



Contingent parental responses are naturally associated with zebra finch song learning

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Active guidance of vocal learning by conspecifics has recently been found in several species, including some cetaceans and primates. However, in the zebra finch, *Taeniopygia guttata*, a commonly studied songbird, vocal learning was traditionally considered the product of memorization and imitation of a song model. Only recently have specific social feedback cues been shown to enhance song learning. What mechanisms drive the superior learning associated with social interactions? We recently found that ‘fluff-ups’, a nonvocal female arousal cue, facilitated song learning when played over video contingently on juvenile song production throughout development. However, it is unknown whether adults naturally respond in a contingent fashion to immature song, and whether young finches incorporate naturally occurring feedback into song learning. To investigate whether social influences affect song learning, the present study addressed the nature and significance of maternal and paternal cues associated with song development. We recorded unmanipulated zebra finch families throughout juvenile development and analysed their social interactions. We found that behaviours of both parents were associated with offspring song outcomes. Juvenile song learning could be predicted by the amount of contingent ‘fluff-up’ behaviours they received from their mothers throughout development. Fathers often sang immediately after a juvenile had sung, and paternal singing after juvenile singing was positively correlated with more accurate song learning in their sons. Conversely, when fathers sang before the juvenile sang, juveniles learned song less accurately. Our data suggest that parental vocal and gestural feedback plays a reinforcing role for song learning in zebra finches. There are many nonavian species, including chiropterans, pachyderms and pinnipeds, that modify their vocalizations in different developmental or social contexts but whose mechanisms of vocal learning are not known. Our findings suggest that these species should be closely examined for adult sensitivity to immature vocalizations and developmental capacity to learn from social feedback.

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Vocal learning is a rare capacity, known within only seven animal orders (Jarvis, 2007). Seemingly rarer still is the capacity for socially guided vocal learning, in which young learners receive social feedback on their immature vocalizations, which influences their learning (West & King, 1985). Until recently, this social learning strategy was known to exist in only two species: humans (Albert, Schwade, & Goldstein, 2017; Goldstein, King, & West, 2003; Gros-Louis et al., 2006) and brown-headed cowbirds, *Molothrus*

ater (West & King, 1988). However, just within the last few years, two well-known and well-studied mammal species were serendipitously discovered to be capable of aspects of socially guided vocal learning, suggesting that this learning strategy may be more common than previously thought. Killer whales, *Orcinus orca*, were cross-socialized with bottlenose dolphins, *Tursiops truncatus*, during development, and found not only to learn to produce dolphin-like vocalizations, but also to alter their use of vocalizations depending on social context (Musser, Bowles, Grebner, & Crance, 2014). Observation of common marmosets, *Callithrix jacchus*, found that parents provided feedback to their offspring during vocal interactions, guiding learning by vocally responding to context-appropriate vocalizations and by failing to do so when

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offspring vocalizations were not appropriate (Chow, Mitchell, & Miller, 2015). Juveniles that received contingent parental feedback developed adult vocal forms more rapidly than those that did not receive feedback (Takahashi, Liao, & Ghazanfar, 2017).

These recent findings of socially guided vocal learning have now been extended to the most commonly studied songbird, the zebra finch, *Taeniopygia guttata*. In this species, juveniles pay more attention to and learn better from tutors with which they can socially interact (Chen, Matheson, & Sakata, 2016) and learn better in the presence of nonsinging females (Adret, 2003; Williams, 2004). We recently found the first causal evidence that cues from females can influence juvenile song development: adult female ‘fluff-ups’ – an arousal behaviour – presented contingently via video on the immature plastic song of juveniles throughout development facilitated song learning (Carouso-Peck & Goldstein, 2019a). However, it is unclear whether zebra finches are true socially guided vocal learners, as it is unknown to what extent females naturally exhibit arousal cues, use those cues to respond to juvenile songs, or whether maternal feedback influences song development in a naturalistic social context. It is also unknown whether paternal reactions, such as adult song production following juvenile song production, influence juvenile song learning outcomes.

Birdsong is the most-studied model system for human speech acquisition due to the behavioural, neural and genetic similarities between the two learning processes (Bolhuis, Okanoya, & Scharff, 2010; Doupe & Kuhl, 1999; Goldstein et al., 2003). One similarity that has received comparatively little attention is dependence on the social environment: many young oscine songbirds and all human babies need to interact with adults to develop vocalizations with proper form and function (Doupe & Kuhl, 1999; Goldstein & Schwade, 2010; Smith, King, & West, 2000).

Nonimitative social guidance of vocal structure was first discovered in the brown-headed cowbird, a nonterritorial brood-parasitic species in which young are not raised by their own parents. Nonsinging females were found to respond selectively to juvenile male song elements with rapid lateral wing movements (‘wing strokes’), which influenced juvenile song development (West & King, 1988). These rapid movements were only perceptible to humans when the females were videorecorded and the recordings were played back at a fraction of real speed. Socially guided vocal learning has not been directly studied in bird species other than the cowbird. Social interactions organized around the immature vocalizations of juveniles have the potential to provide learning opportunities during early development in social species more broadly, but have rarely been investigated.

For territorial species, such as sparrows, the use of song in aggressive interactions makes direct social interaction with adult tutors during the song learning process a dangerous prospect for juvenile learners. This has resulted in an ‘eavesdropping’ learning system in which the young first memorize adult song from a safe distance during an initial ‘sensory’ stage, then practise imitating the song during a temporally distinct ‘sensorimotor’ stage (Beecher, Burt, O’Loughlen, Templeton, & Campbell, 2007; Konishi, 1965; Marler & Peters, 1982; Nelson & Marler, 1994; Soha & Marler, 2001). Song learning in these species may be enhanced by social interaction with tutors (e.g. Beecher & Burt, 2004), but the young do not require social feedback to learn.

