



Adult exploration predicts parental responsiveness to juvenile songs in zebra finch parent–juvenile interactions

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ARTICLE INFO

Article history:

Received 16 April 2021

Initial acceptance 12 July 2021

Final acceptance 24 January 2022

MS. number: A21-00247R

Keywords:

exploration
parental behaviour
personality
song learning
zebra finch

Recent research has established the importance of animal personality traits in behavioural ecology, encompassing domains such as mate choice, cognition and social interactions. However, less is known about how personality traits predict parental behaviour. In the current study, we investigate these relationships in the zebra finch, *Taeniopygia gutatta*, a species that provides biparental care and in which social feedback from parents shapes juvenile song learning. Adults were first assessed on exploratory tendency in a novel environment, then allowed to pair and rear cross-fostered young. Birds were housed in single-family cages within the colony, allowing for visual and auditory interaction between families. We examined foster parent–juvenile interactions over the course of song learning (35–65 days post-hatch), recording parental responsiveness (responses contingent on juvenile songs) as these responses are known to influence song learning outcomes. Exploration scores predicted parental responsiveness in contrasting ways: low-exploring males provided more contingent responses to the immature song of juveniles, while high-exploring females increased their responsiveness to a greater degree over the course of juvenile song development. Over the period of offspring song development, females were more responsive to changes in juvenile vocal production, increasing the number of responses provided as juveniles increased their rate of singing. In contrast, males were less variable in their response rate across development; their contingent singing was not sensitive to changes in the rate of juvenile singing. The importance of exploration as a predictor of parental responsiveness to offspring behaviour demonstrates the possible significance of previous findings that adults pair based on the trait of exploration.

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In many species, communicative skills are learned via parent–offspring interactions over development. Contingent adult responses to juvenile vocalizations facilitate vocal learning and serve as a taxonomically widespread means of communicative development (e.g. humans: Goldstein et al., 2003; marmosets: Gultekin & Hage, 2018; cowbirds: King et al., 2005; zebra finches, *Taeniopygia gutatta*: Carouso-Peck et al., 2020). Individual parents display different amounts of responsiveness to their offspring. External factors that influence individual differences in parental care have been well studied (e.g. the role of experience: Smiley & Adkins-Regan, 2016; Wang & Novak, 2021; the acoustic structure of begging calls: Thornton & McAuliffe, 2006). However, the internal characteristics that influence individual variability in parental responsiveness to immature vocalizations have received less attention (although cf. studies in humans, e.g. depression: Milgrom et al., 2004). Personality, defined as consistent individual

differences in behaviour across context and/or time (Réale et al., 2007), could function as a general attribute that predicts variation in parental responsiveness. The present study examines the influence of exploration on parental responsiveness to juvenile vocalizations in the zebra finch.

At a proximal level, parenting may be constructed from low-level perceptual processes. Perceptual sensitivities to environmental cues, such as offspring vocalizations (e.g. begging calls), form the foundation for providing care to altricial young, with parental responsiveness to immature vocalizations shaping future offspring vocal development (Goldstein et al., 2003). In addition, the vocalizations of offspring are acoustically distinct from mature vocalizations in many species, either in type (e.g. offspring begging calls are not in the adult repertoire), pitch (e.g. larger individuals produce lower-pitched vocalizations; Chabert et al., 2015; Reby & McComb, 2003), or variability (e.g. greater variability in structure and amplitude in immature zebra finch song as compared to mature song; Zann, 1996). Thus, offspring behaviours are potentially a source of perceptual novelty to first-time parents, and possibly to experienced parents as well, due to the variability

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inherent in juveniles' acoustically immature vocalizations. This raises the question of whether individual differences in the tendency to explore novel environments predict parental responses to offspring behaviour. Since personality traits describe general patterns of behaviour that are expressed across contexts (Beausoleil et al., 2012), we examined whether the personality trait of exploration, as shown by adults that were not yet parental, would predict their later responsiveness to offspring cues.

Differences in personality have recently been linked to differences in parental care. Exploration, in particular, has been connected to adult interactions with offspring. For example, fast-exploring female blue tits, *Cyanistes caeruleus*, provision their offspring at higher rates (Mutzel et al., 2013), social exploratory male convict cichlids, *Amatitlania nigrofasciata*, demonstrate more fin digging (a brood-provisioning behaviour; Budaev et al., 1999) and more exploratory male zebra finches raise more offspring (McCowan et al., 2014). In addition, individuals may display consistent differences in communicative behaviours connected to their personalities, such as exploratory male collared flycatchers, *Ficedula albicollis*, singing from riskier perches (Garamszegi et al., 2008), exploratory male great tits, *Parus major*, displaying increased vocal responses to intruders (Snijders et al., 2015) and aggressive male song sparrows, *Melospiza melodia*, responding with increased intensity to alarm calls (Hyman et al., 2013). The above examples are drawn from males as, historically, communicative behaviours (e.g. song) have been examined to a greater extent in males. It remains unclear whether there are sex differences in how vocalizations are expressed and received in individuals with similar personalities. Recent advances in the study of female song (Austin et al., 2021; Odom et al., 2014) and female nonvocal response to male song (Carouso-Peck et al., 2020) provide evidence that females may also vary in parental responsiveness, and merit further investigation.

We examined these relationships (personality and parental behaviour; parental behaviour and offspring song learning) in the zebra finch. This species is monogamous and provides biparental care (Zann, 1996). In addition, personality (Dall & Griffith, 2014) and song learning (Slater et al., 1988) are commonly studied in zebra finches, thus providing a logical study species for investigating the role of personality in communicative development. In this species, only males sing and they learn only one song, which is sung in repeated motifs during courtship. Like many vocal learning species, zebra finches undergo different sensitive periods for song development. Juveniles first listen to and memorize the adult vocalizations that they hear during the sensory period (25–65 days posthatch) and subsequently begin to practise those songs during the sensory-motor period (35–90 days posthatch; Miller et al., 2010). During the overlap of these two periods, juveniles can refine their vocalizations based on sensory feedback from conspecifics.

Recent studies have revealed that both fathers and nonsinging mothers provide important feedback to juvenile males during this overlap window (35–65 days posthatch). When the juvenile produces an immature vocalization, parents may provide a contingent response—one that follows rapidly after the juvenile vocalization. Such contingent responses may include fathers' song or nonvocal arousal-based behaviours from mothers such as fluff-ups (where the female rouses her feathers and performs a full-body shake, unrelated to preening or bathing) and wing strokes (a swift vertical motion of the wing, independent of large body movements). Responses from parents have been shown to facilitate juvenile song development, both in naturalistic family conditions (Carouso-Peck et al., 2020) and in experimental playbacks (Carouso-Peck and Goldstein, 2019). Furthermore, there is natural variation in the number of contingent responses that an individual produces in response to immature song.

What factors underlie such individual differences in parental behaviour? Zebra finch personality traits, including exploration, dominance and neophobia (e.g. David et al., 2011; McCowan et al., 2015), are well studied. Previous studies revealed that personality traits, such as exploration, influence mate preferences (Schuett et al., 2011) and pair bond formation, with individuals pairing with birds of similar exploratory tendency (Faust & Goldstein, 2021). Thus, we theorized that exploration may serve as a domain-general attribute, predicting behaviour in courtship and parental care contexts. Given that higher-exploring individuals have higher rates of provisioning and singing in other species, our first prediction was that high-exploring zebra finches would be more responsive to juvenile vocalizations. As parental responses have been shown to influence song development (Carouso-Peck et al., 2020), our second prediction was that increased parental responsiveness would facilitate song learning.

Adult personality has also been shown to influence the development of offspring personality, with cross-fostered zebra finches more closely resembling the personalities of their foster parents than their genetic parents (Schuett et al., 2013). Specifically, exploration scores of fostered offspring at adulthood resembled those of their foster mothers and were not affected by clutch size or hatch order. Therefore, our third prediction was that the exploration of cross-fostered offspring, measured in adulthood, would resemble that of the foster parents.

