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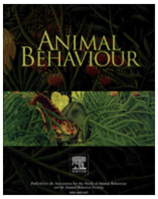

Experimental manipulation of the rearing environment influences adult female zebra finch song preferences

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In songbirds, sensory and social learning processes in juveniles contribute to variation in male song and female preferences. The developmental stress hypothesis proposes that suboptimal early development affects the costly brain structures involved in male song learning and, as a consequence, song quality. As an extension of this hypothesis we tested in this study whether developmental conditions also modulate female song preference acquisition. We tested song preferences in adult female zebra finches, *Taeniopygia guttata*, originating from a brood size manipulation experiment that had induced differences in mass, condition, immune response and levels of plasma testosterone at the early nestling stage. During the song-learning phase, juvenile birds were housed in small mixed-treatment groups with unrelated adult male song tutors. Adult females' song preferences were tested in an operant set-up where females could trigger different song playbacks by pecking different response keys. When females could choose between their own and an unfamiliar tutor's song they preferred their tutors' songs independent of experimental brood size. However, when females chose between two unfamiliar songs there was a significant effect of experimental brood size on preference strength: females from small broods showed significantly stronger preferences than those from medium and large broods. Hence, both females' rearing environment and sensory learning processes appear to contribute to variation in the direction and strength of female preference for male mating signals.

Sexual selection by female mate choice is widely accepted as a powerful selection force (Andersson 1994), but how development and the early rearing environment might contribute to variation in female mating preferences remains poorly understood and has rarely been addressed experimentally (Jennions & Petrie 1997; Widemo & Saether 1999; Cotton et al. 2006). This is in strong contrast to the research effort invested in the now well-documented condition or state dependency of male signals (Andersson 1994). Little is known about how environmental and social conditions experienced during early development might affect receivers' behaviour, such as the perception and decoding of mating signals (Widemo & Saether 1999). Costs and benefits of mate choice behaviour and preferences might shift through suboptimal development (Badyaev & Qvarnström 2002; Cotton et al. 2006). Such effects could play an important role in the evolutionary dynamics of mating signals. Females' preference functions, that is, their ranked preferences for different male phenotypes can be affected by early sensory learning processes, such as sexual imprinting in the visual or auditory domain in birds (ten Cate & Vos 1999; Riebel 2003a) or olfactory imprinting in mammals (Owens et al. 1999) and via as yet unidentified sensory mechanisms in fish (Verzijden & ten Cate 2007). However, at our current state of knowledge, it is unclear how such sensory learning processes during development interact with other environmental factors. Deficits in early nutrition, for instance, could constrain development of central and peripheral nervous systems (e.g. Buchanan et al. 2004; MacDonald et al. 2006) and the nutritional stress hypothesis suggests that this could negatively affect sensory learning (Nowicki et al. 1998).

In songbirds, male song plays an important role in mate choice (Searcy & Yasukawa 1996). Signal development and expression depend critically on sensory learning processes and are limited by a wide array of costs (Gil & Gahr 2002). Consequently, suboptimal conditions at crucial phases of development could be reflected in the accuracy of male song learning ('developmental stress hypothesis' Nowicki et al. 1998; Buchanan et al. 2003; Spencer et al. 2003; Gil et al. 2006; Holveck & Riebel, in press; Zann & Cash 2008).

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Here, we tested the hypothesis that sensory learning processes in females (Riebel 2003a) may be similarly sensitive to conditions experienced during early development. We tested this hypothesis by investigating the effects of brood size manipulation on female song preference development in zebra finches, *Taeniopygia guttata*, a model species for studies of vocal learning and sexual selection (Zann 1996; Riebel 2009). Zebra finches do not fully compensate for the increased nutritional needs of larger broods: chicks from larger broods are smaller and have lower body mass than those from small broods, even under ad libitum feeding conditions in domesticated and wild stock birds (de Kogel & Prijs 1996; Naguib et al. 2004; Tschirren et al. 2009). Brood size manipulations keeping within the natural range thus provide an excellent experimental procedure of inducing ecologically relevant variation in early condition. The females tested in this study originated from a brood size manipulation experiment in which nestling growth, body condition and immune response had been found to be negatively affected by increasing experimental brood size while nestlings' plasma testosterone levels (indicating physiological adjustment to higher levels of competition) increased with number of siblings in the nest (Naguib et al. 2004). Because both male advertising song and female song preferences are influenced by subadult sensory learning processes in songbirds, next to our experimental manipulation of rearing conditions, we also experimentally controlled subjects' song experiences during the sensitive phase for song learning just after nutritional independence (see methods in Gil et al. 2006).

To test whether the experimentally induced variation in early rearing conditions had affected subadult preference learning, upon reaching sexual maturity, each female was given the choice between the specific tutor song she had heard earlier (at the age when song experiences lead to long-lasting preferences, Riebel 2003b) and an unfamiliar song ('tutor versus unfamiliar') in an operant set-up. This set-up allowed us to test female song preferences independently of variation in other male traits or behaviour (Riebel 2000) and song preferences measured this way predict preferences for live males in this species (Holveck & Riebel 2007). Second, to test whether the treatment had affected their preference for qualitatively different stimuli, females were given a choice between two unfamiliar songs of different duration ('short versus long') as female zebra finches have been reported to prefer long over short song (Clayton & Pröve 1989; but see Leadbeater et al. 2005; Holveck & Riebel 2007) and because male song duration can be affected by early nutritional condition in this species (Spencer et al. 2003; but see Gil et al. 2006; Holveck et al. 2008; Zann & Cash 2008).

