et al. 2002

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
great tit (<i>Parus major</i>)	exploration	f=m	11f, 22m	f: $R \pm SE = 0.66 \pm 0.17$, P=0.007; m: $R \pm SE = 0.46 \pm 0.17$, P=0.012;		REP2	Dingemans et al. 2002	
zebra finch (<i>Taeniopygia guttata</i>)	exploration	m>f	12m, 12f	$F_{3,432} = 1.09$, P=0.35 f: $R \pm SE = -0.06 \pm 0.11$, P=0.645; m: $R \pm SE = 0.60 \pm 0.14$, P<0.0001; Z=2.97, P=0.003		REP3	Schuett & Dall, in press	
zebra finch (<i>Taeniopygia guttata</i>)	foraging (time spent)	f>m*	9f, 9m	f: $R \pm SE = 0.68 \pm 0.15$, P=0.0001; m: $R \pm SE = 0.22 \pm 0.23$, P=0.141; Z=1.83, P=0.067		REP3	Schuett & Dall, in press	
zebra finch (<i>Taeniopygia guttata</i>)	foraging with partner (relative time)	m>f*	9f, 9m	f: $R \pm SE = 0.20 \pm 0.23$, P=0.176; m: $R \pm SE = 0.75 \pm 0.13$, P<0.001; Z=1.90, P=0.057		REP3	Schuett & Dall, in press	

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
zebra finch (<i>Taeniopygia guttata</i>)	leadings (number of)	f=m	9f, 9m	f: R \pm SE=0.10 \pm 0.23, P=0.303; m: R \pm SE=0.49 \pm 0.21, P=0.021; Z=1.16, P=0.246		REP3		Schuett & Dall, in press
zebra finch (<i>Taeniopygia guttata</i>)	latency to approach feeder	f=m	9f, 9m	f: R \pm SE=0.50 \pm 0.21, P=0.019; m: R \pm SE=0.25 \pm 0.23, P=0.119; Z=0.74, P=0.457		REP3		Schuett & Dall, in press
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	parental care (activity)	m=f**	23f, 23m	f: α =0.78; m: α =0.77		α		Budaev et al. 1999
convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	parental care (brood provisioning)	f>m**	23f, 23m	f: α =0.90; m: α =0.83		α		Budaev et al. 1999
Long-tailed tit (<i>Aegithalos caudatus</i>)	parental care (brood provisioning)	m>f**	10f, 16m	f: R=0.37, P=?; m: R=0.7, P=?;		REP		MacColl & Hatchwell 2003

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
house sparrow (<i>Passer domesticus</i>)	parental care (feeding rate per chick)	m>f	10-37f, 17-37m, (different years, time span, adjustments)	f: R \pm SE=0.19- 0.35 \pm 0.14-0.29, P=0.006-0.213; m: R \pm SE=0.44- 0.69 \pm 0.10-0.15, P<0.0001-0.003; t ₆ =6.60, P<0.001	REP4		Nakagawa et al. 2007	
house sparrow (<i>Passer domesticus</i>)	parental care (incubation time)	m=f	18-60f, 24-61m, (different years, time span, adjustments)	f: R \pm SE=0.09- 0.35 \pm 0.09-0.22, P<0.0001-0.233; m: R \pm SE=0.21- 0.35 \pm 0.09-0.20, P<0.0001-0.167; t ₆ =6.35, P=0.549	REP4		Nakagawa et al. 2007	
house sparrow (<i>Passer domesticus</i>)	parental care (delivery rate)	m>f**	23f, 30m	f: R \pm SE=-0.06 \pm 0.2, P=0.605; m: R \pm SE=0.38 \pm 0.16, P=0.018	REP		Schwagmeyer & Mock 2003	
house sparrow (<i>Passer domesticus</i>)	parental care (delivery rate, adjusted for brood size & date)	m>f**	23f, 30m	f: R \pm SE=-0.08 \pm 0.2, P=0.64; m: R \pm SE=0.44 \pm 0.15, P=0.008	REP		Schwagmeyer & Mock 2003	

Species	Behavioural trait	Direction	N	Stats	Mean \pm SE	Analyt. ^a	Effect on ^b	Study
savannah	parental care	m>f**	19f, 14m	f: R=0.20, P=0.083; m: R=0.60, P=0.012		REP		Freeman-Gallant & Rothstein 1999
(<i>Passerculus sandwichensis</i>)	(feeding rate)							
(b) Consistency as indicator of quality								
chestnut-sided	5 song variables	h>l	20 cases of EP	t ₁₉ =-4.47-3.53		TT	EP success	Byers 2007
warblers	(coefficients of		offspring	P<0.001-0.012			(paternity	
(<i>Dendroica pensylvanica</i>)	variation)						winner vs.	
							loser)	

For sex differences in the level of behaviour and behaviourally assortative partnerships: only significant results and only a selection of studies are reported due to the vast number of studies published with these aspects. **ass**: assortative; **assertiven.**: assertiveness; **BFI**: Big Five Inventory; **b/w**: between; **conscientiousn.**: conscientiousness; **dat**: dating couple; **dis**: disassortative; **FE**: fast explorers; **f**: female; **FFM**: Five Factor Model; **gregariousn.**: gregariousness; **h**: high; **l**: low; **m**: male; **mar**: married couple; **nona**: non-assortative; **NEO**: Neuroticism-Extraversion-Openness Inventory; **NR**: not reported; **n-sp**: non-spawning; **PCA comp.**: Principle Component Analysis component; **SE**: slow explorers; **sp**: spawning; ; **tendermind.**: tender-mindedness; **ToM**: theory of mind; **w**: with; **w/o**: without; *: trend; **: not statistically tested

^a **Analyt.**: analytical methods: **ACOV**: ANCOVA; **α** : Cronbach alpha; **AOV**: ANOVA; **BT**: binomial test; **χ^2 T**: χ^2 -test; **COR**: correlation; **CQT**: Cochran Q test; **FET**: Fisher's exact test; **GLM**: generalised linear model; **GWM**: generalised Weibull model; **KT**: Krauth test; **KW**: Kruskal-Wallis test; **LMM**: linear mixed model; **MWU**: Mann-Whitney U test; **P-COR**: Pearson's product moment coefficients; **PP-COR**: partial correlation; **Rep-AOV**: repeated ANOVA; **REP**: repeatability; **REP1**: repeatability of female preference function; **REP2**: repeatabilities for sexes compared using F-statistics; **REP3**: repeatabilities for the sexes z-transformed and compared; **REP4**: repeatabilities compared with a type of paired t-test using linear mixed models; **S-COR**: Spearman rank correlation; **Sp-AOV**: split-plot ANOVA; **TT**: t-test; **WT**: Wilcoxon test.

^b **Effect on**: **EPC**: extra-pair copulation; **EP**: extra-pair; **EPP**: extra-pair-paternity rate; **f-MC**: female mate choice; **f-MCI**: female mate choice, dependent on females' activity tendency; **m-MC**: male mate choice; **RS**: reproductive success; **y/n**: yes/no, binary variable

^c the percentage of individuals displaying the behaviour of interest at least once was tested for sex differences, not the mean values

^d Individuals that were exploratory and/or risk-takers sung from lower posts when a human was around. These individuals bonded faster with a partner than individuals singing from higher posts.

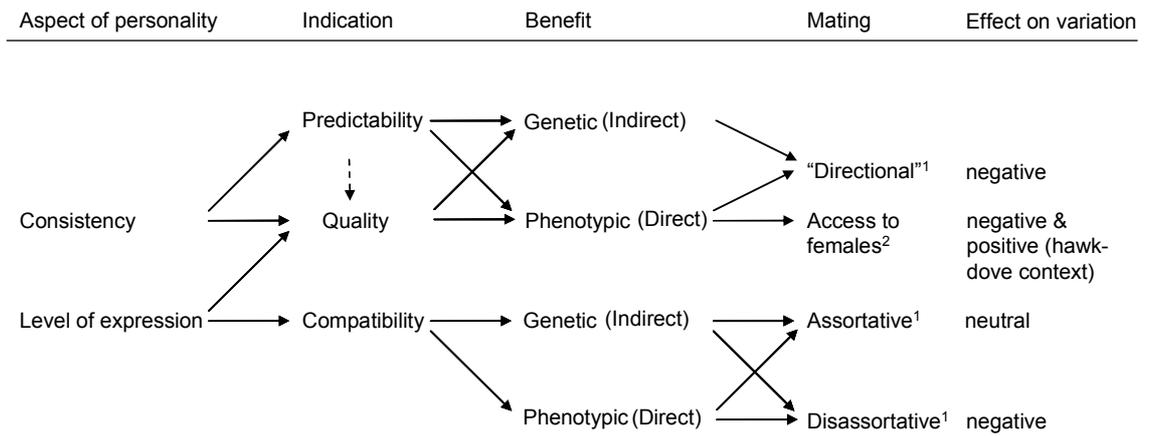


Figure 1. Suggested framework for understanding sexual selection on personality, both behavioural consistency and variation in the level of behaviour. ¹ = selection via mate choice; ² = selection via male-male competition. For more details see text.

Chapter 2

Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*

ABSTRACT

Despite burgeoning interest in consistent individual differences in behaviour (animal “personality”), the influence of social interactions on the performance of different behavioural types is poorly understood. Similarly, the ecological and evolutionary consequences of personality differences in social contexts remain unexplored. Moreover, the possibility that the sexes differ in the degree to which they exhibit personality in both social and non-social contexts has not yet received serious attention, despite the fact that the sexes are usually subject to differing selection pressures. Using a highly gregarious species, the zebra finch, *Taeniopygia guttata*, we tested for consistent behavioural differences (in exploration) among individuals of both sexes in both non-social and social contexts, the latter considering the behavioural influence of opposite-sex companions (Part I). Furthermore, we investigated how exploratory tendencies relate to behaviour in a potentially risky foraging context in mixed-sex dyads of individuals with differing personalities (Part II). Males were not more exploratory on average but were more consistent in their exploratory tendencies than females. Additionally, males behaved more consistently across the social and asocial contexts than females, even though individuals of both sexes similarly influenced each others exploratory behaviour within the social context: the more exploratory the companion, the more exploratory the focal individual (relative to its level of exploration in the asocial context). An individual’s exploration also affected its performance in the social foraging context. Our results stress the importance of looking for sex differences in personality and of considering the influence of social context in animal personality studies. We discuss our findings and their implications in the light of the biology of the species and set them in a broader ecological and evolutionary context.

Keywords: sex differences; individual differences; personality; exploration; foraging; repeatability; novel environment; behavioural synchronisation; leadership

INTRODUCTION

Individuals often differ consistently in their behavioural expression from other members of the local population (Benus et al. 1991; Boissy 1995; Koolhaas et al. 1999; Gosling 2001). Such so-called “personality differences” are frequently correlated among contexts, generating “behavioural syndromes”, i.e. suites of correlated behavioural traits (Sih et al. 2004b). As personality differences are distributed non-randomly along axes of behavioural variation and have fitness consequences (Gosling 2001; Sih et al. 2004a; Sih et al. 2004b; Dingemanse & Réale 2005; Smith & Blumstein 2008), their ecological and evolutionary consequences are expected to be significant (Dall et al. 2004; Sih et al. 2004b). Most personality studies have thus far investigated consistent individual behavioural types and their consequences in non-social contexts (e.g. Dingemanse et al. 2003: relationship between individual exploration under social separation and dispersal distance). Rarer investigations into social contexts mainly consider survival-competitive aspects, such as relationships between exploration and aggression (Verbeek et al. 1996) or dominance (Dingemanse & de Goede 2004), whereas other social aspects have attracted even less attention (but see Marchetti & Drent 2000; van Oers et al. 2005b). So why are social influences worth investigating? Firstly, focal individual behaviour is likely to be influenced by the behaviour of other conspecifics (and individuals of different behavioural types might be influenced differently). Therefore, results obtained from non-social personality tests might not reflect individuals’ responses under (more) natural social situations, particularly in highly social or gregarious species. Consequently, misleading conclusions might be drawn from studies restricted to asocial conditions. Based on contrasting results from social and non-social behavioural tests, some researchers have suggested that the social environment influences an individual’s behaviour via fear reduction (Jones & Merry 1988; Jones et al. 1995; van Oers et al. 2005b). Furthermore, a non-social context can simply limit the behavioural performance, as ‘the social context is a necessary condition for the expression of a broad range of behaviour in organisms, including individual differences’ (Malloy et al. 2005, page 643). Secondly, social behaviour is important for individual survival in many circumstances. For instance, the social environment influences an animal’s foraging performance (reviewed in Galef & Giraldeau 2001). Not only can the presence of conspecifics affect foraging strategies of individuals in general but it can also influence individuals differently, depending on their personality: Marchetti & Drent (2000) showed that individual great tits, *Parus major*, of different exploration types, differed in their tendency to copy a tutor’s foraging decision. Besides effects on foraging decisions, the company of conspecifics can have impacts on perceived predation risk (Clutton-Brock et al. 1999; Lima et al. 1999; Krause & Ruxton 2002) and/or food competition (Janson & Goldsmith 1995). This probably affects the risk-taking behaviour of individuals differently (van Oers et al. 2005b). Finally, sex is social and required for reproduction and therefore crucial for individual fitness. Social interactions between mates

are widespread, particularly in species in which partners stay together after fertilisation of female's gametes. As the sexes have different roles in reproduction and/or are often subject to distinct selection pressures, arising from e.g. intrasexual competition or mate choice, we should also expect sexes to differ consistently in their behavioural performance and to be influenced by their social environments differently. That males and females respond differently in social versus non-social contexts is evident in risk-taking behaviour in great tits studied by van Oers et al. (2005b). However, in this study all individuals experienced non-social tests before social tests which could have confounded any influence of social context *per se*. Also, all companions were males and therefore only the influence of male companions on focal females but not the influence of females on males was assessed. Yet, distinct sex-of-partner effects on the response of the focal individuals of different sexes have been shown in mice, *Mus musculus*, (Malloy et al. 2005) and zebra finches, *Taeniopygia guttata* (Benskin et al. 2002). In the latter, females copied foraging decisions more frequently from male rather than female tutors, whereas males did not appear to distinguish between the sex of the demonstrator. Hence, there is some evidence that personality differences can have substantial impacts on social performance and vice versa. Moreover, these implications seem to differ for males and females. But further work is needed to shore up these findings. Here we focus on how sexes differ in their personality and how personality differences influence the social performance of the sexes. The latter may have implications for behavioural coordination both in mated pairs (e.g. for providing food for the offspring) and in social contexts in general (e.g. via risk dilution when feeding/moving together in groups), which could be particularly crucial in contexts important for survival like foraging.

The aims of this study were to investigate consistent behavioural differences (in exploration) among individuals and between sexes in a non-social and social context, considering the influence of opposite-sex companions in the latter (Part I). Furthermore, we investigated how *a priori* established exploratory tendencies affect behaviour in a potentially risky foraging context in mixed-sex dyads (Part II): we measured individual leadership and foraging behaviour as influenced by the combination of focal individual and companion exploratory tendencies (from Part I). We also recorded the proportion of time the male and female companions spent together at a risky novel food source as influenced by the combination of their exploration types. The latter may reflect behavioural synchronisation in a risky situation which can affect individual fitness (see above: offspring provision, risk dilution). The highly gregarious zebra finch was used as a model study species. In these birds partnerships are socially monogamous and characterised by biparental care (Zann 1996).

Given the general issues discussed above and the biology of the study species we predicted the following: firstly, due to different roles and/or distinct selection pressures we expected males and females to differ in the levels of and/or consistency in exploration. More

specifically, male zebra finches usually lead their female around through the colony except during breeding when the opposite occurs (Zann 1996). Based on the leadership role of males during most of the year, it may be advantageous for a female to have a male who is consistent and therefore predictable in its exploration and leadership behaviour. It could be crucial for a female to be led to feeding sites in a reliable manner in order to gain access to food at a regular rate. Consequently, we expected males (a) to be more consistent in their exploration and leading than females, (b) to influence females' exploratory behaviour more than the other way round and (c) to generally show a higher level of exploration and leading behaviour than females given that tests were conducted outside the breeding season. Secondly, as more exploratory and active individuals are likely to lead more often (see Beauchamp 2000, for tests on mostly males), we expected the two measures to be correlated. Finally, for relationships between the combination of exploratory tendencies in a group and its influence on male and female tendencies to spend time together at a novel risky feeder, we predicted one of two scenarios: exploratory individuals will rarely join their companions (see also Budaev 1997) and should therefore spend more time on their own at the feeder if they have a behaviourally similar companion. However, less exploratory individuals are predicted to join companions more often, resulting in an increased proportion of time spent with a companion (regardless of its exploration tendency). Alternatively, (dis)similar behavioural types may coordinate their foraging and spend more time together at the feeder (for reasons see above, Burley 1983).

METHODS

ETHICAL NOTE

Methodological and animal welfare issues were approved by the Ethical Committee of the University of Exeter and discussed with our Home Office inspector, who agreed that no special license was required. The condition and health of all birds were monitored on a daily basis.

HOUSING AND STUDY SPECIES

We used sexually experienced, adult wild-type zebra finches (1-1.5 years old). They originated from different commercial suppliers in the UK but were kept for more than six months in the University of Exeter, Cornwall Campus aviaries prior to the experiments. All focal birds were housed outdoors in two mixed flocks in free-flight enclosures (84 x 215 cm and 263 cm high). These holding enclosures contained a number of perches at two locations across the width of the cages as well as nest boxes, feeders and drinkers. Commercial seeds (Foreign Finch Mixture; J. E. Haith, Cleethorpes, UK), access to cuttlebone, grit and water were available *ad libitum*.

Supplementary conditioning food (a mixture of Rearing and Conditioning Food (J. E. Haith), Daily Essentials vitamin supplement (The Birdcare Company, Nailsworth, UK) and water) was provided once a week.

PART I: CLASSIFICATION OF EXPLORATORY TENDENCIES

METHODS

Novel environment set-up

The exploratory tendencies of 24 zebra finches (12 of each sex) were assessed in a novel environment between 14 October and 9 November 2006. This novel environment consisted of an outdoor aviary enclosure (65 x 110 cm and 93 cm high), which included eight different features: five perches, a feeder, the mesh of the cage as well as the ground, consisting of gravel. Unlike in the holding enclosures, the perches in the smaller test cage were relatively evenly distributed around the cage and available at a higher density. The mesh at the back of the cage was covered with a white cloth to increase the contrast with the background for videoing. The test cage was visually but not acoustically isolated from the holding enclosures. The focal birds did not have any experience with the experimental cage before the first test.

Experimental procedure

As we were interested in the consistency of individuals' exploration behaviour over time and across contexts, individuals were tested repeatedly in two different contexts, a social and an asocial one. We randomly assigned the focal individuals to one of the following two treatments groups: half of the individuals were tested twice in a mixed-sex pair (social context) and then twice on their own (asocial context), whereas the rest of the individuals experienced the two contexts in the opposite order. Hence, each individual was tested four times, with consecutive tests being one week apart. All tests were conducted within five hours of sunrise as zebra finches are most active in the morning (Cuthill et al. 1997; Dall & Witter 1998). Before the start of each trial the focal individuals were transferred into a cardboard box (22 x 20.5 cm and 13.5 cm high) which was then placed into the test cage. Once the lid of the box was opened from a distance (4 m), using a string, the trials started. A video camera (Sony Handycam DCR-HC90E) recorded the experimental birds for 5 min while W.S. was present (located 4 m from the test cage). The video tapes were later analysed for a number of responses of which we will only present the number of features visited by an individual here as this was the most informative response (e.g. in most of the trials individuals did not revisit any features). After each trial, the

body mass of the focal bird (or focal birds) was measured to the nearest of 0.1 g before the bird was released back into its home enclosure. The sequence in which individuals were tested on the four test days as well as their social partner were randomly chosen pre-experimentally with no two individuals being tested together more than once. Furthermore, the companion was always a familiar flock mate of the opposite sex. Familiar individuals were used in order to minimise potential display behaviour, which we never observed during any of the trials.

Recapture and further measurements

Because all birds were tested repeatedly, the novelty of the test situation was expected to decline due to learning/experience. To reduce this decline in the novelty, we tried to minimise the predictability of each novel environment test. We did this by capturing all individuals once between two consecutive tests and then keeping them under conditions as before the novel environment tests for a few minutes. After this, we released them back into the holding cages. Furthermore, the change of the companion and the two different contexts (with/without companion) were likely to maintain the novelty of the experimental situation for the birds.

In total, we recaptured the individuals four times in the morning (including once a few days after the last test series). The orders of capture during the recaptures were recorded to test whether the capture order was correlated with the degree of exploration of individuals. Furthermore, individuals were weighed when recaptured and morphological measurements (wing chord and tarsus length) were taken once. Wing chord was measured to the nearest 1 mm with a wing ruler, tarsus length to the nearest 0.1 mm with callipers. As wing length and tarsus length were significantly correlated (Pearson's correlation: $r = 0.412$, $N = 24$, $P = 0.045$), only tarsus length is considered in the following to avoid multicollinearity.

Missing data

One male died during the experiment (following three test trials: twice tested alone, only once in a pair: therefore its prospective partner for the partner trial was tested on its own) and one female had to be removed due to illness (following two tests in a pair). Data were used for the trials available (for repeatabilities: data points were included when at least two measurements of an individual were available). Furthermore, two recapture ranks and one weight-measurement of one individual were missing. The latter was replaced by the mean weight of this individual from the seven other measurements taken, as weight within individuals was highly repeatable ($R = 0.945 \pm 0.02$ SE, $F_{23,159} = 131.42$, $P < 0.0001$).

Statistical analyses

To assess how consistent individuals were in their exploratory behaviour over the course of the four trials, we calculated repeatabilities (Lessells & Boag 1987) and their standard errors (SE) for unbalanced design (Becker 1984). Multiple tests were conducted to assess repeatability of individuals of different sexes separately, controlling for the increased probability of type I error rates using the sequentially rejective Bonferroni procedure of Holm (Wright 1992). The experiment-wise type I error rate was set at 0.05. To analyse whether the sexes differed in their exploratory consistency, the repeatability estimates for the two sexes were z-transformed and compared (Stratford 2004). Individual behavioural consistencies were also assessed with linear mixed effect models (using REML estimates) while controlling for the impact of the different test contexts, features of individuals and other measurements on the exploration tendencies. For the assessment of time consistencies and evaluation of the relationship between the number of features visited by an individual and a range of explanatory variables, we started with a maximal model including the between-subject factors as summarised in Table 1a. As variance explained at the within-individual level can be caused by covariance within individuals, we controlled statistically for within-individual covariance by fitting both the mean individual value of weight/tarsus and the deviation of each weight/tarsus value from the individual's mean as outlined by van de Pol & Verhulst (2006) (for a working example see Dingemanse et al. 2007). Our within-subject factors were "home cage" and "individual". In a second linear mixed effect model, we assessed the influence of the companion's exploration on the exploration of the focal individual, with the sex of the focal individual and the order in which it experienced the social and non-social contexts as between-subject factors (for all variables included in the maximal model see Table 1a). The response was the difference between the number of features visited in the social trials and the mean number of features visited in the two asocial tests. Another linear mixed effect model was used to test for behavioural consistencies over the different treatments, i.e. contexts (social, asocial). The response was the number of features visited when tested alone, whereas the number of features visited when tested with a partner was one of the between-subject factors (Table 1a).

Minimal adequate models were obtained by stepwise deletion of non-significant fixed effects ($P > 0.05$), starting with the highest-order interactions and/or the least significant term when fitted last in the model, provided the simplification did not significantly reduce the explanatory power of the model (Crawley 2002). To compare the explanatory power of two subsequent models, maximum likelihood estimates were used (Crawley 2002). The effects of the random terms in the first model were assessed when only significant fixed effects were left in the model following the same approach as described for the fixed effects (see also Pinheiro & Bates 2000; Crawley 2002): the significance of the random term "individual" was estimated and

the repeatability of individuals' exploration tendency was calculated using the variances of the minimal model, accounting for significant effects left in the model.

If an explanatory variable was significant and contained more than two factor levels, the factor levels were collapsed in the manner described by Crawley (2002) to get information about which factor levels differed from one another. If necessary, the data were Box-Cox transformed to conform to the linear mixed effect model assumptions. All statistical analyses were conducted in R 2.1.1 (R Development Core Team 2005).

RESULTS

Overall, the number of features an individual visited over the four trials was significantly repeatable ($R = 0.321 \pm 0.11$ SE, $F_{23,69} = 2.83$, $P < 0.001$). However, when investigating exploratory behaviour of the sexes separately, only males' exploratory tendencies were significantly repeatable (males: $R = 0.595 \pm 0.14$ SE, $F_{11,35} = 6.74$, $P < 0.0001$; females: $R = -0.057 \pm 0.11$ SE, $F_{11,34} = 0.79$, $P = 0.645$; Bonferroni corrected). The difference in consistencies between males and females was highly significant ($Z = 2.97$, $P = 0.003$). To assess whether this difference in time consistency between the sexes occurred (a) because the between-individual variability was greater for males than for females (Figure 1) or (b) because the within-individual variability of males was smaller than the variation within females (Figure 2) or (c) because of both effects, we conducted two ANOVAs. The result of the analyses indicate that both effects combined caused the sex differences in consistencies, as males and females neither differed significantly in the between-individual variability ($F_{1,6} = 2.98$, $P = 0.135$), which was measured as the coefficient of variation for the number of features visited by individuals of one sex within one test series, nor in the within-individual variability ($F_{1,22} = 1.47$, $P = 0.238$). Within-individual variability was measured as the coefficient of variation for the number of features visited by an individual over the trials. Whereas the degree of within-individual variation between different females varied to a great extent (some females were very consistent, others very inconsistent), the males were more similar in their within-individual variation (see also Figure 2).