We examined these three hypotheses by testing parent exploration prior to breeding in a novel environment test and allowing birds to pair (generation 1, G1). We then cross-fostered the resulting offspring (generation 2, G2), to avoid genetic effects on song learning or personality and recorded parent–juvenile interactions over development. Once G2 reached adulthood, we assessed their exploration and recorded their crystallized songs to assess song learning (G2 pupils compared to G1 tutors).

METHODS

Subjects and Housing

We observed parent–juvenile interactions in 11 families of zebra finches, producing a total of 18 male offspring. Prior to commencing the study, two cohorts were planned to allow for constraints of time-intensive observations. The first cohort of birds, containing six families, was recorded in 2015, and the second cohort of five families was recorded in 2017. All birds were from domestic stock, either obtained from Magnolia Bird Farm (Riverside, CA, U.S.A.), or produced from our own breeding colony at Cornell University, originally bred from Magnolia Bird Farms stock, with wild-type plumage. All birds in the colony wore combinations of coloured leg bands for purposes of individual identification, with colours that were visible on video recordings. The colony was kept indoors on a 14:10 h light:dark cycle at constant temperature (22°C) with 40–50% humidity. Within the colony, birds were supplied with ad libitum food (Kaytee FortiFinch Food, Chilton, WI, U.S.A.), water, cuttlefish bone and grit, with supplemental vegetables and hard-boiled egg provided twice per week.

Families were housed in individual aviaries (0.6 × 0.36 × 0.43 m) and were in visual and acoustic contact with other families. Each aviary was equipped with a plastic nestbox, and pairs were provided with coconut fibre as nest-building material. Once the resulting offspring had fledged, the nestboxes were removed.

Ethical Note

To reduce and/or prevent unnecessary stress of our subjects, we observed the behaviour of birds, but found few instances of stress-

related behaviour (e.g. panting, excess flapping or calling). Birds were captured with the lights off, which minimizes handling stress. Additionally, the birds were transported in a small transport cage for <1 min and released directly from the transport cage into the experimental cage, to avoid excess handling. Moreover, during the novel environment tests to assess adult exploration, in which birds were visually and acoustically isolated from the colony, we played a recording of colony noise to reduce stress from isolation. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Cornell University under protocol 2014–0025.

Assessment of Adult Exploration

The parents in the current study had previously participated in an earlier study on personality and mate choice (Faust & Goldstein,

2021). During that study, individuals were first assessed on a variety of personality traits, including exploration, then provided with a variety of potential mates to pair with (free mate choice). Birds that mated served as the first generation (G1; the parents) in the current study, while we refer to birds that did not mate as first generation nonmated (G1N). We used the exploration scores calculated for G1 from the previous study to predict their behaviour in the current study. The methods of our exploration test are described elsewhere (Faust & Goldstein, 2021), but in brief, individuals were introduced into a novel aviary that was visually and acoustically separated from the colony; however, we provided a playback of colony noise to reduce stress from isolation in this gregarious species.

Once in the novel environment, birds' movements to and around the branches of different perches were recorded for 5 min

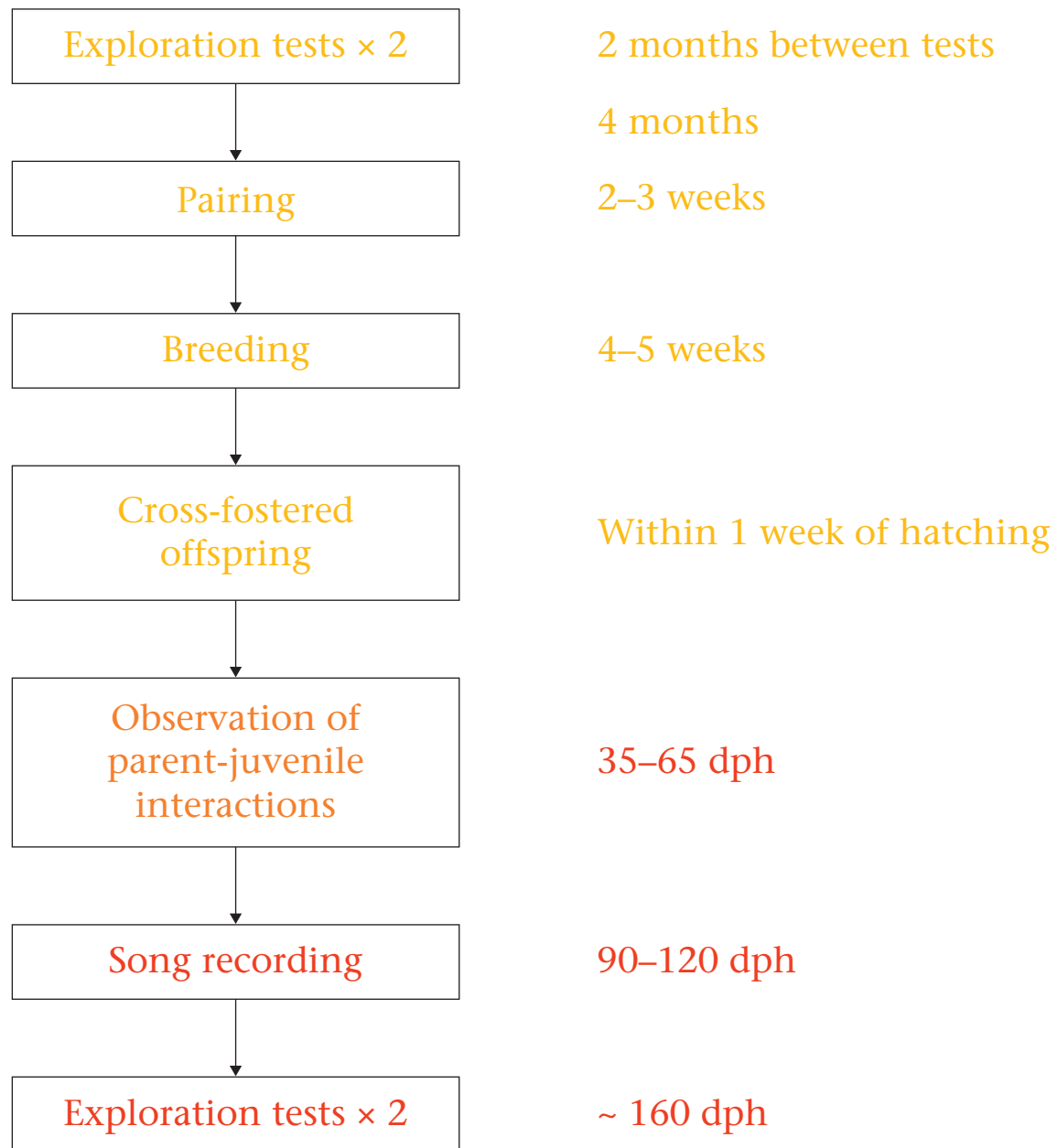


Figure 1. Experimental timeline for different phases of the study. Generation 1 (G1) is represented in yellow, generation 2 (G2) is represented in red, and overlap between the two is represented in orange. dph = days posthatch.

(subsequently, perches are referred to as ‘features’, and branches of perches are referred to as ‘components’). This novel environment test was repeated roughly 2 months later, and the individuals’ scores on the different exploration variables (latency to visit a novel component and novel feature, number of novel components and features visited, number of repeat components and features visited) were averaged between tests. Because this method of assessing exploration produces repeatable results (Faust & Goldstein, 2021), we were able to calculate the repeatability of the exploration of G1 individuals (the parents: $R = 0.489$, 95% CI: [0.264, 0.698]). This score is comparable to other measures of the repeatability of exploration in this species. In the present study, we followed the same methods to assess the exploratory tendencies of the male offspring (the second generation; G2) once they reached adulthood (Fig. 1).

