



Developmental stress and female mate choice behaviour in the zebra finch

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The potential effects of early environmental conditions on adult female mate choice have been largely neglected in studies of sexual selection. Our study tested whether developmental stress affects the mate choice behaviour of female zebra finches, *Taeniopygia guttata*, when choosing between potential mates. In an experiment manipulating developmental condition, female zebra finches were raised under nutritional stress or control conditions. In adulthood, female preferences were assessed using extensive four-stimulus mate choice trials. Nutritional stress affected growth rates during the period of stress, with experimentally stressed females lighter than controls. During mate choice trials stressed females were almost three times less active than controls and made fewer sampling visits to the stimulus males, although we found no evidence of a direct effect of developmental experience on which males were preferred. Thus, developmental experience had a clear effect on behavioural patterns in a mate choice context. To test whether this effect is specific to a mate choice context, we also investigated the effect of developmental stress on female activity rates in three social contexts: isolation, contact with a conspecific male (a potential mate) and contact with a conspecific female. Here, female activity did not differ between the experimental treatments in any of the social situations. Overall, our findings suggest that environmental conditions during early development can have long-term context-dependent consequences for adult female mate choice behaviour, mediated by changes in activity rates.

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Female mate choice is generally accepted to be a fundamental selective force in driving the evolution of elaborate male sexual traits (Andersson 1994). Yet while individual variation in male signal production has been widely studied, factors contributing to individual variation in female choice behaviour remain poorly understood (Jennions & Petrie 1997; Widemo & Saether 1999). Mounting evidence suggests that, like many male ornaments, female preferences can often be condition dependent (reviewed in Cotton et al. 2006), and several recent studies have shown long-term effects of the developmental environment on female choice in

a small number of invertebrate species. Female black field crickets, *Teleogryllus commodus*, reared on a high-protein diet respond more rapidly to male call playbacks and show stronger preferences than those reared on low-protein diets (Hunt et al. 2005). Hebets et al. (2008) manipulated rearing diet in *Schizocosa* wolf spiders and found that females reared on high-quality diets showed strong preferences for males reared on a high-quality diet while females reared on a low-quality diet showed random preferences. In vertebrates, Riebel et al. (2009) found that females reared in large or medium-size broods exhibited weaker song preferences than those from small broods, while Holveck & Riebel (2010) found that female zebra finches reared in small or large broods preferred the song of males reared under similar conditions and suggested that this might be evidence of assortative mating by phenotypic quality. These studies suggest that developmental conditions can be an important source of variation in female choice. However, the potential effects of environmental factors during the rearing period on adult female mate choice remain largely unaddressed.

There are several ways in which environmental factors experienced during early development could affect female choice. These explanations can be understood at both the mechanistic and

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functional levels (Tinbergen 1963). First, when considering the mechanism for such an effect, developmental stress may impair the ability of females to rank potential mates according to the mate choice criteria normally used by females exposed to superior developmental regimes. This may be caused by the deleterious effects of stress on their higher order neural-processing mechanisms (as has been shown previously to occur in males, Buchanan et al. 2004), or even on their visual or auditory systems. According to this hypothesis, stressed females would not rank males in the same way as unstressed females and may show random choice. However, careful experimental tests of discriminatory ability would be needed to determine that this random choice was due to changes in trait perception. Stress has well-documented detrimental effects on neural development (McEwen & Sapolsky 1995; de Kloet 2000), and the inhibitory effect of stress on the development of the song control system is hypothesized to mediate the honesty of song complexity as a signal of past developmental stress (Nowicki et al. 1998, 2002). Although female songbirds of many species do not produce song, most retain the nuclei of the song control system, albeit often at greatly reduced volumes (Nottebohm & Arnold 1976; Ball & MacDougall-Shackleton 2001), and these are involved in female perception of, and preferences for, male song (Brenowitz 1991; Del Negro et al. 1998; MacDougall-Shackleton et al. 1998; Leitner & Catchpole 2002). It is plausible, therefore, that the effects of developmental stress on the developing brain may affect female preference. The effects of stress on neural development are not limited to the song control system (McEwen & Sapolsky 1995; de Kloet 2000), so the ability of females to evaluate and choose between potential mates on the basis of other male signals could also be disrupted by developmental stress.

Alternatively, several functional hypotheses suggest that developmental stress could affect mate choice even without a direct effect of developmental conditions on the mechanisms by which females perceive male traits. Theory suggests that poor-quality females will bear higher costs of choosiness and be less discriminating in their mate choice (Cotton et al. 2006). Poor neonatal nutrition has been shown to have detrimental effects on growth rates as well as long-term effects on a number of life history traits including morphology, fecundity, quality of offspring and possibly longevity (Birkhead et al. 1999; Metcalfe & Monaghan 2001, 2003; Arnold et al. 2007). Less choosy females may benefit, therefore, by investing less time and resources in sampling potential mates (Cotton et al. 2006) and reduced choosiness could affect female preferences in two ways: females may exhibit random choice which would, in practice, be difficult to distinguish from the effects of reduced perceptual ability in mate preference tests. Alternatively, theory suggests that less choosy females might use different traits as mate choice cues, or prioritize cues differently to choosier females (Fawcett & Johnstone 2003b). According to this hypothesis, stressed females would show consistent mate choice preferences as a group, but these preferences would be uncorrelated with those of unstressed females.

Another, functional hypothesis suggests that females may show an active choice for a mate that matches their perception of their own rank, as determined by their developmental history, leading to assortative mating according to developmental stress exposure. If there is costly competition for mates, poorer quality individuals may seek to minimize the costs they incur by preferentially targeting low-quality partners (Fawcett & Johnstone 2003a; Hardling & Kokko 2005), leading to assortative mating by individual quality. This would further benefit females if pairs matched according to early experience have higher reproductive success than mismatched pairs, if, for example, developmental history is related to environmental variation. There is little empirical evidence so far that female quality could affect the direction of

mating preferences, but Holveck & Riebel (2010) found that females raised in experimentally enlarged broods preferred the song of males raised under similar conditions.