A similar pattern as for the sex differences in consistencies over all trials was observed for the sexes in the different contexts: females were neither consistent when tested on their own ($R = 0.183 \pm 0.28$ SE, $F_{10,12} = 1.47$, $P = 0.261$) nor when tested with a companion ($R = 0.327 \pm 0.28$ SE, $F_{10,11} = 1.97$, $P = 0.281$), whereas males were consistent over the asocial trials ($R = 0.666 \pm 0.16$ SE, $F_{11,12} = 4.99$, $P = 0.020$) and showed a trend towards being consistent over the social context, respectively ($R = 0.474 \pm 0.24$ SE, $F_{10,11} = 2.80$, $P = 0.159$, all Bonferroni corrected). The presence of a companion is probably responsible for this absence of a clear

consistency pattern during the social context: the more features the companion visited in the social context, the more features the focal individual visited (relative to the number of features it visited when it was tested alone), whereas a less exploratory companion had the opposite effect on the focal individual ($F_{1,42} = 11.46$, $P = 0.002$; Figure 3). This effect was independent of the sex of the focal individual and the order in which it experienced the test contexts (thus these factors did not remain in the minimal model).

The mean number of features visited did not differ between the sexes but was influenced by the number of tests conducted ($F_{3,83} = 2.88$, $P = 0.041$) and the order in which the tests were administered ($F_{1,83} = 3.83$, $P = 0.043$): individuals were more exploratory during the last trial than during the previous three ($F_{1,85} = 5.55$, $P = 0.021$) and individuals in the group experiencing the asocial context before the social one were more exploratory than the other group. The number of features visited decreased with increasing weight/tarsus length both at the between- and the within-individual level (mean individual value: $F_{1,83} = 6.25$, $P = 0.014$; deviation of each weight/tarsus value: $F_{1,83} = 4.74$, $P = 0.032$). The opposite was true for recapture rank ($F_{1,83} = 4.64$, $P = 0.034$), i.e. more exploratory individuals were harder to catch. Highly significant individual differences in the numbers of features visited were evident (repeatability $R = 0.389 \pm 0.12$ SE; $P < 0.001$) when all significant fixed effects (see above) were fitted in the linear mixed effect model.

Besides temporal consistencies, we also found context consistency: the number of features visited between the two contexts covaried but such covariance differed between the sexes (significant interaction between the number of features visited when tested with a partner and sex: $F_{1,38} = 4.59$, $P = 0.039$) and depended upon which context an individual had experienced first (significant interaction between the number of features visited when tested with a partner and order: $F_{1,38} = 5.57$, $P = 0.024$; Figure 4). Males always positively covaried between the contexts, while females positively covaried if they experienced the novel environment asocially first but negatively if they experienced it socially first.

PART II: SOCIAL FORAGING PERFORMANCE

METHODS

Experimental housing and subjects

Three days prior to the second experimental part, which was conducted between the 15 November 2006 and 26 November 2006 (i.e. outside the breeding period in the UK), we formed

nine groups – consisting of one male and one female each – out of the pool of individuals we had classified in the first experimental part. In four of these groups, individuals with a similar mean number of features visited were kept together, whereas in the remaining five groups, individuals were unmatched based on their exploration in the novel environment. The matched individuals differed in the mean number of features they had visited over the four trials in experimental part I by a maximum of one feature, whereas the unmatched pairs differed by a minimum of 1.5 features (range: 1.5-3.25 features). In four of the non-matched groups the female was more exploratory than its male, vice versa for the remaining group. Each group formed was kept in an outdoor free-flight enclosure, identical to the holding enclosures, under equivalent conditions. The experimental cages were visually but not acoustically isolated from the other zebra finches kept in the aviary.

Experimental procedure

The protocol used was similar to the one applied by Beauchamp (2000), who assessed leadership in a foraging context of (mostly) same-sex zebra finch pairs. Each of our groups experienced three experimental trials, on days 3, 6 and 14 after pairing (owing to weather conditions). All trials were conducted between 1.25 and 3 hours after sunrise following a mild food deprivation of one hour. During the trials a feeder dish (33.5 x 23.5 cm and 5 cm high) filled with seeds was placed on the floor of the cage (a potential risky place). The shape and size of this feeder as well as its location were different to that used for the everyday food supply. The subsequent behaviours of the birds at the feeder were video recorded for 20 min. We were able to video two groups (a block) simultaneously and we also used two video cameras (Sony Handycam DCR-HC90E and Sony Handycam DCR-PCR-PC109E), resulting in a maximum of four groups being tested together. The order in which the blocks of two cages were videoed was randomised *a priori*. The video material was analysed for the latency to approach the feeder, the number of visits, the time an individual spent at the feeder, if it was on its own or with its companion, which individual approached the feeder first in a trial and how often a bird was leading (i.e. visiting the feeder when the companion joined at some point during the feeding bout). If an individual did not approach the feeder within the 20 min of the trial duration, the bird was assigned a maximum latency of 20 min. All groups had experienced the feeder dish on the ground once before the first trial. One female died before the last trial, resulting in a sample size of eight groups for the final test day.

Statistical analyses

Time consistencies within individuals with regard to the measured responses were assessed using repeatability calculations as described above, focussing again primarily on sex

differences. To investigate how the combination of exploratory tendencies in a group influenced males' and females' tendencies to spend time together at the potentially risky feeder, we fitted a linear mixed effect model (Table 1b) using the proportion of total time at the feeder an individual spent with its companion as the response. For assessment of impacts of different measurements on leadership two linear mixed effect models were conducted for the response variables: "being the first individual approaching the feeder in a trial" (binary response) and "proportion of leadings" (number of leadings by an individual/total number of leading events in a pair), respectively (Table 1b). For the binary response we fitted a GLMM with a binomial error distribution.

RESULTS

The sexes differed in their consistencies in a number of behaviours in the feeding context (Table 2): only females were significantly consistent in the total time they spent at the feeder over the trials and in the latency to approach the feeder for the first time during a trial, whereas only males spent a significantly repeatable relative amount of time with their partner at the feeder. Additionally, only males were consistent in the number of times they led. Neither males nor females were consistent in the number of times they visited the food source. The repeatabilities between the sexes differed close to significance for the total time spent at the feeder ($Z = -1.83$, $P = 0.067$) and the relative amount of this time spent with the partner ($Z = 1.90$, $P = 0.057$). Sex difference in the repeatability for the number of leadings ($Z = 1.16$, $P = 0.246$) and for the latency to approach the feeder were not significant ($Z = -0.74$, $P = 0.457$).

Alike companions were not significantly more consistent in the time they spent with their partner at the feeder than unlike individuals ($Z = 0.74$, $P = 0.460$) although only matched groups showed a trend towards spending repeatable amounts of times together at the feeder (Table 2f). Nor did matched groups spend relatively more time with their companion: there was a significant interaction between the type of group and sex ($F_{1,36} = 5.08$, $P = 0.030$), with unmatched grouped males spending relatively more time with their partners at the feeder than the equivalent females did (Figure 5a). There was also a significant interaction between sex and exploratory score for the proportion of time spent with the companion at the feeder ($F_{2,36} = 8.18$, $P = 0.001$, Figure 5b): less exploratory females spent less time with their companion at the feeder than did less exploratory males. The opposite was true for highly exploratory individuals. Furthermore, there was a significant interaction between exploration score and whether individuals were matched or not on the proportion of time spent with the companion at the feeder ($F_{2,36} = 5.94$, $P = 0.006$, Figure 6). Both low and high explorers spent a higher proportion of time with their companion at the feeder if they were in an unmatched than matched group. However, moderately exploratory individuals spent similar proportions with their partner

regardless of how well they were matched behaviourally to their partner. Additionally, the bigger the difference between the numbers of features visited in the novel environment between the partners of pair was, the more relative time spent they together at the feeder ($\chi^2_1 = 5.61$, $P = 0.018$, model comparison between model including the variable “exploration difference” (AIC 20.74) and model without (AIC 24.35)).

Neither sex nor any of the other terms fitted in the model influenced which companion approached the feeder for the first time during a trial. Nevertheless, the random effects explained a significant proportion of the total variance ($P < 0.0001$), indicating that individuals differed consistently in their tendencies to approach the feeders first.

Males and females did not differ in the proportion of leadings to the feeder. However, the difference in the mean number of features visited in the first experiment by prospective companions had an influence on the proportion of leadings in the group trials: the more features an individual had visited in the novel environment relative to its companion, the more it led its partner ($F_{1,38} = 12.13$, $P = 0.001$), regardless of its sex.

DISCUSSION

As predicted, our results suggest that (1) consistent behavioural differences in exploration, feeding performance and leadership (both in a potentially risky context) exist in zebra finches but (a) differ between the sexes and (b) depend on the social environment. The finding that consistent behavioural differences (over time and contexts) in exploration and foraging are present in zebra finches, corroborates other studies that have reported personality differences in the species (e.g. Beauchamp 2000; Forstmeier & Birkhead 2004). Factors, such as body condition (e.g. weight to tarsus length ratio), recapture rank and experience influenced the mean exploration levels observed, which could be driven by variation in metabolic costs, variation in predation risk (Witter & Cuthill 1993), condition-dependence or learning.

We found evidence that the sexes varied in how consistent they were in some behaviours but not others, although the latter effects may have been driven by the limited sample sizes in our experiment. As predicted, males were significantly more consistent in their exploration than females, while mean exploration levels did not differ significantly between the sexes. As we could not disentangle statistically whether this difference in consistency occurred because (a) the within-individual variation in males over time was less than that for females or (b) the between-individual variation in males was greater than for females, our results (see Figures 1 & 2) indicate that both effects were present. One could argue that (b) suggests the

selection on the overall level of female exploration is stronger than it is for males. Nevertheless, if selection favoured an optimal level of female exploration, females should not only show less between-individual variation but also less within-individual variation. However, lower within-individual variation in males (a) could suggest that selection is acting on the degree of exploration consistency in males. Combined with (b) this could mean, that consistency in exploration is selected for in males yet different males follow different exploratory strategies, that is, different levels of exploration are also selected for (e.g. different kinds of females may prefer different kinds of males or, more generally, different strategies may lead to similar pay-offs: see below).

Our finding of repeatability in males' exploration and leadership behaviour supports the hypothesis that exploration is a key male trait as they lead their females through the colony in the wild (Zann 1996) and that females may therefore prefer males whose exploration and leadership is predictable. For instance, following a consistent partner could maximise a female's reliable access to feeding sites. Moreover, only males differed consistently in the proportion of time they spent with their partners at the feeder. This behaviour could be interpreted as differences in attitudes towards risk: foraging alone can be risky (Clutton-Brock et al. 1999; Lima et al. 1999; Krause & Ruxton 2002). Males exhibited consistently different levels of this apparent risk-taking behaviour, indicating variation in individual quality or alternative life-history strategies selected for by strong fitness trade-offs (Stamps 2007; Wolf et al. 2007). In contrast, for females food is usually the limiting resource for reproduction (Andersson 1994) and thus the need for consistent food intake might have sometimes exceeded the potential risk, resulting in inconsistent proportions of time individual females spent with the partner but repeatable total time individual females spent at the feeder. Therefore it may have been important for the females to tie the amount of time spent feeding and the latency to approach the feeder to individual quality or condition, which is likely to vary among birds.

The sex differences in temporal consistencies in zebra finches we document here are suggestive of differential selection acting on male and female personality. These sex differences could arise from intrasexual competition or mate choice as well as from different roles of sexes in reproduction and associated differences in life-history strategies and ecological demands (for detailed discussion on factors that affect sex differences (in size) see Blanckenhorn 2005; Fairbairn et al. 2007). Nevertheless, further work is needed to shore up this interpretation. So far the possibility that males and females experience different selective pressures on consistencies in non-mating behaviours has largely been neglected in evolutionary biology and the study of animal personality. As a consequence, few studies have looked at repeatability of behaviour for the sexes separately and where they do, they focus on consistencies in parental care (see Budaev et al. 1999; Freeman-Gallant & Rothstein 1999; Schwagmeyer & Mock 2003; Nakagawa et al.

2007a). One exception is Dingemanse et al. (2002) who assessed the repeatability of the exploratory behaviour of the sexes independently. Interestingly, Budaev et al. (1999), Freeman-Gallant & Rothstein (1999), Nakagawa et al. (2007a) and Schwagmeyer & Mock (2003) found that male and female convict cichlids, *Cichlasoma (Archocentrus) nigrofasciatum*, savannah and house sparrows, *Passerculus sandwichensis* and *Passer domesticus*, respectively, also differed in behavioural consistencies, all in a parental care context (but note that only Nakagawa et al. 2007a tested this statistically, $P < 0.001$, and that sample sizes vary considerably between studies making it difficult to conclude anything). Whereas the male fish were slightly more unstable in their time spent with the brood than the females (but the effect size was small and unlikely to be biologically significant), males in both bird species were more consistent in their parental feeding rate than their female counterparts. The three bird studies showing males are more consistent in their parental behaviour than females may suggest that females choose males that care at a predictable rate, resulting in selection pressures favouring males showing consistent behaviour.

We found sex differences not only in time consistencies but also in situation consistencies: males always showed a positive relationship between the number of features visited when tested asocially or socially, regardless in which order they experienced the tests. However, if a female experienced the novel environment first in a social context, then her behaviours in the social and asocial context were negatively correlated. This could imply that females are influenced by the behaviour of their male companion when they experience a context for the first time, i.e. they adapt to the male's exploration level only when naive. However, this was not supported by our results: both males and females influenced the behaviour of the other sex in the same way in the social novel environment tests: the more features its companion visited in a trial, the more features the focal individual visited compared to its level of exploration in the asocial context; whereas the opposite effect was true for less exploratory companions. Also, we found that males and females differed in the proportion of time they spent with their partner at the feeder depending on their exploration score in the novel environment test. Less exploratory males in the novel environment spent relatively more time with their partner at the feeder than less exploratory females or more exploratory males. Similar sex differences in context consistencies have been revealed in cichlids, in which parental food provisioning was correlated with novel fish inspection and response to a mirror for males but not for females (Budaev et al. 1999). If the proportion of time spent with the partner at the feeder reflects risk-taking behaviour in our experiment (see above), then it could be that less exploratory males take fewer risks than more exploratory ones (also exploration and risk-taking in great tits are positively correlated, e.g. van Oers et al. 2004a) due to differences in life-history strategies or quality (Stamps 2007; Wolf et al. 2007). Secondly, less exploratory females might

take more risk (in a food context) compared to less exploratory males because of their need for consistent food intake (see above).

Our results regarding males' and females' tendencies to spend time together at the potentially risky feeder depending on their exploration type are not straightforward: we found that only groups matched for exploration tended to be repeatable in the proportion of time they spent together (and not alone) at the feeder; at the same time low and high explorers spent relatively more time with their companion at the feeder when they were in an unmatched than matched group. The first finding supports our prediction that individuals of a similar behavioural type coordinate their behaviour naturally (either functional pairs or conspecifics in general). Coordination of behaviour in functional pairs could lead to behavioural synchronisation and possibly increased reproductive success. Only indirect support for this hypothesis that similar behavioural types can optimise their reproductive performance via behavioural synchronisation is available in the literature: Spoon et al. (2006) showed that pairs of cockatiels, *Nymphicus hollandicus*, with greater behavioural compatibility before breeding (measured as a combination of proximity, behavioural synchrony, copulation, allopreening, responsiveness and total aggression) had greater reproductive success. Furthermore, Budaev et al. (1999) documented that cichlid parents behaved more similarly than did pairs that failed to reproduce. Similarly, Both et al. (2005) showed that great tit pairs with similar exploration tendencies produced offspring in the highest condition and Dingemanse et al. (2004) found that individuals of extreme and similar exploratory types recruited most offspring. However, under some circumstances, assortative mating seems important for only individuals of a certain behavioural type (Groothuis & Carere 2005, Chapter 3: only bold but not shy individuals prefer similar mates) and this appears to be due to behavioural and not genetic compatibility (Chapter 4: only foster parents' but not genetic parents' personality has an influence on offspring condition). Furthermore, disassortative pairing of extreme personalities can sometimes be beneficial (van Oers et al. 2008). The latter fits with our finding that low and high explorers in unmatched groups spent relatively more time with their companion than in matched (or medium explorers, unmatched) groups. Finally, we found that the proportion of time spent with a partner decreased from low to high explorers (Figure 6). This supports the notion that low explorers have a stronger tendency to join their companion (e.g. due to higher risk-averseness, see above). However, this effect was not strong enough to mask the effect of the kind of grouping (unmatched versus matched exploration types). Clearly more research is needed to investigate the circumstances under which similar or dissimilar behavioural types coordinate their behaviour most efficiently.

In sum, we were able to document a range of behavioural consistencies in zebra finches in foraging performance, exploration and leadership and we have shown that the social

environment can influence individuals' behavioural performance in a highly gregarious species. In particular, the link between an individual's exploratory tendency and its social foraging performance in a risky situation, which is likely to have substantial fitness consequences for individuals (e.g. increased predation risk if searching a food patch alone), stresses the need for further consideration of the social environment when studying personalities and their ecological and evolutionary consequences. We also demonstrated that the combination of exploratory tendencies of individuals in dyads influenced their time spent together at a risky foraging patch, which could have implications for behavioural coordination in social contexts in general. Moreover, we showed that males and females differed in a wide range of behavioural consistencies and were influenced differently by the social environments. These sex differences can be interpreted from an adaptive perspective (resulting from both viability and sexual selection) given the natural history of the species. However, further work is required to shore up our interpretation and to establish a general framework for understanding the influence of different selective pressures on animal personality differences (Dingemanse & Réale 2005; Groothuis & Carere 2005, Chapter 1). Nevertheless, in general, females might be expected to be selected for consistency in their choosiness and, as shown in our study, for consistency in their foraging intensities (with different females varying in their choosiness/foraging effort due to differences in body condition) given that reproduction for females is usually more energetically costly than it is for males (Andersson 1994). In contrast, males may be expected to be sexually selected for their consistency in aggressive behaviours, since males who are predictably aggressive may gain advantages in male-male agonistic interactions (Dall et al. 2004). Also, males are likely to be sexually selected for consistency in any behaviour for which predictability enhances performance in a pair, especially in species that form lifelong pair bonds. Different levels of such behaviours could then be selected for in individual males if different females have different needs (e.g. if (dis-)assortative mating leads to better behavioural coordination in pairs and higher reproductive success). Overall then, we hope that the patterns we document here, interpreted in the light of zebra finch biology, encourage further investigation into the rarely considered interaction between the social environment, individual personality and sex and their evolutionary and ecological consequences.

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Table 1. Terms included in the maximal mixed effect models applied to the data collected (a) in novel environment tests prior to pairing and (b) when individuals were tested in feeding contexts after being grouped with an individual of the opposite sex, matched or unmatched, respectively, for their exploratory tendency.

Response	Covariate	Fixed effect	Random effect
(a)			
No. of features visited	Recapture rank	Sex	Individual
	Weight/tarsus length (mean ID)	Test series	Cage number
		Treatment	
	Weight/tarsus deviation	Order	
	Time start trial	Treatment*sex	
		Treatment*order	
Change in no. features visited (social, asocial)	No. of features visited (companion)	Sex	Individual
		Order	Cage number
		No. of features visited (companion)*order	
No. of features visited (asocial)	No. of features visited (social)	Sex	Individual
		Order	Cage number
		No. of features visited (social)*order	
(b)			
Proportion of time at feeder with partner	Exploration difference	Sex	Individual
	Time start trial	Test series	Group number
		No. feeder partner	
		Score	
		Grouping	
		Grouping*sex	
	Score*grouping		
		Score*sex	
Individual approaching feeder first (binary)	Exploration difference	Sex	Individual
	Total time at feeder	Test series	Group number
		Score	
		Grouping	
		Grouping*sex	
	Score*grouping		
No. of leadings/total no. of feeder visits with partner	Exploration difference	Sex	Individual
		Score	Group number
		Grouping	
		Grouping*sex	
		Score* Grouping	

Cage number: number of home cage where an individual was kept; **exploration difference:** difference from the partner in the mean number of features visited in the first experiment; **group number:** each of

nine groups containing two individuals was assigned to a number; **grouping**: kind of group (matched, unmatched for exploratory tendency); **no. of features visited**: number of features visited in novel environment (in **asocial** and/or **social** context); **no. feeder partner**: number of feeder-visits by partner; **order**: order of the treatment (tested with companion first then alone and vice versa); **score**: exploration in novel environment (low, medium, high: individuals' exploratory tendency was classified based on the mean number of features visited as low (mean < 2, range 0.75-1.75), medium (mean 2-3, range 2-2.75) and high explorative (mean > 3, range 3.25-5.75); **test series**: number of trial series conducted (1-4 for novel environment, 1-3 for feeding context); **time start trial**: in minutes since sunrise; **treatment**: kind of context experienced in the novel environment (asocial, social); **weight/tarsus deviation**: deviation of each value from the individual mean; **weight/tarsus (mean ID)**: individual mean value.

Table 2. Repeatabilities and standard errors ($R \pm SE$) of individuals' behaviours in a feeding context.

Component	Mean	$R \pm SE$	d.f.	F	P
(a) Total time spent at feeder (in seconds)					
Overall	240.808	0.346 ± 0.157	17,34	2.528	0.011
Sex					
Female	280.308	0.684 ± 0.152	8,17	7.246	0.0001
Male	201.308	0.223 ± 0.232	8,17	1.827	0.141
(b) Proportion of time at feeder spent with partner					
Overall	0.535	0.510 ± 0.140	17,29	4.003	0.001
Sex					
Female	0.498	0.198 ± 0.231	8,14	1.713	0.176
Male	0.574	0.753 ± 0.126	8,14	9.803	<0.001
(c) No. of leadings					
Overall	1.096	0.112 ± 0.157	17,34	1.363	0.215
Sex					
Female	1.423	0.097 ± 0.225	8,17	1.310	0.303
Male	0.769	0.489 ± 0.206	8,17	3.760	0.021
(d) No. of visits at feeder					
Overall	3.096	-0.077 ± 0.134	17,34	0.795	0.687
Sex					
Female	3.269	-0.011 ± 0.208	8,17	0.967	0.984
Male	2.923	-0.109 ± 0.185	8,17	0.716	0.675
(e) Latency to approach feeder (in seconds)					
Overall	440.731	0.346 ± 0.157	17,34	2.525	0.011
Sex					
Female	392.846	0.496 ± 0.205	8,17	3.839	0.019
Male	488.615	0.247 ± 0.232	8,17	1.944	0.119
(f) Total time a pair spent together at feeder (in seconds)					
Overall	145.731	0.221 ± 0.23	8,17	1.817	0.143
Grouping					
Matched	72.273	0.630 ± 0.28	3,7	5.650	0.055
Unmatched	199.600	0.231 ± 0.31	4,10	1.902	0.187

P-values are Bonferroni corrected. Significant results are given in bold.