Cross-fostering of Offspring

As we were interested in the influence of adult personality on offspring outcomes, we cross-fostered the offspring, swapping them from their natal nest to that of an unrelated pair. Foster parent personality was not controlled for (i.e. we did not swap chicks between the nests of high- and low-exploring parents); chicks were instead assigned to pairs incubating age-matched eggs or chicks. Nest checks were conducted daily during the nesting period to determine hatch dates. All chicks were cross-fostered before their eyes opened, in the first week after hatching, and marked with nontoxic marker for identification. Since the parents in the study were reproductively naïve, not all eggs hatched due to lack of fertilization, failure to incubate or other pre-hatch causes of mortality. To ensure that each family received cross-fostered chicks, we therefore waited until the chicks hatched before moving them to another nest. All chicks from one nest were moved to a new nest together (i.e. siblings were not separated) due to the constraints of finding two nests matched in egg-hatching date. Zebra finches fostered before fledging learn the song of their foster father (Zann, 1996), although exposure to incubation calls in ovo can influence vocal development (Katsis et al., 2018). Once chicks fledged, they were banded, which allowed for individual identification.

Recording of Parent–Juvenile Interactions

In zebra finches, parents are known to respond contingently to juvenile vocalizations, including during the overlap of the sensory and sensory-motor periods (35–65 days posthatch), which creates opportunities for juveniles to modify their song representations as a function of social feedback to their immature vocalizations (Carouso-Peck & Goldstein, 2018). Both mothers and fathers are significantly more likely to produce a parental response following juvenile song than prior to juvenile song, which facilitates song learning (Carouso-Peck et al., 2020). Thus, we recorded parent–juvenile interactions for 1 h in the mornings on days 35, 45, 55 and 65 posthatch; every 10 days during the overlap of sensory and sensory-motor periods. Specifically, we observed juvenile (G2) song and contingent parental (G1) responses that occurred during or after juvenile song: paternal song, maternal fluff-ups and maternal wing strokes. The time window for receiving a contingent response was set at 5 s after the end of juvenile song. This time window was selected based on previous work examining contingent parental responses occurring within 15 s of juvenile song (Carouso-Peck & Goldstein, 2020), and because most parental responses are given during or very shortly after juvenile song (K. M. Faust, personal observation). We also recorded any parental responses that occurred in the 5 s before a juvenile song for comparison with the ‘after’ time period, to determine whether a greater

proportion of parental responses were truly elicited in response to juvenile vocalizations. Given that the size of the family cages ensured that juveniles and their parents were in relatively close proximity (i.e. less than 0.6 m away at all times) and within view of each other, and that zebra finches have wide visual fields that encompass 300° (i.e. a blind spot behind the head of only 60°; Bischof, 1988), we assumed that physical distance between parent and juvenile, or the direction the juvenile faced did not alter the salience of a contingent response.

For each family, on each of the 4 days, we determined the number of juvenile songs, the number of juvenile songs that the foster parents were in view for (i.e. times that the adult bird was clearly visible to an observer in the video recording during and after juvenile song, to observe the presence or absence of a parental response) and the number of juvenile songs that received a contingent response from either parent. We then calculated the proportion of songs (during which a parent was in view) that received a contingent response (i.e. the parental responsiveness for that day).

As some families contained more than one juvenile male, and the juvenile males could sing at overlapping time points, we decided to concentrate our analysis solely on parental response to any juvenile song, as it was ambiguous which juvenile elicited a parental response. This study was primarily designed to focus on the potential relationship between parent exploration and parental responsiveness; thus, the identity of the eliciting juvenile did not matter for the purposes of our analysis, so long as the number of juvenile songs per family were controlled for by calculating proportions of songs that received a parental response for each family.

At 75 days posthatch, offspring were removed from family cages and placed into large aviaries (1.2 × 0.9 × 0.6 m) in groups of 12–16 same-sex conspecifics until they reached at least 90 days posthatch and were considered adults. Parents were returned to the colony.

All recorded videos were coded for the specified behaviours using ELAN, a behavioural coding software created by the Language Archive at the Max Planck Institute for Psycholinguistics in Nijmegen, the Netherlands (v.4.9.4, <https://tla.mpi.nl/tools/tla-tools/elan/>; Sloetjes & Wittenburg, 2008). Juvenile song production was likewise hand-coded in order to confirm that the vocalizations were, in fact, vocalizations (versus miscellaneous cage noise) and that the only vocalizations coded were songs. The presence of songs (versus calls) was determined on the basis of stereotypical song behaviour in this species, which includes an upright posture, a series of rhythmic, rapid head turns, rapid beak movements and occasional plumage erection (e.g. of the head and ear coverts) and/or hop-pivots across perches (Zann, 1996).

Our analysis focused on overall measures of parental responsiveness (averaged across development), as well as an a priori decision to focus on 55 days posthatch. Around this time period, offspring in the wild begin to disperse from the natal nest, congregating with same-age conspecifics that serve as potential mates as individuals approach sexual maturity (Zann, 1996).

Table 1

Principal component loadings of exploration variables (adapted from Faust & Goldstein, 2021)

	PC1	PC2
Novel components	−0.45	0.19
Repeat components	−0.39	0.31
Latency to novel component	0.41	0.46
Novel features	−0.44	−0.05
Repeat features	−0.35	0.61
Latency to novel feature	0.40	0.54
% Variance explained	63.7	11.8

Behaviours with the strongest contribution to each component (>0.4) are shown in bold.

Therefore, we expected feedback at this juncture to have greater influence on song learning.

Offspring Song Learning

Recordings of crystallized song were collected from G2 in the fourth month after hatching (range 91–116 days posthatch), as well as from the fathers. These recordings were obtained by placing the focal individual in an acoustic attenuation chamber; chambers lined with sound-attenuating foam, equipped with lights, airflow and a Sennheiser ME62/K6 omni-directional condenser microphone (described in Carouso-Peck and Goldstein, 2019). Inside, cages ($46 \times 44 \times 36$ cm) contained perches and cuttlebone, and water and seed were provided ad libitum. All recordings were run through a high-pass filter (1000 Hz) to exclude extraneous noise from the chambers' air circulation system. After the focal individual had habituated to the chamber, an unfamiliar female was introduced to induce directed song. We recorded individuals in 2 h sessions, for as long as necessary to obtain 10 high-quality song motif recordings, unobscured by background noises or female calls. If individuals did not produce sufficient song in the first session, they were habituated in the chambers overnight and recorded again the next day, following the same procedure, until sufficient song was collected.

We compared the songs of G2 to their G1 foster fathers, as this species has previously been shown to learn primarily from social, rather than genetic, parents (e.g. Clayton, 1989). Song learning outcomes were assessed using Sound Analysis Pro (Tchernichovski et al., 2000), a software specifically designed for the analysis of zebra finch songs. The similarity module of SAP produces three major components: similarity, which is the overall match between the tutor and the juvenile, computed over a long time segment; accuracy, which reflects match to tutor over much shorter time

segments (e.g. on the level of syllables); and sequential match, which indicates the degree to which the timing and order of the syllables match that of the tutor.

We compared each G2 male's 10 motifs to the two best motifs collected from their tutor (G1 foster father) and averaged the results of these comparisons to create one overall score for similarity, accuracy and sequential match per individual. As some families had multiple males, song learning scores of the juvenile males within each family were averaged to achieve one song learning outcome measure per family.

Statistical Analysis

All analyses were performed in R v.4.0.1 (R Core Team, 2020). Personality variables (the exploration principal components PC1 and PC2) were normally distributed. However, all variables concerning parental responsiveness were non-normally distributed, confirmed via examination of histograms and normal quantile plots. Therefore, analyses involving these variables used nonparametric statistics, such as Spearman's correlations, Wilcoxon signed rank tests, Friedman tests and the $r_{\text{equivalent}}$ effect size calculation (Rosenthal & Rubin, 2003).

