

1 **Fitness costs of female choosiness in a socially monogamous songbird**

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3 Wolfgang Forstmeier^{1*}, Daiping Wang^{1,2*}, Katrin Martin¹ & Bart Kempenaers¹

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5 1 Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for
6 Ornithology, Eberhard-Gwinner-Str. 7, 82319 Seewiesen, Germany

7 2 CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese
8 Academy of Sciences, Beijing, China

9 * Address for correspondence:

10 Wolfgang Forstmeier*, Department of Behavioural Ecology and Evolutionary Genetics, Max Planck
11 Institute for Ornithology, Eberhard-Gwinner-Str. 7, 82319 Seewiesen, Germany, Phone: 0049-8157-
12 932346, Email: forstmeier@orn.mpg.de

13 Daiping Wang*, CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of
14 Zoology, Chinese Academy of Sciences, Beijing, China, [Email: wangdaiping@ioz.ac.cn](mailto:wangdaiping@ioz.ac.cn)

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20 ORCID iDs:

21 Wolfgang Forstmeier <https://orcid.org/0000-0002-5984-8925>

22 Daiping Wang <https://orcid.org/0000-0002-9045-051X>

23 Katrin Martin <https://orcid.org/0000-0003-2477-8397>

24 Bart Kempenaers <https://orcid.org/0000-0002-7505-5458>

25 **Abstract**

26 Female mate choice is thought to be responsible for the evolution of many extravagant male
27 ornaments and displays, but the costs of being too selective may hinder the evolution of choosiness.
28 Selection against choosiness should be strongest in socially monogamous mating systems, because
29 females may end up without a partner and forego reproduction, especially when many females
30 prefer the same few partners (frequency-dependent selection). Here we quantify the fitness costs of
31 having mating preferences that are difficult to satisfy. We capitalise on the recent discovery that
32 female zebra finches (*Taeniopygia guttata*) prefer males of familiar song dialect. We measured
33 female fitness in captive breeding colonies in which one third of females were given ample
34 opportunity to choose a mate of their preferred dialect (two thirds of all males; ‘relaxed
35 competition’), while two thirds of the females had to compete over a limited pool of mates they
36 preferred (one third of all males; ‘high competition’). As expected, social pairings were strongly
37 assortative with regard to song dialect. In the high-competition group, 26% of the females remained
38 unpaired, yet they still obtained relatively high fitness by using brood parasitism as an alternative
39 reproductive tactic. Another 31% of high-competition females paired disassortatively for song
40 dialect. These females showed increased levels of extra-pair paternity, mostly with same-dialect
41 males as sires, suggesting that preferences were not abolished after social pairing. However, females
42 that paired disassortatively for song dialect did not have lower reproductive success. Overall,
43 females in the high-competition group reached equal fitness as those that experienced relaxed
44 competition. Our study suggests that alternative reproductive tactics such as egg dumping can help
45 overcome the frequency-dependent costs of being highly selective in a monogamous mating system,
46 thereby facilitating the evolution of female choosiness.

47

48 **Introduction**

49 Whenever organisms face multiple options to choose from (e.g. choice of food, habitat, mate) they
50 have to weigh the potential benefits of being choosy against potential costs that arise from being
51 too selective [1-8]. Over evolutionary time scales, the behavioural trait “choosiness” may thus evolve
52 to an optimum level [9] or remain flexible depending on circumstances [10-14].

53 Female mate choice has been widely recognized as the driving force behind the evolution of many
54 extravagant male ornaments and displays. Yet, whether such choosiness is expected to evolve
55 should depend critically on how costly it is to be choosy. The costs of choosiness are hence central to
56 sexual selection theory, but they have rarely been measured empirically (see below). The costs of
57 being selective about a mate as opposed to mating with the first potential mate that is encountered
58 will greatly depend on the species’ mating system.

59 The most spectacular examples of sexually selected traits have been observed in lek mating systems
60 with strong reproductive skew, i.e. systems in which most or even all females in a given area can
61 mate with the same male. In general, females can mate with the same male if they do not seek a
62 partner who provides non-shareable direct benefits (e.g. parental care), but only mate to obtain
63 sperm (i.e. genetic benefits), provided sperm depletion is not an issue. Intense selection through
64 female choice for the most attractive males should however erode genetic variation, which will then
65 reduce the genetic benefits that females can obtain from being choosy. The apparently remaining
66 female choosiness in face of diminishing benefits is widely known as the ‘paradox of the lek’, which
67 has been addressed in numerous theoretical and empirical studies [15]. The empirical work has
68 concentrated on quantifying (a) the costs to females of being choosy in terms of time and energy
69 spent or in terms of predation risk [16-19], and (b) the magnitude of genetic benefits from mating
70 with the preferred male [20]. When the costs and benefits are measured on a relevant and
71 comparable scale, i.e. in terms of fitness consequences for the female, they appear to be so small
72 that they can hardly be quantified with sufficient precision to provide an empirical answer to the lek
73 paradox [21, 22].

74 Monogamous mating systems should provide a better opportunity to study the evolution of
75 choosiness empirically, because both costs and benefits of choosiness should be much larger than in
76 lek mating systems. In socially monogamous systems, males typically provide substantial direct
77 benefits in the form of parental care. If the quality or quantity of parental care varies among males,
78 females may obtain large fitness gains from selecting the best partner available [9, 23-25]. However,
79 a female that is too selective might not find any partner that satisfies her choice criteria (“wallflower
80 effect”, [26]), especially because the best partners will rapidly disappear from the available mating

81 pool. Thus, strong female competition over the best mates may lead to selection against being too
82 choosy [27], and hence favour strategies such as accepting the first mate encountered if its quality
83 lies within the top 80% of the males (i.e. only discriminating against the bottom 20%). Yet, such
84 theoretical predictions about optimal female choosiness should critically depend on behavioural
85 tactics that females can adopt when their preferences cannot be satisfied, and on the fitness
86 consequences of these tactics (Figure 1). This choice of tactics can be studied empirically, but we are
87 not aware of any systematic work on this topic despite its central importance for sexual selection
88 theory.

89 When many females compete for a limited number of preferred partners, they pay a cost of
90 engaging in competition (time and energy spent in competition, risk of injury), compared to females
91 that are not constrained by their preferences, either because their preferred partners are
92 overabundant or because they are not choosy (Figure 1). The cost of competition can be equal for
93 both winners and losers of the competition (as in Figure 1), but females might also vary in their
94 abilities to avoid this cost (e.g. by ‘prudent mate choice’; [12]). Females that are unsuccessful at
95 securing a preferred partner, can either settle for a partner they do not prefer, or remain socially
96 unpaired. In the former case, females may suffer a cost (Figure 1; see [25]) – for instance – if they
97 are reluctant to copulate with their partner, resulting in infertility, or if they prefer to copulate with
98 males outside the pair bond, which may lead to aggression [28] and reduced parental care by the
99 social partner [29]. One way to avoid such costs might be to behave similarly towards a preferred
100 and a non-preferred partner once paired. In case females remain socially unpaired, they will also pay
101 a cost, the magnitude of which will depend on how successfully females can achieve fitness through
102 alternative reproductive tactics, including reproduction as a single mother [30] or via brood
103 parasitism (‘egg dumping’, [31-33]).

104 Mate choice in socially monogamous mating systems has the intriguing property that selection on
105 mating preferences works in a negative frequency-dependent manner [34-37]. This means that the
106 fitness consequences of an individual’s preferences depend on what other individuals in the
107 population prefer. For instance, if two thirds of all females would only accept a partner that ranks in
108 the top third of all males (e.g. with regard to ornament size), then at least half of those females will
109 remain unpaired, thereby lowering the mean fitness of all females that carry such preference alleles.
110 As a consequence, such preferences will be strongly selected against, particularly when a male
111 ornament is a poor indicator of benefits to the female [24, 37, 38]. Selection against such
112 preferences will be strongest when the preferences are shared by most females and negative
113 frequency dependence should finally result in relatively little consensus among females about which
114 male is the most attractive [36, 37, 39, 40].

115 To understand the evolution of optimal levels of choosiness in monogamous mating systems, it is
116 essential to quantify empirically the fitness costs of having preferences that are difficult to satisfy.
117 Although several studies have manipulated the costs and/or benefits of choosiness and have
118 subsequently observed female choice behaviour or mating patterns [41-47], no study to date has
119 quantified the costs in terms of female fitness.

120 One practical obstacle is that the costs of choosiness can only be measured if one finds a sufficiently
121 strong preference that will be reliably expressed by the choosing sex. In zebra finches, a socially
122 monogamous bird that forms life-long pair bonds, females reliably prefer (unfamiliar) males that
123 have learnt their song in the same population in which females grew up, over males with song from
124 a different population [48]. Working with four independent captive populations (two domesticated
125 and two recently wild-derived), we used cross-fostering of eggs between populations to produce
126 two different cultural lineages (A and B) within each population that differ only in their song dialects.
127 The lineages were bred in isolation for one additional generation, to obtain birds from the same
128 genetic population that differ only in the song that the foster-grandparents once transmitted to the
129 parents of the current generation. When bringing together equal numbers of unfamiliar males and
130 females of the two song dialects A and B, on average 73% of pairs formed assortatively by dialect
131 (random expectation: 50%, [48]). We made use of this moderately strong assortative mating
132 preference to design an experimental study with pre-registered methods of data collection and
133 analysis plan (<https://osf.io/8md3h>), ensuring maximal objectivity in the quantification of fitness
134 costs of choosiness.

135 We set up a total of 10 experimental aviaries (two or three per genetic population). In each aviary
136 we placed unequal numbers of males and females from lineages A and B (e.g. 4 females of lineage A
137 and 8 females of B, facing 8 males of A and 4 males of B). In this way, we created groups of females
138 that have either plenty of preferred males to choose from ('relaxed competition') or that have to
139 compete for a limited pool of preferred mates ('high competition'). The latter group can thus accept
140 a non-preferred mate (i.e. mate disassortatively) or forego forming a pair to reproduce (Figure 1).
141 This design mimics the above-described example of a two-third majority preferring a male from the
142 top third, while the other group of females are nearly unconstrained by their preference, and it
143 mirrors the principle of negative frequency dependence of preferences in a monogamous system.
144 The treatment thus alters the cost of preferring the same lineage, while the benefits of having that
145 preference should equal zero for both treatment groups (as we assumed in Figure 1, which
146 otherwise can be adapted to accommodate variation in benefits).

147 We allowed all birds to reproduce freely for a fixed period (70 days for egg laying plus 50 days for
148 chick rearing) and quantified the fitness costs of choosiness, closely adhering to the preregistered
149 plan (<https://osf.io/8md3h>). Prior to data collection, we had hypothesized that (1) females from the
150 high-competition treatment will achieve lower relative fitness (measured as the number of
151 independent offspring; primary outcome) compared to the females from the relaxed-competition
152 treatment. Further we hypothesised that these females (2) will lay fewer eggs, and (3) will start egg-
153 laying later (secondary outcome measures). We further present the results of an unplanned,
154 exploratory part of data analysis to elucidate mechanisms by which females coped with the
155 experimental challenge (see Figure 1).

