

1 **Stress hormones, social associations and song learning**
2 **in zebra finches**

3
4 Neeltje J. Boogert^{1*}, Robert F. Lachlan², Karen A. Spencer³, Christopher N. Templeton⁴ &
5 Damien R. Farine^{5,6}

6
7 ¹Centre for Ecology and Conservation, University of Exeter, Penryn Campus, UK

8 *Corresponding author: njboogert@gmail.com

9 ²School of Biological and Chemical Sciences, Queen Mary University of London, UK

10 ³School of Psychology and Neuroscience, University of St. Andrews, UK

11 ⁴Department of Biology, Pacific University, Oregon, USA

12 ⁵Department of Collective Behaviour, Max Planck Institute for Ornithology, Radolfzell, Germany

13 ⁶Chair of Biodiversity and Collective Behaviour, Department of Biology, University of Konstanz,
14 Germany

19 The use of information provided by others is a common short-cut adopted to inform decision-
20 making. However, instead of indiscriminately copying others, animals are often selective in what,
21 when, and whom they copy. How do they decide which “social learning strategy” to use? Previous
22 research indicates that stress hormone exposure in early life may be important: while juvenile zebra
23 finches copied their parents’ behaviour when solving novel foraging tasks, those exposed to elevated
24 levels of corticosterone during development copied only unrelated adults. Here we tested whether
25 this switch in social learning strategy generalises to vocal learning. In zebra finches, juvenile males
26 often copy their father’s song; would corticosterone-treated juveniles in free-flying aviaries switch to
27 copying songs of other males? We found that corticosterone-treated juveniles copied their father’s
28 song less accurately as compared to control juveniles. We hypothesised that this could be due to
29 having weaker social foraging associations with their fathers, and found that sons that spent less
30 time foraging with their fathers produced less similar songs. Our findings are in line with a novel
31 hypothesis linking early-life stress and social learning: early-life corticosterone exposure may affect
32 social learning indirectly as a result of the way it shapes social affiliations.

33

34 Keywords: developmental stress, information use, social networks, social learning, song learning,
35 stress hormones

36 INTRODUCTION

37 While most studies of learning and cognition are conducted on subjects in social isolation, most wild
38 animals live in a social context – be it a territorial or a gregarious one. Animals use information
39 generated by the behaviour of others in species ranging from fruit flies (*Drosophila melanogaster*)
40 [1] to humans [2]. Social information can shape individuals' decisions when tackling virtually every
41 life challenge, from learning to exploit novel food sources [3] and choosing mates [4], to avoiding
42 brood parasites [5] and predators [6]. However, theory suggests that indiscriminate social
43 information use is not adaptive [7], and accumulating evidence shows that animals employ “social
44 learning strategies” in choosing what, when and whom to copy [8,9]. Yet individuals vary in whether
45 they (appear to) use social information [10] and, if so, in which social learning strategy they adopt
46 [11]. Relatively few studies have investigated the mechanisms underlying this inter-individual
47 variation in social information use, but there is accumulating evidence to suggest that early-life
48 conditions [12,13] and social interactions [11,14–18] may be important.

49
50 In two recent studies, we investigated how early-life conditions shape social associations and social
51 learning strategies in the highly gregarious zebra finch (*Taeniopygia guttata*). First, we found that
52 juvenile zebra finches that were fed the avian stress hormone corticosterone during the nestling
53 phase later formed less exclusive (or more random) social bonds in a colony setting (free-flying
54 aviaries containing 6-7 families) relative to their control-treated siblings. In particular,
55 corticosterone-treated juveniles spent less time foraging with their parents [19]. When presented
56 with a novel foraging task, we next found that while control juveniles tended to copy their parents'
57 behaviour to solve the task, their corticosterone-treated siblings exclusively copied unrelated adults
58 [20]. This could be because the corticosterone-treated juveniles may not have perceived their
59 parents as desirable role models, or because the parents may have treated their experimentally
60 stressed (and thus “lower quality”) offspring differently. Regardless of the underlying mechanisms,
61 early-life corticosterone exposure appeared to induce a switch in with whom juveniles affiliated [19]

62 and who they copied when socially acquiring novel foraging behaviours [20]. The aim of the current
63 study was to determine whether early-life corticosterone exposure had a similar effect on the social
64 learning of song. If so, we wanted to identify whether this was due to corticosterone-associated
65 changes in the choice of whom to copy, or a by-product of changes in social affiliation patterns. Bird
66 song is the quintessential example of a socially transmitted trait, and song learning is likely to be
67 important for individuals' fitness: which song an individual sings and how accurately they learn it can
68 have long-lasting consequences for their later ability to compete in territorial disputes or court
69 potential mates [21–23], and can predict individuals' reproductive success and longevity [24].

70

71 In addition to potentially affecting social affiliations and/or song model choices, early-life stress may
72 also influence song learning by impacting cognitive ability. Song learning involves a variety of
73 cognitive processes. Juveniles typically acquire information about species-specific song by listening
74 to the songs of adults (“tutors”) during a relatively short period (the “sensitive window/phase”) in
75 development. They then memorise this information, often for many months, and use it to shape and
76 practise their own song as they mature [25]. Studies that subjected juvenile songbirds to a variety of
77 early-life stressors (e.g. increased brood size, food restriction, corticosterone administration;
78 reviewed in [26]) often found that stressed males sing lower-quality songs; their songs tend to be
79 shorter, contain fewer (unique) songs or syllables, less accurately copied syllables or syntax, and are
80 perceived as less attractive by females. Some developmental stress studies even report a reduction
81 in the volume of the song control nuclei in the brain [26]. The “developmental stress hypothesis”
82 proposes a potential explanation for these findings [26,27]: song control nucleus development in the
83 brain requires considerable energetic resources during a period of rapid physical and neuronal
84 growth. If these energetic resources are constrained by developmental stressors such as sibling
85 competition, food scarcity or predation threat, then song development is likely to be negatively
86 affected. However, the juvenile males in these developmental stress studies, as in most captive
87 studies on song learning, tend to be experimentally constrained to learn from a single adult tutor. It

88 thus remains to be established whether developmentally stressed males show impoverished song
89 learning in more naturalistic social contexts, such as in colonies where young birds are free to
90 choose to associate with and learn from multiple potential song tutors.