In contrast to the sparrows, the zebra finch is not territorial, yet accurate vocal learning in this species is also thought to be the product of memorization and imitation of a song model (e.g. Deshpande, Pirlepsov, & Lints, 2014; Roberts, Gobes, Murugan, Olvezky, & Mooney, 2012; Tchernichovski, Mitra, Lints, & Nottebohm, 2001). However, there have long been hints that social influences affect their song learning. For instance, their song is better learned from live tutors than from tapes or noninteractive

playback paradigms (Chen et al., 2016; Derégnaucourt, Poirier, Kant, Linden, & Gahr, 2013; Eales, 1989). The juveniles also play an active role in selecting their tutor, and this choice is primarily influenced by social interactions, suggesting a learning mechanism beyond mere exposure. The salience of adult tutor song is based on the amount of parental care delivered to fledglings (Williams, 1990), physical proximity (Mann & Slater, 1995), aggression towards the pupil (Clayton, 1987; Jones & Slater, 1996), the tutor’s mating status and partner (Eales, 1987; Mann & Slater, 1994), visual cues such as colour morph (Mann & Slater, 1995; Mann, Slater, Eales, & Richards, 1991) and auditory information, such as song similarity between the father and subsequent song tutors (Clayton, 1987). Juvenile males prefer to learn to sing from their father both in the wild and in laboratory settings, even if other potential song models are available (Bohner, 1983; Zann, 1990), although they learn from multiple tutors depending on the amount of parental care (Williams, 1990). In addition, when multiple male siblings are raised together by an adult male, their song copy fidelity is highly variable, compared to consistently accurate song imitation when a father raises a single male juvenile (Tchernichovski & Nottebohm, 1998). Finally, the structure and timing of song development itself, with a high degree of overlap between the sensory and sensorimotor phases of song learning (Roper & Zann, 2006; Slater, Eales, & Clayton, 1988), offers opportunities for social feedback to influence song learning, as it does in the cowbird.

Nonsinging female listeners also affect zebra finch song development, as males raised with deaf females sing more frequently and develop more atypical songs than those raised with hearing females (Williams, 2004), and blindfolded males develop more accurate song when raised with a female sibling (Adret, 2003). However, the mechanisms underlying such enhanced learning are unknown. Enhanced learning during live interactions may be explained by feedback from parents contingent on a juvenile action, which may increase learning due to heightened arousal or attention (ten Cate, 1991). To date, the sole observational study investigating contingencies in interactions between zebra finch tutors and pupils in natural family settings did not find clear relations supporting that social behaviour of the tutor reinforces vocal learning (Houx & ten Cate, 1998). However, this study examined behaviour in real time, as perceived by a human observer, and not at the finer temporal scale at which birds are capable of perceiving motion (Carouso-Peck & Goldstein, 2019b; Healy, McNally, Ruxton, Cooper, & Jackson, 2013).

Zebra finches are raised jointly by their parents well into the sensorimotor learning phase (Zann, 1996), presenting the opportunity for both paternal and maternal behaviours to influence song development. Discovering which maternal behaviours might be relevant to juvenile song learning requires determining which behaviours females naturally display in response to attractive male displays. Three types of female visual signals have been linked to mate preference in female songbirds: copulation solicitation displays in numerous songbird species (Anderson, 2009; King & West, 1977; O’Loughlen & Beecher, 1997; Searcy & Marler, 1981; Vallet & Kreutzer, 1995), wing strokes in brown-headed cowbirds (West & King, 1988) and shakes or feather-fluff-ups in the zebra finch (Vyas, Harding, Borg, & Bogdan, 2009). Wing strokes and fluff-ups may be signals that females use to indicate song preference and thereby influence vocal development in their sons. Male tutors may similarly sing in response to juvenile song, facilitating vocal development. To investigate whether social influences affect song learning in the zebra finch, the present study addresses the nature and significance of maternal and paternal social interactions associated with the development of juvenile song in unmanipulated families. We analysed video recordings of naturalistic social interactions and annotated the timing of juvenile and adult male

songs as well as female gestures, such as wing strokes and fluff-ups, occurring temporally close to songs of the juvenile males and their fathers. We then investigated whether these interactions were correlated with juvenile song learning, by examining the acoustic similarity between the songs of the juveniles and their fathers.

METHODS

Breeding

Eight male–female pairs of adult zebra finches were selected from an outbred population maintained in an animal facility in the Cornell University Psychology Department accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AALAC). Pairs were placed in single stainless steel cages ($46 \times 44 \times 36$ cm, $N = 6$ pairs; $62 \times 44 \times 36$ cm, $N = 2$ pairs), which contained wooden perches, a plastic nestbox and coconut nesting material, in a communal room that allowed visual and acoustic contact with each other and with birds in other aviaries. The birds were kept on a 14:10 h light:dark cycle with full-spectrum lighting. Housing rooms were maintained at 24°C and 50% relative humidity. Birds were provided with mixed foreign finch seed, water, grit and access to cuttle bone *ad libitum*. The birds received water for bathing and greens as a dietary supplement weekly. Following this study the animals were returned to the colony.

Each pair nested, laid eggs, hatched and fledged two to five young (mean \pm SD = 3.88 ± 1.25 young), which resulted in 14 juvenile males and 15 juvenile females total. Juveniles were colour banded at approximately 3 weeks of age (mean = 21 days, range 17–26 days; age always refers to the hatching date of the oldest juvenile). Families were transferred to larger cages ($62 \times 44 \times 36$ cm) when the oldest chick was 24 days posthatch. The families were housed in acoustic and visual isolation from each other until juveniles entered the sensorimotor period. Individual family cages were then moved to a communal room but kept visually isolated. Because juveniles are unable to learn from tutors with which they cannot directly interact (Clayton, 1988; Williams, 2004), juveniles in the present study did not interact with any adult tutor other than their own father throughout the sensory learning period. Nestboxes were removed at about 35 days post-hatch in order to prevent re-nesting of the parents during the study.

Behavioural Recordings

Video recordings of family interactions began between 21 and 35 days posthatch (mean \pm SD = 27 ± 5.2 days) and continued at approximately 3-day intervals until 70–95 days posthatch. In this study, we focused our analysis on videos recorded between 30 and 75 days posthatch. We chose this time window as it encompasses the overlap period between the sensory and sensorimotor phases of the juvenile zebra finch (Immelmann, 1969), during which it is both practising its song and able to alter its song, such as in response to parental feedback. Within this interval, each family was recorded for about 16 h (mean \pm SD = 16 ± 2.46 h). For each session, the entire cage containing the parents and offspring was placed overnight in a sound-attenuating enclosure ($140 \times 98 \times 80$ cm) lined with Sonex sound-attenuating foam.