156 **Results**

157 **A. Preregistered analyses: costs of choosiness**

158 The 120 experimental females produced a total of 556 offspring that reached independence (mean
159 offspring per female \pm SD = 4.6 ± 3.0 , range 0 – 13). As expected, relative fitness of females
160 decreased with their inbreeding coefficient (mean $F \pm$ SD = 0.051 ± 0.050 , range: 0 – 0.28; $p = 0.006$,
161 S1 Table, model 1a). However, in contrast to our *a priori* prediction, the 80 females in the high-
162 competition treatment achieved a non-significantly higher (rather than lower) relative fitness (1.022
163 ± 0.069) compared to the 40 females in the relaxed-competition treatment (0.955 ± 0.097 ; $p = 0.57$;
164 Figure 2, Table 1, model 1a, S1 Table). This result did not change after additionally controlling for
165 additive genetic and early environmental effects on fitness (S1 Table, model 1b). Moreover, and also
166 in contrast to our predictions, females from the high-competition treatment did not lay fewer eggs
167 (9.2 ± 0.4) than females from the relaxed-competition group (8.6 ± 0.6 ; $p = 0.37$; Table 1, model 2, S2
168 Table) and they did not start egg-laying later (back-transformed means, high-competition: 7.8 days
169 after the start of the experiment, inter-quartile range: 5 – 10.5 days; relaxed-competition: 8.2 days,
170 inter-quartile range: 5 – 10.5 days; $p = 0.63$; Table 1, model 3, S3 Table).

171 **B. Post-hoc data exploration: female coping tactics**

172 The lack of significant treatment effects could be due either to a failed treatment (e.g. because birds
173 did not prefer their natal song dialect) or to female behaviour that reduces the costs of being
174 choosy. Hence, we first examined the efficiency of the treatment, i.e. the degree of assortative
175 mating by song dialect. Second, we investigated the mechanisms by which females reproduced, i.e.
176 we compared success and timing of social pairing, alternative reproductive tactics, and rearing
177 success between the two treatment groups.

178 The degree of assortative mating, i.e. the proportion of assortative pairs, can range from zero to one
179 (see Figure 3). In our experimental setup, a value of zero can theoretically be reached if all pairs
180 mated disassortatively (zero assortative and up to 12 disassortative pairs in each aviary). A value of
181 one, corresponding to perfect assortative pairing, can only be reached if four females per aviary
182 remained unpaired (8 assortative and zero disassortative pairs per aviary). Under random pairing,
183 44.4% of pairings should be assortative (1/3 of females has a 2/3 chance of pairing assortatively, plus
184 2/3 of females has a 1/3 probability; $1/3 \times 2/3 + 2/3 \times 1/3 = 4/9$). If all females would attempt to pair
185 assortatively, but no female would forego pairing, 66.7% of pairings should be assortative (8
186 assortative and 4 disassortative pairs per aviary).

187 Of the 106 social pairs that were observed, 72 (67.9%) were assortative. This significantly deviates
188 from the random expectation of 44.4% (exact goodness-of-fit test $p < 0.0001$). Considering the
189 number of eggs in the nests of those pairs ($N = 1,022$ in total), 730 eggs (71.4%) were cared for by
190 assortative pairs. At the genetic level, out of the 1,074 eggs fertilized and genotyped, 783 (72.9%)
191 had parents that mated assortatively for song dialect. Hence, both at the social and genetic level, we
192 found strong assortative mating, slightly exceeding the 66.7% “assortative if possible” threshold
193 (Figure 3).

194 Females from the two treatment groups differed significantly in their pairing success, with only 4
195 females (10%) from the relaxed-competition treatment remaining unpaired, but 21 females (26%)
196 from the high-competition treatment not observed in a social bond ($p = 0.03$, Figure 4A, B, Table 1,
197 model 4, S4 Table). In the relaxed-competition group, 87.5% of females ($N = 35$) mated assortatively
198 with a male from their natal dialect, and one female (2.5%) was observed in two pair bonds (one
199 assortative, one disassortative; “mixed” in Figure 4A). In contrast, in the high-competition group,
200 only 37.5% of females ($N = 30$) mated exclusively assortatively, 5% ($N = 4$ females) participated in
201 both types of pairing, and 31% ($N = 25$ females) mated exclusively disassortatively (Figure 4B, Table
202 1, models 5-7, S5 Table, S6 Table, S7 Table).

203 Females from the high-competition group took longer to start a social bond compared to females
204 from the relaxed-competition group ($p = 0.008$, Figure 4C, D, Table 1, model 8, S8 Table). For this
205 test, we assigned a maximum latency of 75 days to unpaired females (as in the pre-registered model
206 3), because we cannot exclude that such females would have paired after a longer period. If
207 unpaired females are excluded from the analysis, the difference between treatment groups in
208 latency to pair is no longer significant ($t = 1.24$, $p = 0.22$). Hence, the treatment prevented or delayed
209 social pairing (Table 1, models 4 and 8, S4 Table, S8 Table), but it did not prevent or delay egg-laying
210 (S2 Table, S3 Table).

211 In 18 cases, females attempted to rear offspring as single mothers (14 females attended one clutch
212 and two females each attended two consecutive clutches). Of those, 11 clutches (61%) were reared
213 by females that remained unpaired until the end of the experiment (overall, 25 out of 120 females
214 remained unpaired until the end, 21%). However, the average number of clutches attended to as
215 unpaired female did not differ significantly between the treatment groups (Table 1, model 9, S9
216 Table). Females from the high-competition group on average laid fewer eggs that they actively took
217 care of, although this was not significant ($p = 0.21$, Table 1, model 10, S10 Table). However, females
218 from the high-competition group laid significantly more eggs into clutches that were cared for by
219 other females (egg dumping in the strict sense; $p = 0.038$, Table 1, model 11, S11 Table) and into
220 nests of other females, nests attended by single males, or into unattended nest boxes (egg dumping
221 in the wide sense; $p = 0.009$, Table 1, model 12, S12 Table). Hence the proportion of parasitic eggs
222 among the total number of eggs laid was markedly higher in the high-competition than in the
223 relaxed-competition group (Table 1, models 13 and 14, S13 Table, S14 Table).

224 Splitting the females of each treatment group into subsets according to their social pairing status
225 (Figure 4) shows that the parasitic egg-dumping tactic was used more often by the unpaired females
226 of the high-competition group (compared to relaxed-competition group; t-test with unequal
227 variances, $t_{26.4} = 3.37$, $p = 0.002$), followed by the disassortatively mated females of the high-
228 competition group ($t_{33.4} = 2.09$, $p = 0.044$; Figure 5B). Overall, females from the high-competition
229 group achieved similar fitness as the females from the relaxed-competition group (Figure 5A),
230 because rearing success (the proportion of fertile eggs that became independent offspring) did not
231 differ between the treatment groups (Table 1, model 15, S15 Table).

232 Finally, we examined levels of extra-pair paternity in the different treatment groups, focusing on the
233 84 females that were socially paired to only one partner. As expected, extra-pair paternity was more
234 frequent in the disassortatively paired females from the high-competition group (44%, 81 out of 183
235 eggs from 21 females) than in the assortatively paired females from the same treatment group (18%,
236 42 of 252 eggs from 27 females; t-test based on proportions for each female: $t_{46} = 3.2$, $p = 0.002$;
237 Figure 6). Assortatively paired females from the relaxed-competition group showed intermediate
238 levels of extra-pair paternity (36%, 112 of 312 eggs from 35 females; for additional details see S16
239 Table). In each of the three groups, the majority of extra-pair eggs were sired assortatively (70%,
240 65%, and 89% respectively) and all three numbers clearly exceed the corresponding random
241 expectations (36%, 27%, and 64%, respectively) calculated from the number of potential extra-pair
242 males in the aviary (4, 3, and 7 out of 11, respectively; see also S16 Table).

243

244 **Discussion**

245 Our study illustrates the importance of empirically quantifying the costs and benefits of choosiness
246 to predict selection on the level of choosiness. This can then inform about the expected intensity of
247 sexual selection through female choice. A recent theoretical study highlighted that choosiness in
248 monogamous systems may have high costs and hence will be selected against [27]. Based on this
249 study, we hypothesized that females in the high-competition group would suffer substantial fitness
250 costs compared to the relaxed-competition group (<https://osf.io/8md3h>). However, our empirical
251 findings strongly suggest that female zebra finches have evolved sufficient behavioural flexibility to
252 cope with the challenge of having preferences that are difficult to satisfy such that they did not
253 suffer lower fitness. This flexibility is not trivial, because zebra finches that were force-paired
254 suffered significant fitness costs compared to birds that were allowed to choose their mate [25].

255 Females in the high-competition treatment on average achieved slightly higher relative fitness
256 compared to those in the relaxed-competition group. Thus, the best estimate for the fitness cost of
257 choosiness in our study equals zero. However, when considering reduced pairing success, delayed
258 pairing and reliance on conditional parasitism, one could argue that the biologically most likely
259 fitness cost is small, but positive. Females that relied on the parasitic tactic of egg dumping [31-33]
260 were surprisingly successful in terms of fitness (Figure 5). However, our models on the use of this
261 tactic also suggest that this may be a form of ‘making the best of a bad job’, because the proportion
262 of a female’s eggs that was dumped (in the wide sense) rather than actively cared for was higher in
263 the high-competition treatment group, and also increased with the inbreeding coefficient of the
264 female ($p = 0.002$, S14 Table). These results suggest that the parasitic tactic is associated with poor
265 pairing success and with poor female condition. Hence, overall, there likely is a small net cost of
266 having preferences that are hard to satisfy, but quantifying such a small cost is difficult because of
267 sampling noise.

268 Our study suggests that an alternative reproductive tactic, namely egg dumping, may be important
269 to consider as a mechanism that effectively reduces the costs of choosiness and thereby favors the
270 evolution of choosiness even in monogamous mating systems. Alternative reproductive tactics can
271 thereby increase the intensity of sexual selection through female choice. Note that our analysis of
272 egg dumping is part of the *post hoc* data exploration rather than pre-registered hypothesis testing,
273 which implies that the probability that this result is a chance finding is higher (Figure 5).
274 Nevertheless, we avoided extensive exploratory testing combined with selective reporting and *post-*
275 *hoc* modification of analysis strategy to minimize the risks of false positive findings [49]. Accordingly,
276 Table 1 presents all the exploratory tests that compare the two treatment groups in their original

277 version. The considered hypotheses all directly follow from the observation of equal fitness in both
278 treatment groups, and address the question how females in the high-competition group responded
279 to the given mating opportunities.

