Low-quality females prefer low-quality males when choosing a mate

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Mate choice studies routinely assume female preferences for indicators of high quality in males but rarely consider developmental causes of within-population variation in mating preferences. By contrast, recent mate choice models assume that costs and benefits of searching or competing for high-quality males depend on females' phenotypic quality. A prediction following from these models is that manipulation of female quality should alter her choosiness or even the direction of her mating preferences. We here provide (to our knowledge) the first example where an experimental manipulation of female quality induced a mating preference for low-quality males. Zebra finches (*Taeniopygia guttata*) reared in small or large experimental broods became high- or low-quality adults, respectively. Only high-quality females preferred high-quality males' mate-advertising songs, while all low-quality females preferred low-quality males' song. Subsequent breeding trials confirmed this pattern: latency until egg laying was shortest in quality-matched pairs, indicating that quality-matched birds were accepted faster as partners. Females produced larger eggs when mated with high-quality males, regardless of their own quality, indicating consensus regarding male quality despite the expression of different choices. Our results demonstrate the importance of considering the development of mating preferences to understand their within-population variation and environmentally induced change.

Keywords: state-dependent mate choice; sexual selection; female condition; bird song; assortative mating

1. INTRODUCTION

An animal's fitness hinges on finding a suitable mate. In the majority of animal signalling systems, males are the advertising, and females the choosing sex. Hence, female mating preferences are thought to be an important driving force in the evolution of male sexual signals (Andersson 1994). Sexual selection studies assume a tight link between female preference and male quality as such fitness linked preferences will be positively selected (Andersson 1994; Jennions & Petrie 1997). From this, many empirical studies initially derived the prediction that females should prefer to mate with the highest quality male available. However, it is now recognized that there is often pronounced variation in female preference for different male phenotypes (Jennions & Petrie 1997; Qvarnström *et al.* 2000) and there is increasing interest in the possibility that females' own phenotypic quality might have a substantial contribution to variation in mating preferences (Cotton *et al.* 2006).

Phenotypic variation arises from gene–environment interactions during development (West-Eberhard 2003) which lead to different growth patterns and different physiological phenotypes, which in turn influence the resources an individual can allocate to body maintenance and reproduction, i.e. an individual's condition (*sensu* Rowe & Houle 1996) or quality. The condition dependency of male sexual signals is well documented (Andersson 1994). Similarly, resource allocation to mate

selection and mating preferences may also depend on female condition, but the study of the condition dependency of female mate choice is still in its infancy (Cotton *et al.* 2006).

Optimality models of state-dependent mate choice (Real 1991; Johnstone 1997; McNamara *et al.* 1999; Fawcett & Johnstone 2003; Härdling & Kokko 2005) predict reduced sampling effort or choosiness in low-quality females if (i) females cannot physically afford the costs of prolonged mate search, (ii) and/or they are less successful in competing with their own sex, (iii) and/or are less successful in attracting the opposite sex, or (iv) are more likely to be deserted by their male. If the costs for targeting the best males are sufficiently high (e.g. increase of rarity of high-quality males), then low-quality females might minimize search costs or even lost breeding opportunities by changing the direction of their preferences towards low-quality individuals (Fawcett & Johnstone 2003; Härdling & Kokko 2005). However, to the best of our knowledge, such an effect of female quality on the direction of their mating preferences has never been shown empirically.

We tested this prediction in zebra finches, a socially monogamous passerine bird. Individual quality in zebra finches can be experimentally manipulated through brood size manipulations: wild and domesticated individuals reared in small broods have been shown in previous studies to have higher juvenile growth, condition, survival and stronger immune responses than individuals reared in large broods, and many phenotypic effects of rearing environment are maintained into adulthood (de Kogel & Prijs 1996; de Kogel 1997; Naguib *et al.* 2004; Naguib &

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Table 1. Timeline for the different experimental phases.

experimental phase	age in days post-hatching, mean $\pm$ s.d.	sample sizes
cross-fostering	3.0 ± 1.7^a	113 chicks, 54 from small and 59 from large broods
song tutoring	33.5 ± 3.1 until 69.3 ± 3.0^b	52 chicks, 26 of each treatment in 13 tutor groups ^c
male song recording	141 ± 13^d	26 males ^e , 13 of each treatment
start of song preference tests	164 ± 15^f	24 females, 12 of each treatment ^c
breeding in experimental pairs	487 ± 63^g	48 birds, 24 of each treatment ^h

^a2004: 3.9 ± 1.6 , $n = 56$, 2005: 2.1 ± 1.4 , $n = 57$.