91

92 Zebra finches are the foremost model system for studies of song development [28–30]. Male zebra
93 finch song structure and performance play a crucial role in female mate choice in captivity [31] and
94 predict reproductive success in the wild [32]. Males repeatedly sing a single stereotyped and unique
95 song motif during courtship. Captive studies suggest that juvenile males tend to learn these
96 courtship songs from their fathers, if the latter are available as tutors during the sensitive phase
97 when song templates are acquired, i.e. between ca. 35-65 days post-hatching, after they have
98 fledged [33–36]. Zebra finches are also highly gregarious, non-territorial birds that breed in colonies
99 ranging in size from ca. 4 to 136 pairs [37], making them ideal for studying song learning strategies in
100 a dynamic social context. Even so, most experimental studies on zebra finches in captivity have been
101 based on constrained song tutor choice: birds were usually confined to small cages and only given
102 the choice to copy the song of their father or one alternative tutor, without the opportunity to freely
103 associate in a broader social group. The two studies in which breeding pairs and their offspring were
104 kept in free-flying aviaries containing multiple potential tutors [38,39] generated complementary but
105 contradictory findings: Williams (1990) found that the majority of juveniles produced songs that did
106 not resemble their father's, and they instead appeared to copy the unrelated males that they
107 interacted with the most. Similarly, Mann and Slater (1995) found that most juveniles learnt their
108 songs from the male with whom they maintained greatest proximity, but in contrast to Williams
109 (1990), this was often the father. These studies suggest that there could be considerable variation in
110 the choice of song tutor under (semi-) natural rearing conditions, which is likely related to the social
111 associations that young birds experience, and thus their social preferences. Here we take advantage
112 of being able to quantify fine-scale social associations among all individuals in replicated colonies of

113 zebra finches, combined with experimental manipulations of early-life conditions, to uncover some
114 of the mechanisms that may underlie the observed variation in song tutor selection.

115

116 In the current study, we examined the relationships between early-life exposure to corticosterone,
117 fathers' and sons' social associations, and sons' song tutor choice and song copying accuracy. We
118 used data from the same zebra finches and experimental design as in our previous studies [19,20]:
119 half of the offspring in each of 13 zebra finch families were exposed to experimentally elevated
120 levels of corticosterone in the nest. After fledging, all individuals' feeder visits in two aviaries were
121 recorded using an automated tracking system, generating a social foraging network of birds' co-
122 occurrences at the feeders. Next, we generated a "song similarity matrix" between all males in both
123 aviaries. We then combined these data to test three, not necessarily mutually exclusive, predictions
124 drawn from previous studies: (1) in contrast to control juveniles, corticosterone-treated juveniles
125 will avoid copying their father's song (the "tutor choice hypothesis", based on [20]); (2) the more
126 fathers and sons associate during the sensitive phase for song learning, the more similar the sons'
127 songs will be to those of their fathers (the "social preference hypothesis", based on [38,39]) and (3)
128 corticosterone-treated juveniles will not be capable of copying their father's song as accurately as
129 control juveniles (the "cognitive impairment hypothesis", based on [26]).

130

131 METHODS

132 *Breeding protocol and corticosterone treatment*

133 As described in [19], we housed 24 domesticated adult zebra finch pairs in breeding cages and of
134 these, 13 pairs produced fertile eggs. To facilitate chick age-standardized hormone treatment we
135 synchronised the within-brood hatching dates by replacing eggs with plastic dummies until the
136 brood was complete. Half of the chicks in each brood were assigned to the corticosterone (CORT)
137 treatment following [40]: between days 12 and 28 post-hatching, they were pipette-fed 20 μ l of
138 CORT (Sigma Aldrich; 0.155 mg/ml in peanut oil) twice daily, giving a total dose of 6.2 μ g CORT/day.

139 This dose is known to result in plasma CORT levels comparable to those naturally induced in
140 untreated zebra finch chicks exposed to an acute stressor [40]. Control chicks were fed 20 μ l of pure
141 peanut oil when their siblings received CORT. For additional details, please see the Electronic
142 Supplementary Materials.

143

144 *Social networks in aviaries*

145 When chicks were on average \pm SD = 35 \pm 1 days old (range: 33-38 days), we fitted them and their
146 parents with Passive Integrated Transponder (PIT) tags (Dorset ID) attached to unique colour rings,
147 and released families together into one of two identical indoor aviaries (3x3.1x3.2m) on the same
148 day. The aviaries were visually and acoustically isolated from each other. Each aviary contained
149 seven (N=34 birds: 16 females, 18 males) and six families (N=29 birds: 14 females, 15 males),
150 respectively, and both aviaries were equipped with two identical transparent feeders (28x28x10cm)
151 containing *at libitum* finch seed at all times, except during a 3-day novel foraging task experiment
152 (described in [20]) that was excluded from analyses here. Feeders were designed as enclosed seed
153 trays with two open access points, each fitted with RFID antennae (Dorset ID) to record the PIT tags
154 of zebra finches as they freely entered and exited the feeders. The only way for the birds to obtain
155 food was to visit these feeders. During a 5-day habituation period to the free-flying aviaries we
156 checked that all birds regularly visited the feeders and observed no aggressive interactions around
157 the feeder access points. All birds' feeder visits were subsequently logged for 33 days. From this
158 temporal data stream we extracted bouts of foraging activity using a well-established clustering
159 algorithm [41] to define groups of birds visiting the feeder around the same time. This clustering
160 algorithm generated estimates of flock feeding events lasting on average 290 seconds (2.5th
161 percentile: 0 s (when birds landed on the feeder entrance and immediately left again), 97.5th
162 percentile: 610 s). We then calculated association strengths between each dyad of birds in each
163 aviary as the number of observations of both individuals in the same foraging group divided by the
164 number of observations of at least one individual in a foraging group (i.e. the "simple ratio index",

165 ranging from from 0 = never observed at the same feeder together, to 1 = always observed
166 together; see Supplementary Methods of [20] for more details) with the *asnipe* package Version
167 1.1.3 [42] in R [43]. The social network data can be freely downloaded from [44]. The three social
168 network metrics we extracted as predictors of father-son song similarity were a) the father-son
169 association strength in each of the 33 daily foraging networks [19]; b) the total number and strength
170 of the father's daily associations (i.e. "weighted degree") with all other aviary members excluding
171 the son, as a measure of father "gregariousness" (which could affect his popularity as a song tutor
172 [38]), and c) the son's weighted degree excluding the father (as a highly sociable son may be less
173 likely to pay attention to, and thus copy, the father's song). All social network metrics were
174 calculated including both male and female associates, as this reflects their actual social environment
175 and takes into account any influences that female associations may have had on the males' song
176 learning processes. Females were excluded only from the song metrics (see below) as female zebra
177 finches do not sing.

