ORIGINAL PAPER

Early ontogenetic effects on song quality in the Bengalese finch (*Lonchura striata* var. *domestica*): laying order, sibling competition, and song syntax

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Abstract Birdsong differs from other sexual traits in that the acquisition process involves learning. Especially in close-ended learning species like the Bengalese finch, conditions experienced during the critical song-learning period can have a profound influence on song quality. Therefore, to understand song evolution from a life-history perspective, we investigated early ontogenetic effects on song quality. In particular, we focused on maternal effects and sibling competition. In asynchronously hatching bird species, the age hierarchy among nestlings affects physical development due to competition for food; mothers may influence this competition by adjusting their investment in each egg according to its sequence in the laying order. To independently assess these effects, chicks of the Bengalese finch were cross-fostered so that the age hierarchies formed in fostered broods were independent of the laying order. Our results indicate that song quality partially reflects early ontogenetic conditions, whereas song duration and note-type repertoire were independent of either laying order or age hierarchy. The syntactical complexity of note order declined over the laying sequence. This finding suggests that the song learning ability is influenced by within-clutch variation in maternal investment toward eggs. Considering that song syntactical complexity is subject to female

preference in the Bengalese finch, it is likely that maternal resource allocation strategies play a role in song evolution.

Birdsong is a sexually selected trait that consists of multiple factors. Female songbirds show a preference for various song features, such as performance and elaboration, which have driven the evolution of songs (Catchpole and Slater 2008). Indicator mechanisms of sexual selection suggest that exaggerated sexual traits are preferred by females; such traits indicate male quality by signaling that the male can pay the underlying cost of expressing the trait (Andersson 1994; Andersson and Simmons 2006). In a similar fashion, it is likely that both song performance and elaboration incur costs and thus reflect male quality (reviewed by Gil and Gahr 2002).

Oscine juveniles learn their songs based on model songs of adult males that are heard during a critical period, and the acquired acoustical song features change little after song crystallization, especially in close-ended learners (Marler 1990). Thus, it is possible that a male sings attractive, complex songs simply because he was exposed to good song models in early life. However, most recent literature does not regard song elaboration as completely cost free; it is highly likely that neural and endocrinological controls of song learning impose costs on the acquisition of song complexity (Gil and Gahr 2002; Podos et al. 2004); in this regard, the developmental stress hypothesis predicts that early growth conditions during the song-learning phase affect neural development and therefore song elaboration (Nowicki et al. 1998; Nowicki and Searcy 2004; Nowicki and Searcy 2005). Many studies have shown that the growth of the song control nuclei is obstructed by early

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developmental stresses such as food restriction and stress hormone administration (Nowicki et al. 2002; Buchanan et al. 2004; Spencer et al. 2005; MacDonald et al. 2006; but see also Gil et al. 2006). Although direct evidence showing the effect of early developmental stress on song elaboration is rather scarce (but see Spencer et al. 2003), Zann and Cash (2007) reported that early dietary restrictions can have detrimental effects on the song complexity, calculated as a principal component of six song variables in the zebra finch, *Taeniopygia guttata*. Moreover, Soma et al. (2006a) found that the intensity of sibling competition resulting from variable brood composition affects song quality in the Bengalese finch, *Lonchura striata* var. *domestica*, probably because sibling competition is tied to chick stress and nutrition levels. Specifically, male birds that were reared in large broods had small adult body size and sang songs with short bout durations, while males from large and male-biased broods sang less complex songs regardless of body size in comparison with the birds from small or female-biased broods (Soma et al. 2006a). These results indicate the possibility that neural development associated with song learning is partially independent of physical development.

Another parameter that might influence the development of song and its neural mechanisms is that of asynchronous hatching. In many avian groups, including songbirds, asynchronous hatching results from the onset of incubation before clutch completion, creating an age and size hierarchy within a brood; this hierarchy may cause higher stress levels (Masello and Quillfeldt 2004) and reduced growth or survival (reviewed by Krebs 1999) of nestlings that hatch later in the hierarchy, due in part to disadvantages in the competition for food. Therefore, in a wide range of asynchronously hatching bird species, mothers skew their investment in eggs by investing more (or less in some cases) in eggs that are laid later than in those that are laid earlier (Schwabl 1993; Schwabl et al. 1997; Gil et al. 1999; Reed and Vleck 2001; Pilz et al. 2003; Soma et al. 2007). Numerous studies have identified relationships between laying sequence and maternal investment in both egg size (e.g., Rutkowska and Cichoń 2002; Magrath et al. 2003) and yolk androgens (e.g., Schwabl 1993; Groothuis and Schwabl 2002). In particular, within-clutch variation in yolk androgen hormones (e.g., testosterone) has been well investigated and can have a profound influence on phenotypic differences in early life such as growth, competitive ability, and begging behavior (Groothuis et al. 2005).