^b2004: 34.9 ± 3.1 , $n = 24$ until 70.9 ± 3.1 , $n = 24$, 2005: 32.3 ± 2.7 , $n = 28$ until 67.9 ± 2.1 , $n = 27$.

^cOne female died before the tests. The female paired within the design was not tested either.

^d2004: 141 ± 7 , $n = 12$, 2005: 141 ± 16 , $n = 14$.

^eOne male died before morphological measures at day 180.

^f2004: 159 ± 16 , $n = 12$, 2005: 167 ± 15 , $n = 12$.

^g2004: 554 ± 12 , $n = 22$, 2005: 431 ± 11 , $n = 26$.

^hIn each year, one high-quality female died before pair formation. In 2005, we replaced her with a tape-tutored, instead of live-tutored, high-quality female. The statistical analyses involving this female were rerun without her and gave the same qualitative outcome.

Gil 2005; Verhulst *et al.* 2006; Tschirren *et al.* 2009). We cross-fostered chicks in small or large brood sizes thereby generating high- and low-quality adult phenotypes, and we refer to them as such in the remainder of this paper.

Mating preferences of female zebra finches can be quantified by using operant song preference tests: females can be trained to peck different response keys for different song playback and their song preferences are strongly correlated with their preferences for live males (Riebel 2000; Holveck & Riebel 2007). This method has the advantage that there is no interaction between male and female mutual preference, but instead measures female preference in isolation. In such operant tests, we let females of high or low quality choose between songs of two males that differed in quality (i.e. one reared in a small brood and one reared in a large brood). We then paired all birds with unknown partners that were either of the same quality or the opposite quality and let them breed, to study whether the mating preferences translated into variation in reproductive investment.

2. MATERIAL AND METHODS

(a) *Birds and housing*

Experiments were performed using domesticated zebra finches from an outbred colony at Leiden University (Forstmeier *et al.* 2007). Throughout, birds were housed in standard laboratory cages ($80 \times 40 \times 40$ cm) on a 13.30:10.30 light:dark schedule (lights on at 07.00 central European time) at 20–22°C and 35–50% humidity. Cages had solid side walls and were stacked three cages high in three long rows along the length of the room. Birds could hear and see birds 2 m across the aisle and could hear but not see birds from cages on their side of the aisle. Throughout, birds had ad libitum access to a commercial tropical seed mixture (Tijssen, Hazerswoude, Holland), drinking water and cuttlebone supplemented thrice weekly with egg food (Witte Molen, B.V., Meeuwen, Holland), twice with millet branches and once with germinated seeds.

(b) *Brood size manipulation*

Brood size was manipulated in order to create high-quality (small brood size of rearing) and low-quality (large brood size of rearing) individuals for use in the subsequent experiments.

Breeding of the $n = 113$ experimental birds took place in two rounds of first time breeders (14 pairs in 2004; 16 in