The nutritional stress hypothesis (Nowicki et al. 1998), later extended to encompass a number of potential environmental stressors under the name of the developmental stress hypothesis, relates specifically to the development of male song as a mate choice signal (Buchanan et al. 2003). It suggests that song complexity in songbirds, a sexually selected signal used by females in mate choice decisions, may act as an honest signal of how well a male was able to cope with nutritional or other stress during early development. A number of recent studies have provided empirical support to the hypothesis (Nowicki et al. 2000, 2002; Buchanan et al. 2003, 2004; Spencer et al. 2003, 2004, 2005b; MacDonald et al. 2006; Zann & Cash 2008; although see Gil et al. 2006; Naguib et al. 2008). However, although the effects of developmental conditions on the expression of male traits are well established, there have been no empirical tests to date of whether developmental stress can affect female choice.

In this study we tested the hypothesis that female mate choice behaviour based on visually assessed, or other nonacoustic, traits may be sensitive to the effects of environmental conditions during early development. We investigated the effects of nutritional restriction on female choice in a model species for sexual selection studies, the zebra finch, *Taeniopygia guttata*. We raised female zebra finches under control conditions or conditions of nutritional stress, using an established experimental paradigm for developmental stress that has been found by several previous studies to reduce nestling growth rates and reduce song complexity of adult males (Spencer et al. 2003; Zann & Cash 2008), and which mimics a form of stress to which young birds are particularly vulnerable (Nowicki et al. 1998). In adulthood, we tested female mate choice in an extensive series of 128 four-way male choice tests using a randomized block design.

Our aim in this study was to quantify whether developmental stress in females affects their choice of males in adulthood. Our experimental design allowed us to elucidate in part the mechanisms that underlie any such effect. We predicted that if stressed females could not perceive male sexual traits as effectively as controls, there would be no correlation between the mate choice preferences of stressed and control females. In this case stressed females would show random choice but would invest as much time and energy in choice as controls. If perceptual ability was unaffected but stressed females were less choosy, they may also exhibit random choice but would invest less in sampling potential mates. If stressed females exhibit consistent preferences as a group, but these preferences are uncorrelated with those of controls, it would imply an effect of stress on the way females assess male cues, particularly if stressed females also showed reduced sampling behaviour. Since, in this experiment, we did not manipulate males' developmental histories, it would not be possible to detect assortative mating on the basis of developmental stress.

EXPERIMENT 1: FEMALE CHOICE WITH NONACOUSTIC CUES

Methods

Experimental subjects

Subjects were 32 adult female zebra finches raised at the Max Planck Institute for Ornithology in Seewiesen, Germany, as part of an experiment designed to test the heritability of neural morphology in male zebra finches. These females were the offspring of 20 pairs of laboratory-raised birds which were partnered randomly and allowed to raise two broods in succession. Each pair raised both broods either under control conditions or

under conditions of nutritional stress, with this treatment allocated randomly. Unavoidably, some of the experimental females were genetic siblings.

Experimental manipulations, designed to induce different levels of nutritional stress, took place between days 5 and 30 after the chicks hatched. We used a modified version of the feeding protocol described by Spencer et al. (2003), in which control nests were provided with ad libitum seed mix while those in the stress treatment received a limited mass of seed daily, the amount of seed provided being adjusted for brood size and the age of the chicks. In addition, the seed provided for nests under the stress treatment was mixed with husks in a 1:2 ratio by volume. After 30 days of age all cages received ad libitum seed.

The aims of the larger study necessitated a partial cross-fostering design in which half of the chicks in each brood were cross-fostered to a different brood of similar age (hatching dates within 1 day of each other), within 3 days of hatching, maintaining the original brood size. Seven pairs of genetic sisters originating from the same brood were used in the experiment, of which six pairs had been separated by the cross-fostering and were raised in different nests. One pair of sisters was raised in the same foster nest under control conditions.

Until 60 days of age offspring were housed with their parents or foster-parents in cages measuring $40 \times 40 \times 40$ cm. At 60 days they were removed from their parent's cage but remained housed with their siblings. From day 80 onwards, birds from all treatment groups received identical treatment and were housed together in two sex-specific aviaries with large outdoor (416×242 cm and 302 cm high) and indoor (403×301 cm and 200 cm high) compartments. Throughout the breeding and rearing period the temperature was maintained at 21°C on a 12:12 h light:dark photoperiod. Of 47 broods, 24 were raised under control and 23 under stressed conditions (mean brood size [number of chicks hatched in each brood] ± 1 SD: control broods: 2.8 ± 0.8 ; stressed broods: 3.2 ± 1.1).

As adults (mean age in days \pm SE = 189.7 ± 8.2), the female offspring were transferred to the University of Bristol for mate choice trials. All birds were housed in groups of six to eight per cage (118×50 cm and 212 cm high, Terenziani, Montichiari, Italy) and maintained at 21°C on a 12:12 h light:dark photoperiod, which coincided with the natural daylength in Seewiesen at the time the birds were transferred to Bristol. There were eight possible combinations of the different treatment factors (control or stress treatment, cross-fostered or not, brood 1 or 2), and four females from each combination were used in the mate preference tests. Of the females originally transferred to Bristol, three birds died before the experiment started and a further two were excluded as they were lame and unable to perch. From the remaining pool of birds, four females were selected at random from each of the eight possible combinations of treatments to give a total sample size of 32 females.

Morphological measurements

We weighed the offspring daily until 35 days posthatching and at days 40, 50, 60, 70 and 80, allowing us to look for effects of the stress treatment on nestling growth rates. At day 30, when the stress treatment ceased, we calculated the effect size (d) of the effect of the stress treatment on nestling mass as the difference between the mean mass of nestlings from the control and stress treatment groups divided by the pooled standard deviation in mass. After the completion of experimental trials (mean age in days \pm SE = 649.8 ± 13.4) we measured mass, mean wing length (mean length of both wings) and mean tarsus length (mean of three measurements from each leg) of all but one of the subjects from experiment 1 (one female had died

before the morphological measurements were taken), and all participants in experiment 2.