In general, the early development of asynchronously hatching songbirds can depend considerably on laying and hatching order because of biases in both maternal investment and sibling competition. However, these two factors can have opposite effects on development when maternal investment favors later-hatched chicks to compensate for the disadvantages in sibling competition. Soma et al. (2007) conducted a cross-fostering experiment to independently assess the confounding influences of maternal effect (i.e., egg order) and sibling competition (i.e., age hierarchy in the foster brood) on physical development. Specifically, birds from eggs that were laid later in the laying order could grow larger when reared in older positions in the age hierarchy in fostered broods. Surprisingly, however, when reared in younger positions in the age hierarchy in fostered broods, birds from eggs that were produced earlier in the laying order grew larger than birds from later eggs. This phenomenon could not be explained by within-clutch variation in egg size (i.e., earlier eggs being smaller in size). Presumably, the phenomenon that individuals from earlier laying order eggs had heavier adult body mass under intense sibling competition (younger position in the age hierarchy) is attributable to the qualitative differences among eggs such as androgens that are assumed to enhance the competitive ability of chicks (Schwabl 1996; Lipar and Ketterson 2000; Eising et al. 2001; Rutkowska et al. 2007). In the zebra finch, which is closely related to the Bengalese finch (Zeng et al. 2007), yolk testosterone levels in male eggs decline with laying order (Gilbert et al. 2005), whereas egg mass increases with laying order, at least in a non-wild population (Rutkowska and Cichoń 2002; but also see Zann and Runciman 2003). In contrast, long-term maternal effects from yolk androgens have recently gained attention because sex steroids are strongly involved in the expression of sexual traits (Owens and Short 1995; Kimball and Ligon 1999) and in sexual differentiation of the brain and behaviors (Clark and Galef 1995; Schlinger 1998; also see Godsave et al. 2002). Several studies have experimentally demonstrated the link between maternally derived androgens and morphological secondary sexual traits (Strasser and Schwabl 2004; Eising et al. 2006; Rubolini et al. 2006), whereas behavioral traits have been less well studied, except for an inter-specific comparison suggesting the involvement of yolk testosterone in song evolution (Garamszegi et al. 2007).

We investigated the effects of early ontogenetic conditions on both song output (duration) and complexity (note-type repertoire and syntax of note order). Because we expected maternal effects in relation to laying sequence, in addition to the age hierarchy among brood mates (Soma et al. 2007), nestlings were preliminarily checked for egg order and cross-fostered to experimentally controlled broods. To simulate a natural social environment in a simple experimental setting and to avoid the ceiling effect of a single repertoire from the foster father's song, an unrelated adult male (subtutor) was introduced into the breeding cage around the time of fledging. These breeding situations allowed us to independently assess the potential influences of maternal effects (i.e., egg order) and rearing

conditions (i.e., age hierarchy in the foster brood) on song traits.

Materials and methods

Breeding procedures

Bengalese finches maintained in our laboratory (Brain Science Institute, RIKEN) were used as parents. These birds did not include siblings nor parent–offspring. They were paired in individual breeding cages (45×45×45 cm) equipped with one nest box. Each cage was isolated visually, but not audibly. Throughout the study, the birds were maintained in a controlled environment suitable for breeding (temperature 24±3°C, humidity 30–50%, 14 L:10D photoperiod) and provided with finch seed mixture, foxtail millet coated with egg yolk, water, shell grit, and green vegetables ad libitum. Each nest was checked every morning (i.e., 10:00–11:00 A.M.), and newly laid eggs were marked with nontoxic waterproof colored pens. Newly hatched chicks were marked in the same way and sexed molecularly using DNA extracted from toe clippings (for details see Soma et al. 2007). In most cases, only one chick hatched in a single day in a nest, but in rare cases when two or more chicks hatched on the same day, hatchlings could be assigned to eggs based on the dampness of their nestling down.