178

179 *Song recordings*

180 Male zebra finches each learn one song motif, which is repeated several times to form a song. We
181 recorded the songs of all 17 adult males that were present in the breeding cages when the first
182 chicks started hatching. Only 13 of these males produced fledglings and were present in the aviaries
183 (and thus network analyses), but we also analysed the songs of the unsuccessful breeders (N=4
184 males), as we could not exclude the possibility that their songs were picked up by fledglings in
185 neighbouring breeding cages. Captive-reared zebra finches tend to learn and produce songs heard
186 between 35 and 65 days post-hatching, but they can incorporate elements heard before or after this
187 sensitive phase [28]. CORT-treated (N=12) and control male (N=8) juveniles' songs were recorded
188 when juveniles were at least 100 days old (mean \pm SD = 103 \pm 2 days) and their songs had crystallized
189 to become stereotyped (this is known to occur around day 90 post-hatching [45]). Males were

190 induced to sing by presenting each with an unfamiliar female in a sound-attenuated recording room.
191 For additional details, please see the Electronic Supplementary Materials.

192

193 *Song analyses*

194 We analysed to what extent the song motif of each juvenile male (recorded once they reached
195 adulthood) matched those of the 19 other juvenile males and of all 17 adult males they were
196 acoustically exposed to. We predicted that most learning would occur from the seven (aviary 1) or
197 six (aviary 2) adult males that fathered the juveniles and/or were present in the same free-flying
198 aviaries from post-hatching day 35 onwards. Song elements were compared using dynamic time
199 warping (dtw) in Luscinia (<http://rflachlan.github.io/Luscinia/>). This method has previously been
200 applied successfully to zebra finches and other songbird species [23,46,47] to measure broad-scale
201 features of song organisation as well as copying accuracy. The resulting dissimilarity matrix between
202 all possible pairs of song elements in the dataset served as the basis for comparisons between
203 individuals' song motifs: for each pair of individuals, we found the best fit between each of one's
204 song motifs and those of the other, and averaged these to generate a motif dissimilarity matrix. For
205 each juvenile we then ranked all potential song tutors (i.e. other male juveniles and adults, giving
206 ranks 1-36) according to their song dissimilarity scores. We inferred that the male with the lowest
207 dissimilarity score to the focal individual's song, and thus the most similar song, was the main song
208 tutor, and this individual received rank 1. The individual with the most dissimilar song (i.e. the largest
209 dissimilarity score) received rank 36. These data can be found in Supplementary Dataset 1: Song
210 Similarity Scores. Figure 1 shows examples of high and low father-son song motif similarity, and the
211 song analyses are described in more detail in the Electronic Supplementary Materials.

212

213 STATISTICAL ANALYSES

214 To first determine whether there was a link between CORT treatment and juveniles' use of the
215 father as the primary song tutor, we conducted a generalised linear mixed-effects model (GLMM)

216 with binomial error structure. The response variable was whether the juvenile's father was his main
217 song tutor ("1") or not ("0"), the fixed effect was CORT treatment (=1, control treatment=0), and the
218 random effect was family ID.

219

220 Next, to determine whether CORT treatment and father and son's social foraging association metrics
221 during the sensitive phase for song learning correlated with father-son song similarity, we conducted
222 a linear mixed-effects model with father-son song dissimilarity score as the response variable. Fixed
223 effects were i) CORT treatment; ii) the strength of father-son association in each of the daily foraging
224 networks [19]; iii) the total number and strength of the father's daily associations (i.e. "weighted
225 degree") with all other aviary members excluding the son (to control for "father gregariousness"), iv)
226 the son's weighted degree excluding the father (to control for "son gregariousness"), and v) the
227 number of fledglings in the family (as brood size can affect social learning strategies [12]). We
228 included "family ID" as a random effect, as the 20 juvenile males came from 11 different families
229 (two of the 13 fathers in the aviaries produced only daughters). Previous studies where juvenile
230 males were kept in small song learning groups with a single adult male tutor suggest that the
231 number of male peers present can affect song similarity [48,49]. To test for a correlation between
232 number of male offspring and father-son song similarity, we used the exact same linear mixed-
233 effects model as described above, but replaced the number of fledglings in the family with number
234 of male offspring (as these factors were strongly correlated and so could not both be included in the
235 same model). To test whether CORT treatment was related to the strength of father-son
236 associations, we conducted another linear mixed-effects model: the father-son association in the
237 daily foraging networks was the response variable, CORT treatment was the fixed effect, and family
238 ID the random effect.

239

240 Finally, to test whether CORT treatment was linked to overall song copying accuracy, we conducted
241 a linear mixed-effects model, where the response variable was the song dissimilarity score between

242 juvenile and first-ranked tutor (i.e. with the smallest dissimilarity score), the fixed effect was CORT
243 treatment, and the random effect was family ID.

244

245 All statistical models were constructed using the 'lme4' package version 1.1-11 in R. To calculate the
246 significance of fixed effects involving network metrics, and account for the fact that individuals'
247 social association metrics are not independent of each other, we used a null models approach
248 [50,51]: we compared the "observed" test statistic, i.e. the coefficient of the slope from the linear
249 mixed-effects model of the observed data, to the distribution of test statistics generated by running
250 the same statistical model on 10,000 permutations of the observed social associations using the R
251 package 'asnipe' version 1.1.3 [42]. These permutations maintain the same data structure as the
252 data collected, and only incrementally swap single observations of two individuals occurring in
253 different feeding bouts/flocks [50]. This approach thus maintains, and controls for, aviary ID, the
254 number and ID of individuals in each aviary, the number of times individuals were recorded to visit a
255 feeder, and the specific feeder they visited.

256

257 RESULTS

258 *Link between corticosterone treatment and song tutor choice*

259 We tested whether CORT-treated juveniles were less likely to copy their fathers' song. We found no
260 significant link between CORT treatment and primary song tutor choice (GLMM: slope \pm s.e. = -1.077
261 \pm 1.066, $z_8 = -1.010$, $p = 0.312$). The majority of juveniles (12/20) sang songs most similar to their
262 fathers' (Table 1). Of the eight birds whose songs were most similar to those of alternative tutors, six
263 were CORT-treated juveniles and two were control birds. However, the majority of these eight
264 juveniles' songs were most similar to brothers from the same brood, with the father generally
265 second-ranked ("Father Rank: 2" in Table 1) after a brother. The three exceptions in terms of song
266 tutor choice (with father ranked 5th, 15th and 23rd) were all CORT-treated juveniles (Table 1). These
267 patterns, illustrated in Electronic Supplementary Materials Figure S1, suggest that in some cases

268 CORT-treated juveniles might avoid their father as a song tutor. Replicating this study with a larger
269 sample size would help establish how robust and biologically meaningful this pattern is.