For each recording, family interactions were recorded for 1 h the following morning using a Sennheiser K6/ME64 shotgun microphone connected to a Canon MiniDV ZR930 camcorder with Fuji-film MiniDV cassettes. After each recording, family cages were returned to the communal housing room until the subsequent recording. Families were kept together until about 99 days post-hatch (SD = 9 days). Juveniles were then transferred to single-sex

aviaries (90 cm width, 122 cm height, 60 cm depth), each containing up to 20 juvenile birds.

Ethical Note

All protocols were approved by the Cornell Institutional Animal Care and Use Committee (IACUC protocol 1988–0135). Animal subject treatment complied with the standards defined by the Committee. The study was designed to minimize number of birds used, disturbance and stress.

Behavioural Coding and Analysis

Sound files were created from video recordings using Sound-track Pro (v.3.0.1) and uncompressed sound files were saved as wav files. ELAN Linguistic Annotator software (Wittenberg et al., 2006) was used to synchronize the video and sound files and to code the behaviour of juvenile males and their parents. ELAN permits annotations of multiple categories of behaviour from individual animals with a frame-by-frame accuracy onto different fields associated with the video recording.

Initial analyses examined dynamics of song production between the fathers and juvenile males. Thus, all adult male and juvenile songs were first annotated with single-frame accuracy. Song in zebra finches occurs in bouts, which we defined in behavioural annotations as singing without silent intervals greater than 1 s. Songs were coded as ‘directed’ whenever the singer initiated singing while clearly facing another individual and performing courtship behaviour such as a raised crest, side-to-side head movement or courtship dance (Williams, 2001). All other songs were coded as ‘undirected’. Directed songs were most often performed by the adult male and directed to the adult female. Throughout the observation period, juvenile males rarely directed their songs towards their mothers when their father had recently sung or was about to sing (mean \pm SD = 2 ± 1.77 songs per juvenile); thus, we used the total juvenile male song in subsequent analysis. Thus, directed singing events in the subsequent analysis always refer to adult male song directed towards the adult female. Next, we marked 15 s time windows before and after the songs in ELAN for every adult and juvenile male. Some song bouts were produced in quick succession, leading to overlap between the after and before time windows. When these overlaps occurred, we labelled the time between songs as ‘between’ (Fig. 1).

Because juvenile songs often occurred in quick succession within the 15 s time window, the possibility existed for several juvenile songs to be binned together, counting as only a single event before an ensuing song from the father. Thus, we analysed

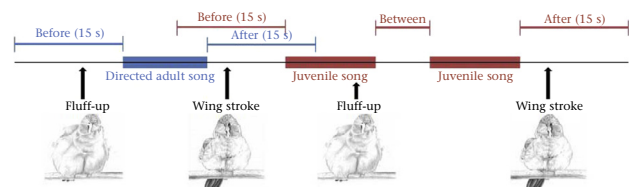


Figure 1. Example of temporal relationships between juvenile song and parental feedback. After coding adult male (blue) and juvenile male (red) song bouts (‘during’ song periods), 15 s time windows were created before each song onset and after each song completion. When two juvenile songs followed in rapid succession (< 15 s), intervening time periods were labelled as ‘between’. Female fluff-ups and wing strokes were coded only in these song-adjacent time windows. Contingent interactions were assessed based on the temporal relations between behaviours occurring within these windows (e.g. ‘directed adult song after juvenile song’, ‘female fluff-up before juvenile song’, etc.).

these events in two ways. First, we counted the number of times that a paternal song followed within 15 s of a juvenile song or song bout. Second, to account for repeated juvenile songs in a bout, we counted the number of individual juvenile songs that preceded a paternal song within 15 s. However, when analysing the incidence of juvenile songs occurring after paternal songs, we noted that fathers never sang multiple times within the 15 s windows. Therefore, we analysed these events only by counting the number of paternal songs that preceded a juvenile song within 15 s.

Wing strokes and fluff-ups by the mother were coded during song and in the 15 s before and after songs. To determine whether more immediate contingent responses have a greater effect on song, analyses were additionally run on contingent behaviours within 5 s after song. Wing strokes were defined as a single fast movement of one (unilateral) or both (bilateral) wings, made independent of large body movements (West & King, 1988). The tallies did not include wing movements made within 1 s of landing from flight, as birds tend to adjust their feathers immediately after landing. Wing strokes were coded after hopping and jumping but only after the female was in contact with the perch. Wing strokes were not coded during preening, or when the movement of the tail appeared to cause the movement of the wing. Tiny wing adjustments during sudden bending were not coded as wing strokes. Any movements not deemed to be wing strokes were not coded. As the movements can be brief and subtle, all wing strokes were independently coded by two individuals. Both coders were blind to hypotheses and were aware of when songs occurred but not the identity of the singer. A third person, blind to hypothesis, coder identity and song timing and singer identity, then checked both coders' annotations and resolved any discrepancies. Wing stroke annotations from this final assessment were used in the data analysis. To assess coder reliability, we calculated the percentage agreement on wing strokes coded. Across all families, the average (\pm SD) agreement between the final assessment and the first coder was $61.3 \pm 0.21\%$, and that between the final assessment and the second coder was $73.3 \pm 0.19\%$.

Fluff-ups are brief erections of the feathers accompanied by a quick shaking movement of the entire body from side to side, followed by smoothing the feathers back down (Vyas et al., 2009). Initially, two independent coders annotated the presence of fluff-ups. After coding random sections of the recordings amounting to 30% of the total data and finding the two coders to be highly consistent for this behaviour (intercoder reliability: mean \pm SD = 0.87 ± 0.24), annotations of only one coder were used in subsequent analyses of the remaining 70% of the data.

Behavioural Contingencies

From the annotations, we determined the occurrence of directed, undirected and total (directed + undirected) adult male songs, juvenile songs and female wing strokes and fluff-ups for the entire developmental period for each family. Juvenile song was rarely classified as directed (mean \pm SD = 2 ± 1.77 songs per juvenile across the entire observation period); thus, we used total juvenile song in all analyses. We also analysed the total number of wing strokes by pooling unilateral and bilateral wing strokes. Behaviours were assigned to categories based on their temporal relationship, namely how many behaviours occurred before, during, after and between adult male or juvenile songs (Fig. 1).

