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Preferred songs predict preferred males: consistency and repeatability of zebra finch females across three test contexts

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Male mating signals are often multidimensional, potentially providing multiple messages to females. However, the relative importance of different signal dimensions and their context dependency are poorly understood. Even in a well-studied species such as the zebra finch, *Taeniopygia guttata*, an important avian model for the study of mate choice, there is little consensus on the relative weighting of visual versus acoustic signals in mate choice. We therefore tested the consistency and repeatability of female mating preferences across different test contexts, presenting male song only or full courtship displays. We concurrently conducted a detailed analysis of male song characteristics and morphological traits. Females' individual preferences were consistent across three commonly used binary test paradigms (operant and phonotaxis tests with songs and association tests with live males). Preference direction was thus independent of test contexts. Preference strength was repeatable only between the operant and live male tests, possibly because these two tests allowed active interaction with songs or males whereas exposure to songs in the phonotaxis test was passive. The song structure parameters that predicted female preferences best were context independent and also predicted male morphology. We conclude from the combined results that song structure (in addition to song rate or absolute output as previously suggested) does contain sufficient information on the singer for female mate choice. We suggest that the earlier focus on song rate rather than song content might partly account for the differences between studies in the importance attributed to acoustic versus visual signals.

Keywords: context-repeatable mating preference; male choice test; mate choice; multiple signals; operant test; phonotaxis test; song structure; *Taeniopygia guttata*; zebra finch

Despite intensive research on female mate choice and the evolution of secondary sexual traits over the past few decades (Andersson 1994), surprisingly little is known about within-population variation in female preference (Jennions & Petrie 1997; Widemo & Saether 1999). Females' mating decisions are often based on multidimensional signals providing a wide range of messages and involving different sensory modalities (e.g. acoustic and visual) propagated on different temporal and spatial scales (Candolin 2003; Hebets & Papaj 2005). Two types of not mutually exclusive functional hypotheses have been suggested to account for multiple ornaments and mating signals: they could provide (1) back-up messages or (2) multiple messages on different aspects of male quality. Within-population variation in female mating preferences (i.e. the response to sample stimuli) can arise through variation in condition or context and/or genetic, cultural or phenotypic compatibility (Jennions & Petrie 1997; Widemo & Saether 1999; Qvarnström 2001). If females within a population differ in whether they predominantly look for direct or indirect benefits (e.g. resource-holding potential versus genetic benefits), they may pay attention to different signals to choose the most suitable male (Candolin 2003). Differences in female mating preferences are also likely to be influenced by social factors such as the intensity of male–male or female–female competition (Jennions & Petrie 1997; Widemo & Saether 1999). For instance, mate density may affect female choosiness (i.e. the time and effort the female is prepared to invest in finding and assessing mates), the cost of sampling and sampling strategies (i.e. the decision rule adopted in mate assessment).

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Both the multiple message and back-up signal scenarios might lead to context dependency of the weighting of particular signals (Wagner 1998; Candolin 2003), a poorly understood issue (Jennions & Petrie 1997; Candolin 2003). It has rightly been pointed out that different test methods might inadvertently lead to context-specific weighting of different signals. For example, they may allow different levels of interaction between males and females (Waas & Wordsworth 1999), which may influence which traits females pay more attention to. Hence, some of the documented variation in female preferences might not arise from differences between females or populations but might be an artefact arising from the wide range of different methods used to measure female mating preferences (Wagner 1998). One of our aims in this study was to examine the impact of the test method on estimated female preferences in zebra finches, *Taeniopygia guttata*.