2005; table 1). Chicks were cross-fostered at 3 ± 1.7 (s.d.) days post-hatching to create small (with two to three chicks per nest, $n = 19$ broods, $n = 54$) and large broods (five to six chicks, $n = 11$ broods, $n = 59$) splitting up full-sibling groups whenever possible (for details see table 1, Holveck *et al.* 2008). We made sure that initial and experimental brood sizes were not correlated (2004: $r_{14} = 0.18$, $p = 0.5$; 2005: $r_{16} = 0.42$, $p = 0.1$) and emulated age composition in foster broods to those of natural broods (Welch two-sample t -test: $t_{57} = 0.85$, $p = 0.4$) using age rank numbers based on hatching order (following de Kogel & Prijs 1996). Average age did not differ between chicks of small and large broods on the day of cross-fostering (2.9 ± 1.7 (s.d.) versus 3.1 ± 1.8 days; generalized linear mixed model with year, hatching nest and foster brood as random effects, $F_{1,26} = 0.00$, $p = 0.98$). Likewise, chick mass (measured with a Sartorius BL600 electronic scale to the nearest 0.1 g) did not vary systematically between brood sizes on the day of cross-fostering (2.6 ± 1.4 for chicks from small broods versus 3.1 ± 1.8 g for chicks from large broods; generalized linear mixed model with year, hatching nest and foster brood as random effects, $F_{1,25.8} = 0.77$, $p = 0.39$). Chicks were housed with the foster parents until nutritional independence at day 35 of age. They were then moved in groups of four chicks (one from each sex and treatment from four different foster nests) to an unfamiliar, unrelated pair for the duration of the sensitive phase for song learning (see below).

We measured offspring tarsus length, an index of structural size, nutritional independence (age 35 days) and at adulthood (180 days). Measurements were taken to the nearest 0.05 mm using callipers (Baumel *et al.* 1979) three times and were highly repeatable (day 35: $F_{104,210} = 96.7$, $p < 0.001$, $R = 0.97 \pm 0.005$; day 180: $F_{99,200} = 142.5$, $p < 0.001$, $R = 0.98 \pm 0.004$). Repeatability $R \pm$ s.e. were calculated following Lessells & Boag (1987) and Becker (1984), respectively. For a related study, standard metabolic rate was measured for the birds bred in 2004 when they were 13 months old (Verhulst *et al.* 2006), and all birds were tested in a mate choice arena when 11 months old (M. J. Holveck 2004, 2006, unpublished data). For all tested birds, this was after the song preference tests and before the breeding trials.

(c) *Female song learning and preference tests*

If females' own phenotypic quality affects their mating preferences, then this should be reflected in females' song

preferences, as song is a predominant cue in zebra finch mate choice (see Riebel 2009 for a review). In zebra finches, although both sexes call frequently, only males produce complex mate advertising song. Each male has an individually specific song motif consisting of three to 14 different elements/syllables and both male song and female song preferences are learned from adult conspecific models early in life at about 35–65 days of age (Slater *et al.* 1988; Riebel 2000; Riebel *et al.* 2002). Housing young fledglings with an adult male or male-female pair during this phase will ensure song learning from this male (the ‘song tutor’) both in males and females (Slater *et al.* 1988; Riebel *et al.* 2002). This allowed us to standardize song learning conditions as follows: at 33.5 ± 3.1 (s.d.) days post-hatching we selected a subsample of 52 fledglings from the foster families to form 13 ‘song tutoring groups’ (six in 2004, seven in 2005; a total of $13 \times 4 = 52$ tutees; table 1). In each tutor group, there were two male and two female fledglings: for each sex, one fledgling had been reared in a small and one in a large brood. Within a tutor group, chicks came from different hatching nests and foster broods. Tutor groups were housed in standard laboratory cages in one of the colony rooms with one unrelated adult male (the tutor) and his mate. At 69.3 ± 3 days post-hatching, when birds reach the end of the sensitive phase for song and song preference learning (and before male song crystallizes around 90 days of age), tutee groups were split. Individuals were now housed in mixed-treatment, mixed-tutor single-sex groups of four to five birds in standard laboratory cages until experiments began after birds were sexually mature (more than 120 days; Zann 1996). For the males ($n = 26$), this entailed recording their spontaneous songs at 141 ± 13 days post-hatching when placed singly in a cage ($70 \times 30 \times 45$ cm) in a sound attenuation chamber ($100 \times 200 \times 220$ cm). Albeit that in zebra finches, solitary ‘undirected’ song is a lower intensity singing mode than courtship song directed to females (for review, see Woolley & Doupe 2008; Riebel 2009), female song preferences for undirected song of different males accurately predict their choices when encountering these males live and in directed singing mode contact (Holveck & Riebel 2007). Opting for solitary undirected song in this experiment allowed us to obtain clean recordings without female calls that could influence female mating decisions (Freed-Brown & White 2009). All songs were recorded under standardized conditions in the same type of sound attenuation chamber at 75 cm distance from the cage (see Holveck *et al.* 2008), with a Sennheiser MKH40 microphone onto a PC’s hard disk (with a CDX-01 soundcard; Digital Audio Labs), using the ISHMAEL software (v. 1.0.2, <http://www.pmel.noaa.gov/vents/acoustics/whales/ishmael/>; automatic energy detection settings for 2000–10 000 Hz, detection threshold 1, detection limits 0.2–100 s, buffer 3 s). From these recordings, we selected the song stimuli for the preference tests. We chose one four-motif song per male, digitally deleted introductory elements, high-pass filtered the songs at 500 Hz (smoothing = 100 Hz) to remove low-frequency background noise and root mean square-equalized amplitudes (peak digitally scaled to 1) with the PRAAT software (4.2.07 for Windows, <http://www.praat.org>). Stimuli were prepared blindly with regard to male treatment.

