The effects of rearing conditions on sexual traits and preferences in zebra finches

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Citation

Holveck, M. J. (2008, February 28). *The effects of rearing conditions on sexual traits and preferences in zebra finches*. Retrieved from https://hdl.handle.net/1887/12621

Chapter 1

General introduction, thesis overview and general conclusions

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Chapter 1

GENERAL INTRODUCTION

Sexual selection and between-individual variation

Sexual selection is an evolutionary force which allows explaining the origin and maintenance of extravagant traits like elaborate songs, conspicuous courtship displays or bright coloration (Darwin, 1871). Such conspicuous traits seem *a priori* to reduce rather than to enhance the survival chance of their bearer, for instance through increased predation risks. However, these traits can evolve because their bearers are more competitive over access to mates and/or attractive towards members of the opposite sex, and therefore have a reproductive advantage. Numerous correlational and experimental studies from many taxa have now confirmed that males with enhanced ornamentation or other preferred attributes, have a mating advantage arising from female mate choice (Andersson, 1994). In accordance with the handicap principle of signaling (Grafen, 1990; Zahavi, 1975), variation in male quality determines the costs incurred with increased investment in ornaments, leading to condition-dependent expression of sexual traits, condition (or quality) in this case being defined as the pool of resources an individual can accumulate and then allocate to the production or maintenance of traits that enhance fitness (Hunt et al., 2005; Rowe and Houle, 1996). However, not only advertising for mates but also choosing mates is likely to incur costs. Therefore, one might also expect that variation in female quality should determine how investment in mate choice, a costly behaviour in many species (Pomiankowski, 1987), is optimized, leading to condition-dependent expression of preferences (Bakker et al., 1999; Jennions and Petrie, 1997). However, while between-male variation in sexually selected traits and in mating success is well-documented, variation in female mating preferences and in reproductive decisions has received relatively less attention from theorists and empiricists alike (Jennions and Petrie, 1997; Widemo and Saether, 1999).Why is it so?

The fact that female mating preferences are not as conspicuous as male ornamentation is probably not the only reason why there is so little documentation on variation in female choice as yet. Mate choice is a complex behaviour. The outcome of mate choice (i.e. mating pattern) not only depends on individual mating preferences but also on the extent to which they can be expressed (e.g. availability of mates), which makes difficult to determine mating preferences solely from the outcome of mate choice (Jennions and Petrie, 1997; Widemo and Saether, 1999). In addition, until recently most studies of sexual selection worked with the assumption that individuals should aim for the highest-quality males available in order to maximize their fitness and tended to discard the variation in female preferences within populations as noise in the data. However, females within a population often show marked variation in mating preferences (Jennions and Petrie, 1997; Widemo and Saether, 1999). It is this variation in female mating preferences and reproductive decisions that will affect the strength and direction of sexual selection and consequently the evolution of preferred male traits (Jennions and Petrie, 1997; Widemo and Saether, 1999). Sexual selection is a co-evolutionary process between females and males so ignoring the presence of variation in females overlooks a key aspect of this process.

Despite the recent increase of studies reporting evidence of between-female variation in their preferences, very little is known about what causes and maintains this variation (Badyaev and Qvarnström, 2002; Cotton et al., 2006; Jennions and Petrie, 1997). Several factors have nevertheless been proposed to account for the observed variation in female preferences like genetic factors, developmental trajectories and environmental factors (for an extensive and detailed list, see Badyaev and Qvarnström, 2002; Cotton et al., 2006; Jennions and Petrie, 1997; Ryan et al., 2007; Widemo and Saether, 1999). Ryan et al. (2007) suggested that these factors might influence the ability to accurately assess potential mates (e.g. decoding of mating signals) and introduce variability to preferences (e.g. state or condition, context and past experiences via learning).

Female mating decisions commonly involve the assessment of multidimensional signals providing a wide range of messages and involving different sensory modalities like acoustic and visual ones (Candolin, 2003; Hebets and Papaj, 2005). Which signals females will pay more attention to may depend on whether females are predominantly looking for direct or indirect benefits (e.g. resource holding potential versus genetic benefits, Candolin, 2003) as well as on the information content and reliability of different signals. It has specifically been proposed that multiple signals provide information on male condition over different time-scales (multiple message hypothesis, Møller and Pomiankowski, 1993). Short-term signals will respond rapidly to momentary variations in condition, while long-term signals lastingly reflect past condition, for instance during the period of juvenile growth and development. If females differ in how they use or rank such signal arrays, this could be one reason for why they show different mating preferences. Several factors could contribute to such inter-individual differences. Next to a genetic base to differences in female preferences, several non-genetic factors can also affect female preferences for different signal variants: e.g. their physiological state and condition (Cotton et al., 2006) and past and present ecological and social contexts, which may also influence which signals females pay more attention to (Candolin, 2003; Jennions and Petrie, 1997; Wagner, 1998). Past experiences can strongly influence subsequent preferences on a short and a long time scale. Female preferences can change based on recent experience gained from previous interactions with males (Collins, 1995; Marler et al., 1997), or due to age (rather than experience *per se*, e.g. Kodric-Brown and Nicoletto, 2001). On a longer time scale, early sensory learning has been well demonstrated as an important source of variation in adult preferences in the context of sexual imprinting in the olfactory domain in mammals (Owens et al., 1999) and in the visual or auditory domain in birds (Riebel, 2003a; Riebel, 2003b; ten Cate and Vos, 1999).

