



Female zebra finches learn to prefer more than one song and from more than one tutor



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Birdsong is a culturally transmitted mating signal: young birds learn specific variants of species-specific song(s) from conspecific models. Female song preferences are also learned early in life, but despite the potential functional implications of such learned mating preferences, we still have a poor understanding of when and from whom females learn. This also holds true for one of the foremost models of vocal learning, the zebra finch, *Taeniopygia guttata*. Both male and female zebra finches memorize their tutor's song motif: as adults, males will sing and females prefer their tutor's song. We here tested whether juvenile females would also learn to prefer the songs of several individuals, and whether the timing and propensity of song preference learning were condition dependent. Young females raised and cross-fostered in experimentally manipulated brood sizes were exposed to several model songs: first their foster father's song until nutritional independence (days 0–35) and then as subadults to playbacks of two different tutor songs (days 35–65). As adults, females preferred all three model songs over unfamiliar songs. There were no interaction effects between females' early rearing conditions (brood size) and preference strength for the different tutor songs. An additional live-tutored group had equally strong preferences for the foster father's song (only heard before day 35) as the tape-tutored females. The combined results demonstrate that subadult females memorize several song types during different times of development and as adults prefer these songs over unfamiliar songs. These findings imply that multiple song learning needs to be taken into account for avian mate choice studies even in species that lack song type repertoires but show individual differences in song.

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Learned mating preferences are increasingly recognized as an evolutionary force but to estimate their qualitative and quantitative impact on population dynamics, the strength and direction of learned versus experience-dependent preferences need to be better documented (e.g. [Verzijden et al., 2012](#)) in order to improve modelling approaches ([Lachlan & Nowicki, 2012](#)). In songbirds (oscines), (learned) song is an important mating signal ([Catchpole & Slater, 2008](#)) but while the process of (male) song learning is relatively well studied, our understanding of female song production and preference learning lags behind in all aspects ([Kroodsma, Vielliard, & Stiles, 1996](#); [Riebel, 2003b](#); [Riebel, Hall, & Langmore, 2005](#)) although the 'when' and 'from whom' females learn their preferences have turned out to be crucial parameters in theoretical models for the evolution of learned birdsong ([Lachlan & Nowicki, 2012](#); [Ritchie, Kirby, & Hawkey, 2008](#)). Zebra finches, *Taeniopygia guttata*, are one of the few species in which song acquisition in

females has seen some systematic study (for reviews see [Riebel, 2003a, 2009](#)). Complex courtship song in zebra finches is produced only by adult males: each male sings an individually distinctive song motif that closely resembles an adult song model (the 'tutor song'). As shown by sequential exposure to different tutors, the peak of the sensitive phase for (male) song production learning is between 35 and 65 days posthatching ([Slater, Eales, & Clayton, 1988](#)). Although females do not sing, several experimental studies have shown that females learn about songs as juveniles too: after maturation, which can be as early as 100 days ([Zann, 1996](#)), adult females have been shown to prefer the song of the adult male with which they had been housed between 35 and 65 days posthatching over the song of an unfamiliar male, showing cultural transmission of song preferences is possible along nongenetic lines ([Clayton, 1988, 1990](#); [Miller, 1979](#); [Riebel, Smallegange, Terpstra, & Bolhuis, 2002](#)). Song preferences in female zebra finches have been validated as predictors of live male preferences and mating decisions (for a review see [Riebel, 2009](#)). Cross-fostering between the subspecies *T. g. guttata* and *T. g. castanostis* has shown that females not only learn preferences for specific songs but also generalize some of the subspecies' structural

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features (Clayton, 1990); however, how generalization processes of learned preferences affect variation at the within-population level is poorly understood (Riebel & Smallegange, 2003). Early exposure to song playback alone ('tape tutoring') is sufficient to induce a stable (repeatable) preference in females for that particular song over unfamiliar songs (Riebel, 2000) which provides us with a method with excellent stimulus control to expand on these earlier studies. Although experimental studies have provided good evidence that adult song preferences develop at least partly by learning from models (Riebel, 2003a), the details regarding when and from whom female zebra finches learn are still poorly understood. For one, there is no clear delineation of the duration of the sensitive phase as there has not been the same experimental work in females as in males (Riebel, 2003a). For males, memorization of song can begin as early as 25 days posthatching but these early song memories translate into adult song (which fully crystallizes at maturation at around 100 days posthatching, Zann, 1996) only if the male is experimentally deprived of further song input during the remainder (and peak) of the sensitive phase (35–65 days posthatching; Böhner, 1990; Jones, ten Cate, & Slater, 1996). Outside such experimental situations, males of this colonial species are, however, continuously exposed to song (Zann, 1996) and will preferentially learn those songs heard during the sensorimotor learning phase (35–65 days) as evidenced by the young male's song resemblance to these later rather than the earlier songs (Slater, Richards, & Mann, 1991). Females can also start memorizing song as early as day 25 as evidenced by increased calling of nestlings towards familiar over unfamiliar songs (Clayton, 1988), but whether these memories persist into adulthood if females are subsequently exposed to other songs has not been tested. Moreover, experiments on juvenile song preference learning have exposed females to only one type of song during the (putative) sensitive phase from 35 to 65 days posthatching. However, in more natural settings young females are likely to hear more than one type of song during this phase. Up until 35 days posthatching birds are cared for by both parents and will have predominantly heard their father's song, but when zebra finches become nutritionally independent at around 35 days posthatching they will start flocking (Zann, 1996). From this stage onwards they are exposed not only to the songs of their father but also to more than one singing male throughout the sensitive period for song learning.