270

271 *Links between corticosterone treatment, social associations and father-son song similarity*

272 Father-son song similarity was strongly affected by the CORT treatment, with CORT-treated juveniles
273 producing songs that were less similar to their fathers' songs than those of control birds (Table 2).

274 Father-son song similarity was also correlated with the strength of father-son social associations
275 (Table 2, illustrated for each network day in Figure S2): the more often fathers and sons were at the
276 same feeder at the same time (Fig.2: thicker lines), the more similar were their songs (Fig.2: redder

277 lines). Further, the number and strength of associations between the father and all other aviary
278 members (excluding the son) showed a negative correlation with father-son song similarity: the

279 more gregarious the father (Fig. 2: larger circles), the less similar his son's song was to his. In

280 contrast, the son's 'gregariousness' showed no significant correlation with father-son song similarity.

281 Finally, father-son song similarity was related to brood size: the more fledglings (of both sexes), the
282 more similar the songs of father and son(s). The number of male fledglings in each nest showed no

283 significant relationship with father-son song similarity (Table 2). These results are robust to the

284 removal of two outliers, except for the effect of brood size, which was no longer significant (see

285 Electronic Supplementary Materials: Results & Table S1).

286

287 The finding that CORT treatment was associated with reduced father-son song similarity, while

288 father-son association strength increased it (Table 2), raises the question whether there might be a

289 direct and negative link between CORT treatment and father-son associations: did CORT juveniles

290 associate less with their fathers as compared to control juveniles? Our post-hoc exploration of the

291 data suggested a weak but significant negative relationship between CORT treatment and father-son

292 association strength that emerged when comparing the observed networks to their randomizations

293 (linear mixed-effects model: slope \pm s.e. = -0.007 ± 0.009 , $t = -0.758$, $p_{\text{rand}} = 0.028$). That is, despite

294 being fairly small, the slope parameter of our model was significantly more negative than expected
295 by chance (i.e. although the confidence interval overlaps 0, the slope is outside the 95% range of
296 slopes generated by the randomisation procedure; see [50] for a detailed explanation of how such
297 patterns can arise). However, absolute father-son association strength differed only slightly between
298 CORT- and control juveniles (CORT ($N=12$): mean \pm SD = 0.175 ± 0.042 ; control ($N=8$): mean \pm SD =
299 0.172 ± 0.046). These results should thus be interpreted as CORT-treated juveniles having weaker
300 associations with their fathers *relative to their potential to associate given their social network*.

301

302 *Link between corticosterone treatment and overall copying accuracy*

303 When we expanded the analysis to include all primary song tutors, rather than just the father, we
304 found no significant relationship between CORT treatment and overall song learning accuracy: when
305 comparing the songs of juveniles to those of their most similar tutor (i.e. the tutor with the smallest
306 song dissimilarity score; see Table 1), control and CORT-treated individuals did not differ in their
307 song dissimilarity scores (linear mixed-effects model: slope \pm s.e. = 0.007 ± 0.013 , $t_8 = 0.554$, $p =$
308 0.587). This finding suggests that corticosterone exposure did not impair juveniles' cognitive ability
309 to learn songs accurately.

310

311 DISCUSSION

312 The aim of this study was to investigate song learning accuracy and tutor choice of juvenile zebra
313 finch males in free-mixing populations, and the social and hormonal mechanisms that might shape
314 these song learning processes. Our results support the "social preference hypothesis": we found that
315 foraging associations between juveniles and their fathers were strongly correlated with their song
316 similarity. This effect was modulated by early-life stress: young males treated with corticosterone
317 were slightly less strongly connected to their fathers than expected by chance, and on average their
318 songs were less similar to those of their fathers when compared to the songs of control males. Our
319 results shed light on the mechanisms by which elevated corticosterone exposure early in life might

320 have downstream effects on song learning: by modulating social preferences of juveniles and their
321 potential song tutors.

322

323 Our results corroborate the results of two previous zebra finch studies showing positive correlations
324 between social associations and tutor-pupil song similarity in an aviary context [38,39], and suggest
325 that the apparent contrasts in tutor choice observed therein may have actually been the by-product
326 of differences in social association patterns. Similar positive correlations between social associations
327 and song or call similarity patterns have been observed in other species, both in captivity (e.g.
328 starlings (*Sturnus vulgaris*) [52]) and in the wild (e.g. song sparrows (*Melospiza melodia*) [53];
329 Campbell's monkeys (*Cercopithecus campbelli campbelli*) [54]).

330

331 We do not claim that our zebra finches were singing (and learning songs) inside the feeders. Instead,
332 our social foraging networks are more likely representative of birds' general social preferences
333 outside the feeders (i.e. by capturing correlations in their behaviour across the day), where singing
334 and song learning presumably occurred. Previous studies suggest that different types of social
335 networks (e.g. proximity vs. interaction networks) do not necessarily correlate [55] nor necessarily
336 concur in predicting information transmission [56]. Work is underway to quantify multi-context
337 social networks in zebra finches to assess the domain-generalty of their foraging associations [57].
338 In addition, the development of light-weight microphone backpacks [58] offers the exciting
339 possibility of tracking vocal interactions and song development throughout the juveniles' sensitive
340 phase for song learning in a free-flying context, and thus map dynamic social association networks
341 onto dynamic communication networks [59] rather than just the end-product of the crystallised
342 song.

343

344 In line with our previous study [19], our results provide greater insights into the effects of early-life
345 corticosterone exposure on social preferences, in this case reducing father-son foraging associations.