In total, 64 nestlings (32 males and 32 females) from 16 broods of 11 pairs were cross-fostered to create 16 broods. Because two male chicks died around the fledging period, a total of 30 males were analyzed. The cross-fostering was designed to create broods with two males and two females. The pairs of nestlings of the same sex were selected randomly to form a size and age hierarchy in each brood to simulate the situation of sibling competition caused by hatching asynchrony (Fig. 1) After cross-fostering, each brood included an older male (mass [mean ± SD]=4.8±1.5 g, median age= 9 days), an older female (mass=5.1±1.4 g, median age= 9 days), a younger male (mass=2.8±0.9, median age=6), and a younger female (mass=3.3±1.6, median age=5), but this size hierarchy among nestlings gradually faded around fledgling period (see also Soma et al. 2007 for the details of physical development). The age hierarchy formed in fostered broods was independent of egg order to distinguish the effect of egg order and sibling competition caused by age hierarchy (Spearman's rank correlation between egg order and age hierarchy: r_s=0.292, n=32, P=0.12). Nine adult pairs served as foster parents, and seven of them reared two broods at 3-month intervals. An additional nine adult males were used as subtutors and were introduced into the breeding cages around the time of fledging (median age=27 days) of the subject chicks. Cross-fostered subjects were kept in the
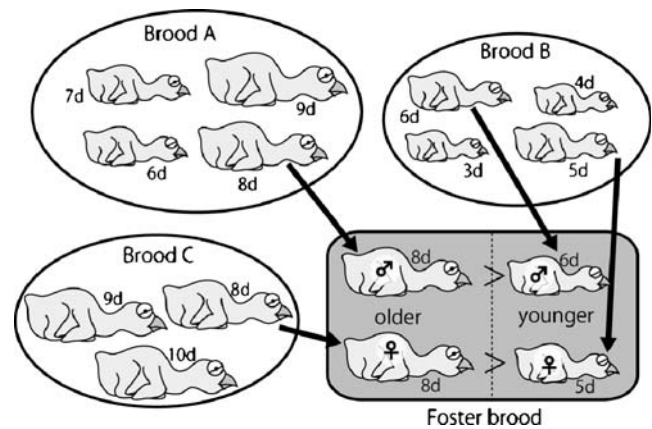
Fig. 1 Representation of cross-fostering design to create broods that involve an older male, an older female, a younger male, and a younger female. Age in day of each chick is indicated. The age hierarchy formed in foster broods was not related with laying and hatching order of natal broods

breeding cages with foster parents and subtutors until maturity when songs were recorded.

Song measurements

Bengalese finch males have a repertoire of one song, which is only used in courtship displays and not for between-male competition (Okanoya 2004b). Individual songs consist of discrete syllables called notes and can be characterized by the type and order of notes included in a song (Honda and Okanoya 1999; Okanoya 2004a; Soma et al. 2006b). Experimental studies have demonstrated that Bengalese finch females prefer syntactically complex songs (Okanoya 2004b).

When the subject males were fully mature (130– 140 days of age), their songs were recorded. Each bird was placed individually in a soundproof room, and its vocal output was recorded using a directional microphone (Sony, ECM-MS975) and a digital audio recorder (Marantz, PMD390) with a sampling rate of 44.1 kHz and 16-bit resolution. At least ten bouts of undirected songs were obtained for each individual. In total, 344 song bouts for 30 subjects were analyzed using the sound analysis software Raven 1.2 (Charif et al. 2004). Based on the computed sonograms, song bout duration and note-type repertoire were calculated for each song bout and averaged for each individual. To estimate the syntactical complexity of note orders, we also calculated the entropy of a first-order Markov model. This model was originally developed in information theory, but is gaining popularity in linguistic analysis and studies of songs sung by Bengalese finch (Nakamura and Okanoya 2004; Soma et al. 2006b) and other songbirds (American redstart, *Setophaga ruticilla*: Lemon et al. 1993; European starling,

Sturnus vulgaris: Gentner and Hulse 2000). The entropy for a song that contains k types of notes is

$$H = -\sum_{j=1}^{k}\sum_{i=1}^{k}P(A_i \cap A_j)\,\text{Log}_2\big(P\big(A_i|A_i \cap A_j\big)\big),$$

where $P(A_i \cap A_j)$ is the probability that note A_i to A_j transition is observed among transitions, and $P(A_i|A_i \cap A_j)$ is the probability that note A_i is followed by note A_j in transitions that are proceeded by A_i. The distinct feature of the entropy model is that it considers transition probabilities. The index will be larger if the note-to-note transition is more versatile (i.e., complex).