280 This study also contributes to our understanding of zebra finch mating preferences with regard to
281 song dialects. Firstly, we confirmed that such preferences exist and that they are sufficiently strong
282 to result in a high degree of assortment even when bringing together unequal numbers of males and
283 females of each dialect. Secondly, assortative mating was present both at the genetic level (72.9% of
284 fertilized eggs had assortative genetic parents) and at the social level (71.4% of eggs were cared for
285 by assortative pairs). As 78.2% of all eggs sired by extra-pair males were assortative, we infer that
286 song dialect preferences affect both social pairing and extra-pair mate choice.

287 The possible adaptive function of these preferences in the wild is not known. They could function to
288 enhance local mating to obtain locally adapted genes, which would be adaptive in both the social
289 and extra-pair context. However, this possibility seems unlikely in light of the lack of genetic
290 differentiation even over a large geographic distance [50]. More widespread sampling of genotypes
291 throughout Australia would be required to rule out this possibility. Alternatively, song preferences
292 could function to find a mate that hatched locally [51, 52] and hence may have gathered local
293 information on ecologically relevant factors such as resources and predation risk. In that case, the
294 song preferences during extra-pair mating might represent a (non-adaptive) spill-over of preferences
295 that are functional in social pairing, or extra-pair mating could function to maintain additional social
296 bonds with similar direct benefits (Maldonado-Chaparro et al. 2018).

297 Our study was designed to estimate the costs of female choosiness, whereby we predicted that
298 these costs would be high in a monogamous mating system [27]. However, this is not what we
299 found. Our study did not fail in the sense that our treatment was effective (Figs. 2 and 3), but
300 females were sufficiently flexible to not suffer substantial fitness costs under high competition for
301 preferred males, at least in our aviary setting. Thus, our study does not support the hypothesis that
302 female choosiness is costly in a socially monogamous system. Females from the high-competition
303 treatment were affected in terms of delayed pairing and reduced pairing success, but they made up
304 for this primarily by the alternative reproductive tactic of egg dumping and only rarely by caring for
305 clutches as a single mother. Females who ended up paired with a non-preferred partner, were more
306 likely to engage in extra-pair copulations, but this did not affect their fitness (see Fig. 4). This stands
307 in contrast to an earlier study that showed that force-paired females responded more negatively to
308 courtships by their social partner, had reduced fertility, and received less paternal care, all resulting

309 in a significant reduction in fitness [25]. Overall, these results emphasize that models on the costs of
310 choosiness need to be informed by empirical research.

311 **Methods**

312 All methods closely adhere to the pre-registration document (<https://osf.io/8md3h>), except for the
313 exploratory post-hoc analyses (presented below).

314 *Ethics*

315 The study was carried out under the housing and breeding permit no. 311.4-si (by Landratsamt
316 Starnberg, Germany) which covers all procedures implemented (including the obtaining of one blood
317 sample per individual for parentage assignment).

318 *Background of study populations and assortative mating*

319 The zebra finches used in this study originate from four captive populations maintained at the Max
320 Planck Institute for Ornithology: two domesticated (referred to as 'Seewiesen' (S) and 'Krakow' (K))
321 and two recently wild-derived populations ('Bielefeld' (B) and 'Melbourne' (M)). For more
322 background and general housing conditions see [25, 53, 54]. The four populations have been
323 maintained in separate aviaries (without visual and with limited auditory contact). When birds from
324 two different populations (combining S with B, and K with M) were brought together in the same
325 breeding aviary, they formed social pairs that were predominantly assortative with regard to
326 population (87% assortative pairs), despite the fact that opposite-sex individuals were unfamiliar
327 with each other ([48], see also [55]). To find out whether this assortative mating took place because
328 of genetic (e.g. body size) or cultural (e.g. song) differences, we produced an offspring generation
329 ('F1') in which half of the birds were cross-fostered between populations (between S and B, or
330 between K and M) and half of the birds were cross-fostered within populations. For this purpose, we
331 used 16 aviaries (4 per population), each containing 8 males and 8 females of the same population
332 that were allowed to freely form pairs and breed. Cross-fostering was carried out at the aviary level,
333 such that 2 aviaries per population served for cross-fostering within population and the other 2 for
334 between-population cross-fostering. This resulted in 8 cultural lines (4 populations x 2 song dialects),
335 each maintained in 2 separate aviaries (16 aviaries). When unfamiliar individuals of the two song
336 dialects were brought together in equal numbers (50:50 sex ratio), they mated assortatively
337 regarding song (79% assortative pairs; Wang et al. 2020) but not regarding genetic population. To
338 disentangle the song effect of interest from possible side-effects of the cross-fostering per se, the 8
339 lines were bred for one more generation ('F2'). These F2 individuals are the focal subjects of this
340 study. Breeding took place in 16 aviaries (2 per song dialect within population), but without cross-

341 fostering. The two replicate aviaries of each song dialect line each contained 8 males and 8 females
342 that produced the next generation. A subset of the resulting offspring ($n = 144$, not used in this
343 study, but see below) were used to test mate choice within each of the 4 genetic populations (here
344 referred to as 'F2 pilot experiment'). Again, we observed assortative pairing for song dialect (73%
345 assortative pairs). The remaining F2 offspring were used as candidates for the experiment, as
346 explained below.

347 *Experimental setup*

348 To quantify the female fitness consequences of having preferences for males that are either rare or
349 overabundant, we used 10 aviaries (3 for populations B and K, and 2 for populations S and M). Each
350 semi-outdoor aviary (measuring 4m x 5m x 2.5m) contained 12 males and 12 females of the same
351 genetic population, but from two different song dialects such that 4 females encountered 8 males of
352 the same dialect, while the remaining 8 females encountered only 4 males of their own dialect.
353 Hence, for each experimental aviary, we used individuals that were raised in 4 separate aviaries (2 of
354 each song dialect) to ensure that opposite-sex individuals were unfamiliar to each other.

355 The allocation of birds to the aviaries followed two principles. First, we listed for each of the 16
356 rearing aviaries the number of available female and male F2 offspring that had not been used
357 previously (in the 'F2 pilot experiment') and that were apparently healthy (374 birds). Depending on
358 the number of available birds, each rearing aviary was then designated to provide either 4 or 8 birds
359 of either sex, such that the total number of experimental breeding aviaries that could be set up was
360 maximized (10 aviaries). Second, the allocation of the available individuals within each rearing aviary
361 to the designated groups of 4 or 8 individuals of a given sex was decided by Excel-generated random
362 numbers. For instance, if a given rearing aviary had 17 candidate female offspring, individuals were
363 randomly allocated to a group of 4 for one experimental aviary, a group of 8 for another aviary, and
364 a group of 5 as leftover (not used). This allocation procedure may have introduced a bias, because
365 rearing aviaries that were highly productive (had more offspring) were more frequently designated
366 to send groups of 8 offspring to an experimental aviary, while those that produced fewer offspring
367 (in the extreme case fewer than 8 of one sex) were more likely used to send a group of 4 offspring to
368 an experimental aviary. This might bias our fitness estimates if offspring production was partly
369 heritable or if housing density prior to the experiment influenced the fitness in the experimental
370 aviaries. We therefore assessed these potential biases in the statistical analysis (see model 1b
371 below).

372 After allocating individuals to the 10 experimental aviaries, one female (designated for aviary 2) and
373 two males (designated for aviary 3) died before the start of the experiment. These individuals were

374 then replaced by randomly choosing individuals of the same sex and rearing aviary, which however
375 had previously taken part in the 'F2 pilot experiment' (17-30 January 2019). These replacement birds
376 differed from the other individuals in the experiment, in that they had previous experience of nest-
377 building and egg-laying >100 days before the start of experiment.

378 The 120 focal females had hatched in one of the 16 natal aviaries between 30 May and 25
379 September 2018 and remained in their natal aviaries initially together with their parents (which
380 were removed between 10 December 2018 and 16 January 2019). On 6 May 2019, all individuals
381 used in the experiment were transferred to the 10 aviaries, whereby the 12 males and 12 females in
382 each aviary were separated by an opaque divider. After one week, the divider was removed and the
383 experiment started. At this time, females were on average 313 days old (range: 230 - 348 days). To
384 facilitate individual identification, each of the 12 males and 12 females within each aviary was
385 randomly assigned two coloured leg bands (using the following 12 combinations: blue-blue, black-
386 black, orange-orange, orange-black, red-red, red-blue, red-black, white-white, white-black, white-
387 orange, yellow-yellow, yellow-blue).

388 *Breeding procedures*

389 Each of the 10 experimental aviaries was equipped with 14 nest boxes. All nest boxes were checked
390 daily during week days (Mon-Fri) for the presence of eggs or offspring. Eggs and offspring were
391 individually marked and a note was made whether eggs were warm. For eggs laid on weekends, we
392 estimated the most likely laying date based on egg development. We collected a DNA sample from
393 all fertilized eggs (including naturally died embryos and nestlings), unless they disappeared before
394 sampling (see below) to determine parentage. Eggs containing naturally died embryos (N = 343)
395 were collected and replaced by plastic dummy eggs (on average 12 ± 4 (SD) days after laying and $7 \pm$
396 4 days after estimated embryo death). Eggs that remained cold (unincubated) for 10 days (N = 7 out
397 of 1,399 eggs) were removed without replacement and were incubated artificially to identify
398 parentage from embryonic tissue. During nest checks we noted the identity of the parent(s) that
399 attended the nest (based on colour bands) to clarify nest ownership for all clutches that were
400 incubated.

401 As the main response variable, we quantified the reproductive success ('fitness') of each female in
402 each experimental aviary as the total number of genetic offspring produced that reached the age of
403 35 days (typical age of independence). All eggs laid within a period of 70 days (between 13 May and
404 22 July 2019; N = 1,399) were allowed to be reared to independence; eggs laid after this period were
405 thrown away and replaced by plastic dummy eggs to terminate a breeding episode without too
406 much disturbance.

407 Out of 1,399 eggs, 319 eggs failed (180 appeared infertile, 101 disappeared, 30 broke, 4 had
408 insufficient DNA, 3 eggs showed only paternal alleles (androgenesis), 1 sample was lost). For the
409 remaining 1,080 eggs we unambiguously assigned maternity and paternity based on 15
410 microsatellite markers (for details see Wang et al. 2017). Of these 1,080 fertile eggs, 750 developed
411 into nestlings and 556 into offspring that reached 35 days of age.

412 The 1,399 eggs were distributed over 289 clutches (allowing for laying gaps of maximally 4 days), of
413 which 190 (1,022 eggs) were attended by a heterosexual pair (involving 106 unique pairs), 55 (120
414 eggs) remained unattended, 24 (120 eggs) were attended by a single female, 12 (41 eggs) were
415 attended by a single male, 3 (36 eggs) were attended by a female-female pair, 2 (30 eggs) were
416 attended by two males and two females, 2 (21 eggs) were attended by a trio with two females, and 1
417 (9 eggs) by a trio with two males.