In songbirds, one of the most intensively studied taxa in current studies of mate choice behaviour, there is ample evidence that male song is important for female choice (Catchpole & Slater 1995; Searcy & Yasukawa 1996). However, the relative weighting of song versus other phenotypic features of males such as morphological traits and display intensity remains poorly understood (Collins et al. 1994; Patricelli et al. 2003). Furthermore, 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 current literature on mating preference in the zebra finch, a species that has been intensively studied experimentally in the laboratory, illustrates rather well how difficult it is to test the relative importance in female mate choice of acoustic and visual signals provided by male courtship displays such as song rate and beak colour (ten Cate & Mug 1984; Collins 1994; Collins & ten Cate 1996; Zann 1996; Forstmeier & Birkhead 2004). Zebra finches therefore provide a good model with which to compare the consistency and the repeatability of female mating preferences as well as to examine what exact attributes make songs attractive to females and what the preferred song features say about the singer. To this end we tested females across three different commonly used test paradigms involving single or multiple sensory modalities. An operant test with song as reinforcer (Houx & ten Cate 1999; Riebel 2000; Riebel et al. 2002; Leadbeater et al. 2005) and a phonotaxis test both tested preferences for the acoustic signal alone (Miller 1979a, b; Clayton 1988; Neubauer 1999). A spatial association test with a choice between two live males presented a test situation where the acoustic signal was combined with additional static and dynamic visual and behavioural signals. The latter is by far the most commonly used mate choice test type (reviewed in Forstmeier & Birkhead 2004). We assessed both preference consistency (identical direction) and repeatability (identical strength) of the within-individual preference for a specific stimulus in different test contexts. Subsequently, we compared the outcome of an in-depth song analysis with female song preferences and male morphological traits to test whether structural song parameters can predict female preferences on the one hand and male quality on the other.

If multiple signals act as multiple messages then we expect more consistency and repeatability in female preferences when comparing the two tests involving song only (operant and phonotaxis tests) than when comparing tests involving single versus multiple sensory modalities (i.e. phonotaxis or operant versus live male tests). However, if multiple signals act as back-up signals, females should not differ in their preference direction between the tests involving song only and the live male tests.

SUBJECTS AND REARING CONDITIONS

We used wild-morph domesticated zebra finches ($N = 35$, 17 males and 18 females) from an outbred breeding colony at Leiden University, The Netherlands. The birds were kept on a 13.5:10.5 h light:dark schedule (lights on between 0700 and 2030 hours CET) at 20–22°C and 35–50% humidity. Birds had ad libitum access to a commercial tropical seed mixture enriched with GistoCal mineral and vitamin powder (Beaphar B.V., Raalte, The Netherlands), drinking water and cuttlebone. This basic diet was supplemented three times a week with 3–4 g of ‘egg food’ (Witte Molen, B.V., Meeuwen, The Netherlands) per bird, twice a week with branches of millet and once a week with germinated tropical seeds. All subjects had been reared by their parents in standard laboratory cages (80 × 40 cm and 40 cm high) equipped with a nestbox. At 65 days (i.e. after the peak of the sensitive period for song learning, Slater et al. 1988), they were moved to be housed in single-sex groups with eight to nine individuals per cage (100 × 60 cm and 60 cm high). All subjects were about 2 years old (20 ± 5 months, $N = 35$) and had no breeding experience when the experiments started. Subjects that encountered each other in preference tests were unfamiliar to each other and had a coefficient of relatedness less than 0.125.

PREFERENCE CONSISTENCY AND REPEATABILITY

Methods

Stimulus preparation

Following Sossinka & Böhner (1980), we call an individual’s specific syllable sequence ‘the motif’. A ‘song’ consists of a series of introductory syllables followed by several repetitions of the motif (range 1–10 for nondirected songs). For the preparation of the stimulus songs, we recorded nondirected songs of 17 males. Males were placed singly in a cage (70 × 30 cm and 45 cm high) on a wooden shelf (100 × 55 cm) at a height of 120 cm in a sound attenuation chamber (100 × 200 cm and 220 cm high). Songs were recorded at a distance of 75 cm from the cage (Sennheiser MKH40 microphone, Wedemark, Germany and Sony TC-D5 Pro II cassette recorder, Tokyo, Japan). Songs were digitized (25 000-Hz sample rate) using Signal/Rts software (Engineering Design, Belmont, MA, U.S.A.) and a lowpass filter (cutoff frequency 10 000 Hz; Frequency Devices 900C/9L8B, Haverhill, MA, U.S.A.). We chose one natural song per male and digitally deleted those introductory syllables at the beginning that were additional to the number of introductory syllables that occurred as part of the motif within songs. All chosen songs had four motifs. Using the Praat sound analysis software (version 4.2.07 for Windows,