Against this background, the aim of this thesis is to address the role of context and developmental condition as two poorly understood factors in causing variation in female preferences. In particular, I experimentally investigated whether, how and to what extent female preferences and their ensuing mating decisions covaried with i) the quantity (i.e. single vs. multiple) and quality of mating signals in combination with the context in which these signals were presented (Chapter 2) and with ii) females' and males' early ecological and social experiences i.e. the interplay between early condition and learning (Chapters 3 to 5). I addressed these questions in songbirds, a model which is particularly interesting to study in this context since learning in the vocal domain occurs both for song production and perception (Riebel, 2003a; Riebel, 2003b; ten Cate, 2000) and preferences for the song are commonly recognized as a strong selection factor (Andersson, 1994; Searcy and Yasukawa, 1996). Therefore in addition to genetic, condition and cultural-transmission dependency of song variation (Catchpole and Slater, 1995), the developmental trajectory and learning process underlying the acquisition of song preferences are likely to influence mating decisions and thus select for specific variants of learned songs.

Song, preference, learning and developmental stress in songbirds

Songbirds show many morphological and behavioural secondary sexual traits, and feature prominently in studies of sexual selection. Although male song undoubtedly plays an important role in female choice (Catchpole and Slater, 1995; Searcy and Yasukawa, 1996), the relative weighting of song versus other male phenotypic features such as morphological traits and display intensity remains poorly understood (Collins et al., 1994; Patricelli et al., 2003). Moreover, surprisingly little is known about which structural features of a song determine its attractiveness to females, and how such features might relate to male quality. The likely reason for this lack of knowledge is that birdsong , like other complex mating displays, varies along many dimensions and each of its features may signal different aspect of male quality (Gil and Gahr, 2002).

Many songbirds have a sensitive period early in life during which exposure to song influences the details of song that a male later produces (Catchpole and Slater, 1995) and that a female later prefers (Riebel, 2003a; Riebel, 2003b). Since variation in male song is mostly culturally inherited, this has raised the question of how this trait may reliably signal male quality. The developmental stress hypothesis (Buchanan et al., 2003; Nowicki et al., 1998; Nowicki et al., 2002a) proposed that learned song can indicate male quality because the development of brain structures mediating song learning and production occurs during the period of fastest development, i.e. when young birds are most vulnerable. Therefore, male learned song could act as a long-term signal of condition and females may gain reliable information about how well males fared in the face of an early developmental stress.

Several empirical studies have now demonstrated effects of various early environmental stressors (i.e. direct manipulation of food availability, corticosterone administration or parasite infection) on nestling and adult condition, song control brain nuclei, song complexity and singing performance (Buchanan et al., 2004; Buchanan et al., 2003; Spencer et al., 2003; Spencer et al., 2004; Spencer et al., 2005a). Supporting the function of song as an indicator of male past developmental history, females have been shown to prefer well-learned songs to poorly-learned songs in song sparrows (Nowicki et al., 2002b) and the songs of early non-stressed males to the ones of early stressed males in zebra finches (Spencer et al., 2005b). However, there is limited evidence that developmental stress causes differences in male song learning in songbirds although it is a fundamental prerequisite of the hypothesis. To date, there have been only two studies that empirically examined the effect of developmental stress on song learning (Gil et al., 2006; Nowicki et al., 2002a), and only one could reported such an effect (Nowicki et al., 2002a). In addition, it is remarkable that both the original hypothesis and empirical tests so far neglected the development of female song preferences, which like male song have a strong learned component (Riebel, 2003a; Riebel, 2003b). Thus, very little is known on whether socially learned preferences are sensitive to early non-social environmental factors.