Table 1
Sample sizes per experimental brood size and days taken to learn the operant task

Brood size	*N*		Number of females		Days to keypecking ($\overline{X}\pm$SD)	
	Broods	Females	SelfLearn*	Training	All SelfLearn†	All training‡
2	5	6	2	4	3.8±3.6	1.0±1.7§
3	5	8	5	3	3.6±2.2	1.3±1.2
4	9	19	10	9	4.2±1.9	1.7±1.6
5	2	6	3	3	3.8±1.6	1.7±2.1
6	6	14	9	5	4.3±2.3	3.4±1.7
All	27	53	29	24	4.0±2.2	1.9±1.7

From the initial 56 adult females from the brood size manipulation experiment, two died before the preference tests started and one (from an experimental brood size of two) never learned to peck the keys, leaning a sample size of $N = 53$ females. Number of days to learn the operant task did not differ between experimental brood sizes (one-way ANOVA: all females: $F_{4,51} = 0.15$, $P = 0.96$; females with training: $F_{4,22} = 1.4$, $P = 0.27$; females without training: $F_{4,24} = 0.9$, $P = 0.49$). Note that the training schedule aimed to maximize the number of females learning and was not standardized with respect to the quantity and timing of training. Hence, the number of days to key pecking is in this context not a proper measure of interindividual differences in learning speed.

* SelfLearn: females learning to press the keys by autoshaping.

† From the day a female was moved into the experimental cage.

‡ From the first day with training to key pecking.

§ Data of one bird excluded because a technical problem required us to repeat the training.

METHODS

Experimental Subjects

We used adult female offspring (≤F4) of laboratory-kept, wild-caught Australian zebra finches at Bielefeld University which had been raised by foster parents in a brood size manipulation experiment (for details see Naguib et al. 2004). Chicks were cross-fostered 1–3 days after hatching in experimental brood sizes varying from two to six nestlings (Table 1) which is within the natural range of this species (Zann 1996). A cross-fostered brood always consisted of siblings from more than one brood and original broods were never wholly cross-fostered. The brood size manipulation had various effects on juvenile morphology and condition: at age 10 days posthatching, body size, body weight, weight in relation to size (tarsus length, see Garcia-Berthou 2001) and immune response decreased with experimental brood size; nestling plasma testosterone levels increased with increasing brood size (for full details see Table 1 and Figures. 1 and 2 in Naguib et al. 2004). Because effects of a brood size manipulation might also affect the father's song output (Verhulst 2003; Brumm et al. 2009) and perhaps also other performance aspects of his song, the young from the different cross-fostered broods were split up at 35 days (full nutritional independence) and assigned to 19 different unrelated adult male song tutors in mixed-sex, mixed-treatment tutor groups (3–9 chicks, mean 5.8) in 19 different indoor aviaries (0.8 × 2.2 m and 1 m high or 0.9 × 1.9 m and 1.9 m high) in large indoor bird-holding facilities with at least three aviaries per room until a mean age ± SD of 89 ± 2 days posthatching. If housed with a live tutor at this age, both males and females will learn the tutor song, even if other males are singing in the same room in cages close by (Riebel et al. 2002). However, we additionally controlled for possible effects of tutor group housing by including tutor group as a random factor in all statistical analyses and by always using songs from a different room as unfamiliar stimuli. At the beginning and at the end of the tutoring phase (at 35 and 90 days posthatching) birds were weighed and measured again. Birds had by now caught up on weight and body condition (weight corrected for size) which no longer differed between the groups while the differences in body size persisted (Naguib et al. 2004). Females were then housed in groups of 15 (from different treatments and different tutor groups) in four indoor aviaries (0.92 × 1.8 m and 1.85 m high or 1 × 3 m and 3.3 m high) in large bird rooms with other single- and mixed-sex aviaries. All aviaries were equipped with wooden perches and were additionally enriched with natural branches as well as a sand floor. At a mean ± SD of 106 ± 19 days, females ($N = 56$) were moved to Leiden University. Here, they were housed in groups of seven or eight birds per cage (0.5 × 1 m and 0.8 m high) in the same bird room (lights on 0745–2145 hours 20–22 °C, and 40–60% humidity). Throughout, birds were maintained on an ad libitum food and water regime consisting of standard seed mix supplemented daily with germinated seeds and three times a week with vitamins (in Bielefeld) or with gisto-cal mineral–vitamin supplement and twice weekly with egg mix, fruit and greens (in Leiden).

Both Bielefeld and Leiden University have licences to keep and breed zebra finches; the experimental procedures we report here were reviewed and approved by Leiden University's animal experimentation ethical committee. After the song preference tests in Leiden, birds were returned to the Bielefeld colony where they were kept in large mixed-sex aviaries (1 × 3 m and 3.3 m high or