Mature Song Recordings

Mature song was recorded from sons ($N = 11$) following song crystallization (Immelmann, 1969), in the fourth month after hatching (mean \pm SD = 104 ± 9.59 days posthatch) and from their

fathers ($N = 8$) (see Fig. 2 for example spectrograms). Three sons did not sing during these initial recording sessions, so their songs were recorded in the fifth month after hatching, between 142 and 153 days posthatch (total $N = 14$). Before all recordings, males were placed in a soundproof room overnight in a $46 \times 44 \times 36$ cm cage. The following morning, an adult female zebra finch was placed in an identical cage next to the male's cage and recording began. If the male did not sing within 60 min, further recordings were attempted on subsequent days until we obtained at least 10 songs. We videorecorded and audiorecorded the mature songs, annotated the video recordings in ELAN software to locate directed songs visually and selected only directed song motifs for subsequent song analyses.

Analysis of Mature Song

Zebra finch song consists of a series of individually distinct acoustic elements, called syllables, which are sequentially organized into a consistent pattern, the song motif. The motif is initially preceded by a train of repetitive introductory elements. A single song bout contains between one and eight motif repetitions (Price, 1979). Zebra finch song is often described as highly stereotyped. In actuality, males usually sing slightly different motif variants, containing different numbers of notes (Helekar, Marsh, Viswanath, & Rosenfield, 2000; Menyhart, Kolodny, Goldstein, DeVoogd, & Edelman, 2015; Scharff & Nottebohm, 1991; Sturdy, Phillimore, & Weisman, 1999). The most common motif occurs in about 60% of song bouts and is termed the 'dominant' or 'canonical' motif (Scharff & Nottebohm, 1991; Zann, 1996). For the purpose of acoustic analysis, we randomly chose 10 renditions of the dominant motif from each recording (both sons and fathers) from samples that did not contain background noise, female calls or cage noise. We also excluded the first motif of each song bout as it tends not to have the consistency of subsequent motifs. To assess song learning, we then compared 10 motifs from the mature song of each son to 10 motifs from their respective fathers, performing 10×10 comparisons within the similarity batch feature of Sound Analysis Pro 2A.04 (SAP) software (Tchernichovski, Nottebohm, Ho, Pesaran, & Mitra, 2000; Tchernichovski, Swigger, & Partha, 2004).

The similarity module of SAP is specifically designed for acoustic analysis and similarity comparisons of zebra finch song, and is widely used in zebra finch song learning studies. Motifs were segmented into syllables according to amplitude, with drops below 43.2 dB, the default value in SAP for segmentation of zebra finch song, providing the boundary for a new section. Fourier transformation was performed on sound segments of 7 ms, with 307 sound pressure samples obtained during each segment, for a

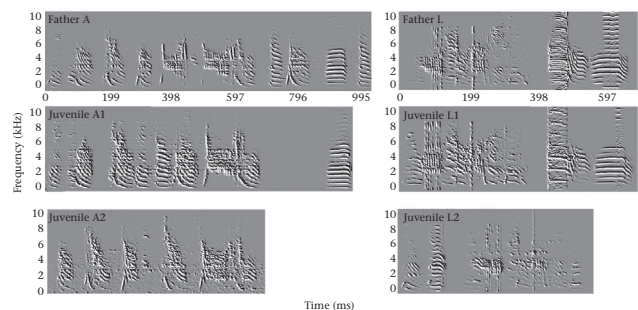


Figure 2. Spectrogram examples of crystallized song outcomes. Spectrograms from two families of subjects, Family A (left) and L (right). The songs of fathers (top row) were compared with the final songs of their sons (second and third rows) following juvenile song crystallization. Song outcomes varied considerably even within the same families, depending on rate, timing and form of parental responsiveness.

frequency resolution of 287 Hz. Each new time window starts 1.4 ms after the beginning of the previous one, resulting in 80% overlap. Similarity sections were set by a threshold for values which were likely to be similar by chance alone with a probability $\leq 1\%$.

We derived the three different measurements of similarity between songs that the SAP software provides: percentage similarity, accuracy and sequential match. Percentage similarity attempts to capture similarity in overall feature values between two songs and is computed over 50 ms intervals of sound. Accuracy is computed across shorter time windows (7 ms) and indicates the accuracy of the vocal match between the two songs across similar segments. The only difference between percentage similarity and accuracy is the time window used. Sequential match accounts for the temporal order (syntax) of sounds. Sequential match is calculated by sorting sections (syllables) of the song according to their temporal order in reference to the tutor's song, and then examining their corresponding order in the juvenile's song. Two sections are sequential if the beginning of a section in the juvenile's song occurred 0–80 ms after the end of the tutor's preceding section. This tolerance level accounts for the durations of stops and for very short sections that are not sequential. This procedure is repeated for all of the consecutive pairs of sections in the tutor's song. The final value represents the percentage of the juvenile's song's sections deemed to be a sequential match to the corresponding sections of the tutor's song. For more detailed technical information on the algorithm underlying the similarity module of SAP, see Tchernichovski et al. (2000).

The relationship between sequential match and accuracy can be illustrated with a metaphor from human language. If the tutor utterance was the sentence 'They went far', then a sentence with scrambled word order ('far went they') would have a high accuracy score but low sequential match, while a sentence with the correct word order but incorrect word pronunciation ('Tay wen fa') would have low accuracy but high sequential match. While our analysis used acoustic similarity to tutor to identify the best-learned juvenile songs, we are now investigating whether the best-copied songs are also the most functional in terms of attracting females.

Statistical Analysis of Song Outcome Measures

To assess the contribution of behavioural interactions during development on song learning, we correlated behaviours occurring in the 15 s time windows with similarity scores obtained between the songs of each father and the mature songs of their sons. To control for effects of juvenile song activity and the number of observations per family, we controlled for amount of singing by partialling out juvenile song rate per hour from the correlations.

Some families contained more than one son, and so the 14 juvenile males could not be treated as independent data points. To analyse the effects of family on the three song outcome measures, we conducted separate intercept-only linear mixed models with family as the random factor and song similarity measures as the dependent variable in each analysis. For the three measures, 4.7% of variance in accuracy, 24% of variance in similarity and 73% of variance in sequential match was attributed to family. Because family accounted for a large proportion of variance on the latter two outcome measures, family identity was controlled for in all subsequent data analyses involving learning measures using partial correlations.