418 We also quantified two additional response variables for every female, namely the latency to start
419 laying eggs (in days since the start of the experiment, counting to the first recorded fertile egg, and
420 ascribing a latency of 75 days to females without fertile eggs) and the total number of fertile eggs
421 laid within the 70-day experimental period (both based on the 1,080 eggs with genetically confirmed
422 maternity). The 319 failed eggs were not considered.

423 Over the course of the experiment (13 May to 22 July 22 for egg laying and until 9 September for
424 rearing young to independence) one male and two females (all of the more abundant type within
425 their aviaries) died of natural causes (a male in aviary 5 on 28 June, a female in aviary 6 on 24 July,
426 and a female in aviary 10 on 22 August). Thus, following the preregistered protocol, no bird was
427 excluded from data analysis.

428 *Data analysis*

429 Following previously used methods [25, 56], we calculated 'relative fitness' for each female as
430 relative fitness of female $i = N * \text{number of offspring of female } i / \text{total number of offspring of all } N$
431 females in the aviary. This index has a mean of 1 for each aviary, and accounts for fitness differences
432 between the 4 genetic populations (note that all birds within an aviary come from the same genetic
433 population). Latency to egg laying was log₁₀-transformed before analysis to approach normality. To
434 control for the effect of inbreeding on fitness, we calculated female inbreeding coefficients F from
435 existing genetic pedigree data (using the R package 'pedigree' V.1.4, [57]). All mixed effect models
436 were built with the R package 'lme4' V1.1-26 [58] in R version 4.0.3 [59] and p-values were
437 calculated from t-values assuming infinite degrees of freedom.

438 Table 1 lists all the statistical models that compare the two treatment groups. These comprise both
439 pre-registered models (1-3) and post-hoc exploratory models (4-15). All models have the same basic
440 structure comparing a fitness-related trait between the two treatment groups (120 rows of data
441 representing 80 high-competition and 40 relaxed-competition females). Thus, we used mixed-effect
442 models with Gaussian (models 1-12) or binomial (models 13-15) errors, with the fitness-related trait
443 as the dependent variable, with treatment as the fixed effect of interest, with a scaled inbreeding
444 coefficient of the female as a covariate, and with the experimental aviary (10 levels) and the natal
445 aviary (16 levels) as random effects.

446 For preregistered model 1 we ran two versions (1a and 1b). Because the dependent variable of this
447 model is relative fitness, which was scaled within experimental aviaries, the model was designed
448 without random effects (as a general linear model, 1a). To control for possible influences of the natal
449 environment and of the genetic F1 mother we added two fixed-effect covariates (in version 1b): (1)
450 the total number of F2 offspring in the natal aviary where the focal female was raised (ranging from
451 29 to 45 offspring across the 16 natal aviaries), (2) the number of independent F2 offspring produced
452 by the genetic mother (one year earlier, also within a 70-day window for egg-laying; mean: 5.7,
453 range: 0-12, N = 66 mothers of the 120 focal females).

454 *Exploratory analyses*

455 To quantify the extent of assortative mating with regard to song dialect at the behavioural level, we
456 relied on the 106 unique heterosexual pairs that were observed caring for at least one of 190
457 clutches (comprising 1,022 eggs). For the quantification of assortment on the genetic level, we relied
458 on the genetic parentage of the 1,080 successfully genotyped eggs, of which 6 eggs had to be
459 excluded because they were sired by males from the females' natal aviaries (due to sperm storage, N
460 = 4), because alleles from two males were detected (presumably due to polyspermy, N = 1), or
461 because no paternal alleles were detected (possible case of parthenogenesis, N = 1), leaving 1,074
462 informative eggs.

463 For each female, we scored their social pairing behaviour, i.e. we noted whether they had been
464 recorded as a member of one of the 106 heterosexual pairs engaging in brood care. We quantified
465 (a) the total number of social bonds (0, 1, or 2), (b) the number of assortative and disassortative
466 bonds and (c) the latency to their first social bond (i.e. the laying date of the first egg in a clutch they
467 attended as one of the 106 pairs, relative to the start of the experiment; ascribing a latency of 75
468 days to females with zero social bonds). Latency was log₁₀-transformed before analysis.

469 For each female, we also counted the number of clutches (0, 1, or 2) attended as a single mother
470 and we quantified (a) the number of eggs (out of the 1,080 genetically assigned eggs) they actively
471 cared for themselves (in whatever social constellation), (b) the number of eggs dumped into nests
472 attended by other females (in whatever social constellation, “egg dumping in the strict sense”) and
473 (c) the number of eggs dumped anywhere (“egg dumping in the wide sense”, including in nests
474 attended by single males and in unattended nest boxes). All exploratory mixed-effect models (4-15)
475 closely follow the design of the preregistered models 2 and 3 (see above).

476 Models 13-15 deal with proportions of eggs, and hence we used binomial models with counts of
477 successes and failures, and controlling for overdispersion by fitting female identity (120 levels) as
478 another random effect.

479 We ran exploratory analyses on the levels of extra-pair paternity of 84 females that were socially
480 paired to only a single male (i.e. recorded with only one male, among the 106 nest-attending
481 heterosexual pairs). These 84 females produced a total of 795 eggs with parentage information.
482 However, we excluded 48 eggs (from 16 females) that were laid before the date of pairing of the
483 focal female (genetic mother). Overall, 239 of the remaining 747 eggs (32%) were sired by a male
484 that was not the social partner (the male with whom the female attended a nest), so these are
485 classified as ‘extra-pair sired’. We calculated levels of extra-pair paternity for three groups of
486 females: (1) assortatively paired females of the relaxed-competition group (n = 35 females), (2)
487 assortatively paired females of the high-competition group (n = 28 females, one of which did not lay
488 any eggs with parentage information), (3) disassortatively paired females of the high-competition
489 group (n = 21 females). To compare levels of extra-pair paternity between the latter two groups of
490 females, we used a t-test on percentages of extra-pair paternity calculated for each female.

491

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495 **Authors’ contributions**

496 WF, DW and BK conceived the study. KM carried out the study and collected the data. WF analyzed
497 and interpreted the data with inputs from BK. WF and BK wrote the manuscript with input from DW.

498 **Competing interests**

499 We have no competing interests.

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502

503 **Data accessibility**

504 All underlying data can be found on the Open Science Framework under

505 <https://osf.io/6e8np>

506

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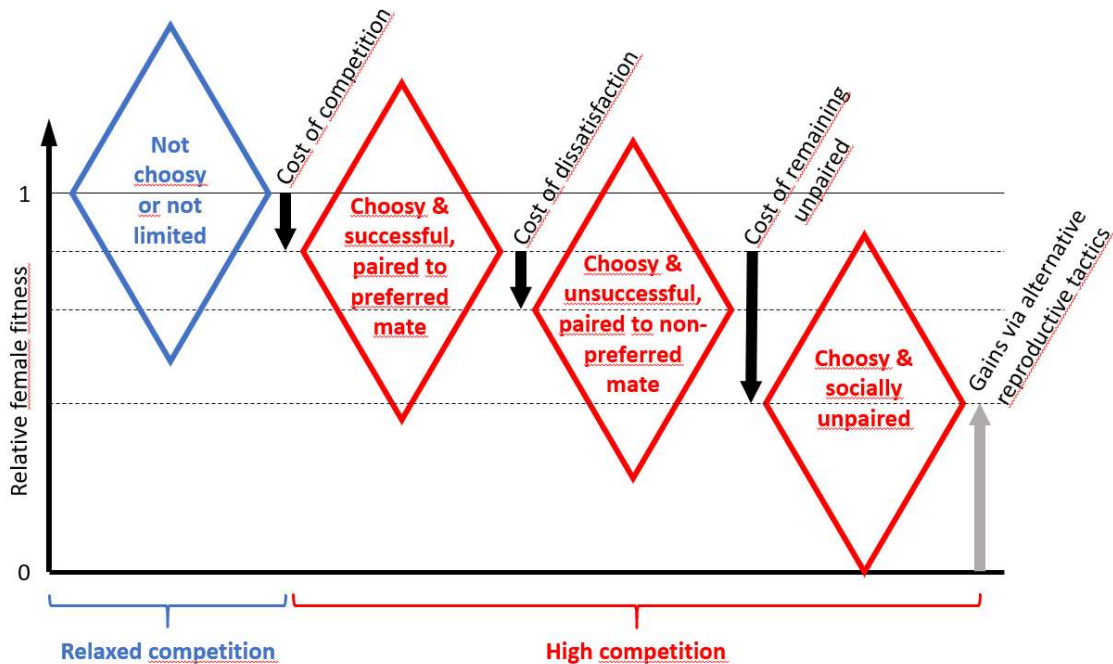
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637 **Table 1.** Comparisons between females of the ‘high-competition’ (n = 80) and ‘relaxed competition’
 638 (n = 40) treatment. Overview of planned tests (models 1-3, as outlined in the pre-registration
 639 document before data collection; <https://osf.io/8md3h>) and post-hoc tests that were conducted
 640 after knowing the results of the planned tests (data exploration, models 4-15). All conducted tests
 641 are reported in their initial form (no selective reporting, no post-hoc modification). Indicated are
 642 average values for the two treatment groups for each dependent variable. Proportions of eggs refer
 643 to means of individual mean proportions. For latencies, back-transformed values after averaging
 644 log₁₀-transformed values are shown. P-values refer to group differences based on glms or glmms.
 645 Covariates are the female’s inbreeding coefficient (F), the size of the peer group in the female’s natal
 646 aviary (peersize), and the fitness of the female’s mother. Random effects are the experimental aviary
 647 (exp AV, 10 levels), the female’s natal aviary (natal AV, 16 levels), and – in binomial models of counts
 648 with overdispersion – female identity (FID, 120 levels) (see S1-S15 Tables for details). Note that the
 649 high significance of the treatment effect in models 6 and 7 is partly caused by the experimental
 650 design.