We started testing females’ song preferences at 164 ± 15 days post-hatching. One female had died, leaving 12 matched pairs with identical song tutoring with one female from a small and a large brood each. Each female’s

preference was tested three times in an operant setup. Females could freely ask for song playbacks by pecking red response buttons (Riebel 2000). For each test, females could choose between songs of two males from the same tutor group (one low-quality and one high-quality male). In the first test, they were offered songs of the two familiar males from their own tutor group, and in the second and third tests, the songs of unfamiliar males from two different tutor groups. Females were paired, in the design, with the other female from their tutor group and each such pair (always one low- and one high-quality female) was given a unique set and order of stimuli for the three tests. Likewise, the songs of the two males within each tutor group were paired as unique stimuli sets. Each set served as the ‘familiar songs’ stimulus set for the two females from their own tutor group and for two females from another tutor group as ‘unfamiliar songs’ stimulus set. Each song stimulus set was used only once in each of the three test types (test 1: familiar, test 2: unfamiliar 1, test 3: unfamiliar 2) and with only one pair of females.

The operant setup used to test song preference has been described and validated previously: females show high within and between trial repeatability (Riebel 2000; Riebel *et al.* 2002) and song preferences are consistent with females’ choices for live males (Holveck & Riebel 2007). Briefly, during the several days of training and preference testing, females were housed individually in sound attenuation chambers in an experimental cage ($70 \times 45 \times 30$ cm; $n = 8$) that contained two small red keys that upon pecking induced the playback of either of two test songs. When moved into the experimental cage for the first time, females still have to learn that key pecking yields song reward but will do so quickly and then can be re-tested even after considerable time spans (e.g. six months later; see Riebel 2000). Females either discover by themselves after a day or two that pecking the red keys yields song reward or otherwise after brief training sessions (for description see Holveck & Riebel 2007). The pecking keys were programmed to play back the test stimuli from the moment the female was moved into the cage (see Holveck & Riebel 2007; Riebel 2000; Riebel *et al.* 2002). The actual preference test started on the morning after the day females were observed to have learned the association between key pecking and song reward (by showing the transition from not pecking at all, to occasional pecking and then to a steep increase in pecking activity at both keys). A test lasted for 2 days during which females had unlimited access to song. Assignment of stimulus songs was fully balanced with regard to presentation on the left and right side, and stimulus presentation was side-reversed on the second test day. For each preference test, we assessed two response variables: (i) the total number of key pecks over the 2 test days, and (ii) song preference, defined as the proportion of key pecks for the song of the high-quality male. Females were housed in the experimental cage during tests and in their home cage for the intervals (8.1 ± 1.4 days) between tests.