Mate choice trials

Female preferences for live males were tested in a mate choice apparatus previously described by Bennett et al. (1996, 1997) in earlier mate choice experiments on zebra finches and Pearn et al. (2001) on budgerigars, *Melopsittacus undulatus*. At the start of each trial, barriers that initially confine a subject female to a central arena are removed using a pulley system operated by the experimenter from outside the room. This leaves the subject female free to enter any of four viewing arms arranged in the shape of a cross, each of which terminates in a stimulus chamber containing a male. The stimulus chambers are separated from the rest of the apparatus by a clear Plexiglas filter such that the female can have visual (and potentially olfactory), but not physical, contact with the males. In an attempt to mask any auditory cues from the males, we played a sound recording of zebra finch vocalizations from their home cage throughout the trials (Pearn et al. 2001; Evans et al. 2006). This was also intended to reduce the stressful effects of isolation.

Electronically monitored perches in each viewing arm logged the number of hops made in front of each male, which has been found to be indicative of female preferences in a number of previous studies (Bennett et al. 1996, 1997; Evans et al. 2006). Opaque barriers beneath the perches ensured that females could only view the males from the perches and not when sitting on the floor. From the perch log data we also deduced how often the female moved from one viewing arm to another and thus how many opportunities she had to sample the potential mates. Although the perch log data indicated when a female switched from one viewing arm to another, it is not possible to determine whether females had returned to the central arena between consecutive hops in front of the same male or whether they remained in the viewing arm but did not move. It is likely, therefore, that while we accurately measured the number of switches from one male to another, this will underestimate the total number of sampling visits since several consecutive visits to the same male will be treated as one. Although it is impossible to determine from the perch logs the frequency or duration of visits to the central arena, observations of a subset of females in the apparatus indicated no difference between females from the control and stress groups. Indeed, the majority of females made few or no visits to the feeders.

During each trial the temperature was maintained at 21°C and all birds were provided with ad libitum seed and water, placed on the floor of each male chamber and in the central arena for the subject female. The apparatus was illuminated by 12 equally spaced 100 W Truelite fluorescent tubes (Durotest, Philadelphia, PA, U.S.A.), which provide spectral emissions similar to natural skylight, powered by high-frequency (>30 kHz) ballasts (Tridonic, Basingstoke, U.K.), to ensure that female preferences would not be affected by artificial lighting conditions (Bennett et al. 1996; Evans et al. 2006), and that lighting conditions were the same as earlier mate choice experiments using zebra finches (Bennett et al. 1996, 1997).

Four quartets of stimulus males were used ($N = 16$) and every quartet was presented to each of the 32 females over the course of the experiment resulting in a repeated measures design. The four males of each quartet were always presented together allowing us to compare the preferences expressed by different females. Each trial lasted 3.5 h and two trials were conducted per day. Each stimulus male was used in 32 trials over the course of the experiment and appeared in no more than one trial every 2 days. Females experienced four trials each with no less than 1 week between each trial. The order in which females were tested was determined

randomly without replacement, such that no female experienced a second trial until all 32 had completed their first trial. The four quartets of males were presented to the four females from each combination according to a randomized block design. In addition, the stimulus chamber in which each male of a quartet was placed was also randomized so that the four females of each treatment combination did not view the same males in the same locations. The time of day was balanced across females so that each female experienced two morning and two afternoon trials.

Acclimatization trials

Over the course of 2 weeks, immediately prior to the start of experimental trials each female experienced four acclimatization trials lasting 3.5 h each, intended to allow them to become familiar with the structure of the apparatus and to overcome any neophobia they might experience. During these acclimatization trials females were released in the apparatus in groups of six to reduce isolation stress and promote exploration of the apparatus. The four stimulus chambers each contained a conspecific female, rather than a male, to ensure that no association was formed between particular arms of the apparatus and preferred males, which could later bias behaviour in the experimental trials.

Stimulus males

The males used in the stimulus chambers of the mate choice apparatus during experimental mate choice trials were obtained from local breeders in the Bristol area. All males were adults (>100 days) at the time they were acquired but no further data were available regarding their ages. Sixteen wild-type males were randomly assigned to the four quartets.

Between trials, males were housed one quartet to a cage in the same room as, but not within visual contact of, the females. Measurements of wing length (mean length of both wings), tarsus length (mean of three measurements from each leg) and mass were taken at the completion of experimental trials.

Statistical analysis

Statistical analyses were performed using Minitab 15 (Minitab Inc., State College, PA, U.S.A.) and SPSS 16.0 (SPSS Inc., Chicago, IL, U.S.A.). To determine the effect of the stress treatment on nestling growth rates, we used two-sample *t* tests to compare the mean mass of nestlings from each treatment at the start of the experimental manipulation (5 days posthatching), and at day 30 when the stress treatment ceased. Two-sample *t* tests were also used to investigate the effects of the stress treatment on the mean adult wing length, tarsus length and mass of all the birds used in experiments 1 and 2.

To investigate the effects of the treatments on female choice we ran a repeated measures general linear model (GLM) using the total number of perches made in front of each male in a quartet over the course of each trial as the dependent variable. The perching data were log transformed to normalize the residuals. Female identity was the random term in the model. The original model included stress treatment, cross-fostering treatment and brood number as between-subjects factors and had two within-subjects terms: quartet and male identity, nested within the quartet with which each male appeared. The original, full-factorial model was simplified by sequential deletion of nonsignificant terms. There was a significant interaction between stress treatment and male quartet ($P < 0.05$). However, this interaction was judged not to be of major interest since it merely reflects variation in the effect of the stress treatment on female activity among randomly chosen male sets. The stress treatment*male quartet interaction term was, therefore, removed from the final model to allow us to calculate accurately the main effect of the stress treatment across all four quartets of

males. The final model included stress treatment as the only between-subjects factor and male quartet and nested male identity as within-subjects factors. Constraining the model to retain the other two between-subjects variables, cross-fostering treatment and brood number, or to retain the stress treatment*male quartet interaction, had no qualitative effect on the results.