346 Further work tracking individual behaviour in finer detail [57] might be able to reveal the factors and
347 their directionality underlying differences in the potential to associate, such as whether they are
348 driven by the juveniles and/or the fathers. Although included primarily as a control variable, we also
349 found that more gregarious fathers had sons with less similar songs. This could suggest that more
350 gregarious fathers might be less preferred as song models, or perhaps that genetic factors that
351 increase father gregariousness also somehow reduce son song copying accuracy. However, it seems
352 more likely that such gregarious fathers create a more complex social and acoustic environment in
353 which accurate song copying is more challenging for their male offspring. A quarter of the sons were
354 also found to have songs most similar to those of their brothers. This could indicate horizontal social
355 transmission of song, a phenomenon previously described amongst juvenile peers in small flocks of
356 captive zebra finches containing a single adult song tutor [60]. Alternatively, brothers might not
357 necessarily copy each other's songs directly, but show similar song learning tendencies (e.g. they
358 may (genetically and/or through early-life effects) be predisposed to attend to the same cues in their
359 social environment), resulting in more similar songs indirectly. It is impossible to distinguish between
360 these hypotheses without further experimental manipulation. Selective feeders, perches or roosting
361 sites (see e.g. [61]) could be used to manipulate the gregariousness of fathers as well as father-son
362 and peer bonds, and help to elucidate the potential causal links between social
363 associations/preferences and song learning patterns.

364

365 Similar to the pattern we previously observed in the context of socially learning to solve a novel
366 foraging task [20], some corticosterone-treated sons appear to have sought out song tutors other
367 than the father. This could be because the father may not have been preferred as a role model due
368 to the negative early-life experiences of the corticosterone-treated offspring in the nest, which
369 would support the "tutor choice hypothesis". Alternatively, fathers may have differentially
370 interacted with corticosterone-treated and control sons, for example because they perceived their
371 corticosterone-treated sons to be of lower quality; corticosterone-treated juveniles weighed less

372 than control juveniles at the end of corticosterone treatment just before fledging ([19]
373 Supplementary Materials) and fathers may have noticed this. We hope that recent developments in
374 tracking techniques [57] will help to determine the directionality of this effect (father to son versus
375 son to father) in the future.

376

377 Previous studies have suggested that developmental stress may hamper the *ability* of birds to learn
378 their songs accurately [62,63] (although see [64,65]). However, our findings suggest that
379 corticosterone-induced changes in social preferences, rather than an impaired cognitive ability,
380 could help explain some of the reported tutor-tutee song (dis)similarities. Our results show that
381 corticosterone-treated juveniles copied their most similar model song as accurately as the control
382 juveniles copied theirs. Similarly, our previous study on the same birds showed that corticosterone-
383 treated juveniles were faster, not slower, to solve a novel foraging task as compared to the control
384 juveniles [20], as has also been found in another zebra finch population that controlled for foraging
385 motivation through quantifying metabolic rate [66]. Our findings thus appear to provide no support
386 for the “cognitive impairment hypothesis” in our specific study population (although this could be a
387 false negative (i.e. type II error) due to small sample size), and suggest that stressors may influence
388 song development indirectly as a consequence of their effects on social preferences. Thus, our study
389 has opened up a new window through which to explore the hormonal and behavioural mechanisms
390 underlying information acquisition (i.e. tutor choice) and use (i.e. copying accuracy) in song learning.
391 Unfortunately, our study does not allow us to completely disentangle the intertwined influences of
392 corticosterone exposure and social preference patterns [19] on song learning due to our limited
393 sample size. In addition, chick sex was unknown at the start of the corticosterone manipulation,
394 resulting in several broods without control sons. However, our findings provide a useful context to,
395 and help to elucidate the contrasting results of previous studies. As a result, we are starting to
396 develop a deeper understanding of factors underlying song learning outcomes.

397

398 Stressors experienced early in life clearly affect juveniles' social learning strategies, both when
399 learning about novel food sources [12,20] and when learning about song (current study). Here, by
400 integrating social and communication networks [59], we suggest that changes in social preferences
401 could play a key role in modulating song learning by juveniles; young males that had strong social
402 bonds with their fathers expressed more similar songs. The functional significance and ecological
403 relevance of juveniles (not) copying their fathers' songs has remained unclear. Most songbirds
404 acquire their songs after dispersing from their natal territory, learning from males other than their
405 fathers, with some species (like the zebra finch) learning during an early critical period, while others
406 (like starlings) continuing to learn throughout life [24]. It has been suggested that learning from the
407 father in early development may facilitate later kinship recognition and inbreeding avoidance in wild
408 zebra finches, where extended breeding seasons and high mortality lead to high rates of re-pairing in
409 the colonies [36]. But if a male was successful in producing offspring, why would any of his sons,
410 even if stressed in early development, decide *not* to copy him? Our study suggests that
411 inaccurate/not copying of the father's song may not be a directed strategy by juvenile males, but
412 instead could be a by-product of other social processes. Our findings, when combined with previous
413 studies, clearly highlight the importance of social preference patterns in modulating song learning,
414 and ultimately the links between early-life conditions, social affiliations and information use.

415 ETHICS

416 All experiments were approved by the local animal ethics committee of the University of St. Andrews
417 (Scotland) and the experiments were conducted in accordance with the Home Office Animals
418 (Scientific) Procedures Act 1986 under project licence no. 60/4068 held by KAS and personal licence
419 no. 60/13491 held by NJB.

420

421 ELECTRONIC SUPPLEMENTARY MATERIALS

422 Methodological details, additional analyses and results have been uploaded as part of the electronic
423 supplementary material.

424

425 DATA ACCESSIBILITY

426 The social network data as first reported in [19] are publicly available via

427 <http://datadryad.org/resource/doi:10.5061/dryad.7qs06>

428 The complete song similarity data and a song-network data summary file have been uploaded as
429 Supplementary Datasets 1 and 2, respectively, and will be published with this manuscript.

430

431 COMPETING INTERESTS

432 We have no competing interests.

433

434 AUTHORS' CONTRIBUTIONS

435 NJB, KAS, and CNT designed the study. NJB collected the data, RL analysed the songs, NJB, DRF and
436 RL planned the statistical analyses and DRF conducted the analyses and created the figures. NJB and
437 DRF wrote the paper with significant input from all co-authors.

438

439 ACKNOWLEDGEMENTS

440 We would like to thank Lysanne Snijders, three reviewers and editor Julie Morand-Ferron for their
441 extensive and constructive feedback, which has greatly improved our manuscript.

442

443 FUNDING

444 NJB was funded by a Netherlands Organisation for Scientific Research Rubicon Fellowship during the
445 experimental phase of this study, and by a Royal Society Dorothy Hodgkin Fellowship during the
446 write-up. KAS was funded by a BBSRC David Phillips Research Fellowship during the experimental
447 phase. CNT was supported by a NERC Postdoctoral Fellowship during the experimental phase of the
448 study. DRF was funded by the Max Planck Society and received additional funding from the Deutsche
449 Forschungsgemeinschaft (FA 1420/4-1).