The experimental procedures and housing conditions were approved by the Institute's Animal Experiments Committee. All of the birds were cared for and treated humanely in accordance with the Institutional Guidelines for Experiments using animals (Brain Science Institute, RIKEN).

Statistical analyses

We used mixed effect models to investigate the effect of early ontogenetic conditions on individual differences in three song variables (i.e., average song duration, average note-type repertoire, and song complexity measured as entropy) while considering the non-independence of the data because of the shared rearing conditions. Specifically, we analyzed each song variable using a linear mixed-effect (LME) model in which the identity of the foster brood was treated as a random effect, and the two variables associated with early ontogenetic conditions, i.e., egg order and age hierarchy (older or younger) in the foster brood, and their interaction were treated as fixed effects. To assess the statistical significance of the fixed effects in each model, we first built maximum models containing all of the fixed effects and then used a backward stepwise procedure to sequentially remove nonsignificant terms. The statistical significance of a term was assessed by the change in deviance (which approximates a chi-square distribution) associated with dropping that term from the model. All statistics were performed using R 2.6.1 (R Development Core Team 2007).

Results

The cross-fostering manipulation revealed a partial impact of early ontogenetic conditions on song elaboration by adult birds. Song duration and note-type repertoire were independent of the foster brood identity ($p > 0.999$) and were not affected by egg order or age hierarchy in the foster brood ($p > 0.4$, Table 1). However, early ontogenetic conditions had an influence on the syntactical complexity of note order measured as entropy. Although age hierarchy and the interaction of age hierarchy × egg order did not have statistically significant effects on song complexity (LME: age hierarchy: $\chi^2 = 0.073$, $p = 0.787$; age hierarchy × egg order: $\chi^2 = 0.814$, $p = 0.367$; Table 1), egg-order influenced the syntactical complexity of songs (LME: $\chi^2 = 5.941$, $p = 0.015$; Table 1). Birds from eggs that were laid earlier in the egg order acquired more complex songs than did birds from eggs that were laid later, regardless of their position in the age hierarchy of the foster brood (Figs. 2 and 3). In addition, the random effect of brood identity was almost significant, suggesting that song complexity tended to be similar among brood mates (LME: $\chi^2 = 2.956$, $p = 0.086$; Table 1).

Discussion

Song quality partially reflected early ontogenetic conditions in the close-ended learner, the Bengalese finch. A performance-related trait (song duration) was independent of