(d) Breeding experiment

After having established females’ mating preferences in the song preference tests, we experimentally paired females either with males of the preferred type (i.e. the same quality as themselves) or the non-preferred type (non-matching quality). For their first breeding attempt (table 1), six pairs of each of the four possible male quality $\times$ female quality

combinations were formed between unfamiliar and genetically unrelated birds, resulting in 12 matched pairs (six high/high and six low/low quality) and 12 mismatched pairs (six high/low and six low/high quality). Females had not encountered their assigned mate prior to the test, neither during housing nor during preference testing. A male and a female were first moved to a breeding cage divided into two compartments by an opaque divider. The male compartment had a nest-box with hay as nesting material. Dividers were removed after 2 days. Nests were checked daily after 10.00 h. Any new eggs were marked and weighed to the nearest 0.1 g. A clutch was considered complete if no new eggs were laid for 4 days. For each pair, we collected data on latency to first egg in the nest, clutch size and mean egg mass per clutch as measures of reproductive investment (Christians 2002).

(e) Statistical analyses

Data were analysed with generalized linear mixed models (two-tailed, $\alpha = 0.05$) in SAS v. 9.1 (SAS Institute Inc., Cary, NC, USA). We started with the full models and then sequentially deleted non-significant higher order interactions and then factors in running backward selection procedures with type III errors. The degrees of freedom were estimated with Satterthwaite's method. Distributions were normal for tarsus length and mean egg mass per clutch, binomial for song preference (with a correction for overdispersion), and Poisson for number of key pecks (with a correction for overdispersion) and latency to first egg. In tests 2 and 3 (both presenting a set of two unfamiliar songs), females had highly repeatable preferences ($F_{23,24} = 7.20$, $p < 0.0001$, $R \pm \text{s.e.} = 0.76 \pm 0.13$) and repeatable numbers of key pecks ($F_{23,24} = 2.12$, $p = 0.037$, $R \pm \text{s.e.} = 0.36 \pm 0.26$). Because of this and because we obtained identical outcomes with models where female identity was entered as random effect, tests 2 and 3 were combined for analyses in summing the number of pecks to keep the model simple. Fixed effects were treatment (brood size at day 10, namely two, three, five or six chicks) in all models, individual age and sex (three-way interaction) in models testing effects on tarsus length, latency to first egg in models testing effects on clutch size, and latency to first egg and clutch size in models testing effects on mean egg mass per clutch. We fitted year, hatching nest and foster brood as random effects. In models including only the birds involved in the song preference tests and in the breeding experiment, we also fitted tutor group as a random factor.

3. RESULTS

The brood size manipulation affected individuals' morphology. Individuals from small broods had longer tarsi than those from large broods at day 35 (15.5 ± 0.5 (s.d.) versus 15.1 ± 0.5 mm, $n = 48$ chicks from small and 57 from large broods; $F_{1,61.1} = 10.72$, $p = 0.0017$). This effect persisted into adulthood for all cross-fostered chicks (day 180: 15.5 ± 0.4 versus 15.1 ± 0.5 mm, $n = 47$ and 53, respectively; $F_{1,60.6} = 20.67$, $p < 0.0001$) and in the subsamples of experimental females (15.6 ± 0.2 versus 15.1 ± 0.5 mm, $n = 12$ and 12, respectively; $F_{1,14.1} = 5.89$, $p = 0.03$) and males, respectively (15.4 ± 0.4 versus 15.0 ± 0.5 mm, $n = 12$ and 13, respectively; $F_{1,12.9} = 4.94$, $p = 0.04$). In the subsample of the experimental birds from 2004, we previously

showed that metabolic efficiency was lower in fledglings from large broods (for details see Verhulst *et al.* 2006). These results fit with the previously found morphological, physiological and reproductive differences between individuals reared in small and large broods which has since led to the categorization of individuals from small broods as high-quality birds and individuals reared in large broods as low-quality birds (de Kogel & Prijs 1996; de Kogel 1997; Naguib *et al.* 2004; Naguib & Gil 2005; Tschirren *et al.* 2009).