There were six pairs and three trios of genetic sisters used in the experiment. To control for the potential nonindependence of sisters we ran a linear mixed model on the number of perches in front of each male, including both female identity and genetic family of origin as random terms. Stress treatment was the only fixed factor in the model.

To test whether trial order had an effect on female activity we ran a GLM using as the dependent variable the total number of perches made in front of all males over the course of a trial. The initial model included female identity as a random term, stress treatment, cross-fostering and brood as between-subjects factors and trial number as a within-subjects factor. After a process of model simplification by sequential deletion of nonsignificant terms the final model retained just subject identity, stress treatment and trial order. The total number of perches made during just the first hour of each trial was also analysed using the same model. To investigate the level of agreement between different females that had experienced the same treatment we calculated the repeatability of females' ranking of males relative to the other males of their quartets. We performed two nested ANOVAs, one for the rankings made by stressed females and one for control females, in which 16 males were nested within their four quartets. We then calculated repeatability using the method outlined by Lessells & Boag (1987), but comparing only the variation within quartets to the within-individual variation, and ignoring that component of the variation attributable to differences between the quartets (Forstmeier & Birkhead 2004). Fisher's *z* transformation was calculated to compare the repeatability of the rankings made by control and stressed females.

The number of switches made from one viewing arm to another did not follow a normal distribution and could not be normalized by transformation. A Kruskal–Wallis test was used to compare the total number of switches made across all four trials by females in the control and stress treatment groups. We also compared the mean number of hops made per visit to a viewing arm (total number of hops across all four trials/total number of switches across all four trials) by stressed and control females using a Kruskal–Wallis test.

Ethical note

The birds used in this study were raised under conditions of ad libitum food supply or nutritional restriction at the Max Planck Institute of Ornithology in compliance with the German animal protection law. Birds were monitored daily for signs of any adverse effect arising from the nutritional stress treatment, by an experienced animal technician, throughout the rearing and experimental periods. Mortality rates of nestlings in the control and stress treatments were very similar (mortality rate from hatching to fledging: controls: 4.3%; stressed: 4.8%). In addition, there were no long-term welfare issues arising from the nutritional restriction and survival rates of adults in the two groups did not differ significantly ($X^2_1 = 0.34$, $P = 0.56$). All birds that died during the experiment were examined by the University of Bristol's Veterinary Officer and the cause of death determined to be unrelated to the experimental protocol. This treatment protocol has previously been used to test the effects of developmental conditions on male sexual signals and neural development indicating there are long-term sublethal effects in males (Spencer et al. 2003; Buchanan et al. 2004). Experimental females were transported to Bristol by car

under the care of an experienced animal handler (S.L.), and in accordance with Defra import requirements (IIN A/9). The journey was made in two stages over the course of approximately 36 h, the females suffering no mortality either during the journey or in the following 48 h. Throughout the journey they were kept in individual compartments (12 × 17 cm and 13 cm high) of specially designed transport cages, provided with food, water and shade at all times, and were checked at regular intervals of 1.5 h during the journey. Experimental trials began approximately 4.5 months after the transfer of the females from Seewiesen to Bristol. The housing of birds in Bristol and the mate preference trials were conducted under approval from the Bristol University Ethics Committee.

Results

Growth rates and adult morphology

In concordance with previous studies (Spencer et al. 2003; Zann & Cash 2008) the stress treatment had a significant effect on nestling growth rates (Fig. 1). At the start of the treatment (day 5) there was no difference between the groups in body mass ($t_{31} = 0.8$, $P = 0.429$), but by the end of the treatment period (day 30) there was a small but significant effect of stress treatment on nestling mass ($t_{25} = 2.49$, $P = 0.02$; effect size, $d = 0.34$). Control nestlings were significantly heavier than those in the stress group. In adulthood there was no difference between the stressed and control females in wing length, tarsus length or mass (all $P > 0.05$).

Female preferences

There was a significant treatment effect on female activity in the mate choice trials (Table 1). Control females were significantly more active than those in the stress group (Fig. 2) and made almost three times as many hops (mean hops per trial ± 1 SE: controls: 654.1 ± 219.9 ; stressed: 230.9 ± 115.6 ; effect size, $d = 0.62$; Table 1). In addition, there was a significant effect of stress treatment on movement within the mate choice apparatus. The number of switches between viewing arms differed significantly, with control females moving between arms more often ($H_1 = 5.49$, $P = 0.019$). However, there was no difference between the treatments in the mean number of hops made per visit to a viewing arm ($H_1 < 0.01$, $P > 0.99$).

Figure 3 illustrates the activity of control and stressed females when viewing each different stimulus male and shows that female

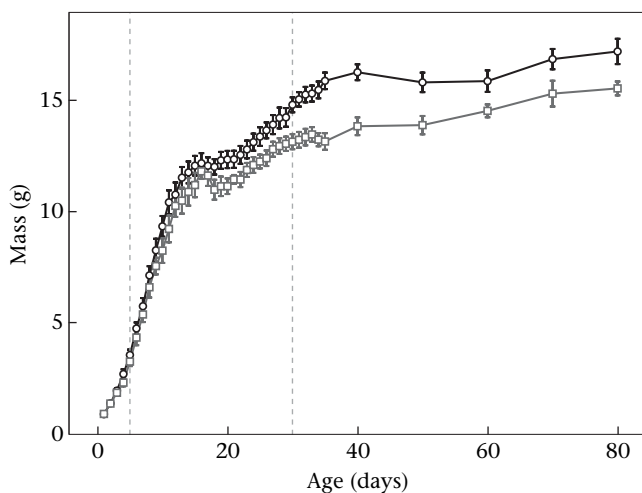


Figure 1. Growth rates of nestling zebra finches (mean mass of nestlings in each brood ± 1 SE) under control (open circles) and stress (open squares) treatments. Dotted lines indicate the start (day 5) and end (day 30) of experimental manipulations.