The zebra finch, *Taeniopygia guttata*, as model species and brood size manipulation as an experimental tool to induce developmental stress

I decided to address the question(s) of effects of the early environment on male traits and females preferences in the zebra finch. The zebra finch is a well established avian model system in current studies on sexual selection, song learning and sensory development. Zebra finches undergo a rapid development, which makes it easy to follow a bird from hatching to maturation and mating. Zebra finches fledge at about 20 days post-hatching, reach nutritional independence at about 35 days, and are sexually mature at around 100 days (Zann, 1996). In zebra finches, only males sing, but both males and females show vocal learning. Male song learning takes place between 25-90 days of age, but the most sensitive period for song acquisition in males ranges mainly from days 35 to 65 (for reviews of male song learning see Jones et al., 1996; Slater et al., 1988). Female song preference learning seems to parallel the time course for song acquisition in males since it ranges mainly between 25 and 70 days of age (Riebel, 2003a). Adult females show repeatable preferences for the song to which they were exposed between 35-65 days of age (Riebel, 2000).

The current literature on mating preferences in zebra finches, despite intensive experimental studies and ample examples of how several male morphological and behavioural traits are involved in mate choice, for example song rate and beak colour (Collins, 1994; Collins and ten Cate, 1996; Forstmeier and Birkhead, 2004; ten Cate and Mug, 1984; Zann, 1996), also illustrates how difficult it is to test the relative importance of acoustic and visual signals provided by males in female mate choice. However, because of the general good background information on mate choice, zebra finches therefore provide a good model system with which to systematically examine the context dependency of different signal dimensions as well as what attributes make songs attractive to females and what the preferred song features say about the singer.

A neglected aspect in this context is the possible interactions between ecological and social factors during development on male song, and on female song preference learning as well as on male and female reproductive decisions. In this thesis I addressed these questions. To manipulate early (nestling) condition I chose brood size manipulations. Among the different methods that have been reported to be efficient in varying nestling condition (i.e. brood size manipulation, direct manipulation of food availability, corticosterone administration or parasite infection), the reduction and enlargement of brood sizes present the advantage to manipulate early condition within an ecological meaningful range. Zebra finches were raised in brood sizes within the natural species-specific range (Zann, 1996), namely in either small (2-3 chicks) or large (5-6 chicks) broods. Brood size manipulation indirectly manipulates food intake during development. An enlargement of brood size induces an increase in nestling competition for access to food (e.g. Neuenschwander et al., 2003) and / or an absence of full parental compensation in food provisioning (Stearns, 1992), which result in a deterioration of nestling body condition. Brood size manipulation has also been shown to affect adult morphology (de Kogel, 1997; Naguib et al., 2004), male secondary sexual traits (de Kogel and Prijs, 1996), survival (de Kogel, 1997) and fitness, for instance the age of the first reproduction (Alonso-Alvarez et al., 2006). In this thesis, I explored the long-term consequences of this phenotypic manipulation early in life on male learned song and female learned song preferences.

THESIS OVERVIEW

The aim of this thesis was to examine the causes of variation in male mating signals and female mating preferences and decisions, using the zebra finch as a model system. I investigated whether female weighing of different mating signals (i.e. acoustic vs. visual) depended upon the context in which they were presented (Chapter 2), whether females could judge male quality based on the information content of the acoustic signal only (Chapters 2 and 5) and whether the information content of the signal as well as the decoding of mating signals was dependent upon males' and females' early social learning and condition

(Chapters 3 to 5), which was manipulated through varying ecological and social factors during development.

In Chapter 2, I examined the relative importance of different signal modalities and their context dependency in female mating preferences. Song is well established to play an important role in mate choice in zebra finch, but its relative role with regard to visual cues and display intensity is unclear as different studies used different test paradigms. Female mating preferences were thus tested across three different widely used testing paradigms, presenting male song only (operant conditioning tests and phonotaxis tests) or full courtship displays (association tests with live males). Other than in classic discrimination task where positive and negative reinforcers like food reward and time out periods are used to test subject discrimination abilities, operant conditioning tests use the song itself as a reinforcer. Females can thus actively control their exposure to songs by pecking keys. Preferences were assessed by comparing the relative frequencies with which one stimulus was chosen over another. In phonotaxis tests and association tests with live males, the number and total duration of approaches to either stimulus (songs or males respectively) were taken as measure of preference. Females showed significant and consistent preferences either for live males or their songs across the three tests. The song structure parameters that predicted female preferences best were context-independent and also predicted male morphology. Besides validating the different designs to assess preferences, these results show that song structure independent of total song output must contain sufficient information on the singer for female mate choice.

In Chapters 3 to 5, I investigated the combined effect of prior ecological and social experiences on individual phenotypes, song learning, song preferences and reproductive decisions in adulthood. Bird nestling and adult condition was experimentally varied by brood size manipulations, which indirectly manipulates food intake during development. After nutritional independence, birds were placed in mixed-treatment, mixed-sex groups of four individuals with an unfamiliar, unrelated, mated adult male that acted as ‘song tutor’ during the song acquisition phase.

