



Song-learning strategies in the Bengalese finch: do chicks choose tutors based on song complexity?

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Birdsong is an important sexually selected trait, and its acoustic features are socially transmitted in the process of song learning. The preference of some female songbirds for song complexity as measured by repertoire size has driven the evolution of many song traits and song-learning programs in males. If juvenile birds adopt the attractiveness of model birds by copying their repertoires, tutor choice in the early song-learning period should be crucial for future reproductive success. Thus, we hypothesized that the song quality of tutors influences the tutor choice of chicks in the Bengalese finch, *Lonchura striata* var. *domestica*. Each subject chick was reared by a foster pair in an individual breeding cage. At around the fledging period, we introduced another unrelated adult male (subtutor) into each cage to simulate the natural social environment in which chicks have opportunities to hear the songs of nonfather males after fledging. Subject chicks learned from both tutors when the total note repertoire size of the two models was small; they tended to learn from the subtutor when the father had a smaller note repertoire size. The acquired note repertoire size was not affected by whether subjects learned songs from the foster father or not. Song learning from the subtutor contributed to a larger note repertoire. Observed patterns in tutor choice, in particular song learning from a subtutor, could be an adaptive strategy that helps chicks compensate for exposure to smaller repertoire size in models.

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Birdsong differs from other major sexually selected traits in that it involves social learning. Learned acoustic features of songs largely affect male reproductive success through female mate choice and territory maintenance (reviewed in Collins 2004; Catchpole & Slater 2008). Songbirds (oscine species) show a great diversity in their song-learning programs with particular regard to the timing of learning (reviewed in Marler 1990; Brenowitz & Beecher 2005), repertoire size (reviewed in MacDougall-Shackleton 1997; Garamszegi & Møller 2004; Garamszegi et al. 2005) and the role of social stimuli associated with song learning (reviewed in Marler 1990; Baptista & Gaunt 1997; Beecher & Burt 2004). This diversity can be explained by the relative importance of two song functions: song sharing with territorial neighbours and attracting mates by singing songs with large repertoires (Beecher & Brenowitz 2005).

Given that birdsong is a culturally transmitted behaviour, social factors play key roles in the transmission process of songs (Freeberg 2000; Beecher & Burt 2004). Because oscine juveniles match the song features of their tutors through vocal learning, tutor selection early in life should have a crucial effect on reproductive success in later life. Evidence from field studies suggests that the father is the most likely tutor in some species, possibly because of its frequent interactions with the chicks (zebra finches, *Taeniopygia guttata*: Zann 1990; Darwin's finches, *Geospiza fortis* and *G. scandens*: Grant & Grant 1996). However, on occasion the chicks can learn from multiple tutors (song sparrows, *Melospiza melodia*: Nordby et al. 2000) and incorporate their repertoires into their own songs (zebra finches: Slater & Mann 1990; Williams 1990). In some territorial species, yearlings learn songs from their territorial neighbours (indigo buntings, *Passerina cyanea*: Payne & Payne 1993; dunnocks, *Prunella modularis*: Langmore 1999; chipping sparrows, *Spizella passerina*: Liu & Kroodsma 2006). Presumably, such a song-learning strategy is favourable for efficient territory establishment among the local males. However, few previous studies have reported on tutor choice patterns that are advantageous for attracting mates.

For approximately two decades, tutor choice among songbirds has often been investigated in the zebra finch. This finch belongs to

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the family Estrildidae and is classified as an age-limited learning species, similar to the Bengalese finch, *Lonchura striata* var. *domestica* (Brenowitz & Beecher 2005). The estrildid finches produce songs mainly for courtship and not for male–male competition (Goodwin 1982; Zann 1996; Okanoya 2004a). Previous studies on captive zebra finches have reported that tutor choice is influenced by multiple factors, including kinship (Böhner 1983; Roper & Zann 2006), social interactions (Clayton 1987), spatial proximity (Mann & Slater 1995; Nordby et al. 2000), morphological similarity to the father (Mann et al. 1991; Mann & Slater 1995) and pairing status (Mann & Slater 1994). These factors seem to facilitate song learning from the fathers under natural breeding conditions and contribute to acquiring species-specific songs. If a father sings unattractive and less complex songs, resulting in inherited song qualities with detrimental effects on the reproductive success of male offspring, the chick may select a different tutor from which to learn the song. However, this hypothesis has not yet been tested. Since song quality affects mate acquisition, song-learning programs including tutor choice have probably evolved under intersexual selection pressure to maximize song complexity, such as song repertoire size.