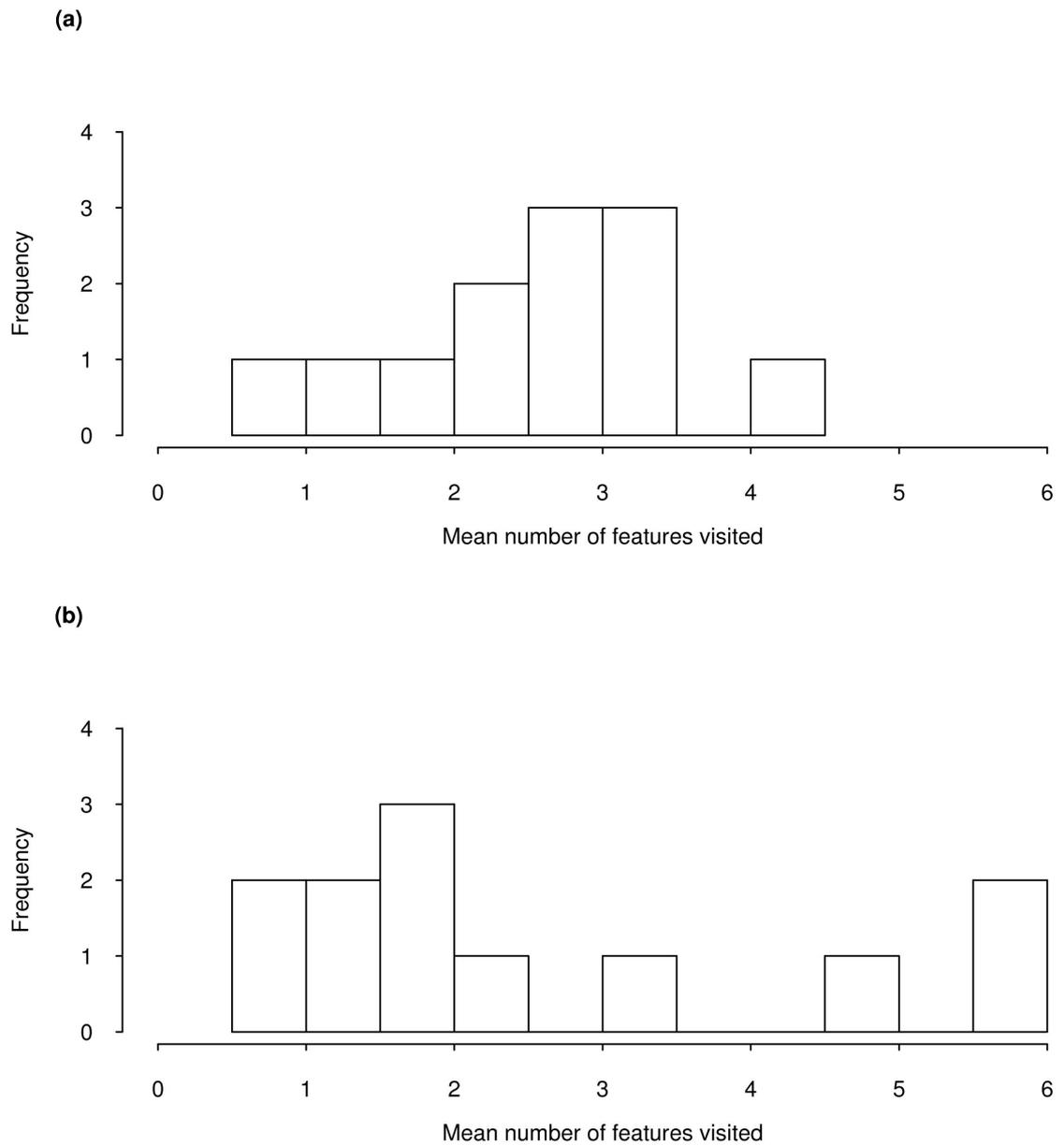


Figure 1. Distribution of the mean number of features visited by (a) females and (b) males in the novel environment over four test series.

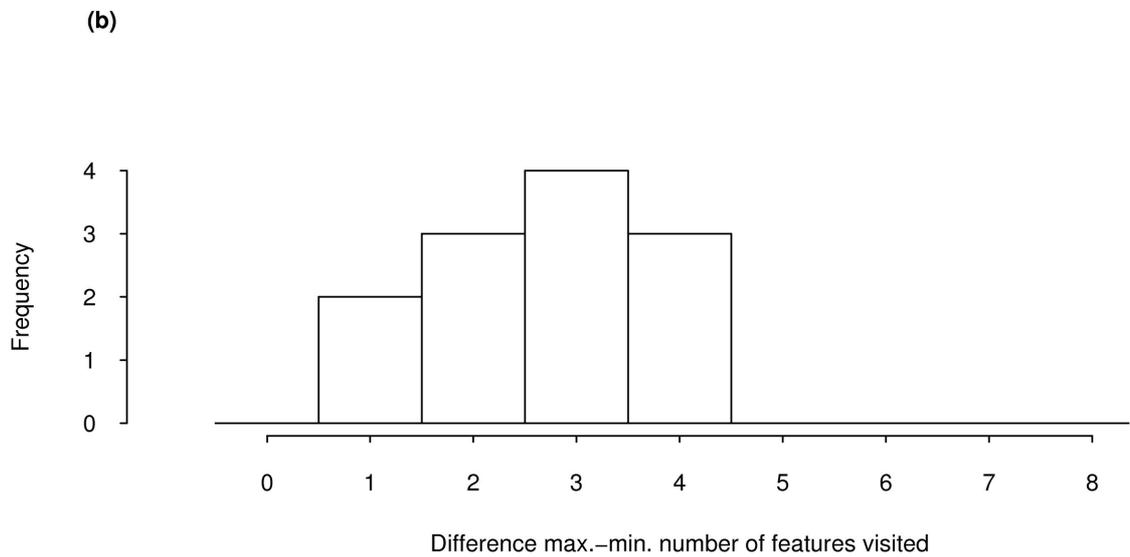
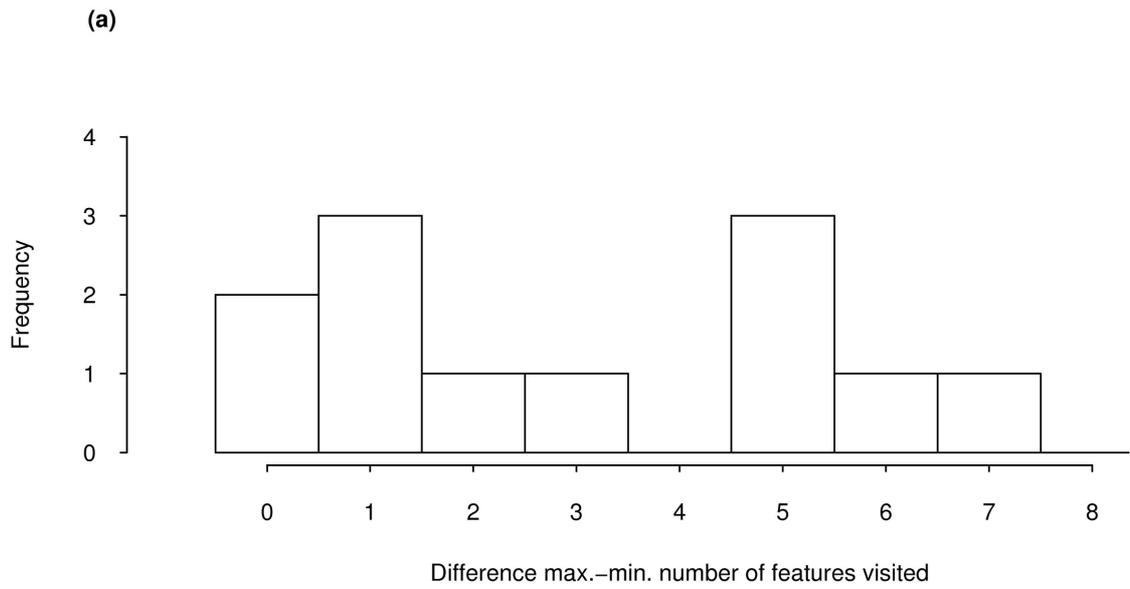


Figure 2. Distribution of the difference between the maximum and minimum number of features visited by (a) individual females and (b) individual males in the novel environment over four test series.

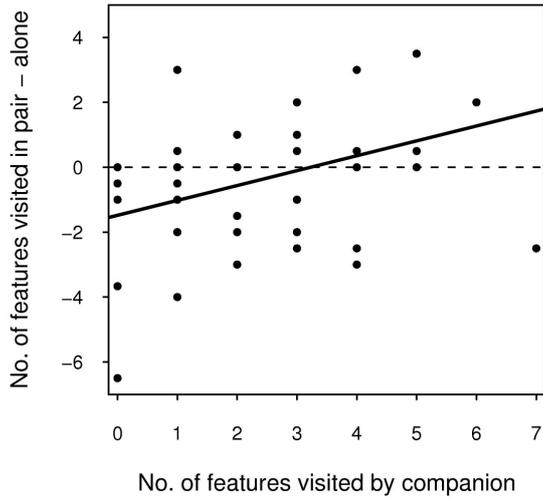


Figure 3. Influence of a companion's exploration (number of features visited) on exploration by the focal individual (number of features visited in social context – mean number of features visited in non-social context) in a novel environment.

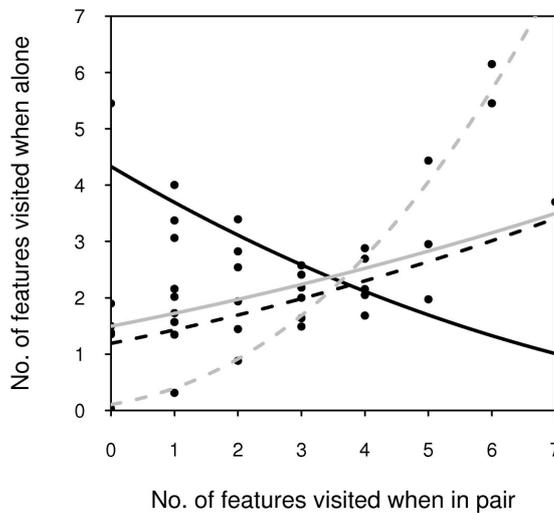


Figure 4. The relationship between the number of features visited by males and females in a social and an asocial context in different orders (back transformed). Black lines: female responses; grey lines: male responses; solid lines: tested in a social context first; dashed lines: tested in an asocial context first. Dots represent fitted values.

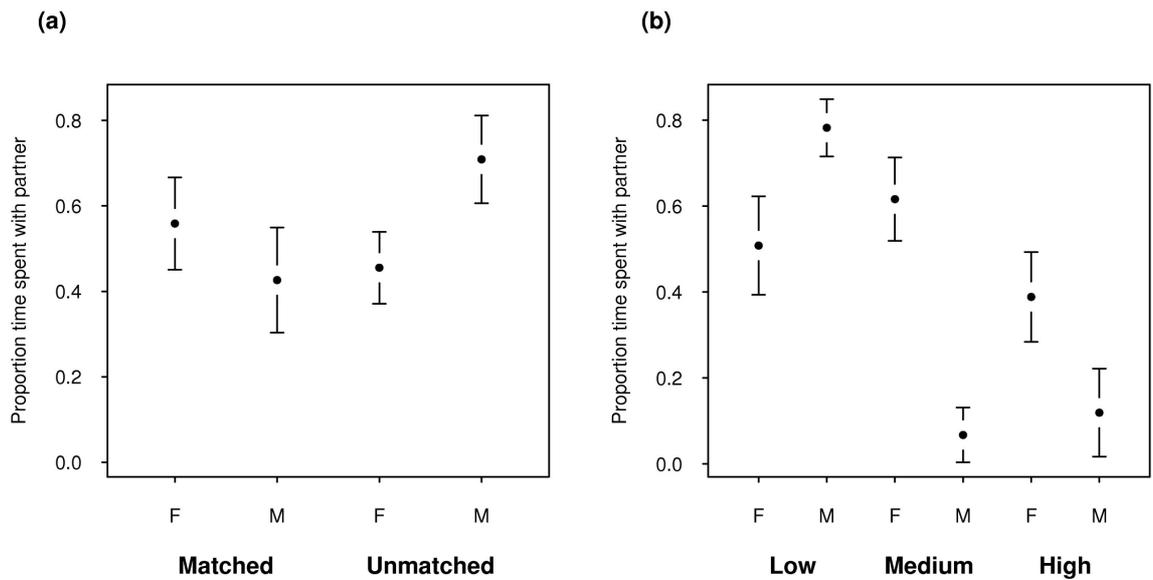


Figure 5. The mean proportion of time (\pm SE) at the feeder that males and females spent with their opposite sex companion depending (a) on the kind of grouping conducted (matched or unmatched for exploratory tendency) and (b) on their exploratory tendency (low, medium, high) in the novel environment (Part I). F: female; M: male.

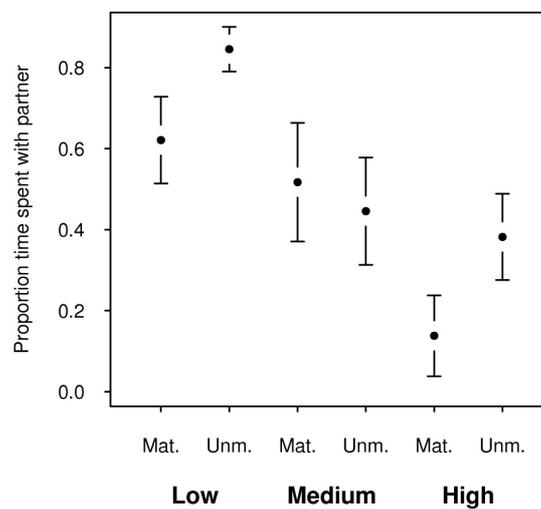


Figure 6. The mean proportion of time (\pm SE) at the feeder that matched (Mat.) and unmatched (Unm.) individuals spent with their companion depending on their exploratory tendency (Part I).

Chapter 3

**Female zebra finches choose males for their
“personality”**

SUMMARY

A major challenge in behavioural and evolutionary ecology is to understand the evolution and maintenance of stable behavioural differences among individuals within populations, often referred to as animal “personalities” (Wilson 1998; Dall et al. 2004; Sih et al. 2004a; Sih et al. 2004b; Dingemanse & Réale 2005; McElreath & Strimling 2006; Nettle 2006; McElreath et al. 2007; Réale et al. 2007; Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008; Wolf et al. 2008; McNamara et al. in press). Here we show that sexual selection may act on such personality differences in zebra finches, *Taeniopygia guttata*, since females choose males on the basis of their exploratory behaviour *per se*, while taking into account their own personality in their choice. After observing a pair of males whose apparent levels of exploration were experimentally manipulated, “unadventurous” females showed no preference during mate choice for males that had appeared to be either “unadventurous” or “adventurous”. However, more adventurous females preferred apparently adventurous males over apparently unadventurous ones. This preference could be driving assortative mating by exploratory personality in the socially monogamous zebra finches, which may in turn facilitate coordinated and successful parenting (Chapter 4). Importantly, such assortative mating based on personality could, in principle, maintain substantial inter-individual behavioural variation within zebra finch populations (Chapter 1).

RESULTS AND DISCUSSION

Increasing evidence suggests that consistent individual differences in behaviour within populations are not just “noise” around (possibly) adaptive population means (Benus et al. 1991; Boissy 1995; Gosling & John 1999; Koolhaas et al. 1999; Gosling 2001; Groothuis & Carere 2005; Réale et al. 2007). Rather, they represent systematic variation along functional continuums or axes of behaviour with measurable fitness consequences (Dingemanse et al. 2004; Sih et al. 2004a; Sih et al. 2004b; Smith & Blumstein 2008). Thus, individual differences in behaviour are subject to selection that can generate, maintain and/or erode such variation. An ongoing challenge in behavioural and evolutionary ecology is to understand how and why consistent behavioural differences, or personalities, persist in populations (Wilson 1998; Dall et al. 2004; Sih et al. 2004a; Sih et al. 2004b; Dingemanse & Réale 2005; McElreath & Strimling 2006; Nettle 2006; McElreath et al. 2007; Réale et al. 2007; Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008; Wolf et al. 2008; McNamara et al. in press). One possibility is that sexual selection is generating and maintaining animal personality differences (Chapter 1). Typically, female mate choice experiments investigate the influence of the physical appearance and sexual behaviour (display, song etc.) of males on a female’s preference behaviour (e.g. Andersson

1994). However, the possibility that other non-sexual behaviours could be also important during mate choice is hardly ever considered (but see Godin & Dugatkin 1996).

If non-sexual behaviours influence mate choice decisions, personality differences among individuals could be maintained via at least two processes. First, behavioural performance could be a reliable indicator of an individual's quality (see Godin & Dugatkin 1996; *sensu* Zahavi 1975; Zahavi & Zahavi 1997), and therefore all females should agree in their choice. If similar levels of behavioural expression are quality-indicating traits in both sexes, then assortative mating is expected (low-quality individuals are left behind and therefore also pair up assortatively: McNamara & Collins 1990; Johnstone 1997), maintaining standing variation in the level of behaviour expressed within a population. Second, females could consider their own behavioural traits during their mate choice process and consequently differ from each other in their preferences (Jennions & Petrie 1997). In this case, females would choose either males similar or dissimilar to themselves in order to achieve genetic (Tregenza & Wedell 2000) or behavioural compatibility (Trivers 1972; Burley 1983) so as to maximise reproductive success. However, only in the case of positive mating assortment would we expect maintenance of behavioural variation in the population (negative assortment would lead to an erosion of variation over time if no other mechanisms are acting; Chapter 1).

In this study, we investigated whether sexual selection is acting to maintain personality differences among individuals by testing if females use the level of non-sexual exploratory behaviour shown by males in their mate choice decisions and if they also consider their own behavioural type during the process. We used the biparental, socially monogamous zebra finch, *Taeniopygia guttata*, as our model study organism. Because highly exploratory (adventurous: A hereafter) zebra finch females raise chicks in better condition when paired to a highly exploratory partner, but not when paired to a low-exploration (unadventurous: UA hereafter) partner, whereas low-exploration females always raise chicks in intermediate condition, regardless of the personality of the partner (Chapter 4), we predicted that exploratory females should prefer A over UA males as mates, but UA females should show no preference.

After first classifying the natural exploratory tendency of test individuals (i) in a novel environment, (ii) towards a novel object, and (iii) the tendency of individual males to interact with a mirror (see Supplemental Data for details), we performed a mate choice experiment, consisting of two experimental phases. In the first phase, we allowed a focal female to observe simultaneously two brothers, each exploring a novel environment. We manipulated (i.e. reduced) the exploratory behaviour of one of the brothers to render him apparently UA, and allowed the other brother to explore the novel environment freely (i.e. apparently A). To do this, each of the two brothers was transferred into an opaque, UV-transmitting box (open to view on

the back and front) placed into their respective similar novel environment (see Figure S1, Supplemental Data). Depending on their respective treatment, one of the stimulus males could leave the box via the back and explore the novel environment (A treatment), whereas the other was restricted to the box (UA treatment). Following the observation period, the female was allowed to choose in a standard mate choice situation between the two stimulus males, which she had previously observed in their novel environment. The brother pairs were presented in different behavioural combinations (A-A, UA-UA, A-UA) to different focal females. Each female experienced all three combinations, while the order of combinations varied between females. Females were assigned randomly to one of three predefined orders, thereby ensuring equal number of females for each order.

We found that both individual females and males were consistent in their exploratory tendency (number of features visited during two pre-experimental novel environment tests), but varied from other members of the same sex in their level of exploration (GLMMs; repeatability of female exploration: $R = 0.447 \pm 0.11$ SE, $P < 0.01$; male exploration: $R = 0.401 \pm 0.08$ SE, $P < 0.001$). For males, the mean number of features visited during the novel environment tests was correlated with both their curiosity towards the novel object (time allocation to different distances from the novel object; Spearman correlation; $r_s = 0.239$, $N = 102$, $P = 0.016$) and their number of aggressive mirror interactions (Spearman correlation; $r_s = 0.342$, $P < 0.001$). For females, there was no such correlation between the mean number of features visited and their behaviour in the novel object test (Spearman correlation; $r_s = -0.049$, $N = 51$, $P = 0.734$). However, they were repeatable in the number of perch visits near either stimulus male during mate choice trials (GLMM; $R = 0.662 \pm 0.06$ SE, $P < 0.0001$), and this behaviour was correlated with the mean number of features visited in the novel environment (Spearman correlation; $r_s = 0.557$, $P < 0.0001$). Finally, the mean number of features males visited in the novel environment pre-experimentally was correlated with their general activity in the box (UA treatment) during the experiment (Spearman correlation; $r_s = 0.271$, $P = 0.006$). Collectively, these results show that personality differences in exploration exist in zebra finches, which corroborate the findings of other studies within this species (Chapter 4, Schuett & Dall in press), and is a prerequisite for assessing the role of sexual selection on personality differences. Further, male exploratory behaviour was correlated with other behaviours, including the tendency to interact aggressively with a mirror, which is commonly taken as a measurement of aggressiveness (e.g. Gerlai 2003). Therefore, a male's level of exploration could potentially be used by females to assess his aggressiveness, which in turn might reflect his ability to defend her or her nest.

In the UA-A trials, a female's choice was influenced by the perceived exploratory level of the stimulus males as well as her own exploratory tendency (Figure 1; GLM; $F_{2,47} = 3.73$, $N = 51$, $P = 0.031$, whilst controlling for time of day). Medium- and high-exploration females

spent more time with the apparently A male than with the apparently UA male, whereas low exploration females did not show a clear preference for either the A or UA male, as we had predicted *a priori*. Low exploration females spent significantly less time with the A male than either the medium- and high-exploration females ($F_{1,48} = 6.30$, $P = 0.015$), which themselves did not differ from each other in the proportion of time they spent near the A male (Figure 1; $F_{1,47} = 1.14$, $P = 0.291$).

There was no statistical interaction between the difference in paired brothers' spontaneous exploration behaviour (difference in number of features visited during the observations in A-A trials and difference in the movement score in the box during observation in UA-UA trials, respectively) and the females' exploratory tendency on female mate choice within our control trials (GLMs; A-A treatment: $F_{2,44} = 1.85$, $P = 0.169$; UA-UA treatment: $F_{2,44} = 0.56$, $P = 0.577$), indicating that the amount of underlying behavioural variation between the stimulus males in either of these control treatments was insufficient to bias female mate choice. Secondly, these findings further indicate that our manipulation of exploratory (A-UA) behaviour was successful in that spontaneous variation within either of the two control treatments did not influence female mating preferences. Thirdly, these results suggest that the way that males use space and apparent shelter is important for female mate choice.

We have demonstrated that female zebra finches choose males on the basis of their exploratory behaviour (i.e. a non-sexual behaviour), which supports the hypothesis that sexual selection acts on personality differences in this species. Similarly, Godin & Dugatkin (1996) showed experimentally that female Trinidadian guppies, *Poecilia reticulata*, preferred males that appeared bold towards a predatory threat over apparently shy males as potential mates. Moreover, female zebra finches vary in their preference for aggression in males (Forstmeier et al. 2004). In our study, female finches differed in their choice of mate, suggesting that some kind of compatibility between partners is important for reproduction. This is supported by findings in cockatiels, *Nymphicus hollandicus*, (Spoon et al. 2006) and convict cichlids, *Cichlasoma (Archocentrus) nigrofasciatum*, (Budaev et al. 1999), where behaviourally compatible and behaviourally similar partners, respectively, were more likely to reproduce successfully. Also, assortatively exploratory pairs of great tits, *Parus major*, rear chicks in best condition (Both et al. 2005) and recruit the most offspring (Dingemanse et al. 2004), although there is some indication that chicks of intermediate pairs have highest life expectancy (Dingemanse et al. 2004). However, sometimes disassortative mating seems to be advantageous (van Oers et al. 2008).

Recently, we have also found that the combination of exploratory tendencies in zebra finch foster parents was crucial while raising hatchlings, even though it did not influence the

onset of their reproduction or egg laying (Chapter 4). This suggests that behavioural compatibility rather than genetic compatibility of the sexual partners is important for successful reproduction in this species. In support of this proposition, we showed here that only more adventurous female zebra finches chose males assortatively on the basis of their exploration behaviour. Similarly, only exploratory females, but not unadventurous ones, have been shown to have reproductive advantages when paired assortatively in this (Chapter 4) and other species (dumpling squid, *Euprymna tasmanica*: Sinn et al. 2006). Also, in great tit males selected for high versus low exploration, only adventurous males have been found to show a preference for similar females, whereas unadventurous males showed no preference for either kind of females (Groothuis & Carere 2005). These findings raise two questions: what is it about exploratory behaviour that makes it an important trait during mate choice/reproduction and why is it only important for exploratory individuals to reproduce with a similar partner? Exploration is correlated with several life-history and behavioural traits in animals (reviewed in Dingemanse & Réale 2005; Groothuis & Carere 2005; Stamps 2007), which could be important in the formation and maintenance of sexual partnerships and for successful parenting. More specifically, exploration in zebra finches is correlated with leading abilities towards novel food sources (Schuett & Dall in press). Therefore, female zebra finches, who are led through the colony by their males during most of the year (Zann 1996), may benefit from choosing a male who is exploratory as he might be able to find high-quality food patches before they become depleted (Schuett & Dall in press). Moreover, having a behaviourally-similar partner might be important for coordinating behaviour within a pair (e.g. parenting or foraging), which may be more challenging for more active and exploratory individuals (for more discussion see Chapter 4).

To our knowledge, our study is the first to have disentangled experimentally the potential influences of the physical appearance of males and their non-sexual behaviour on female mate choice, whilst concurrently taking into account the stable behavioural type of the choosing female. We have shown that female zebra finches use the exploratory behaviour of males *per se* in making mate choice decisions, whilst also considering their own exploratory tendencies; exploratory females preferred behaviourally similar males over males dissimilar to themselves. The resulting assortative mating patterns could potentially maintain inter-individual variation in the level of non-sexual behaviours and in “personalities” within populations, which would have important ecological and evolutionary implications (Dall et al. 2004).