Principal component analysis of exploration

The details of our principal component analysis on the six exploration variables described above are given in Faust and Goldstein (2021). From our PCA, which reduced the dimensionality of our exploration data, we derived two principal components: PC1, which represented novel features and novel components visited, and PC2, which represented latency to visit novel components and features, as well as repeat features visited (Table 1, Appendix, Fig. A1). Together, these two principal components

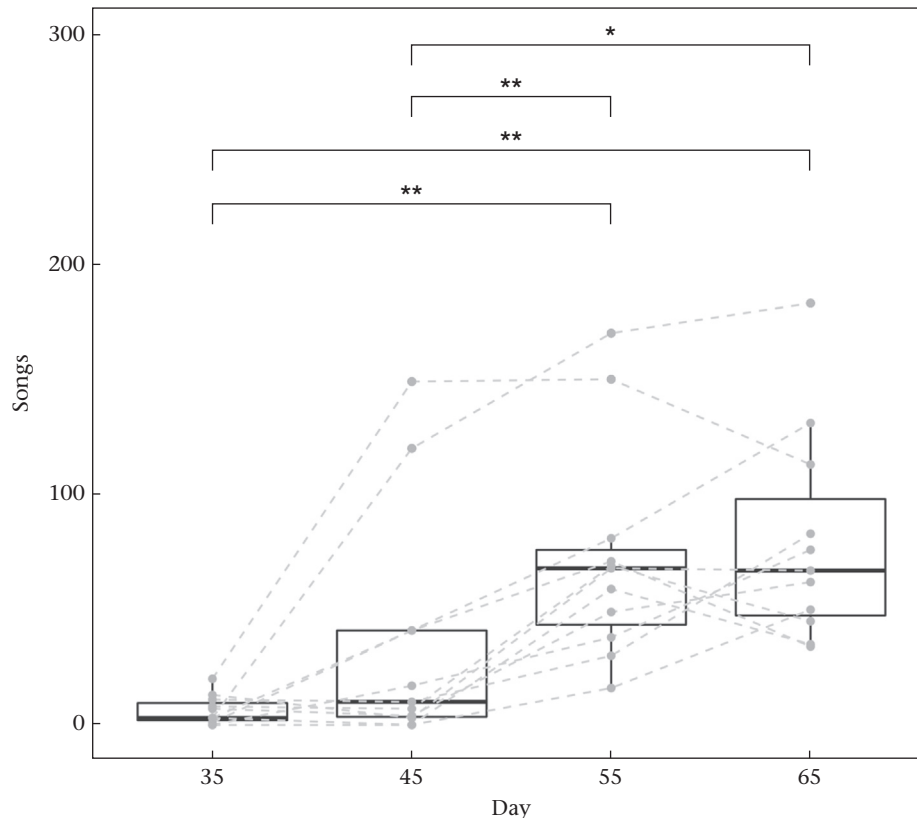


Figure 2. Total number of juvenile songs observed in a 1 h period according to developmental day. Box plots represent median and quartiles; dots represent families. Grey lines track families across development. * $P < 0.05$; ** $P < 0.01$.

explained 75.5% of the variance in exploration that we observed. These principal components may capture different aspects of exploratory behaviour: PC1 may indicate motivation to explore new areas, while PC2 may indicate differences in sampling strategy in a novel environment. Similar to the movement–cognition correlations described by Snell-Rood and Steck (2015), there may be individuals that explore rapidly and less thoroughly, compared to individuals that explore slowly and thoroughly within a given area. However, we did not test explicitly for movement–cognition correlations in the current study.

Using the loadings and rotations of the exploration variables on each principal component from our previous PCA, we then calculated the principal component scores of the G2 males in the current study from their behaviour in the novel environment test. Calculating the scores from an existing PCA equation relied on the implicit assumption that the structure of the exploration trait was identical in G1 and G2; however, given that all personality tests were conducted once the offspring had reached adulthood (>120 days posthatch; that is, all birds were tested on exploration in adulthood), we judged this to be a fair assumption. Our decision was confirmed via scrutiny of G1, G1N and G2 scores on PC1 and PC2 (Appendix, Fig. A2).

Logistic regressions

As zebra finches are known to vary in contingent responsiveness across offspring development (Carouso-Peck et al., 2020), we investigated the effect of developmental day on the likelihood of parental response separately for foster mothers (both for contingent fluff-ups and wing strokes) and foster fathers (contingent song). This was done via logistic regressions using a generalized linear model with the family ‘binomial’, with day as predictor and parental response as the response variable. Model significance was tested using the likelihood ratio test with the ‘car’ package (v.3.0.8; Fox & Weisberg, 2019). Significant models were followed up by post hoc tests with the ‘emmeans’ package (v.1.4.7; Lenth et al., 2020) using a Tukey adjustment.

Correlations

All other analyses were carried out via correlations. Where relevant, we adjusted the *P* values to account for multiple

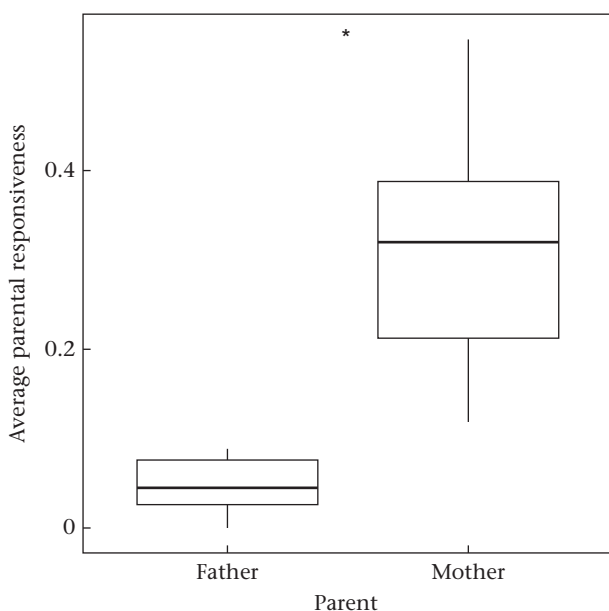


Figure 3. Average responsiveness of mothers and fathers to juvenile songs over the course of development. Box plots represent median and quartiles. **P* < 0.01.

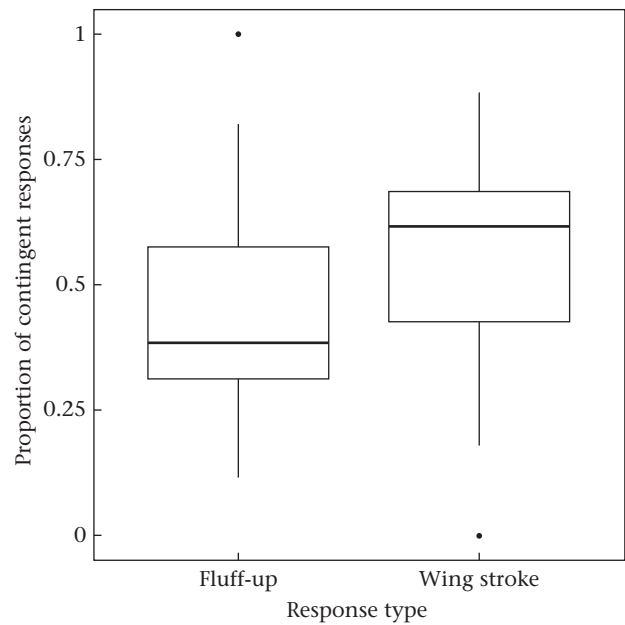


Figure 4. Maternal contingent responses (fluff-up, wing stroke) to juvenile song. Box plots represent median and quartiles; dots are outliers.

comparisons using Benjamini and Hochberg's (1995) ‘false discovery rate’ method.

RESULTS

Juvenile Song

The total amount of juvenile song observed significantly differed depending on developmental day (Friedman test: $\chi^2_3 = 22.16$, $N = 11$, $P < 0.0001$, Kendall's $W = 0.67$; Fig. 2). Pairwise tests revealed that juveniles sang significantly more songs at 55 days posthatch than at 35 days posthatch ($P_{\text{adj}} = 0.006$) or 45 days posthatch ($P_{\text{adj}} = 0.006$), and they sang significantly more songs at 65 days posthatch than at 35 days posthatch ($P_{\text{adj}} = 0.006$) or 45 days posthatch ($P_{\text{adj}} = 0.041$). Juveniles did not sing significantly more at 55 days posthatch than at 65 days posthatch ($P_{\text{adj}} = 1.0$).