Table 1 Results of LME analyses in which the relative effects of age hierarchy and maternal effect (egg order) were tested for each song variable
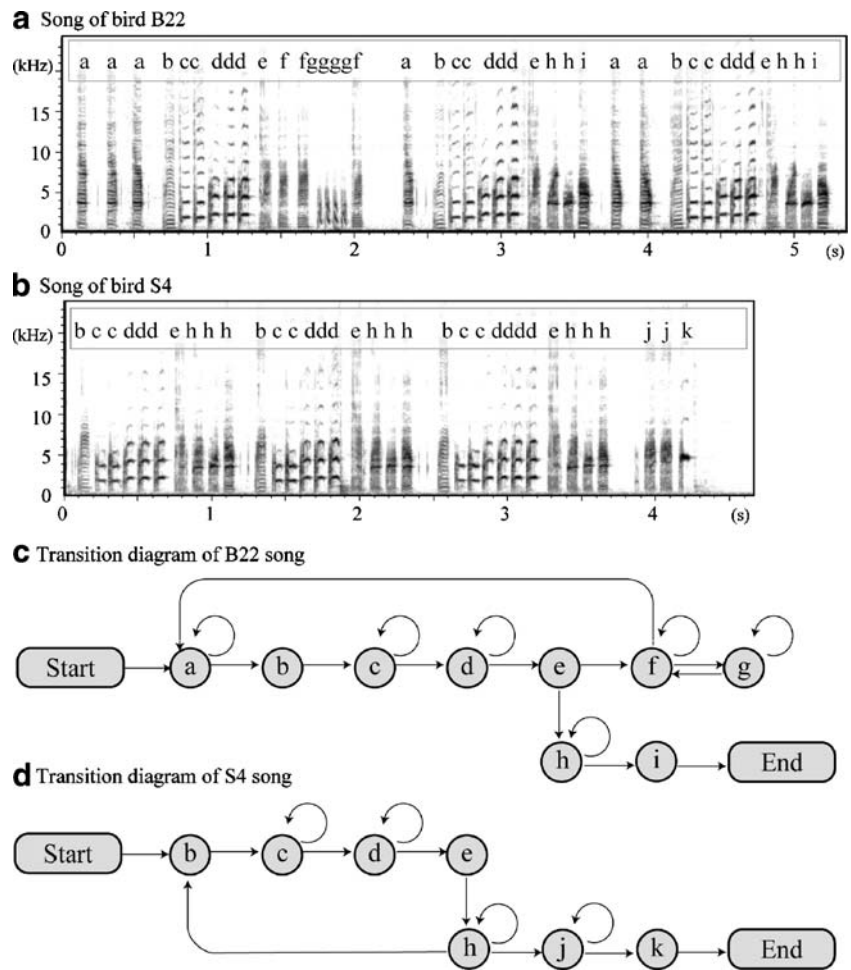
Song variable			Estimate±SD	χ^2	p
Song duration	Random effect	Brood identity		<0.0001	0.999
	Fixed effect	Age hierarchy × Egg order	–	0.0191	0.890
		Age hierarchy	–	0.0191	0.890
		Egg order	–	0.6585	0.417
Note type repertoire	Random effect	Brood identity		<0.0001	0.999
	Fixed effect	Age hierarchy × Egg order	–	0.414	0.520
		Age hierarchy	–	0.337	0.561
		Egg order	–	0.416	0.519
Entropy	Random effect	Brood identity		2.956	0.086
	Fixed effect	Age hierarchy × Egg order	–	0.814	0.367
		Age hierarchy	–	0.073	0.787
		Egg order	−0.039±0.014	5.941	0.015
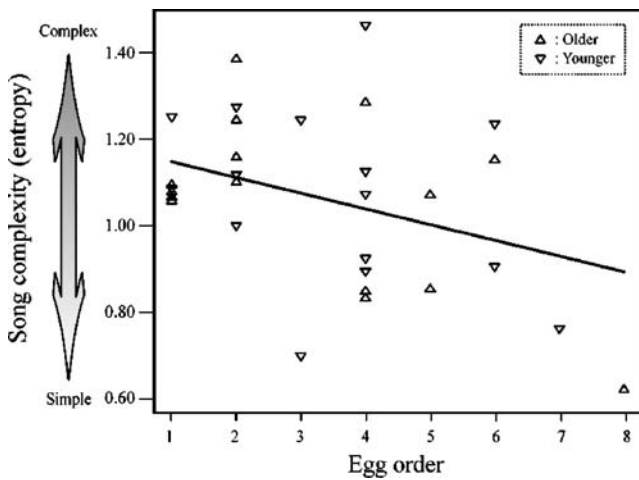
Fig. 2 The relationship between egg order and syntactical complexity of note order, measured as entropy. *Upright triangles* show older individuals in the age hierarchy of the foster brood (*n*=15): *inverted triangles* show younger individuals (*n*=15)

either egg order or age hierarchy in the foster brood, whereas an elaboration-related trait (i.e., syntactical complexity of note order, but not note-type repertoire) was influenced by egg order and also tended to be similar

among unrelated brood mates (Table 1). Overall, these results imply that the conditions experienced in earlier periods of ontogeny can have critical effects on the signal development of individual males because their song's syntactical complexity changes little after sexual maturity (Brenowitz and Beecher 2005) and plays a primary role in mate choice in this species (Okanoya 2004a). Playbacks of experimentally controlled song stimuli have shown that song complexity elicits more reproductive behavior in females (Okanoya 2004b) and that more females choose complex songs in choice tests (Morisaka et al. 2008). Hence, these female preferences for song complexity should provide a trigger for song evolution.