EXPERIMENTAL PROCEDURES

ORIGIN AND MAINTENANCE OF FOCAL BIRDS

We used sexually experienced, adult wild-type zebra finches (51 females, 51 brother pairs), which originated from a large captive population maintained at the Max Planck Institute for Ornithology in Seewiesen, Germany. All focal individuals had been raised by unrelated foster parents (Forstmeier 2005). During the study (October-December 2007), the birds were housed unisexually, with females in groups of five to six and males in pairs of brothers (female cages: 120 x 40 and 45 cm high; male cages: 60 x 40 and 45 cm high). Rooms were lit by full-spectrum fluorescent lights (Osram Lumilux T5 FH 28W/860 Daylight) on a 14.5 L:9.5 D illumination cycle. We kept the birds under controlled conditions of humidity and temperature (see Bolund et al. 2007) and with *ad libitum* access to a millet seed mixture, cuttlebone, grit and water. Supplementary diet (lettuce and multivitamin supplement) was provided on a weekly basis.

PRE-EXPERIMENTAL BEHAVIOURAL TESTS AND MEASUREMENTS

Within 3 weeks prior to the experiment, focal birds were tested for their natural personality in different behavioural tests (for more details see Supplemental Data). Each bird was tested twice (day1, day3) for its tendency to explore a novel environment (number of features visited). After this (day 5), its curiosity towards a novel object was quantified (distance from object weighed by time spent at this distance). Males were also tested once (day8/day9) for their response towards a mirror (number of aggressive interactions). All behavioural tests were carried out in the room in which most of the focal birds were housed, such that birds could hear and see other zebra finches during the tests.

EXPERIMENTAL APPARATUS AND PROCEDURES

The apparatus for the observation period (see Figure 1S, Supplemental Data) consisted of two adjacent novel-environment cages (60 x 40 cm and 45 cm high) and an observation cage for the females (22 x 36 cm and 23 cm high). The novel environment cages included 10 features each (7 branches, an unfamiliar shaped feeder, the mesh of the cage, and a substratum consisting of shavings) which were similarly arranged but mirror-inverted in both novel environments. Furthermore, a cardboard box (11 x 11 cm and 14 cm high) was placed on the substratum in each novel environment; each box initially housed a stimulus male at the onset of a trial. We manipulated the apparent adventurousness of each paired stimulus male by allowing one of the males to explore the novel environment but not the other, as follows. We used two different

types of cardboard boxes depending on the treatment of a male (“unadventurous”: UA or “adventurous”: A): both types were covered with a UV-transmitting Plexiglas (Plexiglas Sunactive ® GS Farblos 2458; measuring 8 x 11.5 cm high) on the front side (facing towards the female). The back of the box was either open or also covered with Plexiglas, allowing the male to either leave the box and freely explore the novel environment (A treatment) or restricting the male to the box (UA treatment).

5 min before a trial started, the focal female was placed into the observation cage. At the end of this acclimatisation, the two focal brothers were transferred into a cardboard box each, which were in accordance to their treatment (see above), and placed into the novel environments. The female was allowed to view the males for 10 min whilst their behaviour was video-recorded (Sony Handycam DCR-HC90E and DCR-PCR-PC109E) by an observer (W.S.) located 2 m away. Video tapes were later analysed for the number of features visited by apparently A males. Apparently UA males were scored for their general activity within their box on a 5-point scale (0 = no movement, 0.5 = few movements, 1 = moderate movements, 1.5 = many movements 2 = many movements, including multiple jumps). At the end of this observation period, the focal female was transferred into a familiar binary mate choice chamber (see Schielzeth et al. 2008). After a 5-min acclimatisation period, during which the female was visually isolated from the males, the focal female was tested for her mating preference for the previously-observed males for 41 min (the first minute of each trial was discarded). Female preference was quantified as the proportion of time spent in each side compartment near one or the other male, weighing the data depending on which of two perches in a side compartment a female was sitting (time spent on perch closest to male x 1 + time spent on perch further away x 0.5; qualitative the same results were obtained for analyses using unweighed proportions, not shown). Such a measure of mating preference is a reliable predictor of sexual preferences in female zebra finches (Clayton 1990; Houtman 1992; Witte 2006; Forstmeier 2007).

Each test female and all stimulus males were used in three consecutive mate choice trials separated by 7-10 days. During these three trials each female viewed three different male brother pairs, appearing in the three possible different behavioural combinations (A-A; UA-UA; A-UA), with different females experiencing the behavioural combinations in different orders. Each male pair was shown in each behavioural combination only once.

During a trial (observation period and choice period), brothers were randomly assigned to a different coloured plastic ring each (white, orange, white-orange, black, black-yellow, orange, white-orange, light pink, A. C. Hughes, Middlesex, UK) to facilitate the female’s discrimination of the two males presented. These particular ring colours used have been shown to be behaviourally “neutral” in our study population (Forstmeier, Schielzeth & Bolund,

unpublished data). None of the focal females encountered a given ring colour twice during the three consecutive mate choice trials and no colour was used twice in a brother pair.

To prevent males from displaying towards the females whilst in their novel environment, we created an increasing light gradient from the female observation cage towards the novel environment cages containing the males by mounting two incandescent lights (60 W) in front of the female cage and directed towards the males' cages (males had been acclimatised towards these lights pre-experimentally). This back light prevented males from seeing the female easily. Secondly, other birds were housed permanently in the part of the room behind the female cage. To prime the interest of the focal female towards the males, she was allowed to watch a bonded zebra finch pair in an adjacent cage for 1 h the day before the experimental trial.

STATISTICAL ANALYSES

For the pre-experimental behavioural tests, we investigated the consistency of behaviour over time and over different test situations for individual birds. To assess behavioural consistency, we calculated the repeatability of each behaviour and its standard error using linear mixed effect models (GLMM) with "individual" as random factor. The significance of the random term (individual) was estimated following Verbeke & Molenberghs (2000) using a mixture of two chi-squared distributions instead of a classical likelihood ratio test (as the variance is not going to go below zero, see also Stram & Lee 1994; Stram & Lee 1995). Because individual differences in exploration were consistent over time, we averaged our repeated measures of female exploration behaviour ("exploration score") for further analyses. The exploration score was used to categorise each female into one of three exploratory types ("low" = mean < 2.5; "medium" = mean 2.5-3.5; "high" = mean > 3.5; these cut-off points were chosen for categorisation as they resulted in the most equally distributed number of individuals in each category, around the median of 3 for the exploration score). Behavioural correlations among behaviours in different tests were assessed with Spearman rank correlations.

We investigated whether females chose males based on male exploration behaviour, whilst considering their own exploratory tendency, using GLMs, one for each behavioural combination in which males were presented (A-A, UA-UA, A-UA). Explanatory variables entered into the models were female exploratory tendency and time of day as a controlling (continuous) variable. For analyses of the UA-UA and A-A trials, we also included the behavioural difference between the brothers during the female observation period (difference between male1 and male2 in features visited during A-A trials and in box activity during UA-UA trials, respectively; males were randomly assigned to be either "male1" or "male2") and their interaction with female exploratory tendency as explanatory variables into the full model.

The response variable in the UA-A analysis was proportion of time spent by the focal female with the A male. In the analyses of UA-UA and A-A trials, the response variable was the proportion of time spent by the female with a randomly chosen “male1”. Where female exploratory tendencies significantly ($P < 0.05$) influenced the response of the model, we applied Crawley’s factor level reduction technique (2002; 2007) to assess which levels significantly differed from one another.

When required, data were transformed appropriately to meet the assumptions of GLMs and GLMMs, respectively.

SUPPLEMENTAL DATA

Supplemental Data include Supplemental Experimental Procedures and one figure.

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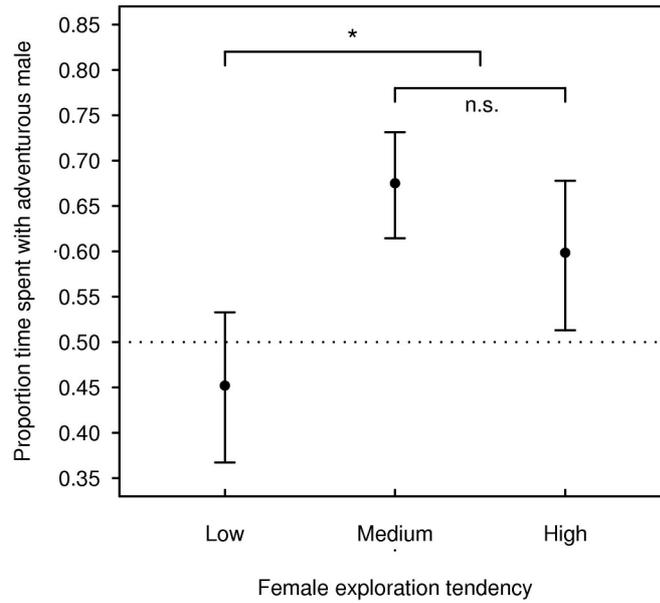


Figure 1. Mean (\pm SE) proportion of time females with different exploratory tendencies (low, medium and high) spent near the apparently adventurous male relative to the male which appeared to be unadventurous in a novel environment (UA-A trials). The females’ exploratory tendencies were categorised based on the mean number of features in a novel environment they had visited over two pre-experimental novel-environment tests (as equally distributed around the median of 3 as possible): low exploration (N = 16), mean < 2.5; medium exploration (N = 23), mean = 2.5-3.5; high exploration (N = 13), mean > 3.5. The figure is based on estimates from a GLM, with “female exploratory tendency” as fixed effect. Estimates have been back-transformed to the original scale for display. The stippled horizontal line denotes random choice. *: significant difference; n.s.: non-significant difference.

SUPPLEMENTAL DATA

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Pre-experimental behavioural tests

Pre-experimental novel-environment tests were conducted using four identical cages (120 x 40 cm and 45 cm high), each containing ten features: six branches of varying diameter, shape, length and “mobility”, serving as perches at unusual locations (compared to what subjects are used to from being housed in standard home cages), one unfamiliar shaped feeder filled with seeds, the mesh at the front of the cage, the substratum covered with shavings (instead of paper as in the home cage), and a wooden balk in the middle of the cage bottom. The features were arranged in the same manner in two of the cages, but mirror-inverted in the remaining two cages. None of the focal birds had experienced the novel environments before the first trial. All birds were tested twice, once in each kind of the two mirror-inverted cage types. Before the start of each trial, four birds were transferred into four cardboard boxes (9 x 11 cm and 9 cm high), which were placed into the four novel environment cages. Once the lid of each box was opened remotely using a string by W.S., the number of features visited by each bird was recorded for 5 min (Sony Handycam DCR-HC90E, Sony Handycam DCR-HC37E). For more details on the test procedure see Chapter 4.

Novel-object tests were conducted in the four cages that had been used for the novel-environment tests but which were set-up in the same manner as the birds’ home cages. Before a trial, individuals were transferred into one half of the cage, which was separated from the other half with an opaque divider. The visually-separated part of the cage contained a novel object at its far end (a green woolly ball of about 8 cm diameter, hanging from the top of the cage). After an acclimatisation time of 3 min, the novel-object trial started with the removal of the divider. Movements and locations of the individuals were video-taped for 5 min. From the times spent at different distances from the novel environment, we calculated a curiosity score (duration at a location [s] * score of location, the latter ranging from 0.5-4.5 with increasing score indicating decreased distance to object) for each bird separately.

Finally, all males were individually tested once for their response towards a mirror, following the procedure described in Chapter 4. In short, following a 5-min acclimatisation period (mirror covered) to the test cage (38.5 x 48 cm and 33.5 cm high) and starting from a box as for the novel-environment test, the number of interactions each male had with a mirror (11 cm and 15 cm high) was quantified for 5 min. Behaviours recorded included directed song towards the mirror, flying against the mirror, beak contact with the mirror (slow movement),

pecking at the mirror (fast movement) and straightening up to full height followed by pecking at the mirror (breast contact with mirror). Two birds were always tested simultaneously, in two mirror-inverted cages, visually separated from each other.

Pre-choice observation

Prior to a mate choice trial, individual females were allowed to observe a pair of stimulus males (brothers), which were manipulated in their level of exploration, in a novel environment for 10 min. The cage set-up is shown in Figure S1.

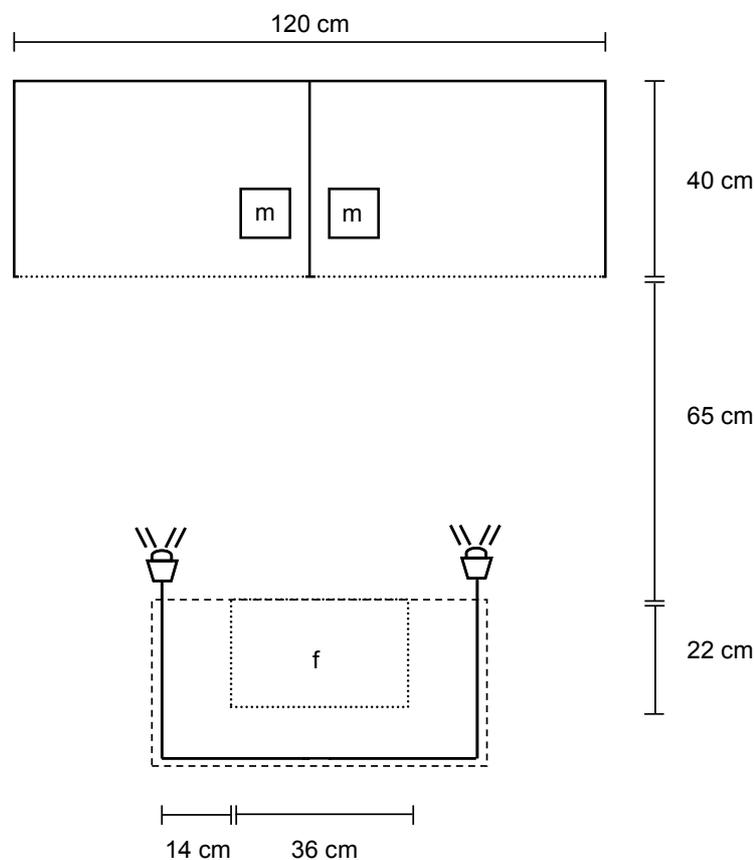


Figure S1. Overhead plan view of the cage set-up for the pre-choice observation period. A focal female (f) observed two brothers (m), each in one novel-environment cage containing 10 features (features not shown). Each male was allowed to either explore the environment (released from box; “adventurous”) or not (kept in a box; “unadventurous”). The males in the two environmental cages could not see each other. The cage of the female was covered on 3 sides and the top (dashed lines) and lights in front of the female cage were directed towards the males to create a light gradient towards the males’ cages. Both males and females had access to food (not shown). Dotted line denotes mesh wire.

Chapter 4

**Pairs of zebra finches with similar “personalities”
make better parents**

SUMMARY

Despite obvious advantages of behavioural flexibility in variable environments, there is growing evidence for consistent behavioural differences between individuals, and, therefore, limited behavioural plasticity under a wide range of conditions in many species (“personalities”, Gosling 2001; Sih et al. 2004b; Dingemanse & Réale 2005). This puzzling phenomenon is currently thought to be driven by trade-offs during development, leading to different paths to maximise fitness and canalisation of alternative life-history strategies (Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008). Here we present evidence for a role of sexual selection in the evolution of “personality” in zebra finches. Females have recently been shown to choose males based on their exploratory tendencies *per se*, indicating that (behavioural or genetic) compatibility is important for reproductive success (Chapter 3). Using a cross-fostering breeding experiment, we demonstrate here that pairs of individuals where both males and females were rated as highly exploratory and aggressive, respectively, fostered heavier offspring that were in better condition at independence than nestlings raised by unmatched or minimally exploratory and aggressive pairs. More importantly, pairs matched for their behavioural consistency (consistent and flexible, respectively) raised better conditioned offspring than pairs in which the individuals differed in their behavioural consistency. In contrast, the personalities of the genetic parents had no effect on offspring state at independence. Furthermore, these effects were pervasive, intergenerational paternal effects: fostered nestlings with adventurous grandfathers showed better condition than those without such grandfathers. These results show that behavioural compatibility has important, pervasive effects on reproductive success, and suggest that personality may be an important indicator of male quality in providing care for young through reduced sexual conflict over the provision of costly parental investment (*sensu* Royle et al. 2002).

RESULTS AND DISCUSSION

Recent evidence suggests that animal personality (stable individual behaviour that varies within populations) may be subject to sexual selection in a wide range of species (Chapter 1). However, virtually all these studies consider only one aspect of personality, variation in the behavioural level *between* individuals (inter-individual variation), while ignoring consistency in behaviour *within* an individual (intra-individual variation). Moreover, such studies rarely investigate the links between sexual selection and personality experimentally, so observed relationships could simply arise from correlations between personality traits and other traits under selection. In particular, there have been no systematic investigations into the processes underlying the observed patterns (e.g. genetic and/or behavioural compatibility).

In a recent experiment, we have shown that female zebra finches choose males on the basis of their exploratory behaviour relative to the females' own exploration type (Chapter 3): moderately and highly exploratory ("adventurous") females preferred behaviourally similar over dissimilar males, whereas unadventurous females did not show any preference, suggesting compatibility between (adventurous) partners is important for reproductive success. Here we test this prediction using an experimental design that utilises a combination of cross-fostering of offspring and parental removal to examine whether the exploratory and aggressive tendencies of individuals in a pair influence their success in parental care. Cross-fostering of clutches and removal of some male parents soon after nestlings hatched (Royle et al. 2002) allowed us to distinguish between effects of genetic and foster parents' personality on different stages of reproductive performance. In order to monitor long-term effects of personality on correlates of fitness, we repeated the experiment the following year using juveniles from the first breeding round as the parental generation.

In the first year (2007) we found a combined effect of the exploratory tendencies of foster mother and father (measured as the average number of features visited by an individual in two novel environment tests pre-breeding) on the mean mass corrected for size (mean mass/head-bill length, hereafter condition) of nestlings at independence (GLM; condition: $F_{1,27} = 4.75$, $P = 0.038$; Figure 1) and a similar trend on the mean mass at independence (GLM; mass: $F_{1,26} = 2.76$, $P = 0.108$) but there were no effects on skeletal size at independence (GLM; head-bill length: $F_{1,26} = 0.04$, $P = 0.846$), or on the mean growth rate of the foster brood (GLM; $F_{1,26} = 0.01$, $P = 0.926$; all $N = 31$): consequently, highly exploratory individuals who were mated assortatively reared nestlings in better condition (which has been shown to have important consequences for nestling fitness prospects in a number of species, e.g. Hochachka & Smith 1991; Whiteman & Parker 2004; Martín et al. 2007) than pairs which differed in their exploratory behaviour or were both unadventurous (Figure 1). For less exploratory males, having a partner with highly exploratory behaviour had negative effects on the mass corrected for size of offspring (condition: $F_{1,27} = 5.92$, $P = 0.022$; see also Figure 1). However, the exploratory tendency of their partners had no influence on the brood rearing success of females at the low end of the exploratory spectrum (condition: $F_{1,27} = 0.52$, $P = 0.476$; see also Figure 1). This finding is congruent with results from our mate choice experiment (Chapter 3) which showed that unadventurous females do not show any preference for either adventurous or unadventurous males, and suggests that this is because they do not gain any fitness advantages from a non-random choice with regard to how adventurous their prospective partner is. On the other hand, assortative mate choice with respect to personality increases the fitness prospects of offspring of exploratory females, which manifests itself in a preference for exploratory males. Similarly, only intermediate and bold dumpling squid, *Euprymna tasmanica*, are more likely to reproduce if they have behaviourally similar mates (Sinn et al. 2006) and only highly

exploratory male great tits choose females assortatively, whereas minimally exploratory males do not choose females on the basis of their exploratory tendencies (Groothuis & Carere 2005).

As for exploration, we found a combined effect of foster parents' tendency to interact with the mirror (number of interactions, exclusive male song, see Experimental Procedures) on the mean mass and condition of nestlings in a clutch at independence (GLM; mass: $F_{1,27} = 4.96$, $P = 0.034$; condition: $F_{1,27} = 4.39$, $P = 0.046$; Figure S3, Supplemental Results) but not on head-bill length ($F_{1,26} = 0.93$, $P = 0.344$; all $N = 31$): highly aggressive individuals in assortative partnerships raised the heaviest chicks in the best condition (Figure S3). However, for only females, but not males, at the low end of the aggressive distribution had the aggressive tendency of the partner a significant effect on offspring condition and weight (for females: condition: $F_{1,27} = 5.65$, $P = 0.025$; mass: $F_{1,27} = 4.91$, $P = 0.035$; for males: condition: $F_{1,27} = 3.86$, $P = 0.060$; mass: $F_{1,27} = 4.11$, $P = 0.053$; see also Figure S3). In contrast to the combined influence of the foster parents' behavioural phenotype on nestlings' fitness prospects, the personality (both aggression and exploration) of the genetic father and mother and their combination in a pair had no influence on the mean absolute mass, condition or skeletal size of their genetic offspring at independence (GLMs; all interactions: $P > 0.60$; all main effects: $P > 0.19$).

In addition to a positive, assortative effect of the level of the behaviour traits of parents (i.e. inter-individual variation) on correlates of nestling fitness there was an even more pronounced combined effect of foster parents behavioural consistency (i.e. intra-individual variation) on their success in parental care: pairs in which both individuals were similarly consistent (i.e. consistent and flexible, respectively) in their latency to explore the novel environment pre-breeding fostered the heaviest offspring in the best condition (GLM; female coefficient of variation (CV) to visit first feature * male CV to visit first feature; mass: $F_{1,27} = 14.11$, $P < 0.001$; condition: $F_{1,27} = 9.79$, $P = 0.004$; all $N = 31$; Figure 2). Again, no such effect was evident for genetic parents (GLMs; interaction: mass: $P = 0.863$; condition: $P = 0.602$). There was also evidence that this effect carried over into the third generation: individuals that had been raised by foster parents which were similar to one another in their behavioural consistency tended to raise themselves nestlings in better mean condition at independence than individuals that had been raised by foster parents unmatched for their consistency (GLMM with "foster brood ID 2007" as random effect; $\chi^2_1 = 3.77$, $P = 0.052$).

These results suggest that genetic compatibility for the behavioural traits we assessed is less important for successful reproduction than behavioural compatibility (in terms of both behavioural consistency and behavioural level, see below) within a pair. In addition, adventurousness in males could also be a signal of quality in this species. This is based upon two findings here: first, only the foster father's mean latency to approach the first feature in the

novel environment prior to breeding influenced the mean mass and condition of offspring at independence, not the foster mother's exploratory behaviour or the interaction between males and females: fast male explorers fostered heaviest offspring in best condition (GLMs; condition: interaction: $F_{1,26} = 0.60$, $P = 0.444$; females: $F_{1,27} = 0.00$, $P = 0.957$; males: $F_{1,29} = 4.18$, $P = 0.050$; mass: interaction: $F_{1,26} = 0.50$, $P = 0.486$; females: $F_{1,27} = 0.02$, $P = 0.901$; males: $F_{1,29} = 4.66$, $P = 0.039$; all $N = 31$; Figure 3). However, neither the condition of the males nor the amount of parental investment they provided when broods were 8-10 days old correlated with this measure of exploration (Spearman correlation; condition: $r_s = -0.011$, $N = 31$, $P = 0.951$; duration food provision: $r_s = 0.270$, $N = 12$, $P = 0.398$; but see Chapter 2: exploratory individuals harder to catch). Second, in the replicate experiment conducted in the following year (2008) we did not find any combined effect of foster parent behavioural phenotypes on their reproductive performance (see Supplemental Results). Instead we found an intergenerational effect of males' behavioural phenotype: adults raised by adventurous foster fathers in 2007 (mean number of features visited prior to breeding in two novel environment tests), reared foster chicks of better mean condition at independence themselves in 2008 (GLMM; $\chi^2_{1} = 5.25$, $N = 56$, $P = 0.022$; Figure 4). The condition of this second generation of foster parents was strongly related to their condition at independence the previous year (Spearman correlation; $r_s = 0.623$, $N = 58$, $P < 0.0001$). This suggests that individuals fostered by adventurous males raised nestlings in better condition, because (1) they were themselves in better condition and were therefore able to provide better care and/or were perceived as higher quality partners, resulting in increased parental care by their mate (i.e. differential allocation, Burley 1988a) or (2) individuals raised by more adventurous foster males may have imprinted on their foster father's parental strategy (as for song: Zann 1996).

These findings corroborate suggestions that levels of non-sexual behavioural traits can signal quality (Godin & Dugatkin 1996), like parental care ability (Barlow 1986; Benus & Røndigs 1996): if offspring fitness is strongly dependent upon male parental investment and males vary in their parental contributions, then selection is expected to favour a degree of female choice for male provisioning behaviour (Schwagmeyer & Mock 2003). Clearly, at the time of pairing, males have no offspring with which to demonstrate their parental skills, so females must use indirect, yet reliable and predictable indicator traits to assess the potential of their mates (e.g. Buchanan & Catchpole 2000; Candolin 2000). One potentially reliable indicator of male ability is his personality or behavioural phenotype.

Behavioural compatibility has been shown to influence pair coordination and reproductive success in pairs of cockatiels, *Nymphicus hollandicus*, (Spoon et al. 2006). Furthermore, correlative studies report benefits of positive assortment for behaviour: reproducing convict cichlid, *Cichlasoma (Archocentrus) nigrofasciatum*, pairs show more

similar behavioural types to one another than non-reproducing pairs are to each other (Budaev et al. 1999). Assortative pairs of low and high exploratory great tits, *Parus major*, raise chicks in better condition (Both et al. 2005) and recruit more offspring than non-assortative pairs although these might suffer a reduced life expectancy (Dingemanse et al. 2004). Finally, disassortative mating by behavioural phenotype may be beneficial under some circumstances, since behaviourally assortative pairs of great tits have higher numbers of extra-pair chicks in their nests than disassortative pairings (van Oers et al. 2008).