Model	Test type	Dependent variable	High competition	Relaxed competition	p (treatment)	Trend in expected direction	Covariates	Random effects
1a	planned	relative fitness (scaled to unity)	1.023	0.953	0.57	no	F	-
1b	planned	relative fitness (scaled to unity)	1.023	0.953	0.32	no	F, peersize, mother fitness	-
2	planned	N genetic eggs laid	9.21	8.58	0.37	no	F	exp AV, natal AV
3	planned	latency to first genetic egg (days)	7.78	8.25	0.63	no	F	exp AV, natal AV
4	exploration	Proportion females socially unpaired	26%	10%	0.03	yes	F	exp AV, natal AV
5	exploration	N social bonds per female	0.863	0.925	0.42	yes	F	exp AV, natal AV
6	exploration	N assortative social bonds	0.450	0.900	0.000002	yes	F	exp AV, natal AV
7	exploration	N disassortative social bonds	0.413	0.025	0.0014	yes	F	exp AV, natal AV
8	exploration	latency to first social bond with eggs (days)	13.48	7.93	0.008	yes	F	exp AV, natal AV
9	exploration	N clutches attended as a single mother	0.163	0.125	0.57	yes	F	exp AV, natal AV
10	exploration	N eggs actively taken care off	6.64	7.40	0.21	yes	F	exp AV, natal AV
11	exploration	N eggs dumped to other females (strict)	1.63	0.80	0.038	yes	F	exp AV, natal AV
12	exploration	N eggs dumped anywhere (wide)	2.58	1.18	0.009	yes	F	exp AV, natal AV
13	exploration	Proportion eggs dumped (strict)	17%	9%	0.027	yes	F	exp AV, natal AV, FID
14	exploration	Proportion eggs dumped (wide)	29%	12%	0.001	yes	F	exp AV, natal AV, FID
15	exploration	Proportion fertile eggs leading to offspring	50.1%	50.2%	0.87	yes	F	exp AV, natal AV, FID

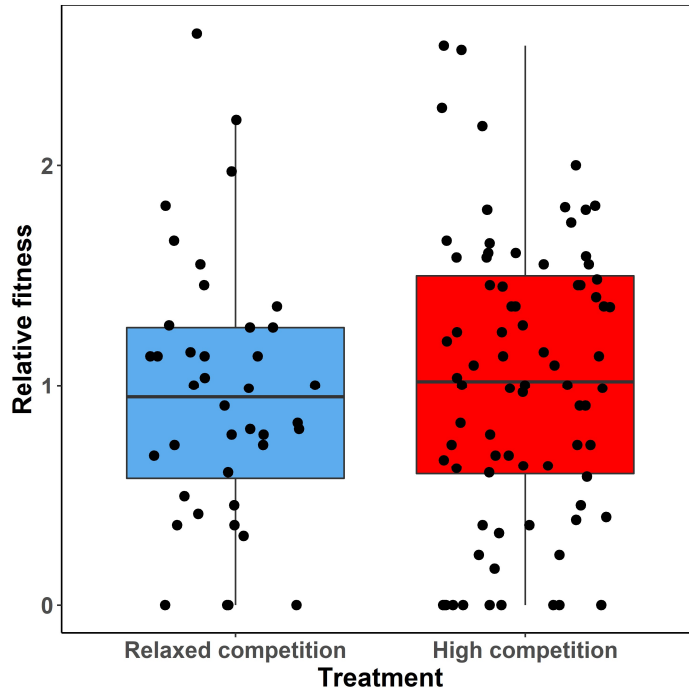
651 **Figure 1.** Schematic representation of the expected fitness costs of choosiness when females are
652 limited by the availability of preferred mates (red, high competition) compared to females that are
653 not limited by their choosiness or by the availability of preferred mates (blue, relaxed competition).
654 For simplicity, we assume that preferred and non-preferred mates do not differentially affect female
655 fitness. Diamonds illustrate variation in individual fitness around the mean fitness of a group of
656 females (centre of diamonds, horizontal lines). Black arrows stand for various aspects of costs of
657 choosiness under competition for mates. The grey arrow represents fitness gains via alternative
658 reproductive tactics of females that remain socially unpaired, including reproduction as single
659 female or via parasitic egg dumping. The cost of socially pairing with a non-preferred male may e.g.
660 result from reduced willingness to copulate leading to infertility, aggression, and reduced male
661 brood care. Note that in empirical studies the apparent costs of pairing with a non-preferred male
662 (cost of “dissatisfaction”) and of remaining unpaired might be confounded by effects of intrinsic
663 quality differences between the three groups of females shown in red. Also note that all choosy
664 females (red) pay a cost of competition, which might also vary between groups, for example if some
665 females avoid to compete.

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667

668 **Figure 2.** Relative fitness (number of independent offspring produced by each female, scaled to a
669 mean of one within each of the 10 experimental aviaries) of the 40 females from the relaxed-
670 competition group (4 females with 8 males of their preferred natal song dialect per aviary)
671 compared to the 80 females from the high-competition group (8 females with 4 males of their
672 preferred natal song dialect per aviary). Group averages of 0.95 and 1.02 are indicated.



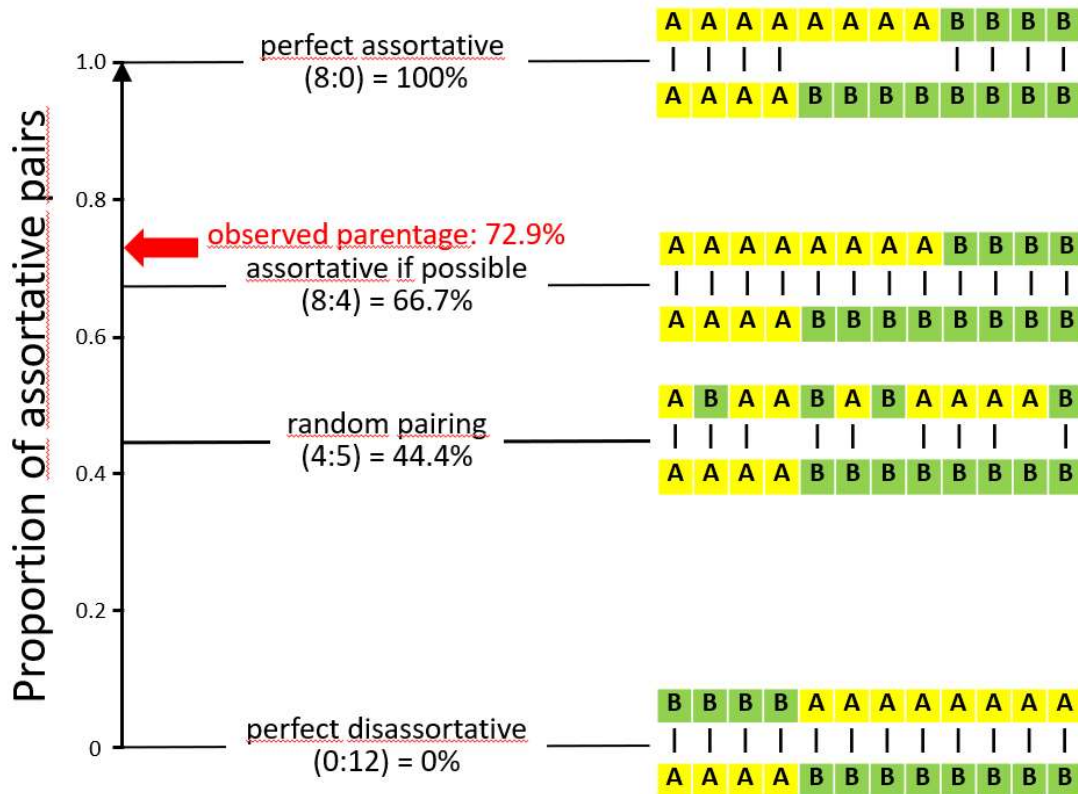
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677 **Figure 3.** Experimental design (letters A and B stand for individuals of different song dialects in an
 678 aviary; each row represents one sex) and possible pair bonds (dashes connecting letters) resulting in
 679 different levels of assortative mating with regard to song dialect. Random pairing on average
 680 produces 44.4% assortative pairs (pairs matched for their song dialect). “Observed parentage” refers
 681 to the proportion of fertilized eggs (N = 1,074) of which the genetic parents were mated
 682 assortatively. For comparison, four idealized scenarios of pairing are indicated together with the
 683 numbers of assortative versus disassortative pairs (in parentheses).