We performed principal component analyses to examine the joint and separate contributions to juvenile song learning outcomes of paternal and maternal responses to immature song. All factors were normalized using Kaiser normalization and orthogonally rotated with Varimax. The analysis included all paternal singing

behaviours, maternal feedback behaviours (wing strokes and fluff-ups) and juvenile singing behaviours. We then performed partial correlations, controlling for family, between each resulting factor with an eigenvalue > 1 and the three song outcome measures of percentage similarity, accuracy and sequential match.

RESULTS

Parental Responses to Juvenile Song

Adult males often produced song immediately following their juvenile's song. They sang more songs after their son sang (mean \pm SD = 14.5 ± 9.99 songs) than before (6.21 ± 4.08 songs) ($t_{13} = -3.832$, $P = 0.002$), and juvenile males sang more songs before their fathers started to sing (26.71 ± 17.93 songs) than after (19.93 ± 12.36 songs) ($t_{13} = 2.519$, $P = 0.026$). We determined the percentage of juvenile vocalizations that preceded adult male song by calculating the percentage of juvenile song occurring immediately before the father's compared to the total juvenile song produced. This varied widely across juveniles (mean \pm SD = $4.26 \pm 2.86\%$, range 0.44–9.12%). Juveniles sang an average of 72.2 ± 50.39 (range 24–216) times per hour, significantly more frequently than the average rate of adult male song of 30.32 ± 23.58 (range 13–84) times per hour ($t_{13} = 4.296$, $P = 0.001$).

Females responded with wing strokes during an average (\pm SD) of $10.8 \pm 0.050\%$ of songs and displayed wing strokes more frequently during the song of their mate (mean \pm SD = $13.4 \pm 5.1\%$) than during the subsong and plastic song of their sons ($9.4 \pm 4.4\%$) ($t_{13} = -2.217$, $P = 0.045$). While the majority of songs did not elicit female wing strokes, those that did often elicited more than one, with an average (\pm SD) of 2.08 ± 0.525 wing strokes per adult song (range 1–19) and 1.07 ± 0.365 wing strokes per juvenile song (range 1–10) within 5 s of singing. Fluff-ups were rare compared to wing strokes. Mothers responded with fluff-ups during only $1.7 \pm 0.016\%$ of songs, and only $2.6 \pm 0.021\%$ of songs received a fluff-up within 15 s of singing. The rate of maternal fluff-ups during adult male song (mean \pm SD = $2.6 \pm 0.021\%$ of songs) was twice that elicited during juvenile songs ($1.3 \pm 0.012\%$ of songs) ($t_{13} = -2.558$, $P = 0.024$).

To determine whether maternal fluff-ups and wing strokes were likely elicited by juvenile song, we compared the rate of maternal cues during juvenile singing (average \pm SD duration of song = 2.85 ± 2.64 s) to that during the silent 15 s periods before and after song. A repeated measures within-subjects ANOVA on number of maternal fluff-ups occurring before, during and after juvenile song showed significant change among periods ($F_{2,26} = 7.777$, $P = 0.002$). A post hoc Tukey HSD test showed a significant increase in fluff-ups between before and during periods, and a significant decrease in fluff-ups between during and after periods ($P < 0.05$; Fig. 3). The number of fluff-ups during singing was significantly higher than during the surrounding nonsinging periods, despite song duration being, on average, only 19% of the duration of 'before' or 'after' periods. Fluff-ups in the before and after periods were not significantly different from each other (Fig. 3). Similarly, a repeated measures ANOVA on numbers of maternal wing strokes occurring before, during and after juvenile song showed a significant change among periods ($F_{2,26} = 10.416$, $P = 0.0005$). A post hoc Tukey revealed that the number of wing strokes significantly increased between before and during periods, and significantly decreased between during and after periods ($P < 0.01$). Number of wing strokes in the before and after periods did not differ significantly (Fig. 4).

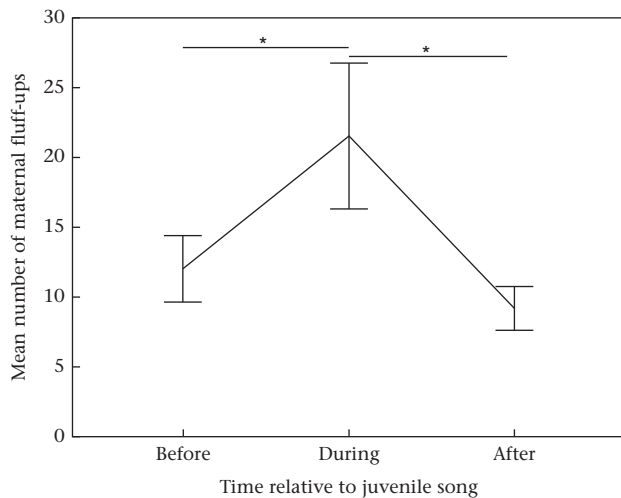


Figure 3. Mean \pm SE number of maternal fluff-ups performed 15 s before, during and 15 s after juvenile song. * $P < 0.05$ (post hoc Tukey tests).

Effects of Social Feedback on Song Learning

Juveniles copied their father's song well, as expected, but with considerable variation between individuals in terms of percentage similarity (mean \pm SD = $73.06 \pm 11.16\%$, range 49.44 – 95.34%), accuracy ($75.3 \pm 2.09\%$, range 71.4 – 79.11%) and sequential match ($59.41 \pm 14.53\%$, range 42.24 – 91.53%). To determine whether this variation in song learning was linked to social interactions between sons and both their fathers and their mothers, we correlated behavioural contingencies occurring in the 15 s time windows surrounding song production with the three measures of final song similarity obtained by comparing the mature song of the son to the song of his father, and found significant effects on sequential match. The incidence of directed songs by the father just after the juvenile male sang was significantly positively correlated with the eventual sequential match to the father's song (Pearson correlation: $r_{10} = 0.734$, $P = 0.007$; Fig. 5a). The number of juvenile songs before directed adult male song was also significantly positively correlated with final sequential match between juvenile and tutor ($r_{10} = 0.775$, $P = 0.003$; Fig. 5b). In contrast, more frequent juvenile song after father song was significantly negatively correlated with