In this study, positive assortment for adventurous and aggressive partnerships produced nestlings in better condition regardless of whether the male was removed shortly after hatching or not (the factor treatment: uni- versus biparental dropped out of the presented analyses). Since the uniparental treatment also involved reducing the brood size so that there was no difference between the treatments in potential workload, this suggests that either (a) the first few days parental care after hatching are critical in determining the developmental pathway that an individual takes, and/or that (b) the female compensates for the male's absence and maintains the level of parental care provided when the partner was around (Markman et al. 1995; Sanz et al. 2000; Johnstone & Hinde 2006). Answering this question is difficult as nothing is known about the mechanisms behind the positive relationship between behavioural compatibility and success in parental care. Video data of the provisioning behaviour of our experimental pairs provided no evidence for differential provisioning rates in relation to compatibility (see Supplemental Data). However, this may be because snap-shots of provisioning behaviour when nestlings are 8-10 days old do not provide a good representation of the amount of effort provided by individuals over the whole nestling period (Royle et al. 2002). Moreover, we are not aware of any studies linking male and female personalities to details of their parental care efforts. Further work is therefore required to elucidate how behaviour-matching in adventurous zebra finch pairs enhances parental care, but our data strongly suggests that compatibility in the personality of collaborating parents reduces sexual conflict over the provision of parental investment (*sensu* Trivers 1972).

One way in which this may arise is if individuals of different personalities have different response rules that they use to provision nestlings. The outcome of sexual conflict, and the relative investment by males and females, is dependent upon the form of these provisioning rules used by parents (Parker et al. 2002). Negotiation models, based on flexible negotiation of effort in real time, predict high responsiveness of individuals to a change in effort by their partners (e.g. McNamara et al. 1999; Johnstone & Hinde 2006). Sealed bid models, on the other hand, predict that individuals should be insensitive to changes in effort by their partner (e.g. Parker 1985). Here individuals commit to a certain level of care at the outset that is independent of partner effort, although it may be modified by variation in environmental resource

availability or brood size (Schwagmeyer & Mock 2003). There is considerable empirical evidence for both flexibility of effort (negotiation) and inflexibility (sealed bids) (reviewed in Sanz et al. 2000; Schwagmeyer & Mock 2003). Life-history theory suggests that individuals should adjust their risk-taking behaviour in relation to their expected future fitness returns (Roff 2002). Consequently, individuals with high future expectations (i.e. with more to lose) should be more risk averse than individuals with lower expected reproductive success (creating an “unadventurous” to “adventurous” continuum of personalities, Wolf et al. 2007; Biro & Stamps 2008). Based on life-history considerations we would therefore expect adventurous individuals to invest relatively more effort in the current breeding attempt than unadventurous individuals. If the personality of an individual provides information about their willingness to trade future for current reproductive opportunities, then it might be expected that adventurous individuals will have different response rules (more flexible) to unadventurous individuals. Consequently, disassortative pairings with respect to personality will have reduced efficiency as a result of dissimilar response rules, whereas assortative pairings will have similar response rules (and increased provisioning efficiency). However, unadventurous-unadventurous pairings will be in greater conflict over provision of current effort than adventurous-adventurous pairings as a consequence of withholding greater resources for future reproductive events. These predictions remain to be tested.

In conclusion, our results show that behavioural compatibility and consistency in personality during parental care, rather than genetic compatibility, has important, long-lasting effects on reproductive success in zebra finches, and suggests that personality may be an important indicator of likely male investment, and help determine the outcome of sexual conflict over parental care. Consequently, we highlight a key role for sexual selection in the evolution and maintenance of animal personalities.

EXPERIMENTAL PROCEDURES

HOUSING AND STUDY SPECIES

We used adult zebra finches, *Taeniopygia guttata*, from a stock of birds kept at the University of Exeter in Cornwall, which were maintained indoors on a 14.5:9.5 h full light:dark photoperiod under controlled temperature (19.0 ± 0.03 SE) and humidity conditions. Water, grit, cuttlebone and commercial seed mixture (Finch Mixture; J. E. Haith, Cleethorpes, UK) were supplied continuously. Prior to breeding, all birds were kept in single-sex groups of between 6-10 individuals. While breeding, each pair was housed in a double-breeder cage (120 x 45 x 40

cm), was provided with an externally attached nest-box (15 cm³), and had access to suitable nesting material.

PERSONALITY TESTS

Prior to pairing and breeding, we tested all focal birds twice for their exploratory behaviour (e.g. number of features visited, latency to visit first feature) in a novel environment containing 10 different features, with a seven day time interval between the consecutive tests. Each individual experienced two further novel environment tests after breeding, before their tendency to interact aggressively with the mirror (number of mirror interactions) was measured twice using a mirror test (for more details see Supplemental Experimental Procedures).

MORPHOLOGICAL MEASUREMENTS

Before pairing, morphological measurements (wing length \pm 1 mm, tarsus and head-bill length \pm 0.1 mm) of the focal birds were taken. As head-bill, tarsus and wing length were significantly correlated (Spearman correlations; head-bill – tarsus: $r_s = 0.289$, $P = 0.01$; head-bill – wing: $r_s = 0.356$, $P = 0.002$; tarsus – wing: $r_s = 0.453$, $P < 0.001$; all $N = 77$), only head-bill length was further considered to avoid multicollinearity.

PAIRING AND BREEDING

Between 27/03/07-19/04/07 77 birds (40 females, 37 males) were paired up to three times (due to failure to lay eggs). Each pair that started reproducing ($N = 31$) was allowed to lay two clutches: the eggs of the first clutch were cross-fostered shortly before hatching and emerging hatchlings were raised by foster parents ($N = 31$ pairs) until independence (day 35), when offspring were transferred into single-sex peer groups. Eggs of the second clutch were removed for further study (beyond the scope of this manuscript) and were replaced by dummy eggs.

MEASUREMENTS OF REPRODUCTIVE SUCCESS

Nest-boxes were checked on a daily basis, and the following measures recorded: latency to start nest building and egg laying (both in days since pairing), number and mass of eggs and hatchlings (\pm 0.01 g) as well as the interval between consecutive clutches (days between laying of first egg of first clutch and first egg of second clutch). Once hatched, individually marked juveniles were weighed on a daily basis until 12-14 days old and again at fledging (day 20) and at independence, when other morphological measurements in addition to mass (wing, head-bill

and tarsus length) were collected. We calculated growth rate (K) for individual nestlings using a logistic model of growth, following the procedure described in Royle et al. (2006).

TREATMENTS

When foster chicks were 3 days old, the foster father was removed in 11 out of the 31 breeding cages until the offspring reached independence, so that the female reared the chicks on her own (uniparental treatment). In the remaining 20 pairs both parents raised their foster chicks together for the duration of the nestling period (biparental treatment). Fostered clutches consisted of 2 (uniparental treatment), 4 or 6 chicks.

REPLICATION OF EXPERIMENT

When we repeated the experiment in 2008, we used the same experimental set-up as in the previous year with the only obvious difference being variation in rearing and housing environments for the adult generations: whereas all of the focal adults in 2007 had been raised by their genetic parents, most of them at the University of Glasgow, the focal adults in 2008 had been raised by foster parents (this study). In the repeated experiment 26 clutches were produced, which were assigned to 29 foster pairs. In one of these 29 foster clutches all chicks died after fledging.

STATISTICAL ANALYSES

The influence of the personality of the genetic and foster parents, respectively, on reproductive success (and parental care, see Supplemental Experimental Procedures) was investigated with a number of generalised linear models (GLMs) with normal error structure: explanatory variables in each model included a measure of personality of either the foster mother and father or the genetic mother and father as well as their interaction and the treatment group (factor with two levels: uniparental versus biparental treatment). Measures of personality concerned either the level of behaviour (i.e. number of features visited in the novel environment, latency to visit the first feature and number of interactions with the mirror) or the behavioural consistency (coefficients of variation (CV) in these measures). For analyses on interactions between female and male number of mirror interactions we excluded the only measurement without physical contact with the mirror: male song rate, in order to make male and female behaviour comparable (female zebra finches do not sing). As the CV is not informative when the mean is close to zero (Spiegel 1991), we only calculated the CV for the latency to visit the first feature in the novel environment but not for the other behavioural measurements which had a mean close to zero. The intergenerational behavioural effects on mean clutch condition of the second generation at

independence (2008) were assessed with two GLMMs (REMLs) with the 3-way and 2-way interactions of the mean number of features visited, and the CV for the latency to visit the first feature, respectively, in the two novel environment tests prior to breeding (2007) by the foster grandmother and foster grandfather and sex of foster parent (2008) as well as their main effects. Foster grandparents' "pair ID" was added as random effect. Minimal adequate models were obtained by stepwise deletion of non-significant fixed effects ($P > 0.05$) following Crawley (2002), providing the explanatory power did not reduce significantly (model comparisons of GLMMs were conducted using maximum likelihoods, Pinheiro & Bates 2000). Non-significant P-values stated stem from terms just before they dropped out of a model, resulting in varying degrees of freedom depending on how many other terms were still in the model. Data were Box-Cox transformed (Crawley 2002) to conform to model assumptions, or non-parametric statistical tests were applied, where appropriate.

SUPPLEMENTAL DATA

Supplemental Data include Supplemental Experimental Procedures and Results, including 1 table and 5 figures.

ACKNOWLEDGEMENTS

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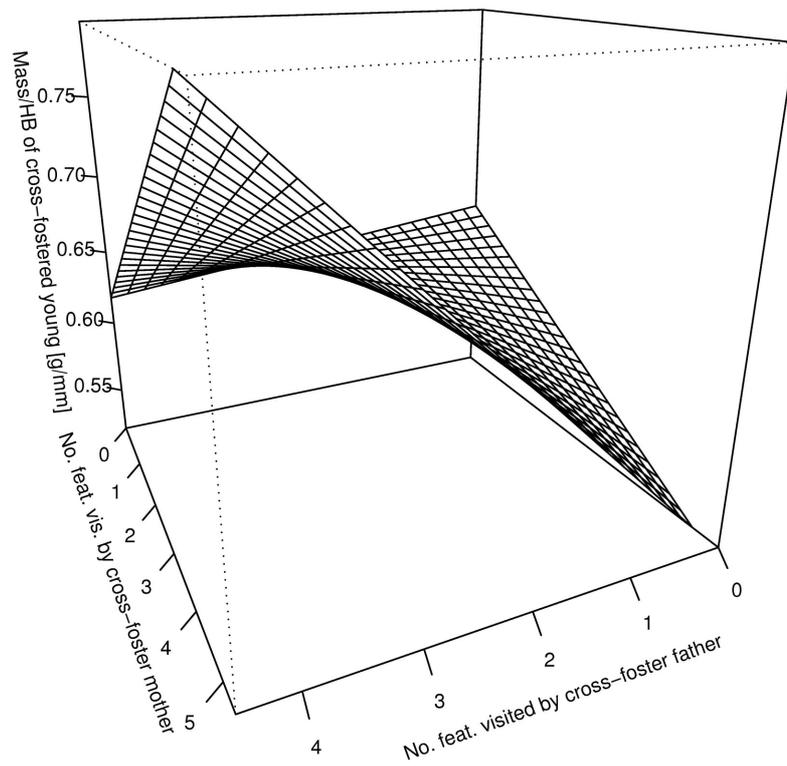


Figure 1. Influence of foster parents' exploratory tendencies on mean brood condition (mass/head-bill length in g/mm) of cross-fostered nestlings at independence. Exploratory tendency was measured as the mean number of features visited in two novel environment tests prior to breeding.

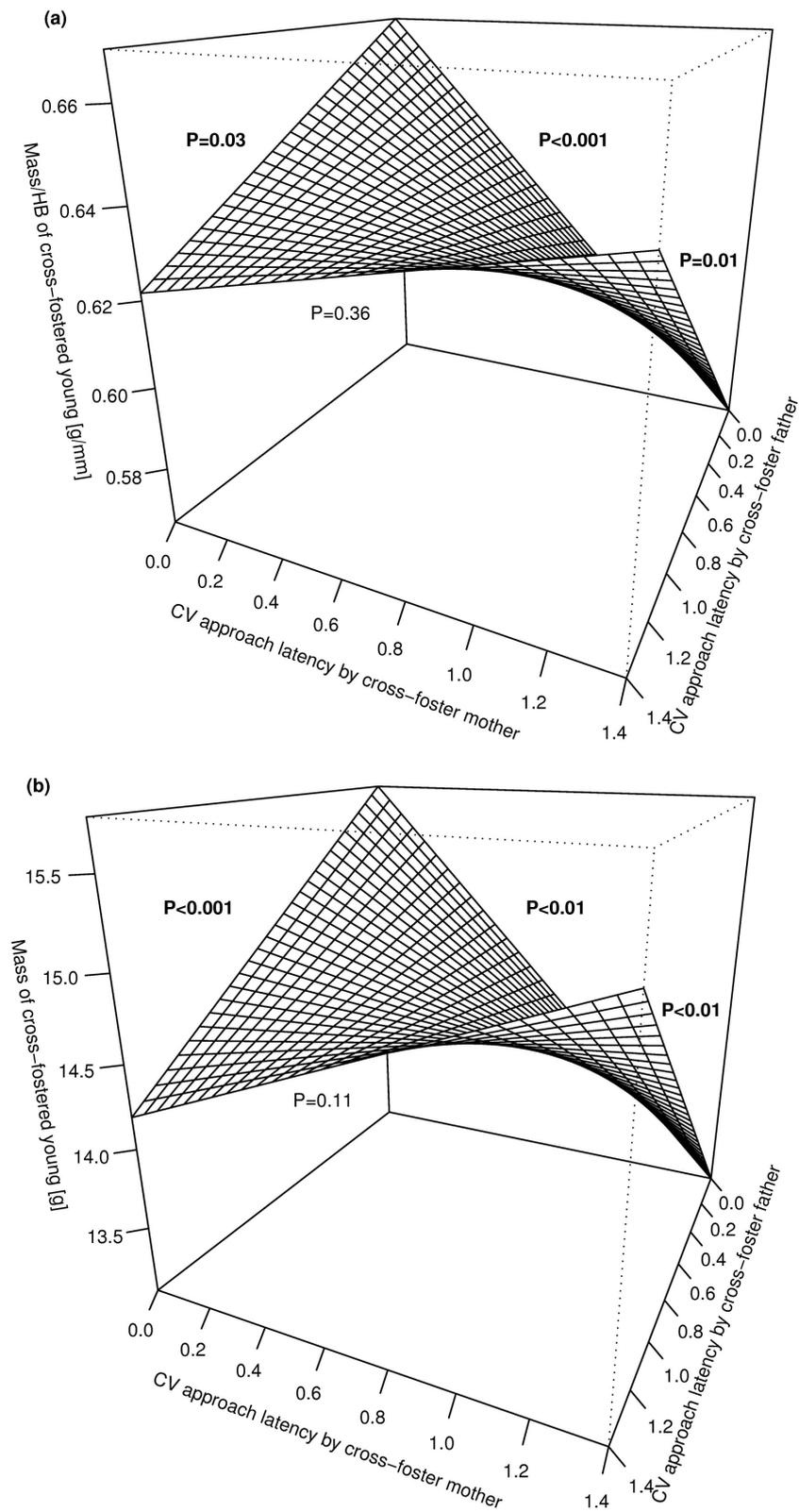


Figure 2. Combined effect of foster parents' behavioural consistency in exploration on mean brood (a) condition and (b) mass of cross-fostered nestlings at independence. Consistency in exploration was measured as the coefficient of variation (CV) for the latency to approach the first feature in two novel environment tests prior to breeding. The P-values show if partners' consistency has an effect on each extreme for foster mothers' and fathers' CV, respectively (e.g. highly consistent foster mothers raise chicks in better condition with a similarly consistent male than with a dissimilar male ($P = 0.03$)). Significant P-values are shown in bold.

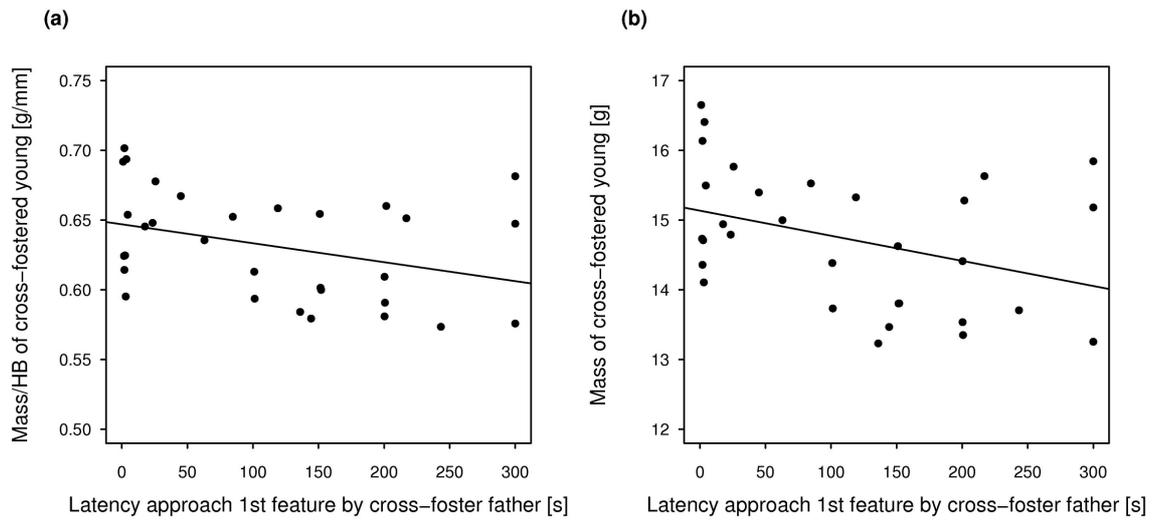


Figure 3. Relation between foster fathers' mean tendency to approach the first feature in a novel environment (pre-breeding) and mean brood (a) condition (mass/head-bill length in g/mm) and (b) mass (in g) of their cross-foster nestlings at independence.

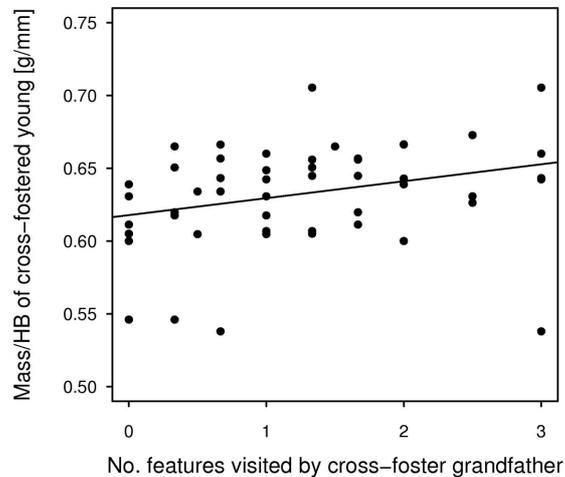


Figure 4. Influence of males' exploratory tendency (2007) on the condition (mass/head-bill length in g/mm) of their second generation foster-offspring at independence (offspring in 2008). Exploratory tendency was measured as the mean number of features visited in two novel environment tests prior to breeding in 2007.

SUPPLEMENTAL DATA

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Novel environment set-up

Novel environment tests were conducted indoors in two cages (120 x 30 cm and 38 cm high) that were visually but not acoustically isolated from the other birds, which were kept in the neighbouring room. The 10 features in each novel environment consisted of 5 branches (of varying diameter, shape and length, serving as perches at random locations), one feeder containing seeds, one drinker, the mesh at the front of the cage, the ground (consisting of bedding) as well as a wooden partition in the middle of the cage bottom. The arrangements of the features in the two novel environment set-ups were mirror-inverted but otherwise identical. The shape and colour of the feeders as well as the shape of the drinkers used were different to the ones in the holding enclosures. Contrary to the novel environment, the home cages contained two commercial, standardised perches at standardised locations and the floor was covered with paper. The focal birds did not have any experience with the experimental cages before the start of the first test trial.

Novel environment test procedure – pre-breeding

Prior to breeding each individual was tested once in each of the two mirror-inverted novel environment cages. Tests were conducted between 10/3/07-20/3/07 within 4 hours of sunrise, as zebra finches are most active during the morning (Cuthill et al. 1997), and lasted 5 min each, during which time the latency to visit the first feature, the total number of features visited, the total number of revisits and the number of times an individual turned around on each feature were recorded. Two birds were tested simultaneously, one in each of the novel environments. The focal individuals could not see but hear each other. Before the start of each trial the focal individuals were transferred into a card box (9 x 11 cm and 9 cm high) each, which was located in the novel environment. The trials started by opening the lid of the box with a string from a distance (of 2 m) and were recorded on a video camera (Sony Handycam DCR-HC90E) while W.S. was present. After each trial the body mass of the focal birds were measured to the nearest of 0.1 g. Due to some disturbances in the neighbouring room during the second test series, 22 individuals were tested for a third time in the novel environment, 3 days after the second series. All data available were presented, as similar results were obtained when the different data subsets were investigated.

Morphological measurements of offspring

As for the adults, the morphological traits of the offspring were significantly correlated (Spearman correlations; head-bill – tarsus: $r_s = 0.343$, $P < 0.001$; head-bill – wing: $r_s = 0.203$, $P = 0.033$; tarsus – wing: $r_s = 0.216$, $P = 0.023$; all $N = 111$), so only head-bill length was considered further in analyses.

Parental care

We videoed foster parents' parental care by mounting an infrared-sensitive video camera with infrared LEDs to the top of the nest-boxes. Provisioning behaviour was recorded at 23 of our 31 nest-boxes for 90 min each, when chicks were 8-10 days old (uniparental treatment: $N = 11$; biparental treatment: $N = 12$). Video data were collected between 1000 and 1500. After a food deprivation of one hour, half of the chicks in a clutch were hand-fed to satiation just before the filming period started (in order to create variation in within-brood levels of hunger; details of which are beyond the scope of this manuscript). We quantified the number and duration of nest attendance events by parents, food provisioning behaviour (rates and regurgitation duration, see Royle et al. 2006) and preening of chicks.

Personality tests – post-breeding

After all breeding pairs had finished laying their second clutch, pairs were split up and returned into single-sex groups, before all successful ($N = 65$) as well as unsuccessful breeders ($N = 11$; 4 individuals of the originally 15 unsuccessful breeders had died) were exposed to further personality tests. The birds were again tested in the novel environments twice (between 24/06/07-24/07/07) under the same procedure as described above, with 6-8 days between two consecutive trials (mean: 6.87 ± 0.08 SE). Subsequently, the mirror tests were conducted (first series: 4-8 days after the last novel environment test, mean: 5.47 ± 0.15 SE; second series: 10-12 days after the first series, mean: 11.0 ± 0.07 SE).

Mirror-test set-up

The mirror-tests were conducted in a mesh-wire cage (38.5 x 48 x 33.5 cm; Figure S1). The cage contained one branch, over the length of same (48 cm), at which end a mirror (11 cm x 15 cm) was placed. Underneath the mirror we positioned a feeder containing seeds. Similarly as for the novel environments tests, we used two mirror-inverted cages, visually but not acoustically separated from each other.

Mirror-test procedure – post-breeding

As for the novel environment test, the focal birds were transferred into a card box (9 x 11 cm and 9 cm high) each, which was then placed into the test cage. As soon as W.S. opened the box from 2 m distance with a string, the trials started and were recorded by two video cameras (Sony Handycam DCR-HC90E and DCR-PCR-PC109E). Trials consisted of two parts, each lasting 5 min: during the first part, in which individuals were allowed to explore and to get used to the novel cages, the mirror was covered. In the second part, the mirror was uncovered thus that the focal individual could interact with the mirror. The following interactions were recorded: flying against the mirror, bill contact with the mirror (slow movement), pecking at the mirror (fast movement) and straightening up to full height followed by pecking at the mirror (breast contact with mirror). For males we also recorded direct song towards the mirror. The latency to interact with the mirror for the first time, the number of times and duration of each interaction with the mirror, the number of turnings on the perch as well as the location of the bird at all times were recorded. The location of the focal bird on the perch was classified as following (Figure S1): zone 1: closest to mirror, within reaching distance of mirror (12 cm long); zone 2: zone between zone 1 and 3 (12 cm long); zone 3: zone furthest away from mirror (24 cm long). From this we calculated a “social score” by weighing the time spent in each zone, i.e. distance to the mirror (time spent in zone 3 + time spent on ground + (time spent in zone 2 * 2) + (time spent in zone 1 * 3)). Therefore, a high social score indicates that a high proportion of time was spent closely to the mirror. We considered this measurement as it might reflect the tendency to affiliate rather than a tendency to behave aggressively: in fish, where mirror tests are used frequently, behaviours like biting the mirror are normally interpreted as aggressive expressions (e.g. Gerlai 2003) but they could as well represent a general measure of tendency to interact socially or to affiliate (Moretz et al. 2007).