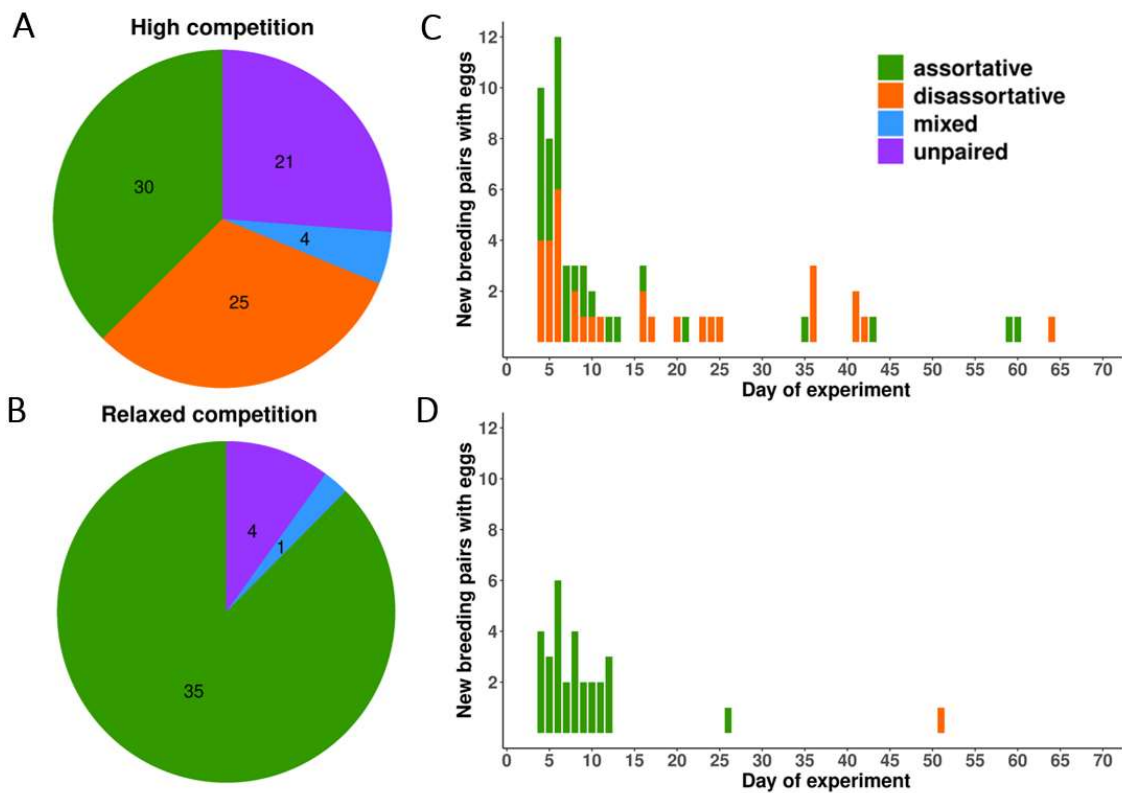


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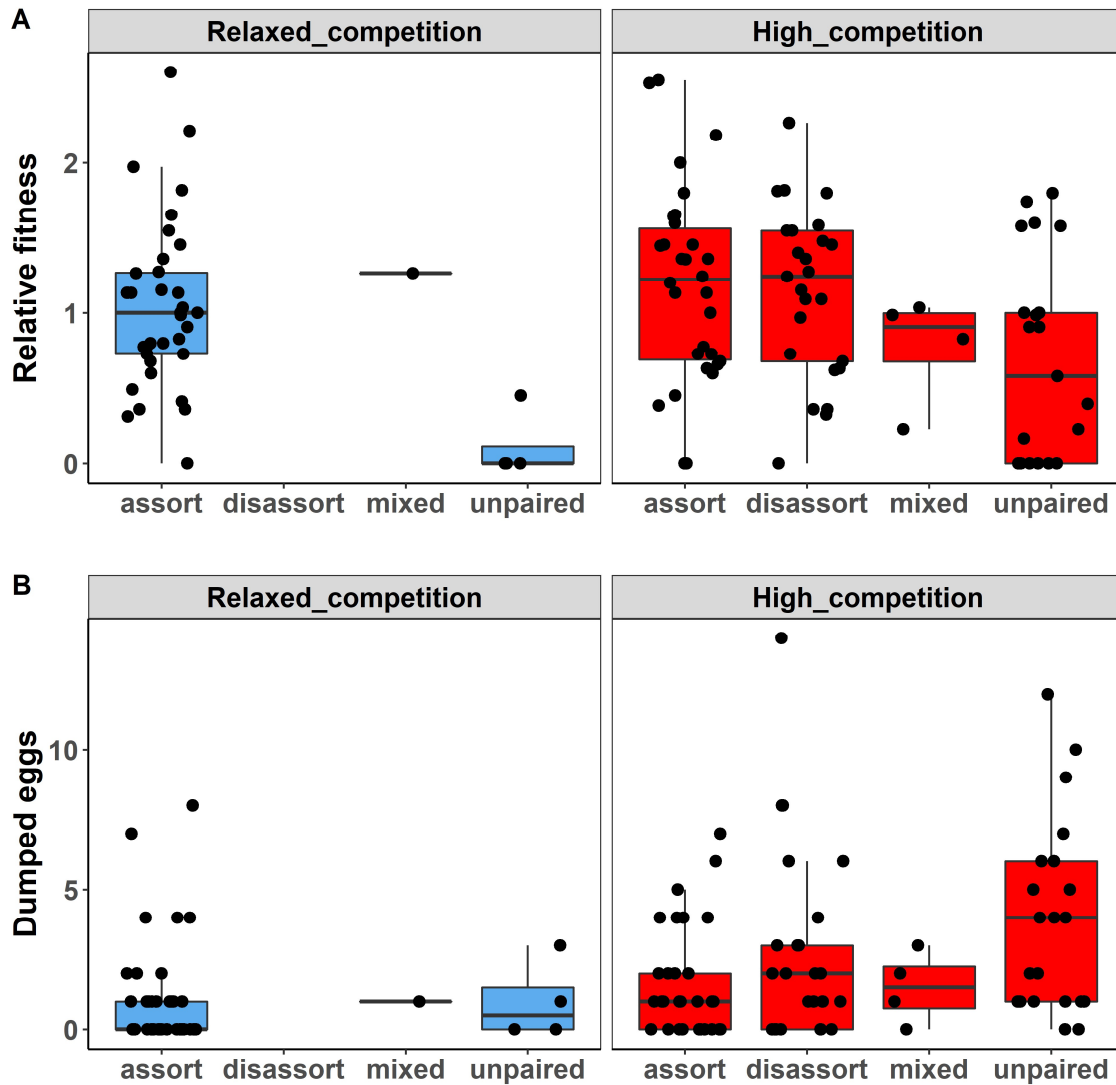
687 **Figure 4.** Observed pair bonds for females from the relaxed and high-competition groups. (A, B) Pie
688 charts showing the proportion of females in each of the two treatment groups that were either not
689 observed as a pair (unpaired), or were seen in assortative, disassortative or both type of pair bonds
690 (mixed). Numbers indicate the count of females in each group. (C, D) Histograms illustrating the
691 temporal patterns of emergence of social bonds (either assortative or disassortative). Shown is the
692 day after the start of the experiment (potentially ranging from 1 to 70) on which the first egg was
693 recorded in a nest taken care of by one of the 106 breeding pairs (note that this may include
694 parasitic eggs not laid by the focal female). The y-axes are scaled to compensate for the two-times
695 larger number of females in the high-competition treatment relative to the relaxed-competition
696 treatment. Note that assortative bonds ($N = 72$) formed significantly earlier than disassortative
697 bonds ($N = 34$; back-transformed estimates 9.3 vs. 17.8 days, t-test on log-transformed latency: $t_{104} =$
698 3.67, $p = 0.0004$).



699

700

701 **Figure 5.** Relative fitness (A, as described in Figure 2) and number of “dumped eggs” laid (B, wide
702 definition of parasitic eggs, see Results) for females of different pairing status (unpaired, or mated
703 assortatively, disassortatively or both, as in Figure 4A, B) in each of the two treatment groups
704 (relaxed competition versus high competition). Horizontal lines indicate group averages.

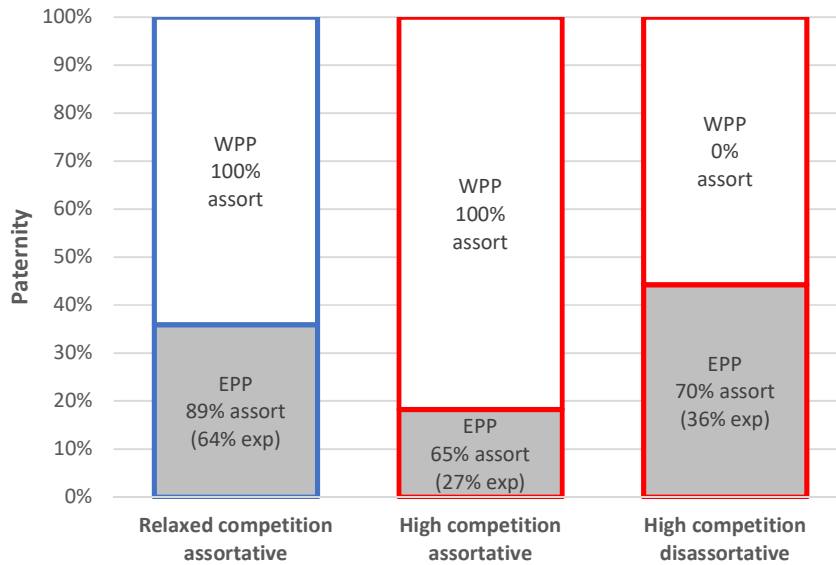


705

706

707

708 **Figure 6.** Proportion of eggs sired outside the monogamous pair bond (extra-pair paternity, EPP,
709 grey bars) versus within-pair paternity (WPP, white bars) for three groups of females with a single
710 social pair bond. These are (1) assortatively paired females (n = 35) from the relaxed competition
711 treatment (blue), (2) assortatively paired females (n = 28, one of which did not lay any eggs) from
712 the high competition treatment (red), and disassortatively paired females (n = 21) from the high
713 competition treatment. For each category of eggs, we indicate the proportion that is sired
714 assortatively ('assort') for song dialect and in parentheses the random expectations ('exp') for this
715 proportion of assortative mating based on the number of available extra-pair males of each song
716 dialect. For more details see also S16 Table.



717

718 **Supporting Information**

719 **S1 Table. Female relative fitness as a function of treatment and confounding factors.**

Model 1	Estimate	SE	<i>t</i>	<i>p</i>
Model 1a				
Intercept	0.955	0.097		
Treatment (high competition)	0.067	0.119	0.57	0.57
Inbreeding coefficient (scaled)	-3.143	1.126	-2.79	0.006
Model 1b				
Intercept	0.914	0.102		
Treatment (high competition)	0.128	0.128	1.01	0.32
Inbreeding coefficient (scaled)	-3.535	1.256	-2.82	0.006
Number of peers in natal aviary (scaled)	-0.017	0.012	-1.46	0.15
Relative fitness of mother (scaled)	0.034	0.020	1.66	0.099

720

721 **S2 Table. Number of genetically verified eggs laid per female as a function of treatment and female**
 722 **inbreeding coefficient (mixed-effect model 2).**

Model 2	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0.16				
Experimental aviary	10	0.22				
Residual	120	12.46				
Fixed effects						
Intercept		8.56	0.59	34.8		
Treatment (high competition)		0.64	0.70	20.1	0.91	0.37
Inbreeding coefficient (scaled)		-18.83	6.73	79.1	-2.80	0.0065

723

724 **S3 Table. Latency (in days, log10-transformed) to lay the first genetically verified egg as a function of**
 725 **treatment and female inbreeding coefficient.**

Model 3	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0.0061				
Experimental aviary	10	0				
Residual	120	0.1012				
Fixed effects						
Intercept		0.92	0.057	37.5		
Treatment (high competition)		-0.033	0.069	45.8	-0.48	0.63
Inbreeding coefficient (scaled)		1.07	0.623	95.1	1.72	0.09

726

727 **S4 Table. Probability of remaining socially unpaired (not recorded participating in one of 106 nest-attending**
 728 **pairs) as a function of treatment and female inbreeding coefficient (binomial model on n=120 females).**

Model 4	Levels	Estimate	SE	<i>z</i>	<i>p</i>
Random effects (variance)					
Natal aviary	15	0.04			
Experimental aviary	10	0.32			
Fixed effects					
Intercept		-2.63	0.66		
Treatment (high competition)		1.49	0.71	2.11	0.035
Inbreeding coefficient (scaled)		20.4	7.00	2.91	0.0036

729

730 **S5 Table. Number of social pair bonds observed per female (range 0-2) as a function of treatment and**
 731 **female inbreeding coefficient (Gaussian mixed-effect model).**

Model 5	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0.015				
Experimental aviary	10	0.007				
Residual	120	0.248				
Fixed effects						
Intercept		0.931	0.092	30.8		
Treatment (high competition)		-0.088	0.108	28.8	-0.82	0.42
Inbreeding coefficient (scaled)		-3.18	0.995	96.7	-3.20	0.0019

732

733 **S6 Table. Number of assortative social pair bonds observed per female (range 0-2) as a function of treatment**
 734 **and female inbreeding coefficient (Gaussian mixed-effect model).**

Model 6	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0				
Experimental aviary	10	0				
Residual	120	0.221				
Fixed effects						
Intercept		0.90	0.074	117		
Treatment (high competition)		-0.45	0.091	117	-4.96	<0.0001
Inbreeding coefficient (scaled)		-2.26	0.863	117	-2.62	0.0099

735

736 **S7 Table. Number of disassortative social pair bonds observed per female (range 0-2) as a function of**
 737 **treatment and female inbreeding coefficient (Gaussian mixed-effect model).**