450

451

452 REFERENCES

- 453 1. Sarin S, Dukas R. 2009 Social learning about egg-laying substrates in fruitflies. *Proc. R. Soc. B*
454 **276**, 4323–4328. (doi:10.1098/rspb.2009.1294)
- 455 2. Dean LG, Kendal RL, Schapiro SJ, Thierry B, Laland KN. 2012 Identification of the social and
456 cognitive processes underlying human cumulative culture. *Science* **335**, 1114–8.
457 (doi:10.1126/science.1213969)
- 458 3. Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015
459 Experimentally induced innovations lead to persistent culture via conformity in wild birds.
460 *Nature* **518**, 538–541. (doi:10.1038/nature13998)
- 461 4. Galef BG, White DJ. 1998 Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*.
462 *Anim. Behav.* **55**, 545–552. (doi:10.1017/CBO9781107415324.004)
- 463 5. Thorogood R, Davies NB. 2016 Combining personal with social information facilitates host
464 defences and explains why cuckoos should be secretive. *Sci. Rep.* **6**, 19872.
465 (doi:10.1038/srep19872)
- 466 6. Coolen I, Dangles O, Casas J. 2005 Social learning in noncolonial insects? *Curr. Biol.* **15**, 1931–
467 5. (doi:10.1016/j.cub.2005.09.015)
- 468 7. Boyd R, Richerson PJ. 1988 An evolutionary model of social learning: The effects of spatial
469 and temporal variation. In *Social learning: A psychological and biological approach* (eds TR
470 Zentall, BG Galef), pp. 29–48. Hillsdale, NJ: Erlbaum.
- 471 8. Laland KN. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14. (doi:10.3758/BF03196002)

- 472 9. Rendell L, Fogarty L, Hoppitt WJE, Morgan TJH, Webster MM, Laland KN. 2011 Cognitive
473 culture: theoretical and empirical insights into social learning strategies. *Trends Cogn. Sci.* **15**,
474 68–76. (doi:10.1016/j.tics.2010.12.002)
- 475 10. Thorogood R, Davies NB. 2012 Cuckoos combat socially transmitted defenses of reed warbler
476 hosts with a plumage polymorphism. *Science* **337**, 578–80. (doi:10.1126/science.1220759)
- 477 11. Dolman CS, Templeton J, Lefebvre L. 1996 Mode of Foraging Competition Is Related to Tutor
478 Preference in *Zenaidura macroura*. *J. Comp. Psychol.* **110**, 45–54. (doi:10.1037//0735-
479 7036.110.1.45)
- 480 12. Riebel K, Spierings MJ, Holveck MJ, Verhulst S. 2012 Phenotypic plasticity of avian social-
481 learning strategies. *Anim. Behav.* **84**, 1533–1539. (doi:10.1016/j.anbehav.2012.09.029)
- 482 13. Boogert NJ, Zimmer C, Spencer KA. 2013 Pre- and post-natal stress have opposing effects on
483 social information use. *Biol. Lett.* **9**, 20121088. (doi:10.1098/rsbl.2012.1088)
- 484 14. Katsnelson E, Motro U, Feldman MW, Lotem A. 2008 Early experience affects producer-
485 scrounger foraging tendencies in the house sparrow. *Anim. Behav.* **75**, 1465–1472.
486 (doi:10.1016/j.anbehav.2007.09.020)
- 487 15. Lindeyer CM, Meaney MJ, Reader SM. 2013 Early maternal care predicts reliance on social
488 learning about food in adult rats. *Dev. Psychobiol.* **55**, 168–75. (doi:10.1002/dev.21009)
- 489 16. Hobaiter C, Poisot T, Zuberbühler K, Hoppitt W, Gruber T. 2014 Social Network Analysis
490 Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. *PLoS Biol.* **12**,
491 e1001960. (doi:10.1371/journal.pbio.1001960)
- 492 17. Leris I, Reader SM. 2016 Age and early social environment influence guppy social learning
493 propensities. *Anim. Behav.* **120**, 11–19. (doi:10.1016/j.anbehav.2016.07.012)
- 494 18. Rawlings B, Flynn E, Kendal R. 2017 To Copy or To Innovate? The Role of Personality and
495 Social Networks in Children’s Learning Strategies. **11**, 39–44. (doi:10.1111/cdep.12206)
- 496 19. Boogert NJ, Farine DR, Spencer KA. 2014 Developmental stress predicts social network
497 position. *Biol. Lett.* **10**, 20140561.
- 498 20. Farine DR, Spencer KA, Boogert NJ. 2015 Early-life stress triggers juvenile zebra finches to
499 switch social learning strategies. *Curr. Biol.* **25**, 2184–2188. (doi:10.1016/j.cub.2015.06.071)
- 500 21. Anderson RC, Peters S, Nowicki S. 2014 Effects of early auditory experience on the
501 development of local song preference in female swamp sparrows. *Behav. Ecol. Sociobiol.* **68**,
502 437–447. (doi:10.1007/s00265-013-1658-7)
- 503 22. Beecher MD, Campbell SE, Nordby JC. 2000 Territory tenure in song sparrows is related to
504 song sharing with neighbours, but not to repertoire size. *Anim. Behav.* **59**, 29–37.
- 505 23. Lachlan RF, Anderson RC, Peters S, Searcy WA, Nowicki S. 2014 Typical versions of learned
506 swamp sparrow song types are more effective signals than are less typical versions. *Proc. R.
507 Soc. B Biol. Sci.* **281**, 20140252. (doi:10.1098/rspb.2014.0252)
- 508 24. Catchpole CK, Slater PJB. 2008 *Bird Song: Biological Themes and Variations*. Cambridge:
509 Cambridge University Press.
- 510 25. Beecher MD, Brenowitz EA. 2005 Functional aspects of song learning in songbirds. *Trends
511 Ecol. Evol.* **20**, 143–149. (doi:10.1016/j.tree.2005.01.004)
- 512 26. Peters S, Searcy WA, Nowicki S. 2014 Developmental Stress , Song-Learning, and Cognition.