Contingency of Parental Responses

Fathers sang significantly more songs during or after their sons sang (mean \pm SD = 8.18 ± 9.03 songs) than before (3.27 ± 4.41 songs) (paired *t* test: $t_{10} = 3.20$, $P = 0.01$). Mothers also produced significantly more wing strokes and fluff-ups during or after their sons sang (35.27 ± 24.17 songs) than before (21.91 ± 17.78 songs) (paired *t* test: $t_{10} = 5.68$, $P = 0.0002$).

Parental Responsiveness

Overall, fathers contingently responded to juvenile vocalizations with song at relatively low rates ($4.62 \pm 3.24\%$ of songs). Mothers contingently responded to juvenile vocalizations at higher rates ($31.14 \pm 13.66\%$ of songs). Maternal responsiveness was significantly higher than paternal responsiveness (Wilcoxon paired signed rank test: $V = 0$, $P = 0.001$; $r_{\text{equivalent}} = 0.994$; Fig. 3). Potentially this is due to differences in the speed of feedback that males and females produce. Female wing strokes and fluff-ups are swifter than male song and can be completed in a shorter interval. The amount of variability in maternal responsiveness across development was also significantly different from that in paternal

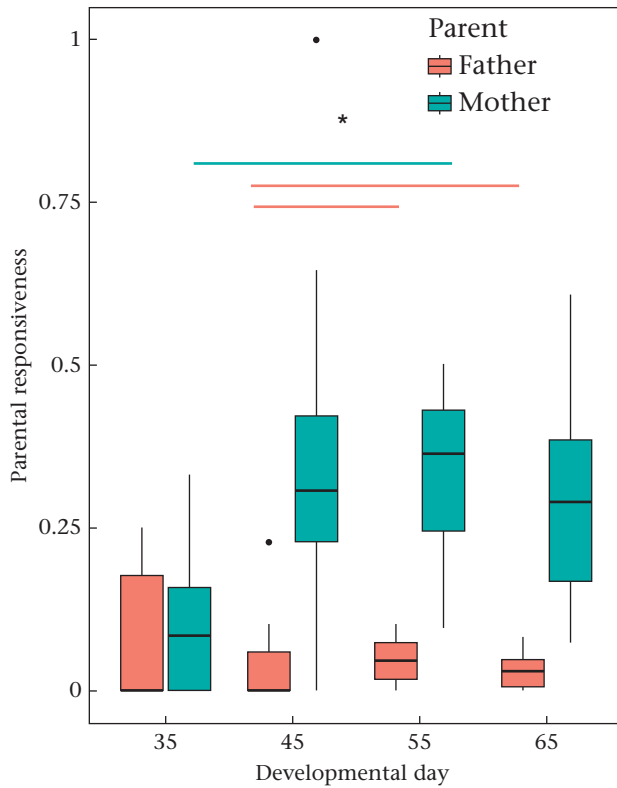


Figure 5. Variation in parental responsiveness (proportion of contingent responses to juvenile vocalizations) across development. Box plots represent median and quartiles; dots are outliers. * $P < 0.01$.

responsiveness (Levene's test on parent*day: $F_{7,67} = 3.23$, $P = 0.005$), with maternal responsiveness exhibiting greater variability.

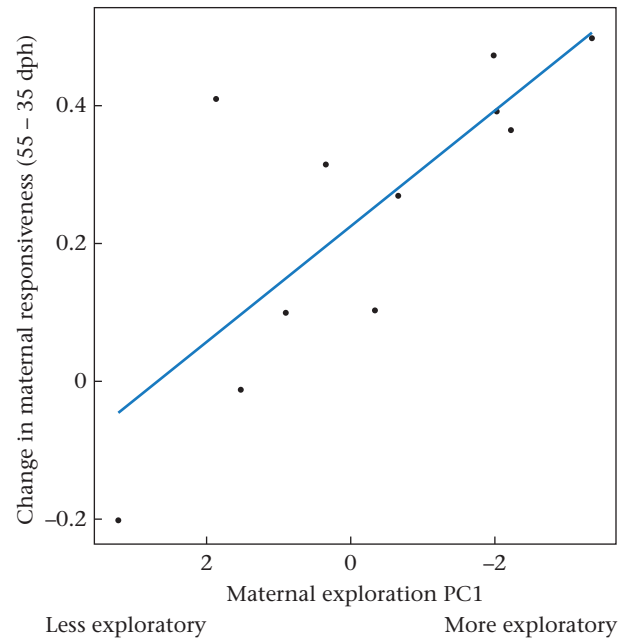


Figure 7. Change in maternal responsiveness to juvenile song in relation to exploratory behaviour (PC1, fewer novel components and fewer novel features visited during the novel environment tests). Change in responsiveness calculated as the proportion of responses at 55 days posthatch (dph) minus the proportion of responses at 35 dph.

Mothers could respond using fluff-ups ($18.82 \pm 12.80\%$ of songs) or wing strokes ($12.32 \pm 11.07\%$ of songs). Of the two maternal responses, there was no significant difference in which was used as the first contingent response to a juvenile song (Wilcoxon paired signed rank test: $V = 25.5$, $P = 0.54$; Fig. 4).

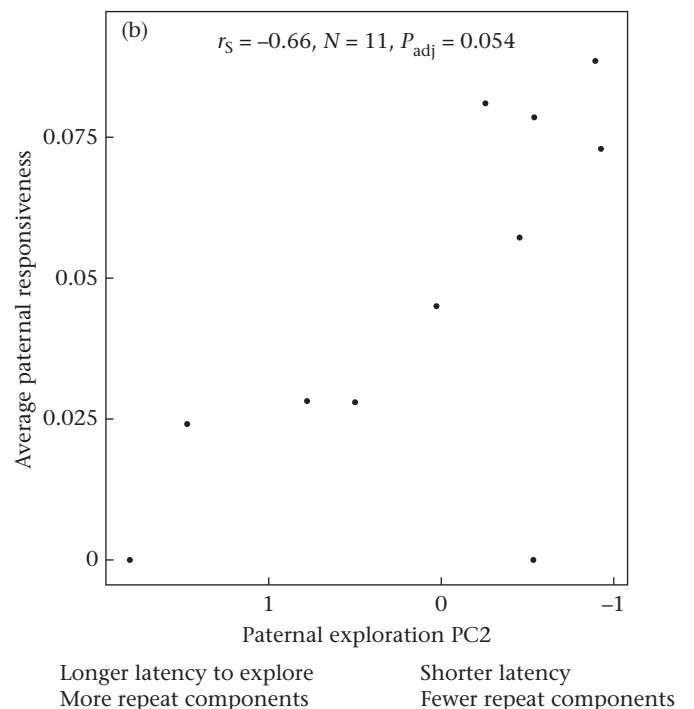
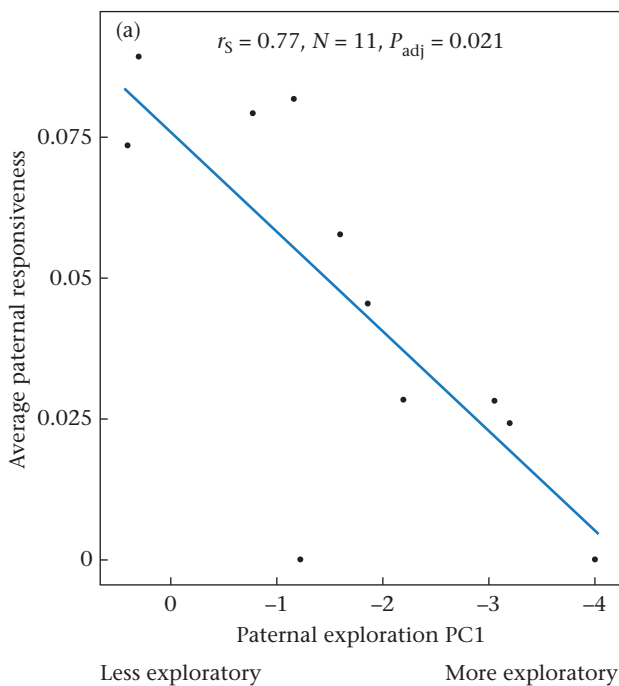


Figure 6. Relation between paternal responsiveness and PCA scores: (a) PC1, novel features and novel components visited; (b) PC2, latency to visit novel components and features, and repeat features visited.