SUPPLEMENTAL RESULTS

PERSONALITY MEASUREMENTS

Exploration of novel environment – pre- and post-breeding

The number of features visited over all novel environment tests (i.e. pre- and post-breeding) was significantly repeatable within individuals of both sexes (GLMMs with “individual” as random term; overall: $R = 0.348 \pm 0.06$ SE, $P < 0.0001$, $N_{\text{trials}} = 322$, $N_{\text{ID}} = 77$; males: $R = 0.291 \pm 0.09$ SE, $P = 0.001$, $N_{\text{trials}} = 161$, $N_{\text{ID}} = 37$; females: $R = 0.414 \pm 0.09$ SE, $P < 0.0001$, $N_{\text{trials}} = 161$, $N_{\text{ID}} = 40$), showing that we measured a behavioural trait that was stable over the experimental

period. Measurements were also repeatable if we consider data from pre- and post-breeding trials separately (GLMMs; pre-breeding: $R = 0.449 \pm 0.08$ SE, $N_{\text{trials}} = 176$, $N_{\text{ID}} = 77$, $P < 0.0001$; post-breeding: $R = 0.531 \pm 0.08$ SE, $N_{\text{trials}} = 146$, $N_{\text{ID}} = 73$, $P < 0.0001$). The mean values per individual for the other behavioural measurements taken during the repeated novel environment trials pre-breeding were all highly correlated to the mean number of features an individual visited (Spearman correlations; mean number of turnings: $r_s = 0.792$, $P < 0.0001$; mean number of revisits: $r_s = 0.722$, $P < 0.0001$; mean latency to visit first feature: $r_s = -0.690$, $P < 0.0001$; all $N = 77$). Both males and females at the extremes of the trait distribution for the latency to approach the first feature pre-breeding were more consistent in their behaviour than intermediate explorers, which showed a higher degree of variability (GLM; overall: mean latency: $F_{1,74} = 41.61$, $N = 77$, $P < 0.0001$, squared mean latency: $F_{1,74} = 59.08$, $P < 0.0001$; females: mean latency: $F_{1,37} = 46.12$, $P < 0.0001$, squared mean latency: $F_{1,37} = 62.24$, $P < 0.0001$; Figure S2a; males: mean latency: $F_{1,34} = 10.97$, $P = 0.002$, squared mean latency: $F_{1,34} = 15.92$, $P < 0.001$; Figure S2b). Finally, mean individuals' responses pre- and post-breeding correlated significantly (Spearman correlation: numbers of features visited: $r_s = 0.333$, $P = 0.004$; latency to approach the first feature: $r_s = 0.483$, $P < 0.0001$; number of turnings: $r_s = 0.301$, $P = 0.010$) apart from the number of revisits ($r_s = 0.268$, $P = 0.155$, all $N = 73$).

Interaction with mirror – post-breeding

Adults of both sexes (37 females and 36 males were available for the mirror test post-breeding) were consistent in the total number of interactions with the mirror over the two trials (Spearman correlations; males: $r_s = 0.373$, $P = 0.023$; females: $r_s = 0.641$, $P < 0.0001$) but this was not true for females if we only assessed behavioural consistencies of individuals that interacted with the mirror when they encountered the mirror for the first time (Spearman correlations; males: $r_s = 0.705$, $N = 24$, $P < 0.001$; females: $r_s = -0.005$, $N = 15$, $P = 0.999$). Also, individuals of both sexes were consistent in their social score (Spearman correlations; overall: $r_s = 0.433$, $P < 0.001$; males: $r_s = 0.412$, $P = 0.012$; females: $r_s = 0.449$, $P = 0.006$), their number of turnings (Spearman correlations; overall: $r_s = 0.536$, $P < 0.0001$; males: $r_s = 0.486$, $P = 0.003$; females: $r_s = 0.562$, $P < 0.001$) and males were consistent in their time spent singing (Spearman correlation; $r_s = 0.811$; $P < 0.0001$). Males interacted more often with their apparent opponent than females (Wilcoxon rank sum test; $W_{37,36} = 417.5$, $P = 0.005$); but the mean individual social score did not vary between the sexes (Wilcoxon rank sum test; $W_{36,37} = 558.5$, $P = 0.237$). The mean number of interactions were correlated positively to the social score (Spearman correlations; overall: $r_s = 0.377$, $P = 0.001$; males: $r_s = 0.367$, $P = 0.026$; females: $r_s = 0.399$, $P = 0.016$) and negatively to the mean latency to interact with the mirror (Spearman correlations; overall: $r_s = -0.864$, $P < 0.001$; males: $r_s = -0.845$, $P < 0.0001$; females: $r_s = -0.868$, $P < 0.0001$).

Associations between exploration and aggression

The mean number of mirror-interactions post-breeding was positively correlated to the mean number of features visited during the novel environment tests for both males and females pre-breeding (Spearman correlations; males: $r_s = 0.336$, $P = 0.046$; females: $r_s = 0.452$, $P = 0.005$) and for males post-breeding (Spearman correlations; males: $r_s = 0.444$, $P = 0.007$; females: $r_s = 0.041$, $P = 0.810$).

Reproductive success

Adults varied substantially in their ability to form a pair bond and ability to start breeding (nest building and egg laying): of the 45 pair combinations 31 started egg laying (69 %). Also, the reproductive success of pairs that did reproduce varied (see Table S1).

BEHAVIOUR AND REPRODUCTIVE SUCCESS

Influence of parents' personality on reproductive success

Males' and females' exploratory tendency (mean number of features visited in the two novel environment tests pre-breeding) and their interaction did not influence whether a male built a nest or not (GLM with binomial error structure; interaction: $\chi^2_1 < 0.01$, $N = 45$, $P = 0.955$; males: $\chi^2_1 < 0.01$, $P = 0.984$; females: $\chi^2_1 = 1.27$, $P = 0.259$) or whether a female laid eggs or not (GLM with binomial error structure; all $P > 0.430$). The occurrence of nest building and egg laying was also independent of a partner's tendency to interact with the mirror (number of interactions without male song) and their social scores (GLMs; interaction: nest building: all $P > 0.200$; egg laying: all $P > 0.330$). Also, in pairs that did reproduce there was no combined effect of genetic parents' exploratory or aggressive tendency on either of two components "reproductive success" obtained from a PCA (GLMs; exploration: all $P_{\text{Comp1}} > 0.380$; all $P_{\text{Comp2}} > 0.220$; aggression: all $P_{\text{Comp1}} > 0.200$; all $P_{\text{Comp2}} > 0.094$; all $N = 25$; the mean egg and hatchling mass of the first clutch and the mean egg mass of the second clutch loaded positively on the first, whereas the number of eggs in the first and second clutch and the number of hatchlings loaded mostly on the second component; varimax rotated; 76% of variance explained by the two components).

Food provision, personality and reproductive success

The total time foster parents spent in the nest-box was a predictor of the duration chicks were fed (Pearson correlation; $r_p = 0.492$, $N = 23$, $P = 0.017$) but not the time spent preening the

chicks (Spearman correlation; $r_s = 0.216$, $N = 23$, $P = 0.319$). The total time an individual spent food provisioning was not correlated to its mean number of features visited during the novel environment test (pre-breeding) (males: $r_p = -0.019$, $N = 12$, $P = 0.954$; females: $r_s = 0.110$, $N = 23$, $P = 0.614$) or to its mean number of mirror interactions (males (without number of songs): $r_s = -0.225$, $N = 12$, $P = 0.484$; females: $r_s = 0.089$, $N = 23$, $P = 0.684$). Similarly, the combination of exploratory or aggressive tendencies in a pair did not influence the total time chicks were fed (GLMs; mean number of features visited: interaction: $F_{1,18} = 1.56$, $P = 0.228$; mean number mirror interactions: interaction: $F_{1,18} = 0.25$, $P = 0.625$; treatment: $F_{1,21} = 7.91$, $P = 0.010$; both $N = 23$). However, these findings should be considered with caution as (a) the duration the parents fed their chicks did not predict chicks' mean clutch mass at independence (GLM; $F_{1,21} = 1.63$, $N = 23$, $P = 0.216$) and (b) the combined effect of parents' personality on offspring mass at independence was not significant in the subset of the broods for which video data were collected (GLM; exploration: interaction: $F_{1,18} = 2.50$, $P = 0.132$; aggression: interaction: $F_{1,18} = 3.23$, $P = 0.089$; both $N = 23$). This could be due to the fact that videos were just taken on one occasion for 90 min, which may not be representative for parental care in general (see Royle et al. 2002).

Personality and reproductive success in 2007 and 2008

Data from the two breeding experiments in 2007 and 2008 were compared with two GLMs. First, we investigated the effect of the mean number of features visited by the cross-foster mother, the cross-foster father and the year, as well as their 2-way and 3-way interactions and the effect of treatment (uni- versus biparental regime) on the mean clutch mass at independence. Both the mean brood mass and condition of nestlings were influenced by the 3-way interaction (GLM; 3-way interaction: mass: $F_{1,51} = 5.34$, $P = 0.025$; condition: $F_{1,51} = 6.48$, $P = 0.014$; both $N = 59$). Contrary to 2007 (see main MS), no combined effects of foster parents' personalities were found in 2008 (GLM for 2008 data: interaction: mass: $F_{1,23} = 2.11$, $P = 0.160$; condition: $F_{1,23} = 1.93$, $P = 0.178$; both $N = 28$). We found a similar 3-way interaction between the behavioural consistency to approach the first feature in a novel environment of the foster mother and the foster father and the year on the brood mean mass at independence (GLM; 3-way interaction: mass: $F_{1,51} = 5.02$, $N = 59$, $P = 0.030$) and a trend for a 3-way interaction on the clutch condition at independence (GLM; 3-way interaction: condition: $F_{1,50} = 3.45$, $P = 0.069$).

Table S1. Reproductive success of zebra finch pairs.

	N	Mean	± SE	Median	Min.	Max.
1st clutch						
Latency to lay egg (days)	31	6.87	0.69	5.00	3	19
Mean egg mass [g]	31	1.24	0.03	1.23	1	1.8
Mean hatchling mass [g]	29 ^a	0.93	0.03	0.92	1	1.65
No. eggs	31	5.16	0.25	5.00	2	8
No. hatchlings	27 ^b	3.93	0.40	5.00	0	7
2nd clutch						
Interval between clutches (days)	31	49.61	1.66	48.00	28	71
Mean egg mass [g]	31	1.13	0.02	1.12	1	1.58
No. eggs	31	4.00	0.22	4.00	1	7

^a two clutches did not hatch

^b in four nests some of the eggs of a clutch (all fertile) were removed for population control.

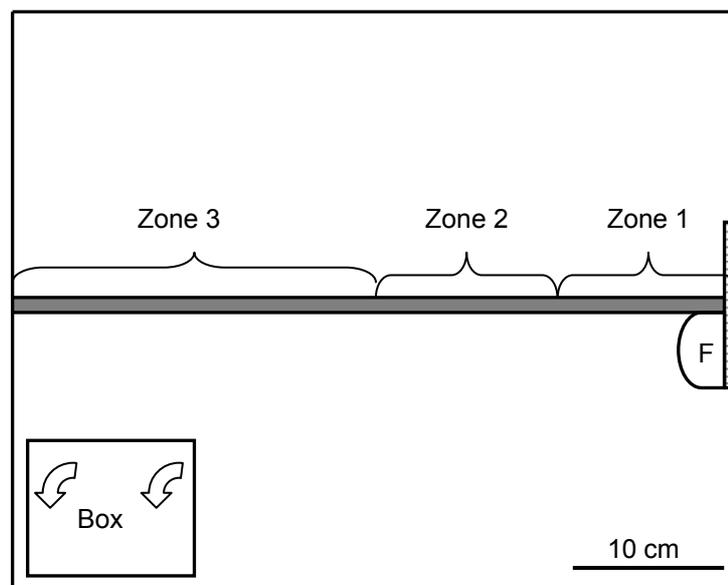


Figure S1. Plan view of the cage set-up for the mirror test. For more details see text. Grey bar: perch; striped bar: mirror. F: feeder placed under the mirror.

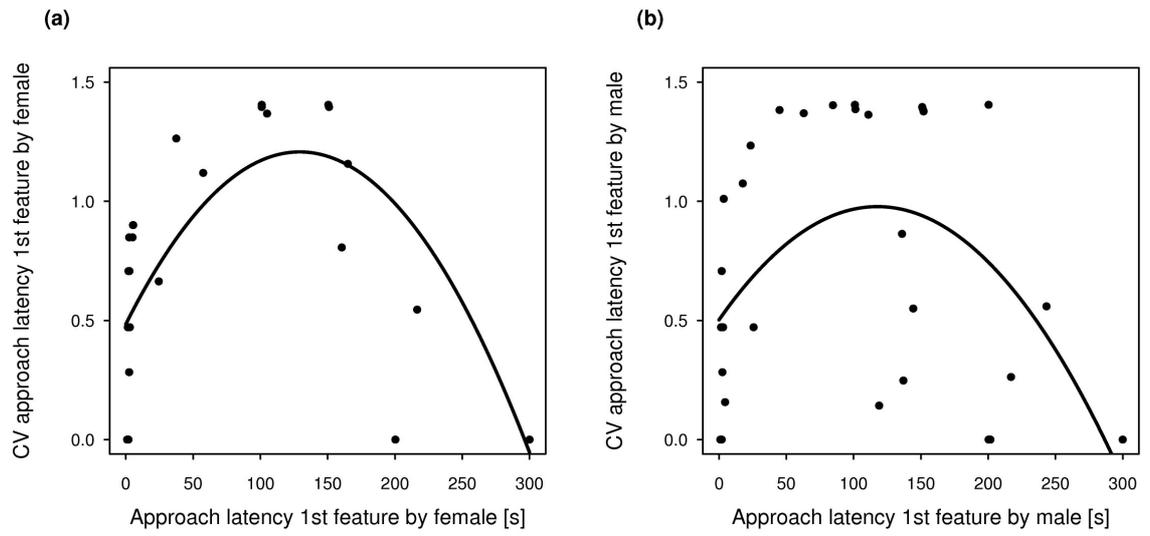


Figure S2. The relationship between the mean latency to approach the first feature in two novel environment tests pre-breeding and the CV for these approach latencies for (a) females and (b) males.

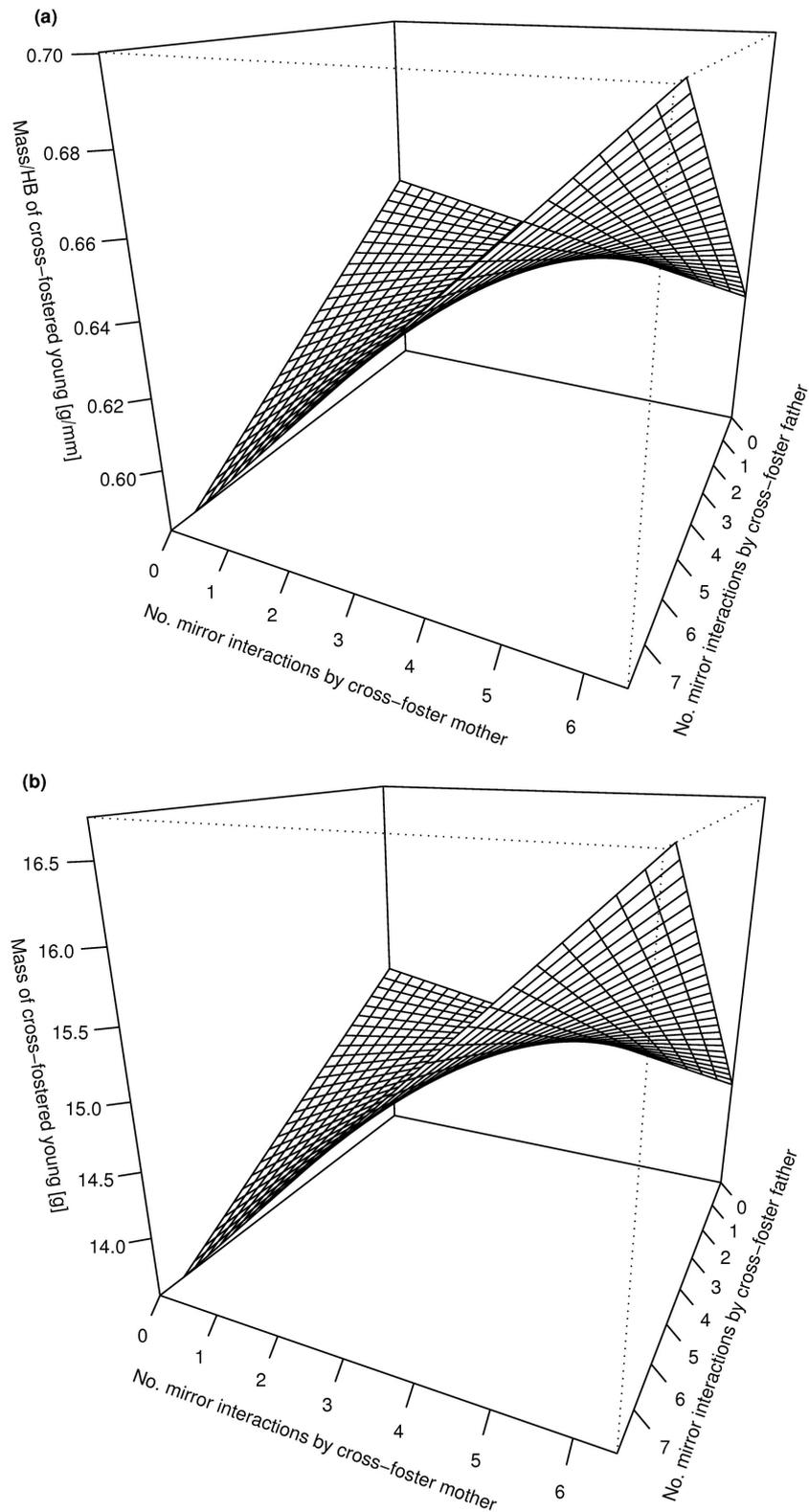


Figure S3. Influence of foster parents' tendencies to interact with a mirror on brood mean (a) condition (mass/head-bill length in g/mm) and (b) mass (in g) of cross-fostered nestlings at independence. This tendency was measured as the mean number of interactions (sum of all interactions shown but song, as song only occurs in males) in two mirror tests after breeding. Two outlier data points are excluded for scaling reasons (but not from the analyses).

Chapter 5

**Appearance, “state” and behaviour in male zebra
finches, *Taeniopygia guttata***

ABSTRACT

Secondary sexual traits are often costly to produce and therefore an individual's appearance can signal its quality. As the quality of an individual influences the payoffs associated with the actions it can perform, its appearance should also influence its behaviour. Here we investigate whether male zebra finches, *Taeniopygia guttata*, change their behaviour (and their energetic states) after artificial manipulations of their appearance, using different coloured leg bands, and if such effects carry over after the end of the manipulation, as might be expected if appearance-mediated social dynamics "lock" individuals into different states. During three experimental phases, in which all males in a group wore neutral coloured leg bands at the beginning (phase I), then got attractive, unattractive and neutral coloured bands, respectively (phase II), before getting the neutral colour again (phase III), we found no evidence of an effect of the appearance manipulation on state, weight or any behavioural traits we measured. Nevertheless, we found that individuals that stored more fat were more likely to initiate and win aggressive interactions but were less likely to be recipients of aggression. This association between energetic state and aggressive behaviour is discussed from both strategic body mass regulation and sexual selection perspectives.

Keywords: state-dependence; aggressive behaviour; fat storage; sexual selection; leg band

INTRODUCTION

Sexual selection: variation in reproductive success due to differential access to mates, is typically manifest via male-male competition (intrasexual competition), female choice (intersexual competition) and male-female conflict (Darwin 1871; Andersson 1994). Consequently, different selective pressures act on males and females, resulting in sex differences in secondary sexual traits like body size or ornamentation, including bright colouration, horns or weapons (reviewed in Andersson 1994). For instance, in a number of species females show a preference for males that are brightly coloured or large (reviewed in e.g. Ryan & Keddy-Hector 1992; Andersson 1994), favouring the evolution of conspicuously colourful and/or large males. If the expression of these appearance traits is costly, then they should reflect a male's quality, including its condition and dominance status (Andersson 1994). Accordingly, at least some features of an individual's appearance should offer conspecifics information about its quality. In male-male interactions (both in sexual and natural selection context) this could be information about an individual's relative fighting ability, which should influence the behaviour shown by its opponents (Bonnie & Earley 2007). Secondly, appearance can affect an individual's behaviour (e.g. during male-male interactions) directly if some features of its appearance reflect its quality and therefore its state (state is a characterisation of an individual at a given point in time, representing features of this individual such as its energy reserves, size, parasite load, physiological or environmental aspects or current behaviour of surrounding individuals, see Houston & McNamara 1999; Dall et al. 2004). This is because such states influence the costs and benefits of the actions an individual can perform (Houston & McNamara 1999; Dall et al. 2004). Indeed, Godin & Dugatkin (1996) showed that the visual conspicuousness of male guppies, *Poecilia reticulata*, which is influenced by their parasite loads (Houde & Torio 1992), determines their predator inspection behaviour and escape abilities.

Often the states underpinning individual behaviour are themselves affected by the consequences of actions they influence (Houston & McNamara 1999). For instance, individuals with few energy reserves will have stronger incentives to compete for food, despite the risks involved, and so are more likely to augment their reserves than individuals showing better condition (Houston et al. 1993). In this way, current actions, via their impacts on the traits influencing behaviour, can determine future behaviour. Indeed, under certain circumstances, arbitrary differences in condition and/or life-history can lock individuals into distinct state trajectories, via positive feedback between state and behaviour, and thereby generate stable behavioural tendencies (Rands et al. 2003; Dall et al. 2004; McElreath et al. 2007). Similarly, variation in individual appearance, via its impact on the social interactions of the individuals

involved (e.g. the intensity of aggression experienced), might generate distinct patterns of individual behaviour.

Given such rationale, we investigated whether an individual's appearance influences its behaviour and if this effect is stable over time. Therefore, we manipulated the appearance of male zebra finches, *Taeniopygia guttata*, using different coloured leg bands and observed their behaviour in male groups before, during and after the manipulations. In the sexually dimorphic zebra finch, different coloured rings have been shown to influence survival (Burley 1985; Burley 1986c), reproductive success (Burley 1986c) and mate choice (Burley et al. 1982; Burley 1988b; but see Jennions 1998), where females prefer red-banded males over orange-banded ones and avoid green-banded males. Furthermore, two studies investigated the influence of coloured leg bands on male-male interactions (Ratcliffe & Boag 1987; Cuthill et al. 1997). However, Ratcliffe & Boag (1987) failed to detect an effect of colour band manipulation on male-male competition for nest boxes and females, or on song rate or agonistic behaviour. In contrast, Cuthill et al. (1997) detected impacts of such colour-ring manipulations on displacement behaviour, mass and fat storage; males with attractive leg bands behaved more dominantly (were more aggressive and stored less fat). Based on the latter study we predict that the male zebra finch social hierarchy will be influenced by colour ring manipulations with individuals wearing an "attractive" ring colour adjusting to their upgraded status by becoming more aggressive and dominant (and vice versa for "unattractive" males). This in turn is expected to influence physiological state variables (e.g. fat reserves) and behavioural performance. More specifically, we predict that these changes will influence the daily feeding and activity patterns consistently, where "unattractive" appearing, "low quality", males will feed more, store more fat but will be less active than "attractive" appearing males. This is predicted to occur as a buffer against a potential nutritive shortfall due to unpredictable food access for subdominants (Ekman & Lilliendahl 1993; Gosler 1996; Clark & Mangel 2000; but see Cuthill & Houston 1997). Thus the changes to the male social hierarchy should persist after the manipulations of attractiveness, if individuals become locked into distinct state trajectories via socially-mediated access to food.

MATERIALS AND METHODS

SUBJECT AND PRE-EXPERIMENTAL HOUSING

The experiment was conducted using captive-bred adult male wild-type zebra finches, *Taeniopygia guttata*, obtained from various breeding stocks in the United Kingdom. Before the experiment all birds were kept in outdoor aviaries (84 x 215 cm and 263 cm high) in three unisex groups which were not acoustically isolated from members of other flocks. Water,

commercial seed mixture (Foreign Finch Mixture; J. E. Haith, Cleethorpes, UK), cuttlebone and grit were available *ad libitum*. Once a week supplementary conditioning food (a mixture of Rearing and Conditioning Food (J. E. Haith), Daily Essentials vitamin supplement (The Birdcare Company, Nailsworth, UK) and water) was provided.