- 513 *Integr. Comp. Biol.* **54**, 555–567. (doi:10.1093/icb/icu020)
- 514 27. Nowicki S, Peters S, Podos J. 1998 Song Learning , Early Nutrition and Sexual Selection in
515 Songbirds. *Am. Zool.* **38**, 179–190.
- 516 28. Slater PJB, Eales LA, Clayton NS. 1988 Song learning in zebra finches (*Taeniopygia guttata*):
517 progress and prospects. *Adv. Study Behav.* **18**, 1–34.
- 518 29. Bolhuis JJ, Gahr M. 2006 Neural mechanisms of birdsong memory. *Nat. Rev. Neurosci.* **7**, 347–
519 57. (doi:10.1038/nrn1904)
- 520 30. Bolhuis JJ, Okanoya K, Scharff C. 2010 Twitter evolution: converging mechanisms in birdsong
521 and human speech. *Nat. Rev. Neurosci.* **11**, 747–59. (doi:10.1038/nrn2931)
- 522 31. Riebel K. 2009 *Song and Female Mate Choice in Zebra Finches : A Review*. 1st edn. Elsevier
523 Inc. (doi:10.1016/S0065-3454(09)40006-8)
- 524 32. Woodgate JL, Mariette MM, Bennett ATD, Griffith SC, Buchanan KL. 2012 Male song structure
525 predicts reproductive success in a wild zebra finch population. *Anim. Behav.* **83**, 773–781.
526 (doi:10.1016/j.anbehav.2011.12.027)
- 527 33. Böhner J. 1983 Song learning in the zebra finch (*Taeniopygia guttata*): Selectivity in the choice
528 of a tutor and accuracy of song copies. *Anim. Behav.* **31**, 231–237. (doi:10.1016/S0003-
529 3472(83)80193-6)
- 530 34. Eales LA. 1985 Song learning in zebra finches: some effects of song model availability on what
531 is learnt and when. *Anim. Behav.* **33**, 1293–1300. (doi:10.1016/S0003-3472(85)80189-5)
- 532 35. Clayton NS. 1987 Song tutor choice in zebra finches. *Anim. Behav.* **35**, 714–721.
- 533 36. Zann R. 1990 Song and call learning in wild zebra finches in south-east Australia. *Anim. Behav.*
534 **40**, 811–828. (doi:http://dx.doi.org/10.1016/S0003-3472(05)80982-0)
- 535 37. McCowan LSC, Mariette MM, Griffith SC. 2015 The size and composition of social groups in
536 the wild zebra finch. *Emu* **115**, 191–198. (doi:10.1071/MU14059)
- 537 38. Williams H. 1990 Models for song learning in the zebra finch: fathers or others? *Anim. Behav.*
538 **39**, 745–757. (doi:10.1016/S0003-3472(05)80386-0)
- 539 39. Mann NI, Slater PJB. 1995 Song tutor choice by zebra finches in aviaries. *Anim. Behav.* **49**,
540 811–820. (doi:10.1016/0003-3472(95)80212-6)
- 541 40. Spencer K a, Evans NP, Monaghan P. 2009 Postnatal stress in birds: a novel model of
542 glucocorticoid programming of the hypothalamic-pituitary-adrenal axis. *Endocrinology* **150**,
543 1931–4. (doi:10.1210/en.2008-1471)
- 544 41. Psorakis I *et al.* 2015 Inferring social structure from temporal data. *Behav. Ecol. Sociobiol.* ,
545 857–866. (doi:10.1007/s00265-015-1906-0)
- 546 42. Farine DR. 2013 Animal social network inference and permutations for ecologists in R using
547 asnipe. *Methods Ecol. Evol.* **4**, 1187–1194. (doi:10.1111/2041-210X.12121)
- 548 43. The R Core Team. 2015 R: A language and environment for statistical computing.
- 549 44. Boogert NJ, Farine DR, Spencer KA. 2014 Data from: Developmental stress predicts social
550 network position. *Biol. Lett.* (doi:doi:10.5061/dryad.7qs06)
- 551 45. Williams H. 2004 Bird song and singing behavior. *Ann. N. Y. Acad. Sci.* **1016**, 1–30.
- 552 46. Lachlan RF, Verhagen L, Peters S, Cate C ten. 2010 Are There Species-Universal Categories in

- 553 Bird Song Phonology and Syntax? A Comparative Study of Chaffinches (*Fringilla coelebs*),
554 Zebra Finches (*Taenopygia guttata*), and Swamp Sparrows (*Melospiza georgiana*). *J. Comp.*
555 *Psychol.* **124**, 92–108. (doi:10.1037/a0016996)
- 556 47. Lachlan RF, Verzijden MN, Bernard CS, Jonker PP, Koese B, Jaarsma S, Spoor W, Slater PJB,
557 Ten Cate C. 2013 The progressive loss of syntactical structure in bird song along an Island
558 colonization chain. *Curr. Biol.* **23**, 1896–1901. (doi:10.1016/j.cub.2013.07.057)
- 559 48. Tchernichovski O, Nottebohm F. 1998 Social inhibition of song imitation among sibling male
560 zebra finches. *Proc. Natl. Acad. Sci. U. S. A.* **95**, 8951–8956. (doi:10.1073/pnas.95.15.8951)
- 561 49. Honarmand M, Riebel K, Naguib M. 2015 Nutrition and peer group composition in early
562 adolescence: Impacts on male song and female preference in zebra finches. *Anim. Behav.*
563 **107**, 147–158. (doi:10.1016/j.anbehav.2015.06.017)
- 564 50. Farine DR. 2017 A guide to null models for animal social network analysis. *Methods Ecol. Evol.*
565 **8**, 1309–1320.
- 566 51. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social
567 network analysis. *J. Anim. Ecol.* **84**, 1144–1163. (doi:10.1111/1365-2656.12418)
- 568 52. Hausberger M, Henry L, Lepage L, Schmidt I. 1995 Song Sharing Reflects the Social
569 Organization in a Captive Group of European Starlings (*Sturnus vulgaris*). **109**, 222–241.
- 570 53. Templeton CN, Reed VA, Campbell SE, Beecher MD. 2012 Spatial movements and social
571 networks in juvenile male song sparrows. *Behav. Ecol.* **23**, 141–152.
572 (doi:10.1093/beheco/arr167)
- 573 54. Lemasson A, Ouattara K, Petit EJ, Zuberbühler K. 2011 Social learning of vocal structure in a
574 nonhuman primate? *BMC Evol. Biol.* **11**. (doi:10.1186/1471-2148-11-362)
- 575 55. Castles M, Heinsohn R, Marshall HH, Lee AEG, Cowlshaw G, Carter AJ. In press. Are social
576 networks created with different techniques comparable? *Anim. Behav.*
- 577 56. Boogert NJ, Nightingale GF, Hoppitt W, Laland KN. 2014 Perching but not foraging networks
578 predict the spread of novel foraging skills in starlings. *Behav. Processes* **109**, 135–144.
579 (doi:10.1016/j.beproc.2014.08.016)
- 580 57. Alarcón-Nieto G, Graving JM, Klarevas-Irby JA, Maldonado-Chaparro AA, Mueller I, Farine DR.
581 2018 An automated barcode tracking system for behavioural studies in birds. *Methods Ecol.*
582 *Evol.* **2018**, 1–12. (doi:10.1111/2041-210X.13005)
- 583 58. Gill LF, D’Amelio PB, Adreani NM, Sagunsky H, Gahr MC, ter Maat A. 2016 A minimum-impact,
584 flexible tool to study vocal communication of small animals with precise individual-level
585 resolution. *Methods Ecol. Evol.* **7**, 1349–1358. (doi:10.1111/2041-210X.12610)
- 586 59. Snijders L, Naguib M. 2017 *Communication in Animal Social Networks: A Missing Link?*
587 Elsevier Ltd. (doi:10.1016/bs.asb.2017.02.004)
- 588 60. Honarmand M, Riebel K, Naguib M. 2015 Nutrition and peer group composition in early
589 adolescence: impacts on male song and female preference in zebra finches. *Anim. Behav.*
590 **107**, 147–158. (doi:10.1016/j.anbehav.2015.06.017)
- 591 61. Firth JA, Voelkl B, Farine DR, Sheldon BC. 2015 Experimental evidence that social relationships
592 determine individual foraging behaviour. *Curr. Biol.* **25**, 3138–3143.
- 593 62. Holveck M-J, Vieira de Castro AC, Lachlan RF, ten Cate C, Riebel K. 2008 Accuracy of song
594 syntax learning and singing consistency signal early condition in zebra finches. *Behav. Ecol.*