With respect to our behavioural measures, we found that females of different quality were equally motivated to hear song: the total amount of key pecks during song preference tests did not differ between high- and low-quality females (test 1, familiar songs: 624 ± 397 versus 806 ± 890 key pecks, $F_{1,14} = 0.36$, $p = 0.56$; tests 2 and 3, unfamiliar songs: 1071 ± 957 versus 668 ± 458 , $F_{1,14.6} = 1.14$, $p = 0.30$).

In the test where females could choose between the two familiar songs of their two peers from the song tutoring phase (test 1), neither low- nor high-quality females systematically preferred high- or low-quality males' singing the familiar song (one-sample t : high-quality females $t_{11} = 0.04$, $p = 0.97$, low-quality females $t_{11} = 0.15$, $p = 0.88$) and preference strength for high-quality males was not related to experimental brood size ($F_{1,13.6} = 0.02$, $p = 0.90$; figure 1). This confirms previous results that familiarity developed early in life interferes with the judgement of male quality (Riebel 2003, 2009).

When females were tested with unfamiliar songs from high- and low-quality males (tests 2 and 3), high- and low-quality females showed a pronounced difference in preference strength for high-quality males ($F_{1,3.66} = 62.04$, $p < 0.002$; figure 1) which was owing to striking assortative song preferences in relation to male quality: high-quality females preferred the song of high-quality males ($t_{11} = 49.5$, $p < 0.001$), and low-quality females preferred the song of low-quality males ($t_{11} = 21.6$, $p < 0.001$). We observed this assortative pattern in 44 out of the 48 tests (2 tests $\times$ 24 females) and when the song preferences for tests 2 and 3 were averaged, every single female preferred males from her own quality category. Interestingly, rather than showing reduced choosiness (Cotton *et al.* 2006), low-quality females had equally strong preferences for quality-matched males as high-quality females ($F_{1,12.6} = 1.47$, $p = 0.25$; figure 1).

The breeding trials showed that the assortative pattern observed in the song preference tests held with live males: the females in quality-matched pairs laid the first egg of their clutch sooner after pairing than females in quality-mismatched pairs (11.5 ± 6.6 (s.d.) versus 21.6 ± 11.4 days; effect of the interaction between female and male quality: $F_{1,11.3} = 6.53$, $p = 0.03$; figure 2). Laying interval was independent of female quality (17.6 ± 10.9 versus 15.9 ± 10.7 days, $F_{1,10.6} = 3.74$, $p = 0.08$) and male quality (18.1 ± 10.2 versus 15.5 ± 11.2 days, $F_{1,12.6} = 3.80$, $p = 0.07$). Moreover, females' investment in mean egg mass per clutch was higher when mated to a high-quality male (1.28 ± 0.07 versus 1.19 ± 0.11 g, $F_{1,4.56} = 16.82$, $p = 0.01$; figure 2; but not clutch size: 5.4 ± 2.2 versus 5.9 ± 0.8 eggs, $F_{1,19.1} = 1.40$, $p = 0.25$), regardless of her own quality (1.23 ± 0.11 versus

Figure 1. Female preference for the song of high-quality males in relation to female quality. Preference was measured as the proportion of choices (pecks in an operant setup) for the song of a high- (versus low-) quality male. All females were tested (a) once with a set of familiar males' songs (test 1) and then (b) twice with different sets of unfamiliar males' songs (tests 2 and 3). High- and low-quality males and females had been produced by experimental manipulation of the brood size of rearing. Males and their songs were considered unfamiliar if they were not from the same hatching nest, foster brood or tutor group as the female. Figures show means $\pm$ s.d. ($n = 12$ females for each data point). Open circle, high-quality females; filled circle, low-quality females.

1.24 ± 0.10 g, $F_{1,14.5} = 0.08$, $p = 0.78$; clutch size: 5.4 ± 2.2 versus 5.9 ± 0.9 eggs, $F_{1,9.5} = 2.39$, $p = 0.15$).