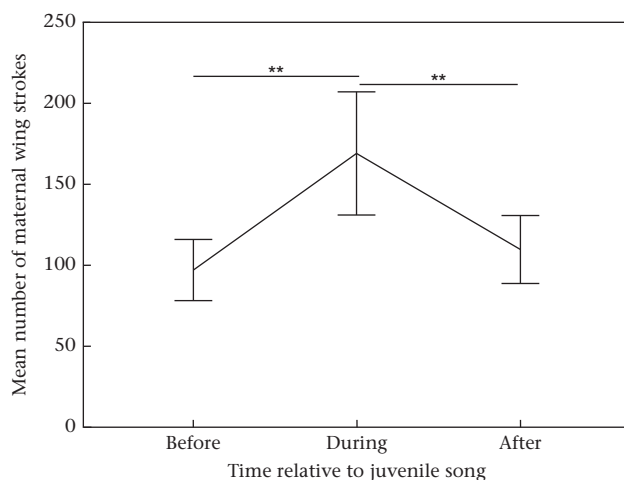


Figure 4. Mean \pm SE number of maternal wing strokes performed 15 s before, during and 15 s after juvenile song. ** $P < 0.01$ (post hoc Tukey tests).

final song accuracy (all father song: $r_{10} = -0.752$, $P = 0.005$; directed father song: $r_{10} = -0.648$, $P = 0.023$; Fig. 6).

Female fluff-ups were associated with higher sequential match between juveniles and their fathers (total number of female fluff-ups around juvenile song: $r_{10} = 0.866$, $P < 0.001$; Fig. 7). Fluff-ups were correlated with sequential match regardless of whether they occurred before juvenile male song ($r_{10} = 0.938$, $P < 0.001$) or following the onset of song (during, after or between: $r_{10} = 0.837$, $P = 0.001$). Maternal fluff-ups during, after or between juvenile songs were also correlated with final percentage similarity to tutor ($r_{10} = 0.581$, $P = 0.047$).

Saliency of Maternal Feedback

We then investigated the saliency of these response behaviours to the juveniles. How obvious is the feedback in the context of background levels of female behaviour? We calculated the signal-to-noise ratio of fluff-ups and wing strokes by subtracting the number of these feedback behaviours performed in a silent 15 s baseline period before juvenile song to that performed during juvenile singing to obtain a difference score for each juvenile. Across subjects, controlling for family, we found a significant positive correlation between fluff-up signal-to-noise ratio and both sequential match ($r_{10} = 0.578$, $P = 0.039$) and overall similarity ($r_{10} = 0.608$, $P = 0.028$). No measure of timing or frequency of female wing stroke signal-to-noise ratio across the developmental period was associated with any of the song outcome measures.

No song outcome measure was significantly correlated with the total amount or rate of paternal song that juveniles were exposed to across development, nor with the amount or rate of song produced by the juveniles ($P_s > 0.05$). Song outcomes were also not correlated with the number of male siblings ($P > 0.05$).

Relative Contributions of Family Members to Song Learning

To examine the joint contributions of various behaviours to song learning outcomes, we performed a principal component analysis constructed from paternal song behaviour, juvenile song timing and maternal feedback behaviours (Table 1), using Varimax rotation. This resulted in a PCA with five components with eigenvalues above 1. The first component (PC1) had an eigenvalue of 8.086 and accounted for 24.79% of variance, and loaded most heavily on maternal fluff-up behaviours around juvenile song, paternal directed song after juvenile song and juvenile singing before paternal directed song. A partial correlation revealed significant correlations between PC1 and the learning outcome measures of percentage similarity ($r_{11} = 0.64$, $P = 0.019$) and sequential match ($r_{11} = 0.854$, $P < 0.001$).

DISCUSSION

We investigated the type and amount of social feedback occurring around subsong and plastic song of juvenile zebra finches by exploring the microstructure of social interactions. We found that interactions with both parents following juvenile singing were correlated with the song learning process and with fidelity of learning in the mature song. This suggests that juvenile plastic song is a potent stimulus for eliciting adult behaviours that function as feedback. Our prior finding that female fluff-ups presented contingently on song in an experimental paradigm facilitated song learning (Carouso-Peck & Goldstein, 2019a) suggests that juveniles may also use naturally occurring contingent maternal fluff-ups as cues that reinforce their song structure. We found that maternal feedback, although given at low rates, influenced song learning. Juveniles experiencing more fluff-ups following their own singing,

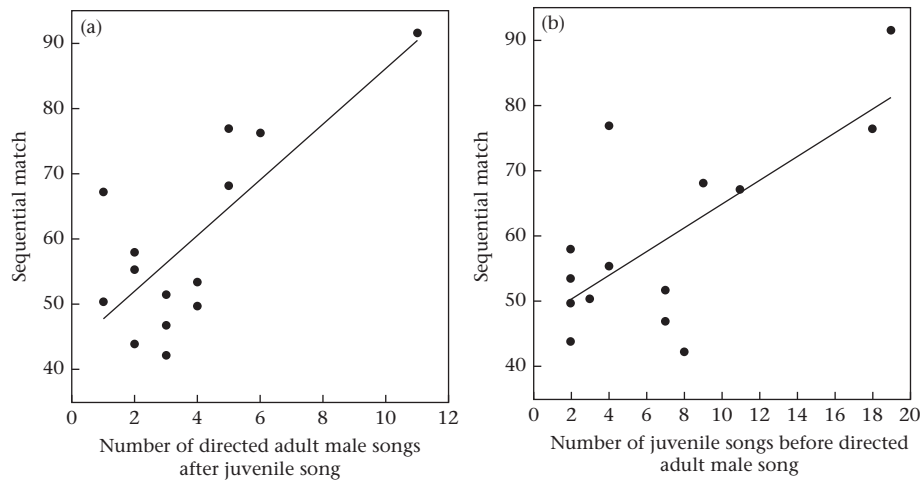


Figure 5. Relation between song sequential match and (a) the number of directed paternal songs performed after juvenile song ($r_{10} = 0.734$, $P = 0.007$) and (b) the number of juvenile songs performed before directed adult male song ($r_{10} = 0.775$, $P = 0.003$).

as well as those that received more fluff-ups during their song than during silent periods surrounding it, learned their father's song more accurately.