Model 7	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0.011				
Experimental aviary	10	0.011				
Residual	120	0.221				
Fixed effects						
Intercept		0.035	0.088	29.2		
Treatment (high competition)		0.365	0.100	21.8	3.65	0.0014
Inbreeding coefficient (scaled)		-0.824	0.944	97.6	-0.87	0.38

738

739 **S8 Table. Latency (in days, log10-transformed) to the first recorded egg in a clutch attended as one of the**
 740 **106 social pairs as a function of treatment and female inbreeding coefficient.**

Model 8	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0				
Experimental aviary	10	0.006				
Residual	120	0.200				
Fixed effects						
Intercept		0.897	0.075	38.2		
Treatment (high competition)		0.234	0.087	105.9	2.70	0.008
Inbreeding coefficient (scaled)		3.650	0.852	88.6	4.28	0.00005

741

742 **S9 Table. Number of clutches attended as a single mother (range 0-2) as a function of treatment and female**
 743 **inbreeding coefficient (Gaussian mixed-effect model).**

Model 9	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0.009				
Experimental aviary	10	0				
Residual	120	0.155				
Fixed effects						
Intercept		0.127	0.070	33.3		
Treatment (high competition)		0.049	0.085	40.8	0.58	0.57
Inbreeding coefficient (scaled)		1.092	0.768	90.7	1.42	0.16

744

745 **S10 Table. Number of eggs which the female took care of (recorded as a social mother in any pairing**
 746 **constellation) as a function of treatment and female inbreeding coefficient.**

Model 10	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0				
Experimental aviary	10	1.13				
Residual	120	10.14				
Fixed effects						
Intercept		7.41	0.61	28.7		
Treatment (high competition)		-0.78	0.62	108.1	-1.27	0.21
Inbreeding coefficient (scaled)		-23.65	6.34	111.7	-3.73	0.0003

747

748 **S11 Table. Number of genetically verified eggs by a female that were cared for by another female as a**
 749 **function of treatment and female inbreeding coefficient (mixed-effect model 2).**

Model 11	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0				
Experimental aviary	10	0				
Residual	120	4.15				
Fixed effects						
Intercept		0.80	0.32	117		
Treatment (high competition)		0.83	0.39	117	2.10	0.038
Inbreeding coefficient (scaled)		2.70	3.74	117	0.72	0.47

750

751 **S12 Table. Number of genetically verified eggs per female that she did not take care of as a function of**
 752 **treatment and female inbreeding coefficient (mixed-effect model 2).**

Model 12	Levels	Estimate	SE	df	<i>t</i>	<i>p</i>
Random effects (variance)						
Natal aviary	15	0.23				
Experimental aviary	10	0				
Residual	120	6.92				
Fixed effects						
Intercept		1.11	0.45	39.0		
Treatment (high competition)		1.48	0.55	44.0	2.72	0.0094
Inbreeding coefficient (scaled)		3.51	5.03	86.5	0.70	0.49

753

754 **S13 Table. Relative counts of eggs that the female dumped (in a strict sense) versus her remaining eggs as a**
 755 **function of treatment and female inbreeding coefficient (binomial mixed-effect model).**

Model 13	Levels	Estimate	SE	<i>z</i>	<i>p</i>
Random effects (variance)					
Female identity	120	1.97			
Natal aviary	15	0			
Experimental aviary	10	0			
Fixed effects					
Intercept		-2.96	0.35		
Treatment (high competition)		0.87	0.39	2.21	0.027
Inbreeding coefficient (scaled)		6.76	3.75	1.80	0.071

756

757 **S14 Table. Relative counts of eggs that the female dumped (in a wide sense) versus took care of as a**
 758 **function of treatment and female inbreeding coefficient (binomial mixed-effect model).**

Model 14	Levels	Estimate	SE	<i>z</i>	<i>p</i>
Random effects (variance)					
Female identity	120	1.54			
Natal aviary	15	0			
Experimental aviary	10	0			
Fixed effects					
Intercept		-2.66	0.36		
Treatment (high competition)		1.36	0.41	3.33	0.0009
Inbreeding coefficient (scaled)		12.45	4.04	3.09	0.002

759

760 **S15 Table. Relative counts of eggs that developed into independent young and her remaining eggs that did**
 761 **not reach independence as a function of treatment and female inbreeding coefficient (binomial mixed-effect**
 762 **model).**

Model 15	Levels	Estimate	SE	<i>z</i>	<i>p</i>
Random effects (variance)					
Female identity	120	0.78			
Natal aviary	15	0			
Experimental aviary	10	0.08			
Fixed effects					
Intercept		0.064	0.21		
Treatment (high competition)		-0.036	0.23	-0.16	0.87
Inbreeding coefficient (scaled)		-6.51	2.85	-2.29	0.022

763

764 **S16 Table. Descriptive statistics on extrapair mating by three groups of females (dependent on competition**
 765 **treatment and social pairing status).**

Dependent variable	Low competition paired assortatively	High competition paired assortatively	High competition paired disassortatively
% females with EPP (N with EPP / N total females)	66 (23/35)	44 (12/27)	81 (17/21)
% EPP (of eggs) in females with EPP \pm SE	55 \pm 7	41 \pm 8	62 \pm 9
% EPP of all eggs (N EPP / N total eggs)	36 (112/312)	18 (46/252)	44 (81/183)
% assortative of EP-eggs (N assortative / N EPP)	89 (100/112)	65 (30/46)	70 (57/81)
% assortative of EP-relationships (N assortative / N total EP-relationships)	87 (40/46)	53 (9/17)	59 (19/32)
% assortative expected of EP-relationships (N assortative / N total EP-males in aviary)	64 (7/11)	27 (3/11)	36 (4/11)
N eggs sired by assortative EP-male per relationship \pm SE (N relationships)	2.5 \pm 0.3 (40)	3.3 \pm 0.6 (9)	3.0 \pm 0.5 (19)
N eggs sired by disassortative EP-male per relationship \pm SE (N relationships)	2.0 \pm 0.4 (6)	2.0 \pm 0.3 (8)	1.8 \pm 0.3 (13)

766 **EPP:** extra-pair paternity

767 **EP:** extra-pair

768 **S1 Text**

769 R-code and model outputs of planned models 1-3 and post-hoc models 4-15.

770 **Explanation of variables:**

771 Dependent variables:

772 relfit = relative fitness, scaled to a mean of one (12 x number of independent young / total number of
773 independent young in the experimental aviary)
774 Neggsvalid = Count of genetically verified eggs produced by a female (total sum = 1,080 eggs)
775 loglatencygen = log10-transformed latency in days to lay the first genetically verified egg
776 unpaired = not participating in any of the 106 heterosexual pair bonds (0 = no, 1 = yes)
777 Nsocbonds = number of social pair bonds observed per female (range 0 – 2, total sum = 106)
778 N_assort_bonds = number of assortative social pair bonds observed per female (range 0 – 2, total sum = 72)
779 N_disassort_bonds = number of disassortative social pair bonds observed per female (range 0 – 2, total sum =
780 34)
781 loglatencysoc = log10-transformed latency in days to the first recorded egg in a clutch attended as one of the
782 106 social pairs
783 Singlemomclutches = number of clutches attended as a single mother (range 0 – 2, total sum = 18)
784 Eggsselfcaredfor = number of eggs for which the female was recorded to attend as a social mother in whatever
785 pairing constellation
786 Eggsdumpedstrict = number of genetically verified eggs of a female that were cared for by another female
787 Eggsdumpedwide = number of genetically verified eggs of a female that she did not care for herself (equal to
788 Neggsvalid – Eggsselfcaredfor)
789 Propdumpedstrict = Relative counts of eggs that a female dumped in the strict sense and her remaining eggs
790 Propdumpedwide = Relative counts of eggs that a female dumped in the wide sense and her remaining eggs
791 Propeggsuccess = Relative counts of eggs of a female that developed into independent young and her
792 remaining eggs that did not reach independence

793

794

795 Fixed effects:

796

797 trt = female treatment (1 = relaxed competition, 2 = high competition)

798 Fped = pedigree-based inbreeding coefficient F of the female

799 Npeers = number of peers reaching independence within the female's natal aviary

800 motherfitness = number of independent offspring produced by the mother in the previous year within an
801 equally-long time window

802

803 Random effects:

804

805 ExpAV = experimental aviary (10 levels)

806 NatalAV = natal aviary (16 levels)

807 Ind_ID = female identity (120 levels)

808

809 **Code :**

810 require(lme4)

811 library("lmerTest")

812 dd<-read.csv("./choosiness1_females.csv",header=T)

813 dd\$NatalAV<-factor(dd\$NatalAV)

814 dd\$ExpAV<-factor(dd\$ExpAV)

815 dd\$trt<-factor(dd\$trt)

816

817

818 **Model 1a**

819

820 `m1a<-glm(relfit~trt+scale(Fped,scale=F),data=dd); summary(m1a)`

821

822 Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	0.95523	0.09704	9.844	< 2e-16	***
trt2	0.06716	0.11884	0.565	0.57308	
scale(Fped, scale = F)	-3.14271	1.12611	-2.791	0.00614	**

827

828 `m1aestimates<-glm(relfit~-1+trt+scale(Fped,scale=F),data=dd); summary(m1aestimates)`

829

830 Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
trt1	0.95523	0.09704	9.844	< 2e-16	***
trt2	1.02239	0.06861	14.901	< 2e-16	***
scale(Fped, scale = F)	-3.14271	1.12611	-2.791	0.00614	**

835

836 **Model 1b**

837

838 `m1b<-glm(relfit~trt+scale(Fped,scale=F)+scale(Npeers,scale=F)+scale(motherfitness,scale=F), data=dd);`

839 `summary(m1b)`

840

841 Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	0.91436	0.10175	8.987	5.94e-15	***
trt2	0.12846	0.12779	1.005	0.31691	
scale(Fped, scale = F)	-3.53541	1.25551	-2.816	0.00573	**
scale(Npeers, scale = F)	-0.01711	0.01174	-1.457	0.14777	
scale(motherfitness, scale = F)	0.03406	0.02049	1.662	0.09925	.