Table 1

Results of GLMs testing the effects of the stress treatment on the number of hops by females in front of different males and whether the total number of hops in each trial or in the first hour of each trial was affected by stress treatment and trial order

| Dependent variable | Model term | F | df | P |
|---|---------------------------------------|------|---------|------------------|
| Hops in each viewing arm | Stress treatment | 8.00 | 1, 30 | 0.008 |
| | Male quartet | 0.27 | 3, 465 | 0.849 |
| | Male identity (nested within quartet) | 3.07 | 12, 465 | <0.001 |
| | <i>Subject identity</i> | 8.86 | 30, 465 | <0.001 |
| Total number of hops per trial | Stress treatment | 8.85 | 1, 30 | 0.006 |
| | Trial order | 1.52 | 3, 90 | 0.215 |
| | Treatment*trial order | 0.34 | 3, 90 | 0.794 |
| | <i>Subject identity</i> | 5.30 | 30, 90 | <0.001 |
| Total number of hops during first hour of trial | Stress treatment | 5.41 | 1, 30 | 0.027 |
| | Trial order | 0.46 | 3, 90 | 0.708 |
| | Treatment*trial order | 1.24 | 3, 90 | 0.299 |
| | <i>Subject identity</i> | 6.32 | 30, 90 | <0.001 |

The random factor in each model, subject identity, is indicated in italics. Significant P values are indicated in bold.

hopping rates (for both control and stressed females) differed significantly between different males (Table 1), implying that some males were preferred to others. There was no difference in female activity rates between quartets of males (Table 1), indicating that, although attractiveness varied between males, no quartet of males received significantly more attention than others. After we controlled for the difference in activity rates noted above, there was no effect of the stress treatment on the difference in female activity between stimulus males ($P > 0.05$), so the stress treatment*male identity interaction term was therefore excluded from the final model. There was no significant difference in activity rates or preference between females raised in their natal nest or a foster nest, nor between females from the first and second broods, so cross-fostering and brood number were also dropped from the final model.

The effect of stress treatment on female activity remained significant when genetic family was included as a random term in the model ($F_{1,29.8} = 7.813$, $P = 0.009$), as did the effect of female identity (Wald $Z = 2.184$, $P = 0.029$). Genetic family did not have a significant effect (Wald $Z = 0.072$, $P = 0.943$).

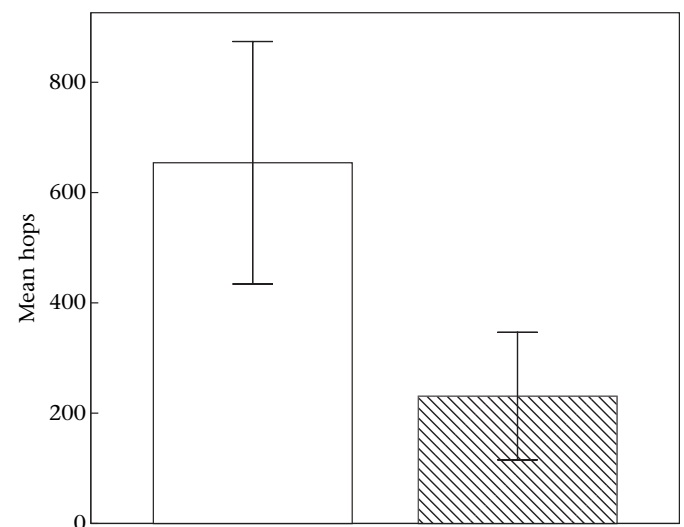


Figure 2. Mean number of hops (±1 SE) made per 3.5 h trial by control (white bars) and stressed (shaded bars) females.

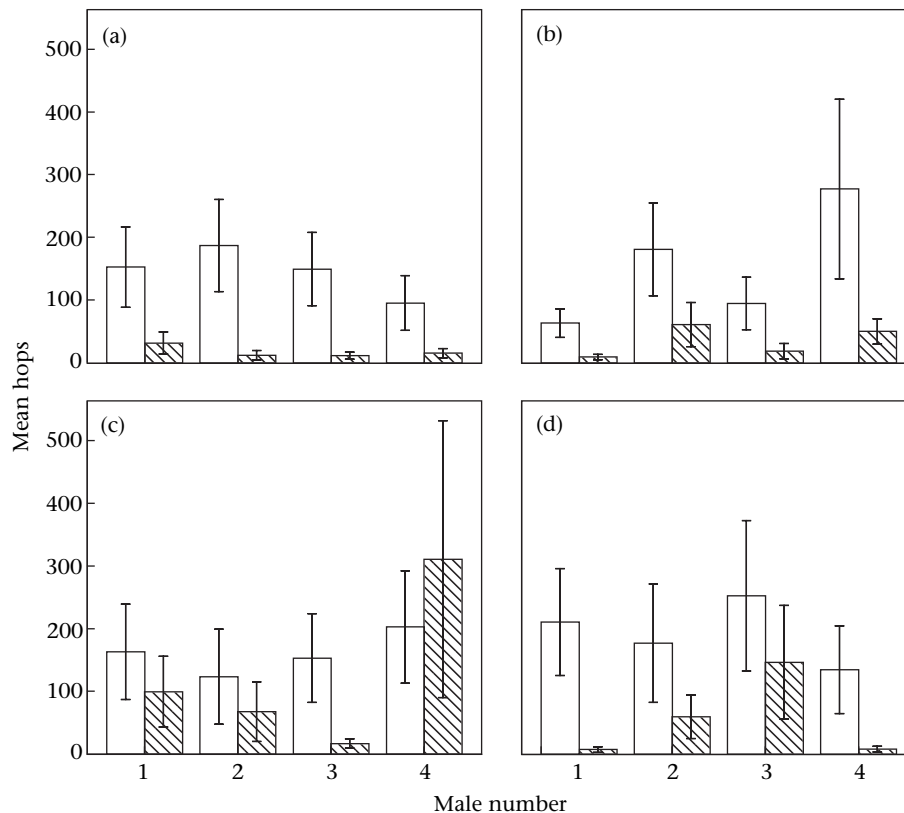


Figure 3. Mean number of hops (± 1 SE) made in front of each stimulus male by control (white bars) and stressed (shaded bars) females. (a–d) The four quartets of males.