- 595 **19**, 1267–1281. (doi:10.1093/beheco/arn078)
- 596 63. Brumm H, Zollinger SA, Slater PJB. 2009 Developmental stress affects song learning but not
597 song complexity and vocal amplitude in zebra finches. *Behav. Ecol. Sociobiol.* **63**, 1387–1395.
598 (doi:10.1007/s00265-009-0749-y)
- 599 64. Gil D, Naguib M, Riebel K, Rutstein A, Gahr M. 2006 Early Condition, Song Learning, and the
600 Volume of Song Brain Nuclei in the Zebra Finch (*Taeniopygia guttata*). *J. Neurobiol.* , 1602–
601 1612. (doi:10.1002/neu)
- 602 65. Zann R, Cash E. 2008 Developmental stress impairs song complexity but not learning accuracy
603 in non-domesticated zebra finches (*Taeniopygia guttata*). *Behav. Ecol. Sociobiol.* **62**, 391–400.
604 (doi:10.1007/s00265-007-0467-2)
- 605 66. Crino OL, Driscoll SC, Ton R, Breuner CW. 2014 Corticosterone exposure during development
606 improves performance on a novel foraging task in zebra finches. *Anim. Behav.* **91**, 27–32.
607 (doi:10.1016/j.anbehav.2014.02.017)
- 608
- 609
- 610
- 611

612 **FIGURE LEGENDS**

613 **Figure 1. Example songs.** The top two panels (a and c) are father songs, and the lower two panels (b
614 and d) are their sons' songs, respectively. a)-b) illustrate a high father-son song similarity (the
615 father's song was the top-ranked model), while c)-d) illustrate a very low song similarity (the father's
616 song was ranked 23rd in similarity to the son's song).

617

618 **Figure 2. The social foraging associations and song similarities of the males in each of the two**
619 **aviaries.** Our social network metrics and analyses included all males and females in the aviaries, but
620 for the purposes of illustration only males are drawn here, as female zebra finches do not sing.
621 Numbers represent family ID. This figure illustrates that fathers (black circles) and sons (grey circles:
622 controls; with black outline: CORT-treated) with stronger social associations (thicker lines) had more
623 similar songs (redder lines), while more gregarious fathers (larger circles) generated less similar
624 songs in their pupils (blue-er lines).

625

626

627

628

629

630 TABLES

631 Table 1. Song tutor choice of control and corticosterone-treated juveniles.

Juvenile treatment	Primary song tutor		Father Rank	Relation to tutor with most similar song
	Father	Not Father ^a		
Control	6	2	2, 2	brother, unrelated adult
Corticosterone	6	6	2, 2, 2, 5, 15, 23	brother, brother, brother, unrelated peer, brother, unrelated adult

632 ^aShaded cells refer to juveniles whose songs were not most similar to their fathers'.

633 The 4th column shows which song-similarity rank the father's song occupied, and the final column
634 shows whom these juveniles copied primarily instead.

635

636

637

638

639

640

641

642 **Table 2. Effect of corticosterone (CORT) treatment and social associations on father-son song**
643 **dissimilarity scores.** Full linear mixed-effects model results (N=13 fathers, 20 sons). P values are
644 calculated by comparing the observed slope coefficients with the distribution of slope coefficients
645 from 10,000 permutations of the social network data. Hence P values do not always exactly match
646 the t-statistic (which is a parametric estimate that depends on sample size, which is not defined for
647 social network data). For each fixed effect, the first row of values was generated by the full model,
648 and the second row represents results of the full model but including number of male offspring
649 instead of number of fledglings for each zebra finch family. Values in bold indicate significant
650 predictors in both models.

Fixed effects	Slope	SE	t	P_{rand}
Intercept	0.226	0.022	10.115	
	0.198	0.023	8.645	
CORT treatment	0.023	0.003	7.803	0.016
	0.023	0.003	7.777	0.003
Father-son association	-0.035	0.017	-2.017	<0.001
	-0.034	0.017	-1.992	0.011
Father gregariousness	0.003	0.001	2.545	<0.001
	0.003	0.001	2.530	0.001
Son gregariousness	-0.002	0.001	-1.981	0.72
	-0.002	0.001	-1.972	0.292
Number of fledglings	-0.012	0.006	-1.973	<0.001
Number of male offspring	-0.007	0.011	-0.605	0.575
Random effects	Variance	SD	% total	
Family	0.001	0.026	47.34%	
	0.001	0.031	55.50%	

651