4. DISCUSSION

We used brood size manipulation to produce 'low-quality' (raised in a large brood) and 'high-quality' (raised in a small brood) zebra finch males and females and showed the following. (i) When offered identical choices between unfamiliar songs, only high-quality females preferred the song of high-quality males, while low-quality females preferred low-quality males. This demonstrates that variation in the rearing environment can have profound effects on the direction of female preference and male mating traits (for the analysis of males' songs, see Holveck *et al.* (2008)). (ii) Regardless of female or male quality, the latency to egg laying was shorter in quality-matched pairs. This confirms the song preference results, suggesting that females prefer mates resembling them in quality and that quality-matched individuals accepted each other faster as mates. (iii) Regardless of their own quality, females laid larger eggs when mated to high-quality males. Such patterns are predicted by the differential allocation hypothesis (Burley 1986, 1988; Sheldon 2000) which states that female investment in offspring can be influenced by perceived male attractiveness (see Burley (1986, 1988) and Gilbert *et al.* (2006) for experimental evidence of positive differential allocation and Bolund *et al.* (2009) for compensatory investment). Thus, despite the opposing preferences shown by high- and low-quality females, their judgement of male quality might nonetheless have been the same.

Female consensus on male quality does not have to mean identical choices, if it pays for some females not to enter the competition for high-quality males (Fawcett & Johnstone 2003; Härdling & Kokko 2005),

Figure 2. Mean egg mass per clutch and latency to the first egg. Birds were experimentally paired by matching or non-matching quality. High- and low-quality males and females had been produced by experimental manipulation of the brood size of rearing. Males and females were unfamiliar to each other, i.e. they were not from the same hatching nest, foster brood or tutor group, and females had not been exposed to the song of their mate in the earlier preference tests. Figures show means $\pm$ s.e.; $n = 6$ for each pair category except for high-quality $\times$ high-quality pairs, where $n = 5$ (one female had still not laid any eggs after 67 days).

for example because they cannot afford the time and energy requirements of a prolonged search, and/or because they lose out in the competition for high-quality males to high-quality females, and/or are rejected by high-quality males in species with mutual mate choice, and/or are divorced in pair bonding species. Any of the above may incur significant fitness costs (Real 1991; Johnstone 1997; McNamara *et al.* 1999; Van de Pol *et al.* 2006). For monogamous seasonal breeders, searching too long for a mate or being deserted by a mate could mean missing a breeding season altogether. Zebra finches form socially monogamous pairs and live in unpredictable habitat with short breeding seasons, and delayed breeding incurs fitness costs (Zann 1996; Alonso-Alvarez *et al.* 2006) in this opportunistic breeder with mutual mate choice (Jones *et al.* 2001). In addition, the larger the quality difference between partners the more likely it is that the higher quality partner deserts its partner, spends more time pursuing extra-pair paternities and/or reduces the time contributing to parental care (Burley 1986; Burley 1988). It is thus conceivable that low-quality individuals gain time, reduce the risks of being rejected or divorced, and hence increase their chance of successfully breeding in a given season by selecting a low-quality mate straight away. This could very well confer a fitness advantage given the low probability of surviving from one season to the next: in the wild, adult annual survival has been estimated to be as low as 4–28% (Zann 1996).

However, to express such quality-matched preferences, females must be able to tell high- from low-quality males as well as to assess their own quality. The results from the song preference tests show that females could tell high- from low-quality males (by listening to their song only). Likewise, our song analyses of the males tested here showed differences between high- and low-quality males' song (Holveck *et al.* 2008), such as syntax and

aspects of singing consistency, but future tests will have to show whether these or other parameters are the cues females use to base their choices on.

Interestingly, while females discriminated between songs of unfamiliar males, the differences in song quality seemed not to affect their preferences when females were choosing between the songs of their familiar male companions from the subadult song-learning phase. Note that these males had not yet produced full adult song when housed with the young females, so that their future adult song was not yet known to females. However, a familiarity effect could also have arisen via voice recognition (Miller 1979; Vignal *et al.* 2004), or if females generalized their tutor song preferences to those males that had learned their songs from the same tutor as themselves (Riebel 2009). Note that the familiar song sets were also used as unfamiliar song sets with two other pairs of females. Here, they were always preferred if the female was of matching and always non-preferred if the tested female was of non-matching quality. Song preference learning thus constitutes an additional source of environmental variation. This is in line with previous findings showing that female subadult experiences with specific song variants can lead to strong preferences for them, which seem to overwrite the importance of other song attributes (Riebel 2000; Riebel *et al.* 2002).