There was no effect of trial order on female activity, nor was there a significant interaction between stress treatment and trial order (Table 1). The significant effect of stress treatment on activity levels noted above emerged even during the first hour of the trials (Table 1). During the first hour there was no interaction between trial order and treatment, nor a main effect of trial order (Table 1).

The relative rankings given to each male were significantly repeatable when the males were ranked by females from either control or stress treatments. However, this repeatability of male attractiveness was low (control females: $r = 0.06$, $F_{12,240} = 2.05$, $P = 0.021$; stressed females: $r = 0.06$, $F_{12,240} = 1.98$, $P = 0.027$) and there was no treatment difference in repeatability ($z = 0.01$, $P = 0.992$).

EXPERIMENT 2: EFFECT OF SOCIAL CONTEXT

Methods

Experimental subjects

The results of experiment 1 indicate an effect of stress treatment on activity rates in the mate choice trials. In experiment 2 we tested whether this effect was specific to a mate choice situation by looking at activity rates in different social contexts. We monitored the activity of control and experimentally stressed females in three contexts: alone, in visual, but not physical, contact with an unfamiliar female, and in visual contact with an unfamiliar male. Of the 32 subjects used in experiment 2, 25 had previously been used in the mate choice trials and the remaining seven chosen at random from a pool of five to seven available females from each combination of treatments. This was because experiment 2 took place 8 months after experiment 1 during which time four of the females used in those trials had died.

Activity rate trials

Females were transferred to a cage (118×50 cm and 50 cm high), identical to their home cages, except that it had a central divider of wire mesh, preventing physical contact but otherwise allowing birds on either side to have visual, acoustic and olfactory contact with one another. Each half of the cage contained two perches, those on the side containing the focal female being monitored so that the number of hops on each was electronically logged by a program (PerchLog, P.G. Lovell, School of Psychology, University of St Andrews, U.K.). The focal female was placed in one half of the cage and the number of hops she made was monitored over a 1 h trial, while the other side of the apparatus contained (1) no bird, (2) an unfamiliar female or (3) an unfamiliar male.

Four stimulus males and four stimulus females were used in this experiment, all of which were acquired from local breeders. Each stimulus male and female was used in eight trials and experienced a maximum of two trials per day. Each subject female experienced three trials, one in each social situation. The order in which females were used was determined randomly without replacement, such that no female experienced a second trial until all 32 had completed their first trial. The order in which females were exposed to the three social situations was allocated according to a randomized block design, and the half of the cage (right or left) in which the female was placed was randomized. Each of the four stimulus males and the four stimulus females was viewed by eight subjects, one from each treatment combination so that no two subject females from the same treatment viewed the same stimulus birds.

Statistical analysis

To investigate the effects of stress on female activity under different social conditions we ran a GLM in which the total number

of hops made by each subject female during each 1 h trial was the dependent variable and subject identity the random factor. Again, the hopping data were log transformed. The original model included stress treatment, cross-fostering treatment and brood number as between-subjects factors, and a single within-subjects term, trial type, which specifies the three social conditions (subject female alone, visual contact with a conspecific female, visual contact with a conspecific male). The original, full-factorial, model was simplified via sequential deletion of nonsignificant terms until a final model was specified, with one between-subjects term (stress treatment), a single within-subjects factor (trial type) and the interaction term between these factors. Constraining the model to include the other two between-subjects variables, cross-fostering treatment and brood number, had no qualitative effect on the results.

We investigated whether female activity levels in experiment 2 were consistent with activity levels in experiment 1. There were 25 females that participated in both experiments and for these birds we used Spearman rank correlation to compare the rank order of their total number of hops across all four trials in experiment 1 with their total activity across all three trials in experiment 2.

Results

Females were more active during trials in which they had visual contact with an unfamiliar conspecific than when they were alone ($F_{2,60} = 4.93$, $P = 0.01$; Tukey's test, pairwise comparison of female activity when alone versus conspecific female present: $t = -2.87$, $P = 0.016$; conspecific male present: $t = -2.55$, $P = 0.035$; Fig. 4). However, there was no difference in activity between trials in which the subject female could view a female or male conspecific (Tukey's test: $t = 0.32$, $P = 0.946$; Fig. 4).

Significant and large differences between the activity rates of control and stressed females were seen in the preference trials in experiment 1 but we found no effect of stress treatment on activity rates in experiment 2 ($F_{1,30} = 1.42$, $P = 0.243$; Fig. 4). There was a nonsignificant tendency for stressed females to be less active than controls under two of the three social contexts (alone; visual contact with unfamiliar male), but the activity differences were not significant in any of the three trial types (Tukey's test, pairwise

comparison of mean activity of control with stressed females in different trial types: female alone: $t = 1.62$, $P = 0.591$; conspecific female present: $t = 0.36$, $P = 0.999$; conspecific male present: $t = 0.87$, $P = 0.952$), and there was no interaction between stress treatment and trial type ($F_{2,60} = 0.40$, $P = 0.671$).

Females' ranked activity levels in this experiment showed a significant correlation with their activity in experiment 1 (Spearman rank correlation: $r_s = 0.48$, $N = 25$, $P = 0.016$).

