



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

VOL 1 OF 1

SUBMITTED BY

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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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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.

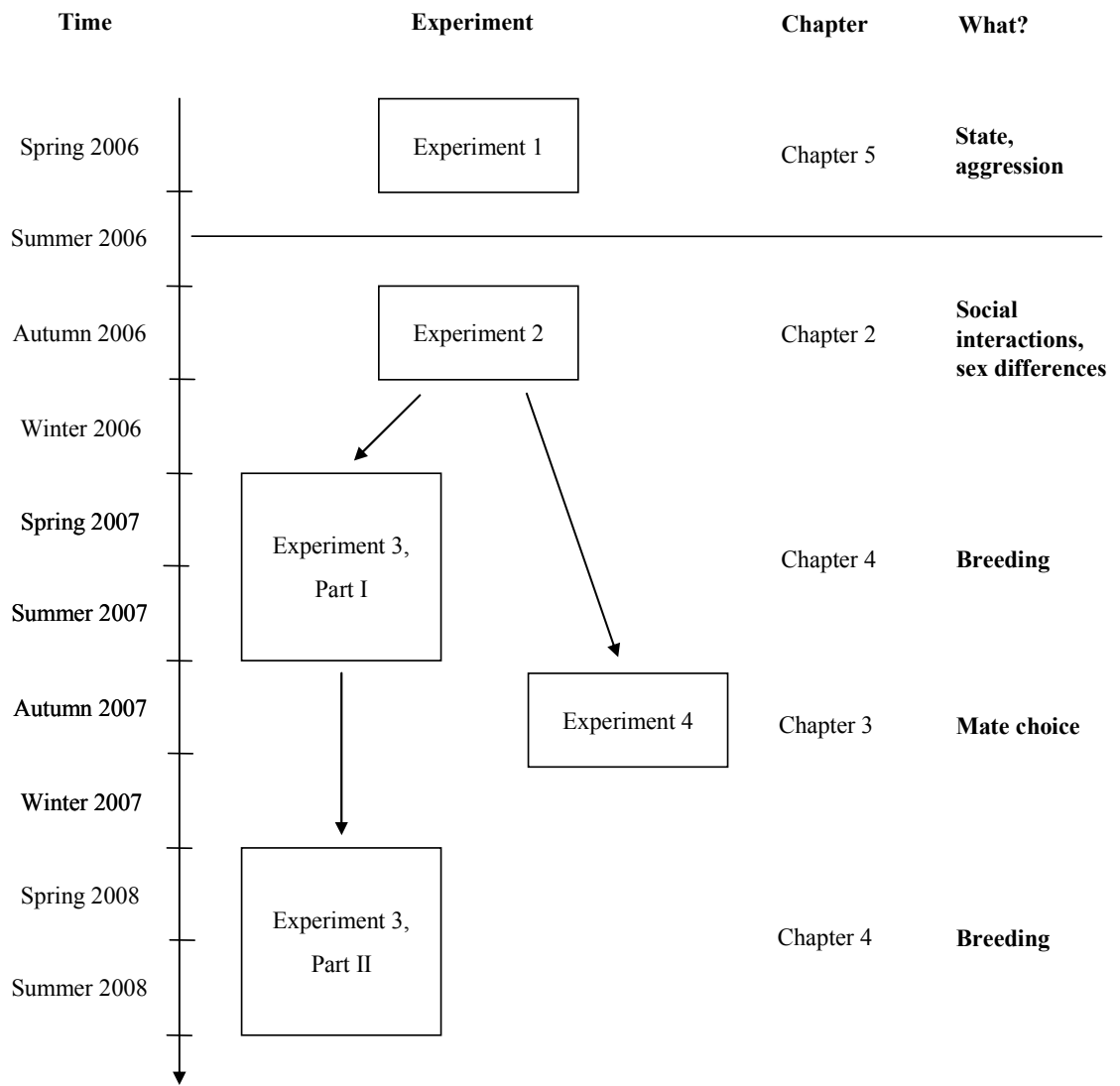


Figure 1. Time line of experiments conducted during my PhD project. The arrows indicate how different experimental parts were followed on from previous findings.