Effect of sibling competition on songs

Indicator mechanisms of sexual selection predict that high-quality signals that attract females should be costly to produce (Andersson 1994; Andersson and Simmons 2006). With regard to song complexity, the developmental stress hypothesis posits that stresses experienced during nestling and fledgling periods can adversely affect brain development and song learning ability (Nowicki et al. 2002;

Fig. 3 Song examples from a pair of unrelated brood mates that learned songs from the same tutors. The egg order of bird B22 is second and that of bird S4 is fourth. **a, b** Sono-grams of the birds' songs; the note-type classification is indi-cated by lowercase letters. **c, d** Transition diagrams showing the patterns of note-to-note transi-tion for the two songs. The song syntactical complexity was higher for bird B22 (*H*=1.243) than for bird S4 (*H*=0.924)

Nowicki and Searcy 2004; Nowicki and Searcy 2005). Although the idea has been tested and supported by experimental manipulations of nutritional conditions and stress hormone levels (Buchanan et al. 2004; Spencer et al. 2004; Zann and Cash 2007), the underlying stress-related ecological factors have received less attention. However, our examinations of the role of sibling competition as such an ecological factor that may affect song learning have produced contrasting results. We previously found that song duration was not the only factor that was affected by poor physical development caused by larger brood size; song syntactical complexity was also impaired in large and male-biased broods (Soma et al. 2006a). However, when we controlled brood size and composition in the present study, we found no significant effect of sibling competition (resulting from age hierarchy) on any song traits. Combining these results, we conclude that age disparities between brood mates do not have as critical an effect on song development as does brood size.

Maternal effect on songs

Our most notable finding is the potent maternal effect on song complexity. Specifically, syntactical complexity, measured as entropy, declined over the laying sequence, but was not affected by the brood's age hierarchy (Table 1, Fig. 2). Although several previous studies focused on the phenomenon of sibling competition among asynchronously hatched brood mates and its effect on physical growth (reviewed by Krebs 1999), the laying order was not assessed independently because it is naturally confounded with the age hierarchy unless the brood composition is controlled experimentally. However, the amounts of resources such as androgens, carotenoids, vitamins, and immune factors that a mother deposits into her eggs varies with the laying sequence in a wide range of avian species (e.g., Schwabl et al. 1997; Reed and Vleck 2001; Rutkowska and Cichoń 2002; Saino et al. 2002) and such skewed investment within a clutch affects the fitness of the hatched chicks (reviewed by Gil 2003; Groothuis et al. 2005). Testosterone in particular has adaptive effects in some species, but causes harm in others (Groothuis et al. 2005). In zebra finch, which is related to the Bengalese finch, testosterone levels decrease with laying order (Gil et al. 1999; Gilbert et al. 2005), and experimentally elevated yolk testosterone in males contributes to survival in early developmental stages (von Engelhardt et al. 2006). Unfortunately, maternal effects on sexual traits have yet to be investigated in estrildid finches. However, a quantitative genetics study of cross-fostered zebra finch found that female choosiness during mate selection declines in relation to laying sequence (Forstmeier et al. 2004). The authors suggested that this phenomenon resulted from variation in egg content derived from the laying order, but they did not investigate song components. Therefore, ours is the first study to suggest a link between within-clutch variation in maternal effects and song traits. Future studies should examine whether maternal investment, especially of testosterone, is responsible for offspring phenotypic divergence in sexual behavior in adult altricial birds.

The Bengalese finch is a domesticated strain of the white-rumped munia (*Lonchura striata*) that resulted from selective breeding for plumage color, but without artificial selection for song. The Bengalese finch sings syntactically complicated songs compared to those of the ancestral strain (Honda and Okanoya 1999; Okanoya 2004a). This greater song complexity probably resulted from a shift in song learning ability. Although Bengalese finch females prefer complex songs, such a change in song complexity may not have directly resulted from female choice because aviculturists would have limited free breeding opportunities in the process of domestication. Maternal effect is one candidate factor that could mediate such intersexual selection (Qvarnström and Price 2001). Our current findings illuminate within-clutch variation, but among-clutch variation in maternal effects is also worth considering. In particular, when females mate with males that have attractive songs and the song features are inherited by the sons through vocal learning, a greater investment in reproduction is expected through the production of more offspring (possibly more sons) or heavier, higher-quality eggs. For example, canary (*Serinus canaria*) females that are exposed to playbacks of more attractive songs lay larger eggs (Leitner et al. 2006) or produce eggs with greater amounts of testosterone (Gil et al. 2004). Similarly, such indirect parental effects may be involved in the evolution of song traits and the song-learning capacity of the Bengalese finch.

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