EXPERIMENTAL HOUSING

The experiment was performed on 30 randomly chosen male zebra finches from the outdoor stocks. Out of these adults ten groups of three males each were formed, with birds in each group originating from different flocks. Males within groups were matched for weight, but otherwise randomly allocated to ten experimental cages (30 x 60 cm and 40 cm high) which were visually but not acoustically separated from each other. During the experiment the birds were kept indoors on a 14:10 h light:dark photoperiod (10 min of the beginning and end of each dark period was twilight) with temperatures ranging between 18.51 °C (\pm 0.21 SD) and 20.22 °C (\pm 0.32 SD). Water and commercial seed mixture were supplied continuously. Food was provided from a single source (feeder) and each cage also contained two perches as well as grit and cuttlebone.

EXPERIMENTAL PROCEDURE

One day before males were transferred into the indoor cages (day 0), each experimental bird was weighed and its wing chords were measured (to the nearest of 0.1 mm using a wing ruler) before it got one numbered orange coloured leg band (supplied by A. C. Hughes, Middlesex, UK) on each leg. Orange leg bands have been shown to be behaviourally neutral in zebra finches (e.g. Burley et al. 1982). After transferring the birds on the next morning (day 1), the males were allowed to acclimatise before observations of the first of three experimental phases started the following day (day 2; Table 1). Observations of this first phase took place over a period of six days (day 2 - 7), with five groups being observed per day (i.e. one block), resulting in observations for each group every second day. The groups (within a block) were videoed (Sony Handycam DCR-HC90E) in a random order twice a day: once in the morning (within three hours after dawn) and once in the evenings (within three hours of dusk). At dawn all feeders in the cages within the block being observed were removed and replaced in each cage just before recordings started. Moreover, before each group was videoed, its members were caught and scored for the amount of fat they stored. This was done by scoring the amount of fat stored in the intrafurcular groove as well as in the abdomen on a subjective 10-point scale (modified after Helms & Drury 1960). Fat scores of both regions were averaged in order to get one overall fat score. Furthermore, the weights of individuals were measured to the nearest 0.1 g

on an electronic balance. After being released into their cage again, males were given 2 min to settle before they were videoed for 15 min.

After the six days of observations, the second phase of the experiment started and of the three zebra finches in each group one was allocated to two red (“attractive”, Burley et al. 1982), one to two orange (“neutral”) and one to two green (“unattractive”, Burley et al. 1982) leg bands (day 8, Table 1). As for the first phase, the birds again had an acclimatisation period of one day before the observations (day 10 - 15) started in the same manner as before. The set-up of the third phase, in which all individuals carried orange coloured leg bands again, was the same as described before (observations: day 18 - 23). All birds (including the neutral treatment birds) had their rings removed and replaced for each phase. In order to increase the competition between the males in a group, one day after the last observations in each phase (day 8, 16, 24), a female was released into each male cage for 25 min. A different female was used for each of the 30 trials.

To eliminate interobserver bias, all videos were analysed by W.S. who recorded the following behaviours of the focal birds every 5 s over the 15 min trials (scan sampling Lehner 1996): (a) inactive/resting or gazing (no observable activity or looking around), (b) drinking (performed at the water dispenser), (c) feeding (primarily at the feeder but also on spilt seeds on the cage floor), (d) self-preening (including also wiping, scratching, stretching or body shaking), (e) locomotory behaviour (including hopping, flying, movements on the floor), (f) allo-preening (preening of another individual) and (g) other (every behaviour which did not fit into any of the aforementioned categories). Furthermore, all social interactions (allo-preening and aggressive encounters) between the group members were noted, including who initiated them, and their outcomes (all-occurrence sampling, Lehner 1996). We distinguished the following aggressive behaviours: supplanting (an individual flies towards an opponent who flees just before the initiator lands on its place or an individual chases another one on the floor), bill-fencing (each bird jabs its closed bill at the head and bill of the opponent – two-way interaction) and pecking (an individual pecks another one, who might escape – one-way interaction).

STATISTICAL ANALYSES

In order to decrease the number of variables analysed, we conducted principal component analyses (PCA) using SPSS 14.0 before subsequent statistical analyses. The first PCA was conducted on the frequencies of all behaviours scanned (a-g above), as well as fat score, weight, wing length and weight-wing length ratio, for each individual in each trial (3 x 2 observations x 3 individuals x 10 groups x 3 phases = 540 values per response). Following Field (2005), variables that did not intercorrelate (drinking, others, fat score) or were correlated too highly

with other variables (weight-wing length ratio correlated to weight: $r > 0.9$) were excluded. The second set of data subjected to PCA included six behavioural responses measured in relation to aggression (Table 3). These variables were analysed separately as agonistic interactions did not occur that frequently so that for each individual the total number of each agonistic behaviour over the six observations per phase were considered in the analysis instead of six values per individual (e.g. in the PCA above). None of the variables included were either multicollinear or not correlated to any other variable. In all PCAs only factors with an eigenvalue of at least one were kept (Field 2005). We run both orthogonal (varimax) and oblique rotations (oblimin) on the data as we did not know *a priori* if the underlying factors were unrelated to each other. The oblimin rotations revealed that the correlations between the extracted factors were negligible ($< \pm 0.2$) and are therefore not further considered. The reliability of the PCAs were assessed using the “Kaiser-Meyer-Olkin measure of sampling adequacy” (KMO), which is the ratio of the squared correlation between variables to the squared partial correlation between them (Field 2005). A value close to zero indicates a diffusion in the pattern of the correlation which is likely to result in unreliable components, whereas values close to one indicate that the factors should be reliable (Field 2005).

To estimate the impact of the different coloured leg bands on behaviour, weight and fat storage of zebra finches and possible carry-over effects, linear mixed effect models using residual maximum likelihoods (REML) were conducted using R 2.1.1 (R Development Core Team 2005) with the extension package lme4. We always included “group” as a within-subject random term in our models. In doing so, we controlled for the repeated measurements of groups, i.e. we controlled for the non-independence of the data points which occurred because individuals in a cage could have influenced each others’ behaviour. A summary of the full models fitted is found in Table 4. Minimal adequate models were estimated by stepwise deletion of the highest non-significant effects ($P > 0.05$), starting with the highest-order interactions, providing the simplification did not significantly reduce the explanatory power of the model (Crawley 2002). Consecutive models were compared using maximum likelihoods (ML, Pinheiro & Bates 2000). If an explanatory variable had a significant effect in the minimal model and contained more than two factor levels, factor levels were collapsed as described by Crawley (2002) to get information about which factor levels differed from one another (see Table 4). The residuals from each model were checked for normality and variance homogeneity; if required, appropriate Box-Cox transformations of the responses were done following Crawley (2002).

ETHICAL NOTE

Methodological issues were discussed with our Home Office inspector and the Ethical Review Group of the University of Exeter. All birds were monitored for their well-being on a daily

basis. None of the individuals showed any signs of stress during the experiment and no long-term adverse effects were detected afterwards.

RESULTS

PRINCIPLE COMPONENT ANALYSES

The PCA conducted on the scan sampled behaviours as well as weight and morphological measurements resulted in three factors “activity”, “morphology” and “preening” (Table 2). Feeding and locomotory behaviour loaded positively on “activity”, resting negatively. Weight and wing length loaded mostly on the second component and both allo- and self-preening loaded positively on the third factor “preening”. However, confidence in this analysis is minimal (KMO = 0.196).

One final component emerged from the data on aggressive interactions (Table 3): on which the proportion of fights initiated or won by a focal individual loaded positively, while the proportion of fights it received aggression from its partners loaded negatively. The KMO for the PCA (0.825) allows for a high degree of confidence in its utility.

EFFECTS OF APPEARANCE MANIPULATION

A linear mixed effect model with the PCA component “activity” as response did not reveal a significant interaction between treatment and phase (Table 4a) as would be expected if colour of band influenced behaviour – because e.g. treatment “red” stands for the colour combination orange-red-orange (Table 1) – and so a significant treatment effect is not sufficient in its own to signal any changes in behaviour and/or state due to colour ring treatment (i.e. in phase 2 and/or 3). Because the KMO of the PCA was low (see above) and the outcome consequently not necessarily reliable, we decided to repeat the analyses on each of variables separately (Table 4a). However, none of the variables by themselves were influenced significantly by a treatment - phase interaction either (Table 4a). As colour effects might only have been detectable at the end of each phase (time lag to respond to changes), we repeated the same analyses with only data included for the last day of observation for each group in each phase (not shown here); but again no influences of the band manipulation could be detected.

Most behaviours recorded (apart from resting) increased significantly over the experimental phases, as did weight (Figure 1) and fat score as well as overall “body condition” (weight/wing length; Table 4a). Furthermore, the incidence of all behaviours (apart from

resting) was higher in the mornings than in the evenings. In contrast, weight and fat measures increased over the day. The treatment groups differed significantly in a number of variables recorded (Table 4a): individuals in the treatment group “green” stored less fat and rested less than those in the groups “orange” and “red”. Wing lengths did not differ significantly in the “red” and “green” group but were significantly smaller than those of individuals in the “orange” control group. Individuals in the “red” treatment group weighed relatively (weight/wing length) and absolutely (Figure 1) less than individuals in the other groups (Table 4a). Nevertheless, the weights of the birds in the three prospective treatment groups did not differ significantly from one another (ANOVA: $F_{2,27} = 0.21$, $N = 30$, $P = 0.809$) on the day before the transfer into the experimental cages took place (day 0).

Once more, when we conducted the analysis on the PCA component “aggression”, we could not detect any indication for a behavioural change due to the leg band manipulation (no significant treatment - phase interaction). Individuals of the “green” and “orange” treatment groups were more likely to receive aggression but less likely to either win or initiate aggression than birds in the “red” treatment group (Table 4b). In contrast, none of the treatment groups was more likely to initiate allo-preening behaviour than the others (Table 4b).

CORRELATIONS BETWEEN AGGRESSIVE BEHAVIOURS AND OTHER MEASUREMENTS

In a final analysis (Table 4c) we investigated how aggressive behaviour (PCA component “aggression”) was influenced by absolute and relative weight as well as fat score independent of the ring colour manipulation: individuals with higher fat scores initiated aggression more, won more fights and received less aggression than those with lower fat scores (Table 4c, Figure 2). None of the other factors included in the model influenced aggressive behaviour (Table 4c).

DISCUSSION

Contrary to expectation – that secondary sexual traits are costly to express and therefore reflect (and influence) an individual’s state and quality, which determine the behavioural options available to it – we failed to detect a change in behaviour or body mass regulation after artificial manipulations of male zebra finch appearance with coloured leg bands. Consequently, we failed to establish whether arbitrary differences in state can generate consistent individual differences as a result of positive feedback between state and behaviour (Dall et al. 2004). Nevertheless, we did detect an association between a measure of individual state, an individual’s fat score, and an individual’s aggressiveness.

The lack of an effect of band colour is at odds with findings from a number of experiments conducted on different bird species (e.g. rock ptarmigan, *Lagopus mutus*: Brodsky 1988; red-cockaded woodpecker, *Picoides borealis*: Hagan & Reed 1988). Also, in zebra finches numerous studies have documented effects of these artificial ornaments on life-history traits (like mortality rates), reproductive success, extra-pair copulations, mate choice, parental investment, offspring traits (including brood sex ratio) and male-male interactions (for a summary of studies on leg bands in zebra finches and their findings see Table 5). However, a smaller number of published studies, along with a number of unpublished studies (S Griffith, personal communication; W Forstmeier, personal communication; both mate choice experiments), failed to detect any effects of coloured leg bands on at least some of the aforementioned aspects of zebra finch biology (see Table 5). A similar pattern is also evident for beak colour preferences in female zebra finches, where results of different experiments seem to contradict each other (reviewed in Collins & tenCate 1996).

There are a number of possible explanations for the absence of an effect of the artificial manipulation of male appearance both in our study and some of the others done on zebra finches. First of all, we observed a quite substantial increase in the measured state variables (weight, weight/wing and fat score; Figure 1) over the course of the experiment which could have masked any potential treatment effects. Secondly, a lack of sufficient ambient UV light could have affected the colour perception and therefore the perceived appearance of the males in our experiment. Hunt et al. (1997) showed that female preference for males wearing red leg bands was evident when UV light was present, but not in its absence. However, even though all of the few studies that used full-spectrum light documented coloured band effects (Table 5), it seems unlikely that the presence of UV light is always necessary for leg bands to be effective: most studies that detected impacts of leg bands do not specify the light conditions in the experimental arenas (Table 5) and are therefore unlikely to have used expensive full-spectrum light sources. In particular, the first studies conducted on leg bands in laboratories in the 1980s (e.g. Burley 1981; Burley et al. 1982; Burley 1985) are unlikely to have considered the possible role of avian UV sensitivity in their experimental design, as this issue was first raised in the 1990s (e.g. Bennett et al. 1996). Further reasons for the absence of colour band effects in some studies could lie in differences in other aspects of the experimental design, like the duration of the study or the density of individuals in a cage, as well as pre-exposure to coloured rings, amongst others. For instance, Ratcliffe & Boag (1987) argued that the strong male-male competition in their experiment, in which males with different colour bands competed for access to a limited number of nest boxes and females, respectively, could have masked the beneficial impacts of attractive band colours. A high level of competition could have been present in our experiment as well (see below) because males had far less space available during the experiment than in their home free-flight aviaries. Also, the space in the cage per individual in our

experiment was smaller than the space per individual in the experiment of Cuthill et al. (1997), which detected an impact of leg band colour on male-male interactions. Furthermore, Ratcliffe & Boag (1987) discuss the possibility that the duration of a leg band application of one week for parts of their experiment might have been too short for males to perceive the manipulated changes in their own attractiveness. However, Cuthill et al. (1997) found an influence of band colour on male-male interactions within one day. Another possible factor influencing results is the leg band treatment itself: in contrast to most other studies conducted (but see for instance Cuthill et al. 1997), we applied neutral coloured bands to every bird in each group before they experienced different colour ring treatments. The birds within one group were therefore familiar with each other and their social hierarchy could have been established prior to the experimental phase when the apparent “attractive” and “unattractive” colours were applied, swamping any effect of the band colour change. Nonetheless, in Cuthill et al.’s (1997) study a reversal of the effects of colour band treatments was present when colour bands were swapped. Overall, the effects of different experimental designs on leg band impacts are very difficult to judge due to a variety of potential confounding factors.

Besides any influences of different experimental designs, another reason for the discrepancy in results from different leg band studies could be due to variation in (behavioural) traits between different strains or populations of the same species. Moretz et al. (2007) demonstrated that different strains of zebrafishes, *Danio rerio*, (two laboratory strains and one wild-derived strain) diverged profoundly in a number of behaviours including whole behavioural syndromes. These differences could be a result of captivity (see below) or a result of divergent selection pressures acting on wild populations (see also Bell 2005; Dingemanse et al. 2007: different wild populations of sticklebacks, *Gasterosteus aculeatus*, differ in behavioural syndromes depending on predation risk) or both. But there are some hints that different populations of wild zebra finches might vary in the degree to which red or green bands serve as artificial cues of appearance: a study on wild zebra finches in Victoria, Australia, revealed female preference for males wearing red coloured leg bands (Burley 1988b), whereas a similar experiment with descendants of wild zebra finches from Sydney, Australia, failed to show similar preferences (S Griffith, personal communication). In a comparative study between zebra finches and the closely related double-bar finch, *Taeniopygia bichenovii*, Burley (1986a) found support for the hypothesis that species display preferences for species-typical colours and avoid species-atypical colours, particularly colours displayed on closely related, sympatric species. This hypothesis is also corroborated by Hagan & Reed’s (1988) observations on red-cockaded woodpeckers. Therefore, if colour preferences/aversions are costly, only populations that occur sympatrically with closely related species should evolve these visual preferences as a mechanism of species recognition. One final explanation for differences in colour preferences or their absence is due to captivity and captive breeding (“domestication”). Domestication is a

‘complex of behavioural, morphological, and physiological changes due both to intentional selection for desirable traits as well as inadvertent selection and a reduction of natural selection’ (Moretz et al. 2007, page 556). Examples of changes due to captivity in the morphology of mammals and behaviour in cultivated fish can be found in reviews by O’Regan & Kitchener (2005) and Huntingford (2004), respectively. In zebra finches domestication had obvious effects on the plumage colour of many individuals, resulting in various morphs (Zann 1996). Domestication could have similar impacts on the colour preferences of zebra finches leading to a loss of colour preferences in some captive-bred strains. All these effects could be caused at the very least by selection for reliable and rapid reproduction which could have weakened female choosiness and sexual selection.

In sum, we regard divergent selection pressures on different populations, either wild or domesticated, as most likely to be responsible for the absence or presence of leg band effects or colour preferences in zebra finches. This is supported by the finding that some females consistently prefer males with redder natural beaks, whereas other consistently prefer males with more orange beaks within the same experiment (Forstmeier & Birkhead 2004).

Besides resting, all other behaviours as well as body mass (and condition) and intrafurcular fat stores increased with each experimental phase. One could argue that the experimental conditions were less energetically stressful than those in the outdoor holding enclosures, as the environmental conditions indoors were strictly controlled (regulated temperature, no rainfall etc.), so that individuals could afford to increase their activity levels as the experiment progressed. Also, the birds had less space during the experiment, shortening travel to food and limiting the potential for activity, especially energetic costly flying, all of which saves energy as well as time that could be dedicated to feeding. Furthermore, increased activity could have arisen due to habituation to the experimental conditions, promoting patterns of behaviour that were uninhibited by the perceived risk associated with novel environments. Alternatively, the limited space could also have increased male-male competition, resulting in more feeding, fat storage and weight gain when possible to buffer against unpredictable nutritive shortfalls due to interference at the lone feeder in each cage (McNamara et al. 1994). Indeed, Witter & Swaddle (1995) documented increased storage of fat reserves under heightened levels of competition in European starlings, *Sturnus vulgaris*. Nonetheless, our finding that zebra finches increased their locomotory activity as the experiment progressed argues against the latter interpretation as zebra finches have been observed to decrease their locomotory activity when experiencing food stress (Dall & Witter 1998).

Similarly to Dall & Witter (1998) and Cuthill et al. (1997), we found that body mass, fat stores and the time spent resting were higher in the evenings than in the mornings, whereas the

frequencies of feeding and preening decreased over the day. These daily routines are as predicted by theoretical work on body mass regulation under risk (e.g. McNamara et al. 1994).

In our study birds with high levels of aggression stored also more fat. Similar associations, usually between dominance status and energy reserves (e.g. fat score, body mass or an external food store) have been documented in the literature. Most of these studies, however, argue for a negative relationship between aggression/dominance and reserve levels, both empirically (e.g. Ekman & Lilliendahl 1993; Witter & Swaddle 1995; Gosler 1996; but see Koivula et al. 1995: positive relationship; Lundborg & Brodin 2003: no relationship) and theoretically (Clark & Ekman 1995; Brodin et al. 2001). Such relationships are usually interpreted from a survival selection perspective, such that the amount of fat stored depends on a trade-off between the costs, like mass-dependent predation risk, and benefits, like offsetting starvation risk, of fat storage (reviewed in Witter & Cuthill 1993), with dominants and subdominants experiencing different costs and benefits. A negative relationship between dominance rank and fat/reserve levels has often been interpreted as a strategic response of the subdominants to an unpredictable food supply due to displacement from feeding sites by more dominant individuals. Less frequently observed positive correlations between rank and energetic reserves have been suggested to result from dominants having access to higher quality food sites than the subdominants (Piper & Wiley 1990). Rarely, other possible explanations for the relationships have been proposed, involving differential energetic expenditure or predation risk as well as differential influences of more general ecological circumstances for individuals of different dominance status (Witter & Swaddle 1995; Cuthill & Houston 1997).

Unlike the studies mentioned above, we did not assess the stable outcome of aggression in our social groups: their dominance hierarchies, where the most aggressive individuals are not necessarily the most dominant ones (Drews 1993) and which are also often only based on pair-wise displacements at feeders (Ekman & Lilliendahl 1993; Koivula et al. 1995; Lundborg & Brodin 2003). Instead, we recorded all of the aggressive interactions in our male groups. The question arising then is what the adaptive value of aggression is and how should it vary with fat stores. Houston & McNamara (1988) showed that an animal should play Hawk (fight for a resource) when its energy reserves fall below a threshold level, but play Dove (never fight and escape when attacked) otherwise. This is because, if energy reserves are high, an individual should play Dove to minimise the likelihood of dying in a fight, while when they are low obtaining food at all costs is a priority to avoid starvation. Interestingly, this is opposite to the pattern we observed here, which requires further consideration. From a sexual selection perspective, if an individual's state influences the actions available to it, including the adaptive value of aggression (which may decline with energy reserves as it is an energetically costly activity), and its behaviour influences its state, then (a) a female choosing a male could get

information on what she can expect in terms of behavioural performance from the male after pairing by assessing the male's state, possibly via his appearance or aggressiveness, or (b) a male can similarly obtain information about the likely future actions of an opponent (also important from a viability selection perspective). What is clear from the work we report here is that further research is required to elucidate the relationship between an individual's appearance, its state and its influence on behavioural actions in either aggressive male-male interactions, competing for access to resources (females, food) or on female choice.

ACKNOWLEDGEMENTS

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Table 1. Experimental design: the three males in each cage were randomly assigned to one of three treatments each, consisting of different leg band colour combinations (number of replicates: 10). Each of the ten groups was videoed six times per each phase, resulting in 180 trials.

Cage x	Treatment	Phase 1	Phase 2	Phase 3
male a _x	“red” (r)	orange	red	orange
male b _x	“orange” (o)	orange	orange	orange
male c _x	“green” (g)	orange	green	orange

Table 2. Component loadings (varimax rotated) of behavioural and morphological measurements as quantified by principal component analysis.

Variable	Mean	SD	Principal component		
			Activity	Morphology	Preening
Resting	0.685	0.218	-0.828	-0.063	-0.540
Feeding	0.116	0.124	0.843	0.021	-0.094
Locomotory	0.047	0.052	0.750	-0.045	-0.023
Self-preening	0.138	0.143	0.241	0.082	0.842
Allo-preening	0.005	0.015	-0.173	0.098	0.660
Weight	17.552	1.932	0.047	0.881	0.054
Wing length	59.467	1.747	-0.047	0.861	0.131
Eigenvalue			2.333	1.656	1.069
% variance explained			33.331	23.659	15.267

Loadings over ± 0.6 are marked in bold. N = 540.

Table 3. Component loadings (varimax rotated) of aggressive interactions as quantified by principal component analysis.

Variable	Mean	SD	Principal component
			Aggression
No. initiated / No. aggressive IA per focal individual	0.464	0.319	0.934
No. initiated / No. of aggressive IA in group	0.317	0.266	0.862
No. wins / No. aggressive IA per focal individual	0.337	0.314	0.886
No. wins / No. of aggressive IA in group	0.241	0.260	0.819
No. received / No. aggressive IA per focal individual	0.447	0.321	-0.921
No. received / No. of aggressive IA in group	0.317	0.270	-0.786
Eigenvalue			4.537
% variance explained			75.622

Loadings over ± 0.6 are marked in bold. N = 87. IA: interactions; /: divided by.

Table 4. Summary of minimal linear mixed effect models for (a) scan sampled behaviour, weight, size and fat measurements^a, (b) all social interactions occurred (all-occurrence sampling)^b, and (c) PCA component “aggression”^c.

Response	N	Δ AIC	Significant term	F (d.f.)	P	Dir	F dir (d.f.)	P dir
(a) “Activity” (Table 2)	540	71.4	Phase	4.52 (2,534)	0.011	1<2=3	6.23 (1,536)	0.013
			Time day	72.81 (1,534)	<0.0001	am>pm	72.94 (1,536)	<0.0001
			Time day*phase	6.37 (2,534)	0.0018		12.70 (1,536)	0.0004
Resting	540	68.6	Treatment	5.06 (2,532)	0.007	g<o=r	8.25 (2,533)	0.004
			Phase	17.50 (2,532)	<0.0001	1>2>3	17.50 (1,533)	<0.0001
			Time day	111.42 (1,532)	<0.0001	am<pm	111.24 (1,533)	<0.0001
			Time day*phase	9.10 (2,532)	0.00013		9.08 (2,533)	0.00013
Feeding	540	89.11	Phase	5.89 (2,536)	0.003	1=2<3	10.45 (1,537)	0.001
			Time of day	116.66 (1,536)	<0.0001	am>pm	116.66 (1,537)	<0.0001
Locomotory	540	97.2	(Phase)	2.70 (2,534)	0.068	1<2=3	4.201 (1,536)	0.041
			Time day	35.13 (1,534)	<0.0001	am>pm	35.20 (1,536)	<0.0001
			Time day*phase	10.01 (2,534)	<0.0001		20.05 (1,536)	<0.0001
Self-preen	540	84.6	Phase	10.42 (2,534)	<0.0001	1<2=3	18.37 (1,536)	<0.0001
			Time day	24.80 (1,534)	<0.0001	am>pm	24.70 (1,536)	<0.0001
			Time day*phase	7.37 (2,534)	<0.001		12.73 (1,536)	<0.001
Weight	540	43.9	Treatment	31.04 (2,534)	<0.0001	r<g<o		
			Phase	39.23 (2,534)	<0.0001	1<2<3		
			Time day	136.30 (1,534)	<0.0001	am<pm		
Wing	540	362.8	Treatment	91.28 (2,537)	<0.0001	g=r<o	180.29 (1,538)	<0.0001
Weight/wing	540	150.4	Treatment	12.52 (2,534)	<0.0001	g>o>r		

Response	N	Δ AIC	Significant term	F (d.f.)	P	Dir	F dir (d.f.)	P dir
			Phase	144.78 (1,534)	<0.0001	1<2<3		
			Time day	41.73 (2,534)	<0.0001	am<pm		
Fat score	540	34.4	Treatment	13.56 (2,532)	<0.0001	g<o<r	13.58 (2,534)	<0.0001
			Phase	5.93 (1,532)	0.003	1<2=3	5.81 (1,534)	0.016
			Time day	131.17 (2,532)	<0.0001	am<pm	131.35 (1,534)	<0.0001
			Time day*phase	3.83 (2,532)	0.022		7.39 (1,534)	0.007
(b) “Aggression”	87	16.6	Treatment	4.682 (2,84)	0.012	g=o<r	9.054 (1,85)	0.003
(Table 3)								
In/no allo-pr	78	26.7	None					
(c) “Aggression”	87	5.1	Fat score	9.982 (1,85)	0.002	positive		
(Table 3)								

^a fixed effects and covariates included in maximal models: treatment*phase*time of day; treatment; phase; time of day; sum; random effects: group no.; observation day

^b fixed effects and covariates included in maximal models: treatment*phase; treatment; phase; random effect: group no.