Changes in Parental Responses over Development

We conducted separate logistic regressions to examine the effect of developmental day on the likelihood of a song receiving a contingent parental response from the mother or the father (Fig. 5). For fathers, there was a significant effect of day on the likelihood of providing a contingent response to juvenile song (likelihood ratio test: $\chi^2_1 = 13.09$, $P = 0.004$). Post hoc tests using the Tukey method of adjustment revealed that the likelihood of juvenile songs receiving a contingent paternal response was significantly higher at 55 days posthatch ($Z = 2.83$, $P = 0.024$) and 65 days posthatch ($Z = 3.33$, $P = 0.005$) than at 45 days posthatch.

For mothers, there was also a significant effect of day on the likelihood of providing a contingent response to juvenile song (likelihood ratio test: $\chi^2_1 = 9.38$, $P = 0.025$). Post hoc tests revealed that the likelihood of juvenile songs receiving a contingent maternal response was significantly higher at 55 days posthatch than at 35 days posthatch ($Z = -2.606$, $P = 0.045$), and there was a tendency for juvenile songs to have a higher likelihood of receiving a contingent maternal response at 65 days posthatch than at 35 days posthatch ($Z = -2.42$, $P = 0.073$). There was no effect of day on the type of response; that is, the likelihood of first responding with a contingent wing stroke or fluff-up did not vary depending on developmental day (all P s > 0.46).

Personality and Parental Response

We next tested whether adult personality, in terms of exploration, predicted responsiveness to offspring. We examined the correlation between parental responsiveness and PCA scores. For foster fathers, there was a significant positive correlation between PC1 and overall responsiveness (Spearman correlation: $r_s = 0.77$, $N = 11$, $P_{\text{adj}} = 0.021$). That is, fathers who tended to visit fewer novel components and fewer novel features were more likely to respond to juvenile vocalizations with contingent song (Fig. 6a). There was also a tendency towards a relationship between PC2 and overall paternal responsiveness (Spearman correlation: $r_s = -0.66$, $N = 11$, $P_{\text{adj}} = 0.054$). In other words, fathers who had a longer latency to commence exploration, and who visited more repeat features, tended to be less likely to respond to juvenile vocalizations with contingent song (Fig. 6b).

There was no significant relationship between the exploratory tendencies of foster mothers and their overall responsiveness (all $P_{\text{adj}} > 0.17$). We next investigated whether maternal personality predicted responsiveness on any of the developmental days individually, but found no significant correlation (all $P_{\text{adj}} > 0.33$). However, this was not unexpected given that maternal responsiveness varies depending on developmental day to a greater extent than does paternal responsiveness, as reported above.

After conducting the previous analyses, we became interested in whether maternal responsiveness flexibly adjusted to the increase in juvenile vocalizations at day 55, and whether that was predicted by maternal exploration score. We conducted a post hoc follow-up analysis to examine the change in maternal responsiveness from day 35 to day 55, as day 55 was of previous interest due to juvenile dispersal, as well as a time point of significant increase in both juvenile song rate and maternal response rate. We found that maternal exploration PC1 predicted the increase in responsiveness from day 35 to day 55, with a significant negative correlation between the two (Spearman correlation: $r_s = -0.66$, $N = 11$, $P = 0.031$). That is, females who were more exploratory were more likely to modulate their response over time, increasing the rate of contingent responses to their offspring from 35 to 55 days posthatch (Fig. 7). There was no significant relationship between maternal exploration PC2 and change in maternal responsiveness

from 35 to 55 days posthatch (Spearman correlation: $r_s = 0.31$, $N = 11$, $P = 0.37$).

We ran a parallel analysis for the fathers to examine whether paternal responsiveness flexibly adjusted to juvenile vocal productions at day 55, and whether that correlated with paternal exploration score. Neither paternal exploration PC1 nor paternal exploration PC2 had significant correlations with the change in paternal responsiveness from 35 to 55 days posthatch (Spearman correlations: all $P_{\text{adj}} > 0.14$).

Parental Response and Offspring Song Learning

G2 juveniles' mean (\pm SD) percentage match to tutor was $81.08 \pm 14.13\%$ for song similarity (overall match between the tutor and the juvenile), $77.68 \pm 3.67\%$ for accuracy (match to tutor over shorter time segments, on the level of syllables) and $73.51 \pm 12.45\%$ for sequential match (degree to which the juvenile's syllable order and timing matched that of the tutor). We compared overall parental responsiveness with G2 song learning outcomes. There was no significant effect of overall responsiveness on any of the G2 song learning measures, for foster fathers (Spearman correlations: all $P_{\text{adj}} > 0.88$) or foster mothers (Spearman correlations: all $P_{\text{adj}} > 0.96$).

Next, we examined the effect of parental responsiveness on G2 song learning specifically on 55 days posthatch, when juveniles increase song production. There was no significant effect of parental responsiveness on any of the G2 song learning measures, for foster fathers (Spearman correlations: all $P_{\text{adj}} > 0.96$) or foster mothers (Spearman correlations: all $P_{\text{adj}} > 0.36$), nor when looking only at wing strokes (Spearman correlations: all $P_{\text{adj}} > 0.80$) or fluff-ups (Spearman correlations: all $P_{\text{adj}} > 0.99$).

Personality and Offspring Song Learning

Neither paternal nor maternal personality predicted G2 song learning (Spearman correlations: all $P_{\text{adj}} > 0.65$). G2 personality did not predict any of the song learning outcome measures (Spearman correlations: all $P_{\text{adj}} > 0.86$).

Transgenerational Transmission of Personality Traits

We compared the personality traits of the two generations. G2 scored significantly higher on exploration PC1 than G1 (Wilcoxon signed rank test: $W = 293$, $P = 0.009$; $r_{\text{equivalent}} = 0.615$). There was no significant difference in exploration PC2 scores between the generations (Wilcoxon signed rank test: $W = 213$, $P = 0.70$). However, we also compared the PC1 scores of G1 and G2 with the other birds from G1 that did not reproduce (G1N). We found a significant effect of group (Kruskal–Wallis test: $\chi^2_2 = 10.93$, $P = 0.004$). Following up with pairwise comparisons, we determined that G1 significantly differed from G2 ($P = 0.014$) and G1N ($P = 0.007$), but there was no significant difference between G2 and G1N (Appendix, Fig. A3). There was no significant difference when comparing PC2 scores for G1, G1N and G2 (Kruskal–Wallis test: $\chi^2_2 = 0.21$, $P = 0.90$). Thus, although G2 scored higher on PC1 than did G1, the G2 group did not have unusually high PC1 scores when compared to a bigger sample of birds. There were no significant differences in PC2 scores.

We found no evidence for transgenerational transmission of exploration between G1 foster parents and G2 (Spearman correlations: all $P_{\text{adj}} > 0.61$), nor between G1 genetic parents and G2 (Spearman correlations: all $P_{\text{adj}} > 0.12$). Overall parental responsiveness did not influence G2 personality development (Spearman correlations: all $P_{\text{adj}} > 0.37$).

DISCUSSION

We found that individual differences in parental behaviour were predicted by exploration scores. This finding demonstrates the possible adaptive significance of adults pairing based on the trait of exploration, as previously shown (Faust & Goldstein, 2021). Parental responsiveness changed over juvenile development; however, the nature and direction of this change differed by parental sex. Foster fathers were more likely to sing contingently in response to juvenile vocalizations at 55 days posthatch and 65 days posthatch than at 45 days posthatch. Foster mothers were also more likely to respond at 55 days posthatch, as compared to 35 days posthatch. In general, mothers responded to juvenile song at significantly higher rates than fathers, and with greater variability. Changes in maternal responsiveness were linked to offspring song rate. Juveniles increased the number of songs that they produced as they matured, with significantly more songs produced at 55 days posthatch than at 35 days posthatch. This increase is in line with previous studies on song development, which report an inverted U-shape of song production over the course of song learning, with a peak around 55 days posthatch (Carouso-Peck et al., 2021; Johnson et al., 2002).