Because the direction of preference for songs of unfamiliar males was linked to female quality, females must have had some 'knowledge' of their own quality or 'market value' (Noë & Hammerstein 1995). During the song preference tests, males were absent and females were naive with respect to male judgement of their quality. We can thus exclude the possibility that low-quality females avoided songs of high-quality males because males rejected them during the tests, or because they had previously experienced rejection by such males in a mate choice context (Jones *et al.* 2001), or because they were outcompeted by other females (Otter & Ratcliffe 1996). The causes of females' differential self-assessment must thus have preceded their first mate-choice event. There are at least two, not mutually exclusive explanations we think worth testing in future studies. First, the effects of non-sexual social experiences could have triggered a female's learning about her competitive abilities. Prior to the tests, both in the tutor groups and later in the all-female groups, females were housed in mixed-treatment groups. Competitive interactions about access to feeders or favourite perches, and resulting dominance relationships within the group might have provided a female with feedback about her quality relative to her peers. Second, our experimental birds differed in their physiology: standard metabolic rate was higher in birds from large broods (Verhulst *et al.* 2006)—internal physiological monitoring processes might provide feedback affecting behavioural decisions.

Our findings of female phenotypic quality affecting the direction of female preferences are reminiscent of correlative patterns of mating preferences so far only reported from humans. Women with low self-perceived attractiveness preferred to date men with lower attractiveness when compared with women with higher self-perceived attractiveness (Little *et al.* 2001; Buston & Emlen 2003; Todd *et al.* 2007). The finding that two such diverse species express the same pattern of assortative mating

preferences suggests that it could be a general aspect of mate choice.

Such effects of phenotypic quality (or 'condition' or 'state') on mate choice is an emerging research field. Empirical studies to date have concentrated on effects of quality on choosiness emphasizing preference strength as behavioural currency (Cotton *et al.* 2006). We found no difference in preference strength between the high- and low-quality females, but a change in the direction of preferences. In zebra finches, two earlier studies testing effects of condition on female preference showed reduced preference strength rather than changes in the direction of preference (Burley & Foster 2006; Riebel *et al.* in press), but neither study had manipulated both male and female conditions symmetrically (as we have in the present study, which might be the reason why we were able to detect such clear assortative pattern) and neither study searched for assortative patterns in the analyses. Future experimental studies will have to elucidate whether choosiness and preferences are dependent on context and whether they might constitute alternative ways for optimizing mate choice to one's own quality.

For now, this study might be seen as proof of principle: even under benign sheltered laboratory conditions, the increased competition resulting from the brood size manipulations revealed that in zebra finches, mechanisms are in place which can set off an environmental determination of female mating preferences for low-quality males. In a recent independent brood size manipulation experiment, wild and domesticated zebra finches showed comparable change in morphology and life-history traits (Tschirren *et al.* 2009). This makes it unlikely that we observed an artefact and raises the exciting possibilities of concerted change in male trait and female preference as response even to short-term environmental variation—an avenue worth exploring in future mate choice studies.

All procedures followed the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research and Dutch laws and were approved by Leiden University Committee for Animal Experimentation.

We thank Kate Lessells, Simon Verhulst, Peter Slater, Tim Fawcett, Carel ten Cate, Hans Slabbekoorn, Machteld Verzijden, Cerrisse Allen and Diego Gil for comments on the manuscript and Simon Verhulst for critical discussion and input regarding the design of the breeding experiment. We also thank Pauline Manhes, Peter Snelderswaard, Paula den Hartog, Erwin Ripmeester, Robert Lachlan, Hans Slabbekoorn, Padu Franco and Ardie den Boer-Visser for assisting in collecting data and Henny Koolmoes for assistance with animal care. This work was supported by the Research Council for Earth and Life Sciences (ALW) with financial aid from the Netherlands Organization for Scientific Research (NWO).

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