Chapter 3 is concerned with investigating the potential metabolic constraints underlying the long-term effects of developmental condition on survival and fitness prospects. In a collaborative project (with Simon Verhulst from Groningen University), I found that the metabolic rate of 1-year-old zebra finches was higher when they had been reared in large broods. In combination with earlier observations in these species (de Kogel, 1997), that birds reared in large broods live for a shorter time, our finding suggests that metabolic efficiency may play a role in mediating the long-term survival and fitness consequences of rearing conditions.

In Chapter 4, I examined whether prior ecological and social experiences affected male song learning and song features, while including multiple song parameters to account for songs' multidimensionality. I recorded all adult males from the brood size manipulation experiment once they reached sexual maturity and analyzed several song features and the amount of elements and element transitions learned from the song tutor with computer-based acoustic analysis. I found that the birds from large broods learned fewer element transitions as they appear in the song of their tutor than the birds from small broods. In addition, the birds from large broods showed less consistent singing than the birds from small broods. These results therefore support the developmental stress hypothesis (Buchanan et al., 2003; Nowicki et al., 1998; Nowicki et al., 2002a): the natural variation of early nutritional and social environment created through brood size manipulation affected the accuracy with which the syntactical structure of the song is learned and induced condition dependence in male singing consistency.

In Chapter 5, I examined how females' early social learning and condition contributed to variation in their mating preferences and reproductive decisions. Using the well-established operant conditioning set-up (Chapter 2), I tested preferences of adult females reared in either small or large broods for songs of males reared in either small or large broods. Females showed condition-dependent preferences: females from small broods (i.e. high condition females) preferred males from small broods, but females from large broods (i.e. low condition females) preferred males from large broods over males from small broods. In a breeding experiment, females paired up with males assortatively with respect to rearing conditions had shorter egg laying latency than females in disassortative pairs, which is consistent with the song choice results. It also suggests that males and females with a similar developmental background accepted each others faster as partners, which can increase their lifetime reproductive success (Alonso-Alvarez et al., 2006). Importantly, the perception that females from large broods had of male condition was not impaired since all females invested more in egg mass when paired with males from small broods. Thus females from both rearing conditions agreed on the phenotypic quality of the males they were paired to, despite showing different preferences. These results provide evidence that the early environmental variation induced variation in individual condition, which translated to substantial phenotypic plasticity, notably in the direction of female mating preferences.

GENERAL CONCLUSIONS

This thesis shows that female mating preferences and their reproductive decisions but not their perception of male condition vary substantially according to variation in early social learning and condition they experienced. Therefore, developmental condition is an important source of variation in female mating preferences and reproductive decisions. The effects could go as far as females actively preferring low quality males. This condition-dependency of the direction of female preferences indicates that not all females aimed for the highest-quality males available. Such condition-dependent preferences are likely to result into assortative mating by condition, which, as reported, can be beneficial in term of an increase of lifetime reproductive success for both individuals in the pair. This is at first counter-intuitive as sexual selection theory predicts that females should always prefer the highest-quality males when they are given the choice, but recent theoretical modelling work suggests that a preference for low-quality individuals could be an adaptive strategy under certain selection pressures. When the competition over mate access is high or when mutual mate choice exists, low-quality females are likely to be out-competed by higher-quality females or to be avoided or deserted by males in favour of high-quality females. Thus in those cases, an active preference for low- instead of high-quality males could allow females to save time and energy and thus increase their fitness.

Male song appeared to play a major role in mediating the observed variation in female preferences. The difference in preference direction between females from small and large broods occurred while females had access to the song only and this variation in their song preferences was confirmed by the timing of their reproductive decisions. Furthermore, preferences for song were consistent across different test contexts and translated into identical preferences for the singer. Taken together, these findings strongly suggest that the song contains sufficient information on the singer for female mate choice. In support of this, I showed evidence that some song features reflected male morphology and/or male past developmental history. Thus, males' learned song can act as long-term signal of their past condition thereby providing reliable information to females about how well males fared in the face of an early developmental stress.

To conclude, this thesis provides evidence that both male song learning and female socially learned preferences are co-dependent on variation in early social and non-social environmental factors. Both mating preferences and aspects of song production lastingly reflect individual past condition. Therefore, an approach that takes into account past experiences and state-dependent life-history traits might prove extremely fruitful to further our understanding of sexual selection and of the evolutionary dynamics between preferences and sexually selected, culturally transmitted traits.