Our results on parental responsiveness parallel those of previous work examining parent–juvenile interactions in this species. We found that fathers responded to juvenile vocalization with contingent song at relatively low rates (mean \pm SD = $4.62 \pm 3.24\%$ of songs), comparable to the paternal responsiveness found by others ($4.26 \pm 2.86\%$; Carouso-Peck et al., 2020). Mothers produced contingent wing strokes ($12.32 \pm 11.07\%$ of songs) and fluff-ups ($18.82 \pm 12.80\%$ of songs) in response to juvenile song. These rates are higher and more variable than those found previously in females (wing strokes $10.8 \pm 0.050\%$, fluff-ups $1.3 \pm 0.016\%$, Carouso-Peck et al., 2020), which we discuss in more detail below.

We next examined the relationship between personality traits, specifically exploration, and parental responsiveness. Our first prediction was that individuals with higher exploration scores would respond to juvenile song at higher rates (i.e. higher paternal responsiveness), due to previous studies that found that more exploratory males were also more vocal in response to social stimuli (e.g. Hyman et al., 2013; Snijders et al., 2015). However, the opposite pattern was found in fathers: more exploratory males were significantly less responsive to juvenile song. There was also a tendency for individuals with longer latencies to explore and that visited more repeat perches to be less responsive. In mothers, on the other hand, our hypothesis was borne out: more exploratory females were more likely to increase responsiveness to juvenile song from 35 days posthatch to 55 days posthatch. There was no correlation between overall responsiveness and exploration for females as there was in males, possibly stemming from greater changes in maternal responsiveness over time as their offspring matured, relative to fathers.

While these results linking personality and parental responsiveness were somewhat surprising, we find them particularly intriguing in light of previous work on the influence of exploration on mate choice. Faust and Goldstein (2021) found that zebra finches selected pair partners that were similar to them in exploration. Thus, the contrasting pattern in males (negative correlation between exploration and paternal responsiveness) and females (positive correlation between exploration and maternal responsiveness) would lead to stabilizing influences on offspring song learning across families. For example, a pair of low explorers would result in a more responsive father and a less responsive mother, while a pair of high explorers would result in a less responsive father and a more responsive mother. Song learning might therefore be equivalent across different pairs of assortatively mated parents.

The opposite relation between exploration and parental responsiveness in mothers and fathers points to differences in how females and males recognize and react to cues from their offspring. Females appear to be far more responsive to the development of juveniles, with their responsiveness varying by developmental day. This may be due to the nature of zebra finch reproductive cues: when optimal conditions for breeding (i.e. sufficient humidity) are present, females will attempt to renest. Renesting is common in the wild, with 52 ± 16 days between successful renesting attempts, and birds averaging 1.7 clutches (females) or 1.9 clutches (males) per season (Zann, 1996). The beginning of a second breeding attempt marks a transition in behaviour in the wild, with females concentrating primarily on the new clutch, and males providing care for the existing fledglings (Zann, 1996). The physiological changes that accompany the ramping-up period for a second reproductive attempt might thus predispose females to be more responsive to more mature-sounding juvenile songs, which are produced more frequently around this point (e.g. 55 days posthatch) in offspring development. Thus, increased responsiveness may be a side-effect of increased physiological readiness for courtship and reproduction by responding to the songs of adult males. Some evidence for this is provided by previous studies: treating nonbreeding adult females with oestradiol induced similar stages of physiological breeding readiness as in breeding females (Williams, 1989), and implants of 17β -oestradiol have been used to increase response to song in zebra finches, eliciting tail quivers (a copulation solicitation display; Clayton & Pröve, 1989).

Together, females responding at higher rates to juveniles just as juveniles are, in turn, vocalizing at higher rates and with more mature-sounding songs could result in increased scaffolding of offspring song learning. The term scaffolding is connected to Vygotsky's (1978) 'zone of proximal development', which distinguishes between infant behaviours that are possible given an infant's current capabilities and infant behaviours that are facilitated by the presence of an adult. Under this framework, scaffolding refers to the structuring of parent–infant interactions in ways that benefit learning or task performance (Pea, 2004; Wood et al., 1976). Thus, the structured nature of parent–juvenile interactions in zebra finches, with parental responses contingent on the juvenile's immature song, could facilitate song learning. Other species also demonstrate forms of scaffolding that rely on acoustic cues to provide the appropriate level of parental care (Faust et al., 2020). For example, meerkats, *Suricata suricatta*, differentially provision their young with scorpions in varying states (e.g. dead, live but with the stinger removed, live and with stinger intact) depending on the vocalizations of the young (Thornton & McAuliffe, 2006). These begging calls correlate with pup size and prey-handling skill. Together, the parent–offspring system facilitates pup learning of adaptive foraging skills.

Fathers, however, may have a different parental niche, according to our findings. They are lower and less variable in responsiveness to juvenile song than mothers are, and thus appear to be less responsive than mothers to variation in juvenile song production. There are a few potential explanations for this occurrence. As males' period of parental care may extend for longer than that of the females (who commence renesting; Zann, 1996), their responsiveness to offspring behaviour may not alter as much over time. Alternatively, given that renesting may occur, fathers might need to be more selective as to whom their song is directed: the mother, for courtship purposes, or the juvenile. Previous studies have elucidated the importance of pupil-directed song in this species for offspring song learning outcomes (Chen et al., 2016). As paternal responsiveness does not change to a large extent depending on developmental day, despite renesting efforts that might be occurring (and thus necessitating increased female-

directed song), it would be interesting to investigate rates of pupil-directed song in particular. Future studies in our laboratory are planned to investigate paternal selectivity in song directedness.

While the ideas above are preliminary explanations of the patterns we observed, they provide guidance for future research. The relationship between paternal exploration and rate of pupil-directed songs, as well as the potential relationship between maternal exploration and physiological readiness to breed, offer interesting avenues for future studies. In particular, we encourage further examination of the reneating period (50–55 days post-hatch) and its effects on song learning outcomes.

Zebra finches, and other species with both biparental care and socially guided vocal learning, provide a means to examine the interface of personality, parental care and offspring learning outcomes. However, in such highly social species, it is important to consider the influence of housing methods on learning outcomes. As described above, the rates of paternal responsiveness in the present study were comparable to previous studies (Carouso-Peck et al., 2020), but the rates of maternal responsiveness were higher and more variable than those previously found (e.g. contingent wing strokes in response to $12.32 \pm 11.07\%$ of songs versus $10.8 \pm 0.050\%$, and contingent fluff-ups in response to $18.82 \pm 12.80\%$ of songs versus $1.3 \pm 0.016\%$, respectively). This divergence is potentially explained by differences in methodology. Our families were housed in a common aviary room, rather than in acoustic isolation, as in Carouso-Peck et al. (2020). This housing situation allowed for interaction between families, as adjacent families were within close visual and auditory range. Therefore, our females could have been responding to hearing the mature vocalizations of other adult males as well as juvenile males, as wing strokes and fluff-ups are arousal-based behaviours (Carouso-Peck and Goldstein, 2019). As the females would not be responding to the juveniles' songs alone, this would reduce the signal-to-noise ratio of the females' responses from the perspective of a juvenile. Indeed, we suspect the reduced signal-to-noise ratio may explain the lack of correlation between parental responsiveness and offspring song learning. Accordingly, future studies might explore the relationship between exploration and parental responsiveness either in acoustic attenuation chambers, or in families with only one juvenile male, to reduce noise in contingent responsiveness to other male offspring and to reduce chance contingencies between juveniles (i.e. a juvenile receives a contingent response from his brother) that might reduce song learning (Tchernichovski & Nottebohm, 1998). Alternately, playback experiments of immature song towards nonbreeding adults of known exploration might provide more insight into the relationship.