Paternal singing also influenced song learning. Juveniles whose immature song received more directed song from their fathers learned more similar copies of their father's song, and learned his sequence more correctly. Conversely, increased juvenile singing after the father's song was correlated with less accurate learning. Why do juveniles learn from feedback provided by the father, rather than by singing after the presentation of a song model? According to the action-based learning model, juvenile songbirds may adjust their repertoire depending on vocal interactions and retain elements that elicit reactions from the receivers, such as their territorial neighbours or their father (Nelson & Marler, 1994). It is also possible that adult singing following their own song helps to organize juvenile attention. Given that adult zebra finches are

known to simplify their song in the presence of juveniles (Chen et al., 2016), simplified song presented immediately after practice song could make it easier to reproduce.

Directed song by the father was an especially powerful signal, as juvenile learning outcome was correlated with directed tutor song rather than undirected singing, despite being produced about one-third as often in conjunction with immature song. Courtship song may be a more salient communication signal than undirected singing for a number of reasons: it is frequently accompanied by dynamic choreography aimed at the female (Williams, 2001) and is delivered with a faster tempo and less spectral variability than undirected song (Kao & Brainard, 2006; Sossinka & Böhner, 1980). Moreover, the song of adult males elicited more wing strokes from adult females than did juvenile song. As both song from adult males and fluff-ups from adult females were correlated with song learning, these behaviours may be working in conjunction to

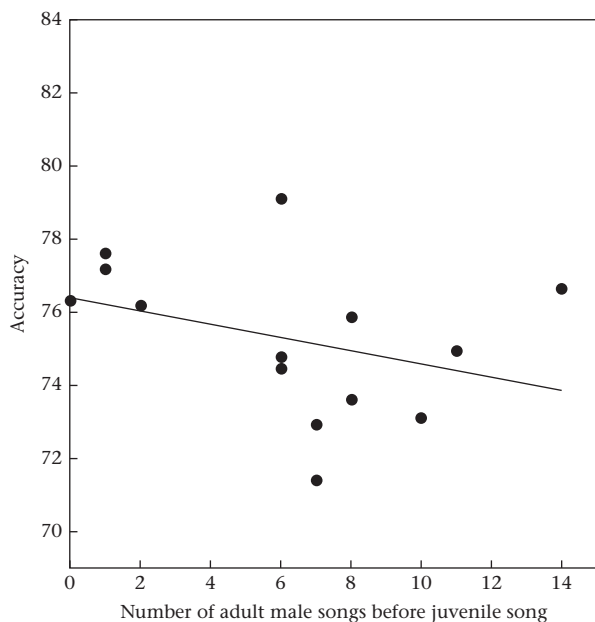


Figure 6. Relation between the accuracy of final juvenile song and the total number of adult male songs (both directed and undirected) performed before juvenile song ($r_{10} = -0.752$, $P = 0.005$).

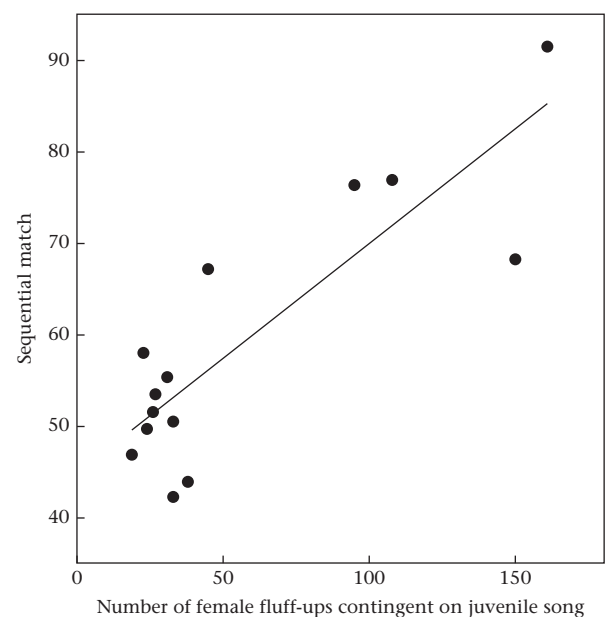


Figure 7. Relation between the number of maternal fluff-ups performed in response to juvenile song and the final sequential match between juvenile and tutor songs ($r_{10} = 0.837$, $P = 0.001$).

Table 1
Principal component analysis constructed from paternal song behaviour, juvenile song timing and maternal feedback behaviours

	Components derived				
	1	2	3	4	5
Number of WS before JS	0.163	-0.045	0.972	0.024	-0.042
Number of WS during JS	0.179	-0.003	0.952	-0.040	-0.076
Number of WS between JS	0.064	0.099	0.920	0.021	-0.222
Number of WS after JS	0.161	0.069	0.960	-0.077	-0.024
Number of FU before JS	0.865	-0.122	0.245	0.213	-0.005
Number of FU during JS	0.865	0.075	0.470	-0.042	0.002
Number of FU between JS	0.932	0.084	0.298	0.044	-0.116
Number of FU after JS	0.836	-0.031	0.192	0.149	0.039
Number of undirected AS before JS	-0.004	0.790	0.394	-0.058	0.069
Number of undirected AS during JS	-0.147	0.816	0.017	-0.104	0.516
Number of AS between JS	0.364	0.871	-0.092	0.149	0.211
Number of undirected AS after JS	0.451	0.386	0.678	-0.077	0.124
Number of directed AS before JS	0.136	-0.033	0.010	0.880	0.153
Number of directed AS during JS	0.466	0.019	-0.269	0.460	0.641
Number of directed AS after JS	0.885	0.335	-0.099	0.077	0.119
Number of JS before undirected AS	0.398	0.841	0.021	0.237	-0.106
Number of JS during undirected AS	-0.148	0.362	-0.149	0.233	0.832
Number of JS after undirected AS	-0.004	0.942	0.165	0.050	-0.126
Number of JS between total AS	0.073	0.935	-0.050	0.058	0.253
Number of JS before directed AS	0.677	0.451	-0.037	0.300	-0.176
Number of JS during directed AS	-0.066	0.456	-0.323	0.561	0.245
Number of JS after directed AS	0.525	0.185	0.069	0.788	0.023
Eigenvalue	5.453	5.404	4.897	2.255	1.727
% Variance	24.787	24.564	22.260	10.252	7.848