848

849 **Model 2**

850

851 `require(lme4)`

852 `m2<-lmer(Neggvalid~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m2)`

853

854 Random effects:

Groups	Name	Variance	Std.Dev.
NatalAV	(Intercept)	0.1557	0.3945
ExpAV	(Intercept)	0.2179	0.4668
Residual		12.4647	3.5305

859 Number of obs: 120, groups: NatalAV, 15; ExpAV, 10

860

861 Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)	
(Intercept)	8.5633	0.5931	34.7822	14.439	2.94e-16	***
trt2	0.6400	0.7032	20.1072	0.910	0.37351	
scale(Fped, scale = F)	-18.8353	6.7343	79.0559	-2.797	0.00648	**

866

867 **Model 3**

868

869 `m3<-lmer(loglatencygen~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m3)`

870

871 Random effects:

Groups	Name	Variance	Std.Dev.
NatalAV	(Intercept)	0.006107	0.07815
ExpAV	(Intercept)	0.000000	0.00000
Residual		0.101216	0.31814

876 Number of obs: 120, groups: NatalAV, 15; ExpAV, 10

877

878 Fixed effects:

```
879             Estimate Std. Error      df t value Pr(>|t|)
880 (Intercept)          0.92029    0.05662 37.45131 16.255 <2e-16 ***
881 trt2                 -0.03294    0.06884 45.81581 -0.479 0.6346
882 scale(Fped, scale = F) 1.06877    0.62299 95.07132 1.716 0.0895 .
883
884 Model 4
885
886 m4<-glmer(unpaired~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd, family=binomial);
887 summary(m4)
888
889 Random effects:
890   Groups Name          Variance Std.Dev.
891 NatalAV (Intercept) 0.03969 0.1992
892 ExpAV   (Intercept) 0.32334 0.5686
893 Number of obs: 120, groups: NatalAV, 15; ExpAV, 10
894
895 Fixed effects:
896             Estimate Std. Error z value Pr(>|z|)
897 (Intercept)      -2.6337    0.6646  -3.963 7.4e-05 ***
898 trt2              1.4886    0.7055   2.110 0.03485 *
899 scale(Fped, scale = F) 20.4028    7.0019   2.914 0.00357 **
900
901 Model 5
902
903 m5<-lmer(Nsocbonds~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m5)
904
905 Random effects:
906   Groups Name          Variance Std.Dev.
907 NatalAV (Intercept) 0.014594 0.12081
908 ExpAV   (Intercept) 0.007147 0.08454
909 Residual                0.247540 0.49753
910 Number of obs: 120, groups: NatalAV, 15; ExpAV, 10
911
912 Fixed effects:
913             Estimate Std. Error      df t value Pr(>|t|)
914 (Intercept)          0.93126    0.09239 30.78383 10.080 2.86e-11 ***
915 trt2                 -0.08796    0.10762 28.81111 -0.817 0.42042
916 scale(Fped, scale = F) -3.17993    0.99468 96.68667 -3.197 0.00188 **
917
918 Model 6
919
920 m6<-lmer(N_assort_bonds~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m6)
921
922 Random effects:
923   Groups Name          Variance Std.Dev.
924 NatalAV (Intercept) 0.0000 0.0000
925 ExpAV   (Intercept) 0.0000 0.0000
926 Residual                0.2212 0.4703
927 Number of obs: 120, groups: NatalAV, 15; ExpAV, 10
928
929 Fixed effects:
930             Estimate Std. Error      df t value Pr(>|t|)
931 (Intercept)          0.90133    0.07436 117.00000 12.121 < 2e-16 ***
932 trt2                 -0.45200    0.09108 117.00000 -4.963 2.38e-06 ***
933 scale(Fped, scale = F) -2.26344    0.86299 117.00000 -2.623 0.00988 **
934
935 Model 7
936
937 m7<-lmer(N_disassort_bonds~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m7)
938
939 Random effects:
```

```
940   Groups   Name          Variance Std.Dev.
941   NatalAV  (Intercept) 0.01057 0.1028
942   ExpAV    (Intercept) 0.01089 0.1044
943   Residual                0.22068 0.4698
944   Number of obs: 120, groups:  NatalAV, 15; ExpAV, 10
945
946   Fixed effects:
947               Estimate Std. Error      df t value Pr(>|t|)
948   (Intercept)      0.03545    0.08836 29.21410   0.401 0.69119
949   trt2              0.36459    0.09995 21.79147   3.648 0.00144 **
950   scale(Fped, scale = F) -0.82400    0.94355 97.62335  -0.873 0.38464
951
952   Model 8
953
954   m8<-lmer(loglatencysoc~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m8)
955
956   Random effects:
957   Groups   Name          Variance Std.Dev.
958   NatalAV  (Intercept) 0.000000 0.00000
959   ExpAV    (Intercept) 0.006349 0.07968
960   Residual                0.199917 0.44712
961   Number of obs: 120, groups:  NatalAV, 15; ExpAV, 10
962
963   Fixed effects:
964               Estimate Std. Error      df t value Pr(>|t|)
965   (Intercept)      0.89686    0.07505 38.17114  11.950 1.81e-14 ***
966   trt2              0.23380    0.08659 105.88609   2.700 0.00807 **
967   scale(Fped, scale = F) 3.65047    0.85214 88.57020   4.284 4.65e-05 ***
968
969   Model 9
970
971   m9<-lmer(Singlemomclutches~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m9)
972
973   Random effects:
974   Groups   Name          Variance Std.Dev.
975   NatalAV  (Intercept) 0.008803 0.09383
976   ExpAV    (Intercept) 0.000000 0.00000
977   Residual                0.154795 0.39344
978   Number of obs: 120, groups:  NatalAV, 15; ExpAV, 10
979
980   Fixed effects:
981               Estimate Std. Error      df t value Pr(>|t|)
982   (Intercept)      0.12673    0.06962 33.27238   1.820 0.0777 .
983   trt2              0.04872    0.08470 40.78098   0.575 0.5684
984   scale(Fped, scale = F) 1.09214    0.76845 90.67711   1.421 0.1587
985
986
```

```
987 Model 10
988
989 m10<-lmer(Eggsselfcaredfor~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m10)
990
991 Random effects:
992   Groups   Name                Variance Std.Dev.
993   NatalAV  (Intercept)           0.00    0.000
994   ExpAV    (Intercept)           1.13    1.063
995   Residual                            10.14    3.185
996 Number of obs: 120, groups:  NatalAV, 15; ExpAV, 10
997
998 Fixed effects:
999               Estimate Std. Error      df t value Pr(>|t|)
1000 (Intercept)          7.4139    0.6055  28.6811  12.245 6.51e-13 ***
1001 trt2                 -0.7834    0.6167  108.0893  -1.270 0.206713
1002 scale(Fped, scale = F) -23.6450    6.3432  111.6922  -3.728 0.000305 ***
1003
1004 Model 11
1005
1006 m11<-lmer(Eggsdumpedstrict~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m11)
1007
1008 Random effects:
1009   Groups   Name                Variance Std.Dev.
1010   NatalAV  (Intercept)           0.000    0.000
1011   ExpAV    (Intercept)           0.000    0.000
1012   Residual                            4.145    2.036
1013 Number of obs: 120, groups:  NatalAV, 15; ExpAV, 10
1014
1015 Fixed effects:
1016               Estimate Std. Error      df t value Pr(>|t|)
1017 (Intercept)          0.7984    0.3219  117.0000   2.480  0.0146 *
1018 trt2                 0.8274    0.3943  117.0000   2.098  0.0380 *
1019 scale(Fped, scale = F)  2.6959    3.7360  117.0000   0.722  0.4720
1020
1021 Model 12
1022
1023 m12<-lmer(Eggsdumpedwide~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m12)
1024
1025 Random effects:
1026   Groups   Name                Variance Std.Dev.
1027   NatalAV  (Intercept)           0.2326    0.4823
1028   ExpAV    (Intercept)           0.0000    0.0000
1029   Residual                            6.9173    2.6301
1030 Number of obs: 120, groups:  NatalAV, 15; ExpAV, 10
1031
1032 Fixed effects:
1033               Estimate Std. Error      df t value Pr(>|t|)
1034 (Intercept)          1.1143    0.4466  38.9532   2.495  0.01694 *
1035 trt2                 1.4819    0.5455  44.0411   2.717  0.00939 **
1036 scale(Fped, scale = F)  3.5141    5.0345  86.4795   0.698  0.48704
1037
1038
```

```
1039 Model 13
1040
1041 dd$Propdumpedstrict<-cbind(dd$Eggsdumpedstrict,dd$Eggsnotstrictlydumped)
1042 m13<-glmer(Propdumpedstrict~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV)+(1|Ind_ID),data=dd,
1043 family=binomial); summary(m13)
1044
1045 Random effects:
1046   Groups Name          Variance Std.Dev.
1047   Ind_ID  (Intercept) 1.969e+00 1.403e+00
1048   NatalAV (Intercept) 2.590e-10 1.609e-05
1049   ExpAV   (Intercept) 1.431e-09 3.783e-05
1050 Number of obs: 120, groups:  Ind_ID, 120; NatalAV, 15; ExpAV, 10
1051
1052 Fixed effects:
1053             Estimate Std. Error z value Pr(>|z|)
1054 (Intercept)      -2.9587    0.3536  -8.367  <2e-16 ***
1055 trt2              0.8687    0.3931   2.210  0.0271 *
1056 scale(Fped, scale = F)  6.7587    3.7493   1.803  0.0714 .
1057
1058 Model 14
1059
1060 dd$Propdumpedwide<-cbind(dd$Eggsdumpedwide,dd$Eggsnotwidelydumped)
1061 m14<-glmer(Propdumpedwide~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV)+(1|Ind_ID),data=dd,
1062 family=binomial); summary(m14)
1063
1064 Random effects:
1065   Groups Name          Variance Std.Dev.
1066   Ind_ID  (Intercept) 2.38    1.543
1067   NatalAV (Intercept) 0.00    0.000
1068   ExpAV   (Intercept) 0.00    0.000
1069 Number of obs: 120, groups:  Ind_ID, 120; NatalAV, 15; ExpAV, 10
1070
1071 Fixed effects:
1072             Estimate Std. Error z value Pr(>|z|)
1073 (Intercept)      -2.6595    0.3582  -7.425 1.13e-13 ***
1074 trt2              1.3551    0.4065   3.334 0.000857 ***
1075 scale(Fped, scale = F) 12.4515    4.0355   3.085 0.002032 **
1076
1077 Model 15
1078
1079 dd$Propeggsuccess<-cbind(dd$juvd35,dd$Eggsfailed)
1080 m15<-glmer(Propeggsuccess~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV)+(1|Ind_ID),data=dd,
1081 family=binomial); summary(m15)
1082
1083 Random effects:
1084   Groups Name          Variance Std.Dev.
1085   Ind_ID  (Intercept) 7.807e-01 8.836e-01
1086   NatalAV (Intercept) 1.758e-10 1.326e-05
1087   ExpAV   (Intercept) 7.669e-02 2.769e-01
1088 Number of obs: 120, groups:  Ind_ID, 120; NatalAV, 15; ExpAV, 10
1089
1090 Fixed effects:
1091             Estimate Std. Error z value Pr(>|z|)
1092 (Intercept)      0.06413    0.20909   0.307  0.7591
1093 trt2             -0.03649    0.23081  -0.158  0.8744
1094 scale(Fped, scale = F) -6.50954    2.84856  -2.285  0.0223 *
1095
```