DISCUSSION

In recent years there has been considerable interest in how developmental conditions can affect male signalling and attractiveness (Buchanan et al. 1999, 2003; Griffith et al. 1999; Nowicki et al. 2002; Spencer et al. 2003, 2004, 2005a, b; Gil et al. 2006; Naguib & Nemitz 2007; Naguib et al. 2008; Zann & Cash 2008). The condition dependence of many male signals is now evident (Andersson 1994), even when the signal is produced a long time after the cessation of the stressor (Buchanan et al. 2003; Spencer et al. 2003, 2005a; Naguib & Nemitz 2007; Zann & Cash 2008). This study constitutes the first experimental test of the effects of developmental stress on female preferences for live males.

Stressed females were almost three times less active than controls during the mate choice trials. The subjects in this study included several sets of genetic sisters. Since female activity levels in mate choice tests are likely to be heritable (Forstmeier 2005), the activity of sisters cannot be considered to be fully independent. However, the effect of stress treatment remains robust when genetic family is accounted for as a random effect. This demonstrates the potential for mate choice effects, owing to a reduction in the participation or possibly the motivation of stressed females for mate assessment. If such a reduction translated into a change in male assessment in the wild we predict that we would see altered mate choice behaviour in individuals that experienced stress during early development. Similar reductions in activity levels in a choice chamber have been observed in inbred female zebra finches (Bolund et al. 2010), perhaps implying a general difference in mate choice behaviour between high- and low-quality females.

We found a clear effect of male identity on female activity, demonstrating that males varied in their attractiveness to the test females. However, despite this, and despite the significant effect of the stress treatment on female activity, we found no difference between the treatment groups in their preferences for males. However, differences in the way females sample potential mates could still affect the outcome of mate choice even where females do not differ in preference since females that sample few potential mates will show less bias in their mate choice than those that choose between many (Wagner 1998).

Two- and four-way mate choice trials have previously detected strong, population level female preferences when a trait of interest in the stimulus males has been manipulated (e.g. Burley et al. 1982; Swaddle & Cuthill 1994; Bennett et al. 1996), but since we were investigating the possibility of an effect of stress on females' ability to discriminate between males, rather than on preference for a particular trait, we chose to allow subjects to choose between unmanipulated males on the basis of naturally occurring variation between them. Several studies have successfully used these experimental protocols to investigate female preferences for unmanipulated stimulus males (e.g. Bennett et al. 1997; Evans et al. 2006), and Holveck & Riebel (2007) found that female preference for live males in a two-way choice test was repeatable across several test paradigms and predicted female choice for song alone. However, Forstmeier & Birkhead (2004) found low levels of between-female agreement for unmanipulated males in a similar

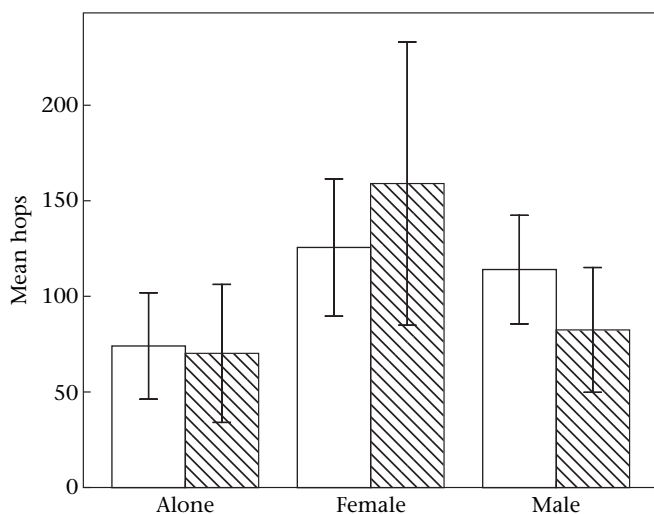


Figure 4. Mean number of hops (± 1 SE) made by control (white bars) and stressed (shaded bars) females in three social contexts: alone: focal female alone in apparatus; female: focal female had visual contact with an unfamiliar female; male: focal female had visual contact with an unfamiliar male.

choice environment. Although the relative rank preferences accorded to the stimulus males in experiment 1 were found to be repeatable, the repeatability was extremely low, in line with (although even lower than) those reported by Forstmeier & Birkhead (2004). These low levels of agreement between females imply that their preferences were relatively weak or that they varied between females, making it difficult to identify any treatment effect on preference. There was no effect of the stress treatment on the level of agreement between females.

Another criticism levelled at this methodology is that it is not possible to separate preference from sampling behaviour (Wagner 1998; Rutstein et al. 2007). If an individual samples potential mates more often before making a choice it can be harder to detect a preference (Wagner 1998): the female is likely to be more active in front of the less preferred males as part of her sampling behaviour, making it appear that her preference is weaker than that of a female that makes a choice after less sampling. It seems likely that, when the differences between stimulus males are less obvious, females will have to sample each male more often before making a choice, so our results may underestimate the strength of female preferences in this study. Additionally, the apparatus constitutes a novel environment and may promote stress in females. This could lead to reduced willingness to move around the apparatus with the result that females were unable to sample males sufficiently to make a choice. A final way in which our methodology may have underestimated preference strength is due to the stimulus males and experimental females being drawn from different populations. Genetic differences have been demonstrated to exist between populations (Forstmeier et al. 2007), and female preferences for various traits are known to be learned (e.g. Burley 2006), so it is possible that females might exhibit stronger preferences for males from their own population and be less able to assess attractiveness in males from other populations.