Our first aim in this study was therefore to test the hypothesis that females could simultaneously learn more than one tutor song during the putative peak of the sensitive phase postindependence (i.e. 35–65 days posthatching, see Riebel, 2003a) if exposed to recordings of two different songs throughout this phase. If both songs were memorized, as adults females should show preferences for both tutor songs over unfamiliar songs. Our second aim was to test whether females would also learn several songs sequentially, more specifically whether females would also prefer the song they had only heard before independence (i.e. until 35 days posthatching) even if thereafter they heard only other songs. Again we predicted that if all sequentially heard songs were memorized, as adults, females should show preferences for all tutor songs over unfamiliar songs. Third, because effects of rearing condition on cognitive functions within mate choice contexts are increasingly hypothesized but rarely tested empirically (Boogert, Fawcett, & Lefebvre, 2011; Buchanan, Grindstaff, & Pravosudov, 2013; Riebel, 2011; Ritchie et al., 2008) we tested whether female condition would affect the timing and/or quantity of learned songs. If adverse developmental conditions affect memorization then, as adults, females from low-quality rearing environments should show weaker (or even no) preferences for the tutor songs over unfamiliar songs than females from high-quality rearing environments. To this end, all tests were run with females from an experimental brood size

manipulation that in past studies and in our birds had induced significant differences between birds from small and large brood sizes in morphology, physiology, adult song and social-learning preferences (Holveck & Riebel, 2010; Riebel, Naguib, & Gil, 2009; Riebel, Spierings, Holveck, & Verhulst, 2012; Verhulst, Holveck, & Riebel, 2006). All females first heard the song of their foster father while being reared in experimental small (two to three chicks) or large (five to six chicks) brood sizes. Upon reaching nutritional independence at day 35 posthatching, females from different rearing nests were experimentally matched to form pairs consisting of one female from a large and one from a small brood. From then onwards each pair of tape-tutored females was exposed to playbacks of two different songs for the remainder of the sensitive phase for song learning. This allowed us later on to compare individual pairs of females of different rearing backgrounds for the quantity and strength of song preference learning by testing how many of the early tutor song types they would prefer (and how strongly) over unfamiliar songs in adulthood. No previous study has investigated whether early live tutoring (until nutritional independence at day 35 days posthatching) preceding the tape tutoring might bias song memorization of females towards the live tutor of the early juvenile phase. The timing and model selection in male song learning can be affected by when and how males encounter a live tutor (Böhner, 1990; Jones et al., 1996) and this might also hold for female preference learning. We hypothesized that the absence of a live tutor postindependence could potentially bias preferences towards the preindependence tutor in tape-tutored females more so than in live-tutored females. Therefore, when females were tested for preferences for the early live tutor (i.e. their foster father) an additional group of females from the same brood size manipulation but raised in live-tutored, mixed-sex groups (Holveck & Riebel, 2010) was also tested for preferences for the songs they had heard before day 35 posthatching.

METHODS

Subjects and Housing Conditions

The subjects were a subsample from a large brood size manipulation experiment conducted in two breeding rounds in 2 different years (2004 and 2005) in the zebra finch breeding colony at Leiden University (Holveck, de Castro, Lachlan, ten Cate, & Riebel, 2008; Holveck & Riebel, 2010). To break correlations between parental quality and brood size and possible genetic links between fathers' songs and females' preferences, chicks ($N = 113$) of first-time breeders were assigned to nests of unrelated foster parents at 3 ± 2 days posthatching (mean ± 1 SD) to form either small (two to three chicks per nest) or large broods (five to six chicks) assigning siblings to different foster nests in different brood size categories (Holveck et al., 2008). Chicks were housed with their foster parents in standard laboratory cages (80×40 cm and 40 cm high) on a 13.5:10.5 h light:dark schedule (lights on 0700–2030 hours Central European Time) at 20–22 °C and 35–50% humidity. Cages had solid sidewalls and were stacked three cages high in three rows along the length of the room and with other birds in earshot and in sight at 2 m across the aisle. Throughout, birds had ad libitum access to a commercial tropical seed mixture (Tijssen, Hazerswoude, Holland), drinking water and cuttlebone. This was supplemented thrice weekly with egg food (Witte Molen, B.V., Meeuwen, Holland), twice with millet branches and once with germinated seeds. After the study, we returned the experimental birds to the colony.

All procedures followed to the ASAB/ABS Guidelines for the Use of Animals in Research and Dutch laws and were approved by Leiden University's Animal Experimentation Committee (Dier-experimentencommissie Universiteit Leiden, permit DEC 04090).

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