Our second prediction, that increased parental response would facilitate song learning, was not supported by the data. Prior studies have strongly linked contingent responses to juvenile vocalizations with their eventual song learning, as playbacks of a female fluff-up contingent on juvenile song result in significantly better song learning outcomes than playbacks not contingent on a juvenile's behaviour (yoked playbacks; Carouso-Peck & Goldstein, 2019). Signals that occur rarely (e.g. 1.3% of zebra finch songs receive fluff-ups, Carouso-Peck et al., 2020; 1.1% of cowbird songs receive wing strokes, West & King, 1988) can provide potent feedback for learning if they only occur contingently on a juvenile's song. However, if such signals occur at a higher rate and are only partially dependent on a juvenile's song—as might occur outside of acoustic isolation chambers—it might be more difficult to form an association between the two events. Examination of zebra finch breeding conditions in the wild reinforce the importance of high signal-to-noise response ratios. Wild zebra finches nest in colonies where pairs tend to synchronize their breeding (Brandl et al., 2019) and

where individuals may either nest in separate bushes or have multiple nests—up to 21—in the same bush (Zann, 1996). Parents spend more time foraging at a distance (e.g. colony members may forage up to 400 m from the nearest nesting trees). The limited interactions with parents in the wild might heighten the salience, and thus the reward value, of any contingent responses that occur, mimicking the conditions of rearing in acoustic isolation chambers.

Our third hypothesis, that the exploration of cross-fostered offspring (G2) measured in adulthood, would most closely match that of the foster parents, was not supported. Indeed, we found no significant effect of personality or parental responsiveness on G2 song learning or G2 personality. Although G2 personality did not resemble that of their genetic parents, it did not significantly resemble that of the G1 foster parents either. These results were somewhat unexpected given the results of previous studies on the transgenerational transmission of personality (e.g. Schuett et al., 2013), which found that offspring resembled the personality of their foster parents but not that of their genetic parents. However, unlike previous studies, we only examined the personality of male G2 birds and not that of their sisters. It is possible that males are not as influenced by foster parent personality as females, or that our small sample size prevented us from detecting small or moderate effects on offspring personality. Alternatively, perhaps differences in housing might explain our results. In Schuett et al.'s (2013) study, offspring were removed from single family cages at 35 days posthatch and transferred to cages with same-sex peers. In our study, families were housed in single family cages in visual and auditory contact with other families until 75 days posthatch. While this allowed us to examine parent–juvenile interactions surrounding song development, it also allowed for prolonged family and nonfamily interactions that might have influenced personality development.

Conclusion

We found that adult personality predicted parental behaviour in zebra finches. In particular, exploration predicted parental responsiveness to their offspring's immature songs. Juveniles increased the number of songs produced over development, with a rise at 55 days posthatch that parallels an increase in maternal responsiveness at this same period. Paternal responsiveness remained consistent throughout development. However, the relationship between personality and parental responsiveness differed by sex. High-exploring mothers and low-exploring fathers were more likely to respond to the immature vocalizations of their offspring. We suggest that differences in maternal and paternal responsiveness may stem from differences in reproductive strategies, such as division of care during reneating. While parental responsiveness did not predict offspring song learning in this study, personality did predict information provisioning by the parents, in terms of the number of contingent responses offspring receive. These responses provide opportunities for offspring learning.

Author Contributions

Both authors designed the study, conducted statistical analyses of results and wrote the manuscript. K.M.F. carried out the experiments and behavioural analysis.

Acknowledgments

We thank Samantha Carouso-Peck for her valuable feedback on earlier drafts of this manuscript. We also thank the many research assistants who coded our videos for their assistance in data collection. Research reported in this publication was supported by

the Eunice Kennedy Shriver National Institute of Child Health & Human Development of the U.S. National Institutes of Health under Award Number F31HD096848 to K.M.F. The content is solely the responsibility of the authors and does not necessarily represent the official views of the U.S. National Institutes of Health. K.M.F. was also supported by a grant from the Cornell University Field of Psychology Graduate Student Research Awards Fund.

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Appendix

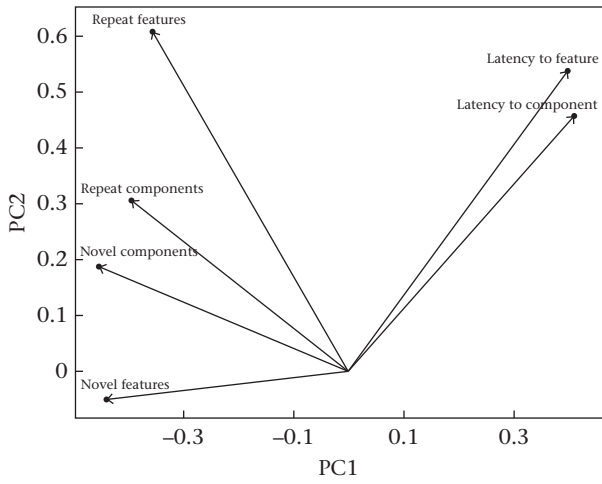


Figure A1. Principal components loading plot for PC1 and PC2. Figure reprinted from Faust and Goldstein (2021). PC1 primarily loaded on novel features and novel components visited; PC2 loaded primarily on latency to visit novel features or components, as well as repeat features visited.

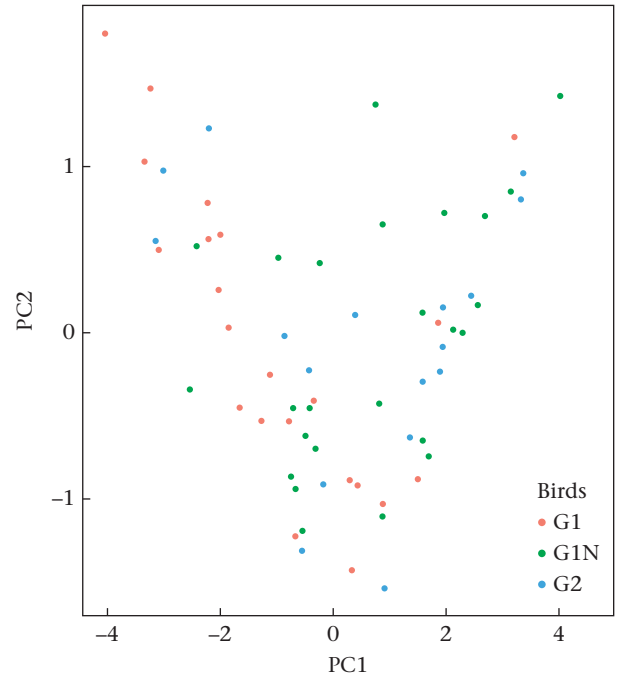


Figure A2. Principal component analysis scores for exploratory behaviour of each generation (G1, G1N, G2). Overlap between generational scores confirmed our assumption of similar underlying structure of exploration across generations.

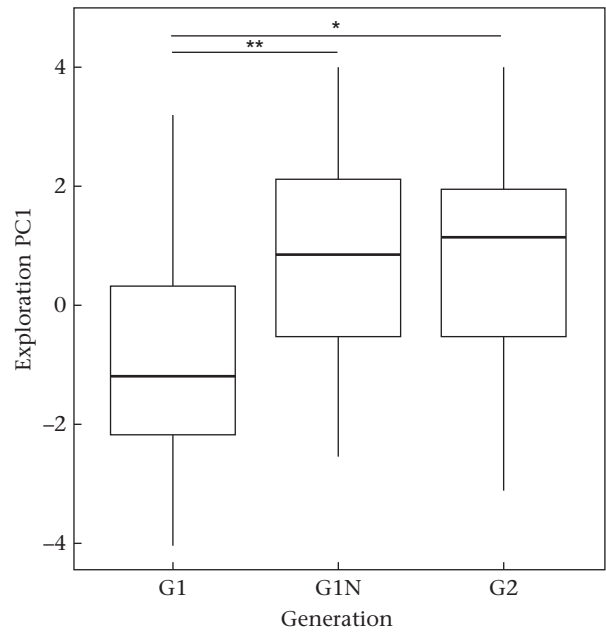


Figure A3. PC1 scores by generation. * $P < 0.05$; ** $P < 0.01$.