Females' relative activity levels in experiment 1 were significantly correlated with those in experiment 2, indicating that female activity is consistent over time and across different behavioural contexts. However, stress treatment had a significant effect on the overall activity rates of females during four-way mate choice trials in experiment 1 but not in no-choice trials in experiment 2. This difference in activity was not observed under any of the three trial types in experiment 2, allowing us to conclude that stress does not have a fundamental effect on activity rates per se, but instead has a context-dependent effect on behaviour. The two experiments differed in a number of ways (including novelty of the apparatus, length of the trials, time of year, age of the females, masking of potential acoustic cues, etc.), so it is impossible to draw clear conclusions from these data about exactly what behaviour is affected by stress. There are, however, several intriguing possibilities that should be addressed by future studies.

Experiment 1 used a traditional four-way mate choice design of a type that does not separate female preference from sampling behaviour (Wagner 1998; Rutstein et al. 2007), whereas the methods used in experiment 2 can be thought of as a no-choice trial in which sampling behaviour is not measured. An effect of stress on mate-sampling strategies would lead to a difference between control and stressed females in their behaviour in experiment 1 but remain undetected in experiment 2. If stressed females expend less time and resources on sampling potential mates this would support the prediction that females of lower quality should be less choosy (Cotton et al. 2006) and, moreover, could affect the outcome of mate choice in a natural context even if stress has no effect on preference function (Wagner 1998). In experiment 1, the number of switches made between viewing arms by control females (an estimate of how many sampling visits were made to the potential mates) was significantly greater than that of stressed females, but

there was no effect of stress treatment on the mean number of hops they made per visit. This supports the hypothesis that the difference in activity rates was the result of reduced sampling by stressed females. If there had been a difference in hopping activity per se, we would expect to see no difference in the number of switches, with stressed birds making fewer hops per visit than controls. Although the switching data may underestimate the number of visits females made to the viewing arms, since consecutive visits to the same arm could not be detected, observation of a subset of females in the apparatus suggests this bias is consistent across the treatment groups. We suggest, therefore, that our conclusion that control females made more sampling visits, switching more often between males, is robust, implying their mate choice sampling behaviour allows them greater opportunities to compare the available males.

There were several factors that differed between the two experiments and might have potentially led to a difference in behaviour unassociated with mate choice. One such factor was the novelty of the apparatus. In experiment 2 this was an adapted home cage while the mate choice chamber used in experiment 1 was largely unfamiliar. Females from the control and stress treatments differed significantly in their behaviour in this novel environment but not in the more familiar setting. A large body of evidence suggests that individuals differ consistently in suites of behavioural and physiological traits known as personalities or behavioural syndromes which are often measured by individual differences in behaviour in a novel environment (Sih et al. 2004; Groothuis & Carere 2005). It is an intriguing possibility that our results might represent an effect of early environmental conditions on females' propensity to explore a novel environment, and one that it would be interesting to see addressed in future studies. However, if the difference in activity levels between stressed and control females in experiment 1 was due to differences in exploratory behaviour or coping styles in a novel environment, we might expect an interaction between stress treatment and trial order with the difference between the treatment groups being reduced in later trials as the females became more acclimatized to the mate choice apparatus, which was not the case.

The duration of the trials in the two experiments was also markedly different: 3.5 h in experiment 1 and only 1 h in experiment 2. If the effects of developmental stress underlying the difference in activity levels observed in experiment 1 displayed a temporal pattern, emerging only over long periods of activity, the trials of experiment 2 might have been too short for them to appear. However, analysis of just the first hour's activity in experiment 1 reveals the same pattern as can be seen in the main analysis, with controls hopping significantly more often than stressed females.

Experiment 2 took place 8 months after experiment 1, so seasonal variation in mate choice behaviour could underlie the lack of consistency between the two. Wild zebra finch populations often breed continuously for 7–10 months of the year and breeding appears to be triggered by rainfall and the ripening of new supplies of seed (Zann et al. 1995; Zann 1996). Unlike periodically breeding species, zebra finch females' ovaries are maintained in a medium-developed resting state allowing rapid ovulation (Sossinka 1980). Because of these traits the zebra finch has traditionally been considered a nonseasonal, opportunistic breeder and it has been assumed that if diet, photoperiod, humidity and temperature are kept constant, as in our two experiments, there will be no effect of season on breeding behaviour. However, Williamson et al. (2008) found seasonal differences in maternal reproductive investment even under constant conditions. It is unknown whether there may be similar seasonal effects on behaviour in mate choice contexts.

Because of the difference in timing of the two experiments, the subject females were 8 months older during experiment 2 than they were at the end of experiment 1. The possibility cannot be

discounted that the difference in hops observed in experiment 1 is due to age-dependent rather than context-dependent effects of developmental stress. Age-dependent changes in reproductive success are found across the majority of bird species, reproductive success usually increasing with age (Martin 1995). If such age-dependent effects interacted with the effects of the stress treatment it is possible that any differences in activity levels or choosiness between control and stressed females reduce with age.

Our results clearly demonstrate that early developmental stress caused a reduction in female activity in a mate choice situation, which might potentially have profound consequences for both mate assessment and reproductive behaviour in natural populations. Both stressed and control females showed preferences for some males over others, which indicates that developmental stress did not reduce females' ability to differentiate between potential mates. There was no significant difference between the preferences of stressed and control females which we would expect if females preferred males with similar developmental histories to themselves, or if control and stressed females were assessing males according to different criteria. Stressed females were less active in a mate choice context than controls, and made fewer visits to the viewing arms, consistent with the hypothesis that stressed females invest less in sampling potential mates. Reduced sampling effort is an expected outcome of reduced choosiness in females.

Although our results do not allow us to differentiate clearly between all possible hypotheses, they are most consistent with the possibility that developmental stress causes reduced choosiness in females. This hypothesis is in concordance with several previous studies that have looked at the effects of the rearing environment on female choice (Hingle et al. 2001; Hunt et al. 2005; Hebets et al. 2008). The long-term repercussions of the early environment on adult behaviour, and their implications for mate choice, have been hitherto largely neglected, but our study demonstrates the importance of understanding the contribution of environmental factors to variation between individuals in mate choice behaviour.

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