The males of the Bengalese finch have a repertoire of one song, which consists of discrete syllables (notes). In previous studies of this species, song complexity has been measured by the number of distinct note types and the versatility of note-to-note order (respectively referred to below as note repertoire size and syntactical complexity), and the latter measure is especially associated with attractiveness of males (Honda & Okanoya 1999; Okanoya 2004a, b; Soma et al. 2006b). The Bengalese finch is a domesticated strain of the white-rumped munia, *Lonchura striata*, resulting from selective breeding for plumage colour, but without artificial selection for song (Okanoya 2004a, b). Bengalese finches sing songs with syntactically complicated (i.e. nonlinear) note order compared to the ancestral strain (Honda & Okanoya 1999; Okanoya 2004a). This greater song complexity has probably developed via a shift in the species' song-learning ability under intersexual selection pressure because Bengalese finch females prefer complex songs (Okanoya 2004a). In previous studies, playbacks of syntactically complex songs elicited increased reproductive behaviour in females (Okanoya 2004b), and more females chose complex songs in perch choice tests (Morisaka et al. 2008). The wild strain of the Bengalese finch moves around and breeds in small flocks and shows almost no aggressiveness to conspecifics even when breeding, similar to the domesticated strain (Goodwin 1982; Restall 1996). This sociality might give rise to the opportunity for young birds to learn songs from unrelated adult males.

Our aim in this study was to test whether the tutor choice of young Bengalese finches is affected by the song quality of tutor males to which they are exposed. Each subject chick was reared by a foster pair in an individual breeding cage. At around the fledging period, we introduced another unrelated adult male (subtutor) into each cage to simulate the natural social environment in which chicks are exposed to the songs of nonfather males after fledging. We hypothesized that the tutor choice of young birds contributes to the acquisition of attractive songs that are acoustically complex in terms of note repertoire size and syntactical complexity. Estrildid juveniles are assumed to show a tendency to learn songs from the foster father (main tutor), according to previous studies of tutor choice in the zebra finch (Böhner 1983; Mann et al. 1991; Mann & Slater 1995; Roper & Zann 2006). However, we predicted that young birds would be able to incorporate note repertoires from another male (subtutor) into their songs to acquire more complex songs. Hence, in this study, we investigated whether tutor choice of the Bengalese finch is affected not only by tutor status (main or sub) or the duration of time chicks are exposed to tutors, but also by tutor song complexity.

METHODS

Study Species

Although the song-learning period of the Bengalese finch has not been well examined, it is usually assumed to be close to that of the zebra finch, which begins as early as 25 days of age and ends around 80–90 days of age (Zann 1997) or somewhat later (Takahasi et al. 2006). According to our experience with captive populations of the Bengalese finch, birds that are caged with parents until 120 days of age develop normal song, and the song features recorded at around 4 months of age do not change afterwards.

Breeding Procedures and Song Tutoring

Bengalese finches were maintained in our laboratory (Brain Science Institute (BSI), RIKEN, Japan) and were paired in individual breeding cages (45 × 45 × 45 cm) equipped with one nestbox each. Each cage was isolated visually, but not acoustically. These rearing conditions were sufficient to prevent young birds from learning songs from birds in other cages because song learning in this species requires social interactions (Immelmann 1969). Throughout this study, birds were maintained in a controlled environment suitable for breeding (24 ± 3 °C, 30–50% humidity and 14: 10 h light: dark photoperiod) and provided ad libitum with a finch seed mixture, foxtail millet coated with egg yolk, water, shell grit and green vegetables. We checked each nest every morning, and the newly hatched chicks were marked with nontoxic waterproof coloured pens for individual identification.

Colour marking was sufficient for individual identification, but we also needed to obtain DNA samples for sexing subjects while young for the experimental fostering design. Therefore, we clipped the tip of one toe (approximately 1 mm, only tissue without bone) of each hatchling with dissecting scissors for DNA sexing. This procedure was usually accompanied by little or no bleeding. In rare cases when birds bled, the toe was treated with pressure haemostasis and antiseptic. Toe clipping was used because it allowed minimal handling time and we thought it would cause minimal stress, compared to blood sampling or removal of a growing feather. Anaesthetic could not be used because it could cause serious harm to hatchlings of this altricial species, which are very tiny and undeveloped. We carefully monitored the condition and health of all birds on a daily basis, especially after the toe clipping, and observed no incidence of infection or mobility problems. Although the toenails did not regrow, the birds were able to perch normally as adults.

Molecular sexing was performed from genomic DNA extracted from toe clippings using a standard phenol–chloroform extraction (Soma et al. 2007). As our previous study has revealed, the stress of sibling competition (e.g. brood size and sex ratio) affects song-learning ability (Soma et al. 2006b). Thus, all subject chicks were reared in a controlled brood environment by cross-fostering manipulation. The cross-fostering was designed to create broods with two males and two females.

In total, 64 nestlings (32 males and 32 females) from 16 broods of 11 pairs were cross-fostered to 16 broods after molecular sexing (at 2–13 days of age). Because two male chicks died at around the fledging period, 30 males were analysed in the present study. Each brood was reared by a foster pair until around the fledging period of the subject chicks (median age = 27 days, range 22–33 days) when the subtutors were additionally introduced into each breeding cage. The foster father is referred to below as the main tutor. Nine paired main and subtutors were used and seven of them were exposed to two broods. Because main and subtutors belonged to different breeding lineages of laboratory breeding populations, the two groups of tutors did not share the same note types. The

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