^c fixed effects and covariates included in maximal models: weight; fat score; wing length; weight/wing length; random effect: group no.

“**Activity**”, “**aggression**”: Values obtained for PCA component “activity” and “aggression”, respectively; Δ **AIC**: difference between AIC of maximal and minimal model; **Dir**: direction of effect; **F dir**: F-values after factor collapsing; **g, o, r**: indicate the colour of leg bands worn by an individual in the second experimental phase, **g**: green, **o**: orange, **r**: red; **group no.**: number of each group consisting of three males in one cage, factor with ten levels; **In/no allo-pr**: no. of initiated divided by the no. of allopreens involved; **observation day**: day of observation, factor with 18 levels; **P dir**: P-values after factor collapsing; **phase**: experimental phase, factor with three levels; **self-preen**: self-preening; **sum**: number of scans (usually 180 but in 5 out of 540 cases an individual was out of sight for some scans), covariate; **time day**: time of observation, factor with two levels (**am**: morning, **pm**: evening); **treatment**: assignment of certain leg band colour combination over time, factor with the three factor levels “green” (**g**), “orange” (**o**), “red” (**r**), where treatment “red” refers to the colour combination: orange-red-orange etc.); * indicating interaction between effects.

Table 5. Summary of studies on effects of coloured leg bands in zebra finches.

Author	Leg band ^a	Short description of experiment	No effect on	Effect on	Light ^b
I. Studies on wild populations					
Burley (1988b)	m: r, lg, no	mate choice trials (f choose)		f preference	NR
Zann (1994)	m: r, lg, others f: bl, lb, others	field data	survivorship bill colour mass moult no. independent young clutch size re-pairing pair-bond duration no. fledglings (MR) no. eggs (FR) no. clutches (FR)	no. eggs (MR) no. clutches (MR) no. fledglings (FR)	NAT
II. Studies in captivity					
(a) Mate choice/preference					
Burley et al. (1982)	m: r, bl, p, lb, lg, o, no	mate choice trials (f choose)		f preference	IN (270 lux)
	f: r, bl, p, lb, lg, o, no	mate choice trials (m choose)		m preference	IN (270 lux)
Burley (1986a)	m: r, lb, no	mate choice trials (f choose), comparison to double-bar finches		f preference	NR

Author	Leg band ^a	Short description of experiment	No effect on	Effect on	Light ^b
Hunt et al. (1997)	f: r, lb, no m: r, lg, o, no	mate choice trials (m choose), comparison to double-bar finches mate choice trials (f choose) in presence/absence of UV	f preference (without UV)	m preference f preference (with UV)	FT (DL vs SA) FT
Jennions (1998)	m: r, lg	mate choice trials (f choose)	f preference		
(b) Reproduction/breeding					
Burley (1981)	m: r, lg, o f: bl, lb, o	f and m with attractive, neutral, unattractive colour allowed to breed freely		sex ratio offspring no. independent young mortality	NR NR
Burley (1985)	m: r, lg, o f: bl, lb, o	exp1: m with leg bands; exp2: f with leg bands, both exp: unbanded individuals of other sex released, free breeding (different colours in 1 aviary)			
Burley (1986b)	m: r, lg, o f: bl, lb, o	exp1: m with leg bands; exp2: f with leg bands, both exp: unbanded individuals of other sex released, free breeding (different colours in 1 aviary)		sex ratio offspring	IN
Burley (1986c)	m: r, lg, o f: bl, lb, o	exp1: m with leg bands; exp2: f with leg bands, both exp: unbanded individuals of other sex released, free breeding (different colours in 1 aviary)	clutch duration interclutch interval clutch size number mates no. successful clutch attempts (in f)	no. independent young mortality no. successful clutch attempts (in m)	NR
Burley (1988a)	m: r, lg, o f: bl, lb, o	exp1: m with leg bands; exp2: f with leg bands, both exp: unbanded individuals of other sex released, free breeding	nest defence	paternal expenditure	NR

Author	Leg band ^a	Short description of experiment	No effect on	Effect on	Light ^b
		(different colours in 1 aviary)			
		(exp3: no leg bands); exp4: leg bands exchanged (m: red or green)			
Burley et al. (1994)	m: r, lg f: neutral	m and f breeding in 1 aviary		extra-pair copulations	IN
Burley et al. (1996)	m: r, g f: neutral	m and f allowed to breed freely		exclusion rate	NR
Gil et al. (1999)	m: r, g	f assigned to red or green banded m group for breeding; 2 nd breeding round: f assigned to m with other colour band		amount of T and DHT in eggs	NR
Rutstein et al. (2004)	m: r, g	each m paired with 1 f each in individual cage; 2 nd breeding round: each f assigned to a m with other colour band; 3 rd round: each f assigned to a m with colour band as in 2 nd round	no. days to laying clutch size egg mass (3 rd round) primary sex ratio hatching success amount T, DHT in eggs	egg mass (1 st and 2 nd round)	FS
Rutstein et al. (2005)	m: r, g	expl: m with different colours in separated aviaries, f assigned exp2: each f randomly assigned to a red or green banded m	sex ratio (at laying, hatching, fledging) sex ratio (at laying, hatching)	sex ratio (adulthood)	OUT
Gilbert et al. (2006)	m: r, lg	each m paired with 1 f each in individual cage (cross-fostering of clutches)	clutch size no. hatchlings offspring survival	sex ratio (fledging, adulthood) tarsus growth rate offspring egg mass maturation rate offspring	IN, FS IN, FS

Author	Leg band ^a	Short description of experiment	No effect on	Effect on	Light ^b
(c) Social learning					
Benskin et al. (2002)	m: r, lg	choice to copy red or green-banded demonstrators in food context	body size m offspring	begging duration offspring body size f offspring	IN
(d) Male-male competition					
Ratcliffe & Boag (1987)	m: r, lg	expl: m with different colours in 1 aviary, competition for limited no. of nest boxes and f; exp2: bands randomly reassigned	obtaining nest obtaining f song rate supplanting		IN
Cuthill et al. (1997)	expl: m: r, lg, o, no exp2: m: r, lg	expl: 4 m per cage, single food and water source exp2: 2 m per cage, single food and water source, switch of colours after 10 days	feeding (no. and time) mass gain (expl) seeds in crop (expl) aggressive pecking behaviour	displacement daily fat regulation daily mass regulation (exp2)	FT, DL

DHT: dihydrotestosterone; **exp:** experiment; **f:** females; **FR:** female ring; **m:** males; **MR:** male ring; **T:** testosterone

^a **Leg band:** leg band colours; **bl:** black; **g:** green; **lg:** light blue; **lg:** light green; **o:** orange; **p:** pink; **o:** orange; **r:** red

^b **Light:** light conditions; **DL:** daylight-mimicking light; **FS:** full-spectrum light; **FT:** fluorescent tubes; **IN:** indoors; **NAT:** natural light; **NR:** not reported; **OUT:** outdoors; **SA:** standard artificial light; **vs:** versus.

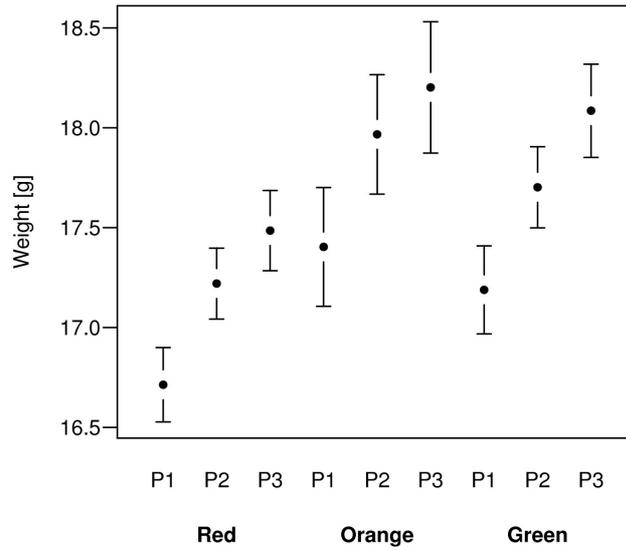


Figure 1. Mean (\pm SE) weights of the different treatment groups (“red”, “orange”, “green”) over the three experimental phases. The graph is based on the raw data and not on the model output. For more details see text and Table 4a. P: phase.

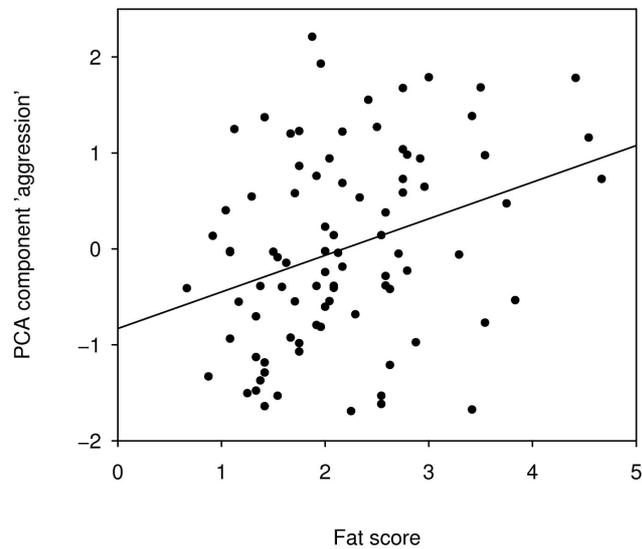


Figure 2. Relation between the principle component “aggression” and fat score.

Chapter 6

Conclusions and prospects: sexual selection and personality

In this thesis I have shown that sex differences in zebra finch personality exist (Chapter 2-4), that individuals with different personalities react differently in social interactions (Chapter 2), that links between an individual's state and its behaviour are likely (e.g. Chapter 4, Chapter 5), that the combination of personalities (both behavioural level and consistency) in a pair are important for successfully raising young (but not to start reproduction; Chapter 4) and that females choose males on the basis of their behaviour while considering their own behavioural type (Chapter 3). The female choice patterns corresponded with pairings leading to highest reproductive success (Chapter 4). Furthermore, some reproductive advantages were long-lasting, intergenerational effects (Chapter 4). Besides giving insights into some ecological consequences of personality, these findings support the hypothesis that personality is subject to sexual selection, at least in zebra finches. More specifically, the results could be used to identify some hypothesised underlying mechanisms (Chapter 1): behavioural compatibility (and not genetic compatibility) seems most important for reproduction/raising young for most behavioural traits measured, but sometimes male behavioural traits seem to reflect general male quality (either genetic, parental or partner quality). The support, experimentally obtained, for the link between sexual selection and personality, particularly the discovery of the importance of the combination of behavioural consistency in this context, and the first identification of underlying mechanisms provided in this thesis hopefully gives a good basis for further research: the findings provide some clarification but also raise a number of new questions at the same time. A few of these questions and prospects are briefly outlined below.

FROM CHARACTERISTICS OF ZEBRA FINCHES TO WIDESPREAD PATTERNS

– WHAT CAN WE LEARN?

As for most studies on a single system, we need to ask ourselves how much of the results found are specific to the species investigated, i.e. how much can be extrapolated to other species. Or even more drastically, how many of the findings obtained from a few (here: 3) captive populations of zebra finches actually apply to wild-type zebra finches? To what extent can underlying mechanisms relevant for wild individuals be elucidated using captive breeding populations? Therefore, the challenge will be to look at different perspectives: explaining patterns found at a species level, integrating the biology of this particular species, but also considering the existence of potential general patterns. For the results in this thesis, I provided a number of explanations and hypothesis/predictions as to what patterns to expect both on the species-specific and -general level. Some of these ideas have been tested in the thesis, others need further investigations. Moreover, some of the results presented seem to be species-specific due to certain biological traits of this taxon (e.g. sex differences in exploration in zebra finches, see below), other findings seem more generalisable (e.g. not only highly exploratory zebra

finches: Chapter 3 and Chapter 4, but also exploratory great tits: Groothuis & Carere 2005; and dumpling squid: Sinn et al. 2006 seem to gain advantages from choosing a behaviourally similar partner).

SEX DIFFERENCES IN PERSONALITY & SOCIAL INTERACTIONS

I showed that sexes can differ in the personalities that individuals exhibit, not only in the level of behavioural traits, as shown for many species previously, but also in their behavioural consistency, an aspect mostly neglected so far. This stresses the importance of considering sex differences for both aspects of personality in future studies (see below). Hopefully, assessing personality of sexes separately more often will help understanding in more detail why sexes differ in this respect, i.e. to facilitate the elucidation of underlying evolutionary processes and resulting ecological consequences. Throughout the chapters I provided some possible explanations for each of the sex differences found, both considering the biology of my study species, but also making general predictions which could be tested in other species as well (as outlined above). For instance, in Chapter 2 I found that males were significantly more consistent in their exploration of a novel environment than females, for which individuals were found instead to be consistent in their time spent foraging. I could explain these patterns with reference to the biology of wild zebra finches: male zebra finches lead their females around through the colony for the majority of the time (Zann 1996). Females might gain benefits from choosing males who are consistent in their leading and exploratory behaviour, since they can expect to be led to foraging sites in a reliable manner. However, in later chapters (Chapter 3, Chapter 4), males and females were similarly consistent in their exploration of the novel environments. In order to assess the overall pattern in a statistical manner, I conducted a meta-analysis on the repeatabilities of exploration (number of features visited in a novel environment) of males and females obtained in the different experiments. To make the repeatabilities of the three experiments comparable, I converted them into dimensionless, standardised effect sizes (for detailed discussion see e.g. Nakagawa & Cuthill 2007) by applying Fisher z-transformations for repeatabilities and calculated 95% confidence intervals (CIs) and their variances as outlined by Stratford (2004) and Donner (1985). The z-transformed repeatabilities (Z_R , effect size values) were entered as the response into a linear mixed model (REML, nlme package in R, R Development Core Team 2008), with sex as a fixed effect and study as a random term (for a similar procedure see Nakagawa et al. 2007a). The mean effect sizes for the two sexes were estimated as a weighted mean as outlined by Nakagawa et al. (2007b). With this procedure, more weight is put onto more powerful studies. I tested whether the effect sizes from the three experiments were homogenous, by computing the total heterogeneity, Q_{REML} , of my studies (see Nakagawa et al. 2007b). The result from the meta-analysis suggests that overall males and

females did not differ in how consistent they were in the number of features they visited in the novel environment (Figure 1; $F_{1,2} < 0.001$, $P = 0.988$, effect sizes and 95% CI: males: $R = 0.335$, $CI_{lower} = -0.066$, $CI_{upper} = 0.782$; $Z_R = 0.492$, $CI_{lower} = -0.066$, $CI_{upper} = 1.050$; females: $R = 0.337$, $CI_{lower} = -0.159$, $CI_{upper} = 0.819$; $Z_R = 0.496$, $CI_{lower} = -0.161$, $CI_{upper} = 1.152$; heterogeneity: $Q_{REML} = 0.04$, d.f. = 5, $P = 0.99$). This result is not surprising given that sex differences were only found in Chapter 2 and the results in Chapter 3 & 4 were based on much bigger sample sizes than results in Chapter 2, and were therefore given more weight in the analysis. Furthermore, the result should be taken with caution, as the analysis was only based on a sample size of three studies. Thus, the obtained estimates were very uncertain, resulting in huge confidence intervals for the overall estimates for the sexes (see Figure 1). Future studies need to explore if male and female zebra finches differ in their consistency in exploration. If no overall sex differences can be found, investigations should reveal if this is a result of either (a) an absence of sex differences in this behavioural trait in the zebra finch (i.e. type I error in Chapter 2) or if (b) sex differences in consistency do exist but only under certain circumstances. For instance, populations may vary in the extent to which sex differences in consistency occur (see e.g. Chapter 5 for general discussion on behavioural differences between populations). Also, females may only be inconsistent in their exploration if they are kept in mixed-sex groups (as in Chapter 2) where they can rely on males' exploration, whereas may be consistent if they are kept in female groups (as in Chapter 3 & 4). This could be for instance the case if consistency endures a cost to individuals (cf. Chapter 1).

Although in Chapter 3 & 4 the finding that males were significantly more consistent in their exploration of a novel environment could not be replicated, I found throughout that males showed more complex exploration "behavioural syndromes" than females. For instance, only male behaviour in the novel environment was correlated with male exploration of a novel object, whereas for females there was no such relationship between these potentially ecologically significant behaviours (Chapter 3). Contrary to the likely species-specific sex differences in exploration, the consistency in food intake by females but not by males might be a more generic sex difference in personality: due to nutritionally expensive reproduction (Andersson 1994), females might generally have a need for consistency in foraging (see Chapter 2). More examples for behaviours likely to reveal sex differences in consistency are outlined in Chapter 1.

Furthermore, throughout the thesis I have shown that the influence of social interactions on personality (and vice versa) can be quite substantial. Therefore, their further investigation may be crucial for identifying both ecological and evolutionary consequences of animal personality (empirical data shown in Chapter 2-4). For instance, the presence of an opposite-sex companion influenced individual exploration of the novel environment (Chapter 2), the

combination of both personalities in a pair had an impact on how well offspring were cared for (Chapter 4) and females did not merely choose males on the basis of their behaviour but also considered their own behavioural traits in their choice (Chapter 3). If we had only considered the overall preference for exploratory versus non-exploratory males in that mate choice experiment, we would have (wrongly) concluded that overall females showed a slight preference for exploratory males (33 out of 51 females spent more time with the apparent exploratory male; Binomial test, $P = 0.048$, 95% confidence interval: 0.501-0.776) but this was only due to the fact that both medium and high exploration females spent more time with the apparent exploratory males (but not the low exploration females). These findings highlight the importance of considering social interactions when studying animal personality.

The more we understand the influence of social interactions on individuals with different personalities (and vice versa), as well as the existence of sex differences in personality and reactions to social interactions or more generic ecological factors, the more likely we are to understand and predict underlying evolutionary mechanisms. For instance, if female zebra finches gain advantages from choosing males who lead in a reliable manner, consistent male leading behaviour should be selected for via intersexual selection. Related to this would be to test how parents in biparental species, characterised by more or less different personalities, interact with each other, particularly while breeding. More detailed knowledge about these interactions could offer more specific insights into the behavioural traits that are an important focus of mate choice.

BEHAVIOURAL COMPATIBILITY AND REPRODUCTION

One next step would be to test more explicitly how personality relates to parental care and parental rules within a pair to address the question of how personality compatibility may be important for raising young. This could include investigating what it is about highly exploratory and aggressive assortative pairings that makes them so successful in raising chicks (Chapter 4). Is it that similar partners in general and/or highly exploratory partners in particular are better able to synchronise their behaviour than other behavioural combinations and are therefore able to provide better parental care? But what does such “best ways” imply? For instance, reliable food provisioning could be most important for chick development (e.g. Royle et al. 2006). Alternatively, maximising the amount or quality of food might be most crucial for raising the young most efficiently. Also, it may be that the first few days of parental care after hatching are most crucial in shaping the developmental path of individual chicks (e.g. in Chapter 4 offspring condition at independence was unaffected when the foster father was removed at an early hatchling stage). As suggested in Chapter 4, rules on parental care may depend on the

personality of the individuals and might explain why some personality combinations in a pair are more or less successful in raising young than others: i.e. some pairings might be more efficient in coordinating their care. Indeed, a future challenge will be to disentangle the role of the two aspects of personality, behavioural consistency and level of behaviour, in order to assess how important each of these components is for parental care (directly or for predicting parental care) and/or mate choice. A first step towards this would be to conduct a similar mate choice experiment to the one presented in Chapter 3. However, instead of investigating the effect of the behavioural level on mate choice, the effect of behavioural consistency on mate choice should be tested by direct manipulation. Or more effectively, both approaches could be linked with each other. This would mean giving females the choice between males showing a high or low level of a certain behaviour while either being inconsistent or consistent, respectively. Mate preferences could then be linked to both aspects of female personality (behavioural level and degree of consistency).

PERSONALITY AS A QUALITY INDICATOR

Apart from behavioural compatibility being important for mate choice and for successful raising offspring, I presented some results (Chapter 4) indicating that certain behavioural traits are also likely to indicate male quality (which could be either parenting or genetic quality) with advantageous effects on foster offspring which carried over into the next (unrelated) generation. Future research could focus on why foster chicks which had been raised by highly exploratory foster males themselves reared chicks in best condition. For this the two possible mechanisms outlined in Chapter 4 would have to be separated: foster offspring could be imprinted on the successful paternal strategy or foster offspring could have an increased ability to invest into paternal care if they are themselves in better condition when raised by foster fathers in good condition. Therefore, it could be the parental strategy and/or the individual condition that is linked to individual personality (see also Chapter 2: weight/tarsus correlated to exploration; Chapter 5: amount fat stored correlated to aggression) and results in increased reproductive success.

WHY PERSONALITY AND WHY VARIATION?

I have outlined a few avenues for future research which could help elucidate the patterns observed in this thesis, which focus mostly on studying the links between sexual selection and personality in more detail. Eventually, I think it would be desirable to integrate findings on this topic with other general hypothesis concerning the existence of personality, which aim to

explain why personalities evolve and how they are maintained (Dall et al. 2004; Sih et al. 2004b; McElreath & Strimling 2006; Stamps 2007; McElreath et al. 2007; Wolf et al. 2007; Biro & Stamps 2008; Wolf et al. 2008; McNamara et al. in press). For instance, do sexual selection and viability selection have counteracting effects on personality, resulting in trade-offs and consequently in a mix of personalities? If this was the case, could it be that better conditioned chicks raised by exploratory or aggressive partnerships are more at risk of predation, equalising the fitness of exploratory and non-exploratory individuals? Further general mechanisms that could generate consistent variation in behavioural traits and which are not mutually exclusive should be considered, like frequency-dependence, life-history trade-offs, condition-dependence, and the fact that changing environment might favour different optima (for detailed discussion see for instance Dall et al. 2004; Sih et al. 2004b; McElreath & Strimling 2006; Stamps 2007; McElreath et al. 2007; Wolf et al. 2007; Biro & Stamps 2008; Wolf et al. 2008), in order to achieve a comprehensive understanding of the evolution of personality.

Taken together, I hope the results presented in this thesis, along with the interpretations and predictions provided, will motivate further studies on the roles of sexual and viability selection in maintaining individual differences to better understand the evolutionary and ecological consequences of a seemingly important (both human and non-human) animal trait: personality.

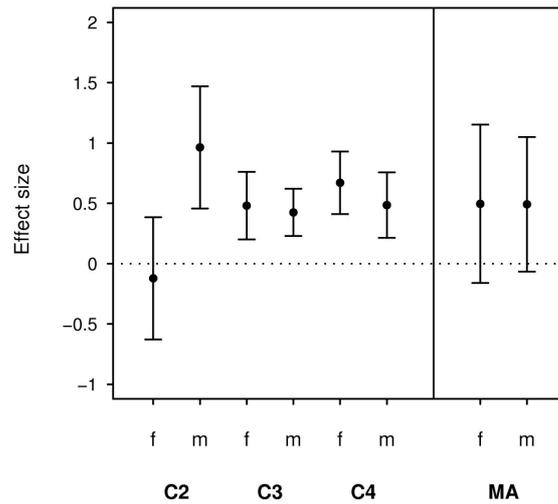


Figure 1. Standardised repeatabilities (\pm 95% confidence intervals, CIs) of males' (m) and females' (f) exploration. C2, C3, C4: standardised repeatabilities (\pm 95% CIs) for data from Chapter 2, Chapter 3 and Chapter 4, respectively. MA: overall estimates from meta-analysis. 95% CIs were calculated as standardised repeatability \pm 1.96 SE for data from Chapter 2-4; whereas a t-distribution with appropriate d.f.s, rather than 1.96, was used for the estimates from the meta-analysis due to the small sample size (see Nakagawa & Cuthill 2007 for discussion).

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