WS = wing stroke; JS = juvenile song; FU = fluff-up; AS = adult song. Behaviours with the strongest contribution to each component are shown in bold. PC1 loaded most heavily with maternal fluff-ups, directed adult song after juvenile song and juvenile song before directed adult song and was significantly correlated with final song percentage similarity to tutor ($r = 0.640$, $P = 0.019$), sequential match ($r = 0.854$, $P < 0.0001$) and overall similarity ($r = 0.902$, $P < 0.0001$).

improve juvenile learning, as suggested by our principal component analysis showing that maternal and paternal behaviours jointly contribute to song sequence learning. Exposure to multi-sensory information (song of the adult male, visual signals from the adult female) may organize juvenile perception and enhance learning via increased attention to social cues (Chen et al., 2016) or arousal (Carouso-Peck & Goldstein, 2018, 2019a), effects that may be enhanced if the signals co-occur. Exposure to concurrent auditory and visual stimuli has been shown to enhance learning in nightingales, *Luscinia megarhynchos*, as juveniles exposed to stroboscope flashes during tutoring developed larger repertoires and produced better copies of the song model than controls exposed only to the tutor songs (Hultsch, Schleuss, & Todt, 1999). Human infants appear to use a similar mechanism. Infants aged 7.5 months old use visual information that is synchronized with the speech stream to aid perceptual segmentation (Gogate & Bahrick, 1998; Hollich, Newman, & Jusczyk, 2005).

Rare or less obvious forms of experiential factors during development are infrequently studied but have been shown to be important, such as auditory exposure in ovo affecting visual preference (domestic mallard (Peking) ducklings: Johnston & Gottlieb, 1981) and vocal learning (superb fairy-wrens, *Malurus cyaneus*: Colombelli-Negrel et al., 2012; zebra finches: Katsis et al., 2018). Our results emphasize the importance of microanalytic approaches to quantifying the form and timing of behaviour, as infrequent adult behaviours performed in response to juvenile song may have a strong impact on the learning process. Only 1.3% of juvenile songs elicited a maternal fluff-up. Visual feedback cues to juveniles from female cowbirds are also extremely rare behaviours, as on average 1.1 wing strokes occur per 100 juvenile songs (West & King, 1988). Among our zebra finch subjects, about 4% of juvenile song elicited feedback from adult males, and directed song by the father

produced immediately following juvenile song accounted for less than 2% of total adult male song. Nevertheless, these types and rates of social cues robustly shape juvenile cowbird song and change its content as well as its developmental trajectory (Smith et al., 2000), similar to the effect we observed with the rare but potent zebra finch maternal fluff-ups.

How could such infrequent parental responses become so salient for learning? Juveniles may also learn from observing social interactions among other adults (Pepperberg, 1985). For example, female brown-headed cowbirds eavesdrop on interactions between other males and females and use the information available in the social group for preference formation (Gros-Louis, White, King, & West, 2003). Parental responsiveness may also vary over developmental time, such that there may be periods of more frequent feedback. We assessed the overall impact of parental feedback on the final song outcome of juvenile males, but we did not analyse how parental feedback may differently impact song learning when received at specific ontogenetic time points. While we did not find wing strokes to be associated with song outcomes when pooled across development, it is possible that they are relevant only during a specific window. To uncover development in progress, we are currently observing changes in juvenile singing activity and in the associated parental feedback as they unfold over time.

Our results offer an alternative to the traditional model of song learning, which describes song development in terms of an early sensory memorization phase followed by a later sensorimotor practice phase that is based on recalled memories of the tutor song (Konishi, 1965; Marler, 1976). Such a model of song learning may be appropriate only for territorial songbirds, in which the two phases are typically temporally distinct and immature vocalizations develop through a process of being compared to the mature songs of territorial neighbours (Beecher et al., 2007). In contrast, the sensory and sensorimotor phases overlap in time for the gregarious, nonterritorial zebra finches and brown-headed cowbirds, creating the developmental opportunity to both receive social feedback on their immature song and to use it to update an incomplete song representation. Given that these species use song exclusively for mate attraction, learning about song quality from females is also more reproductively adaptive for these species than for solitary territorial species. Given the diversity of life history strategies and developmental trajectories of song learning across passerines, it is unsurprising that a single model of song learning does not generalize across species (Beecher & Brenowitz, 2005; DeVoogd, 2004; Marler & Nelson, 1992), but socially guided vocal learning may be present in more species than previously thought.

While our findings are correlational and do not demonstrate that zebra finch parents are actively guiding their offspring towards more accurately learned song, the finding that female fluff-ups performed in response to juvenile song facilitates learning (Carouso-Peck & Goldstein, 2019a) suggests that juveniles may take advantage of these cues to improve their song. In cowbirds, wing strokes and fluff-ups are believed to be precursors of the copulation solicitation preference display, suggesting that female feedback has its origins in signals that evolved for a different function, a process called 'inadvertent coaching' (Hoppitt & Laland, 2008). The developmental process bears striking similarity to vocal learning in human infants. Infant babbling elicits rapid contingent social responses from caregivers, and these responses influence infant vocal learning in real time and developmental time (Albert et al., 2017; Elmlinger, Schwade, & Goldstein, 2019; Goldstein & Schwade, 2008; Goldstein, Schwade, & Bornstein, 2009). In a strong parallel with the songbird findings, contingent parental feedback can induce more developmentally advanced vocalizations even when it consists only of nonvocal responses such as touching, moving closer or smiling at the infants (Goldstein et al., 2003).

Our results support the existence of a dynamic system of socially guided learning, in which senders and receivers alternate roles as they participate in multisensory information exchange. We have shown that paternal song produced after, but not before, juvenile song correlates with positive learning outcomes, contrary to what would be predicted by a traditional imitation model. We have previously shown that female fluff-ups presented contingently on juvenile song production result in more accurate song learning in a video playback paradigm (Carouso-Peck & Goldstein, 2019a) and have now demonstrated a similar effect in a naturalistic context in which mothers selectively responded to their sons. In summary, both parents contribute to successful song development. In nature, juvenile songbirds can rely on parental feedback, because their altricial state requires the presence of caregivers. Thus, young songbirds are born into a structured social environment, with the essential developmental task of extracting information from it.

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