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

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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].

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

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

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

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

Results

A. Preregistered analyses: costs of choosiness

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

B. Post-hoc data exploration: female coping tactics

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

The degree of assortative mating, i.e. the proportion of assortative pairs, can range from zero to one (see Figure 3). In our experimental setup, a value of zero can theoretically be reached if all pairs mated disassortatively (zero assortative and up to 12 disassortative pairs in each aviary). A value of one, corresponding to perfect assortative pairing, can only be reached if four females per aviary remained unpaired (8 assortative and zero disassortative pairs per aviary). Under random pairing, 44.4% of pairings should be assortative (1/3 of females has a 2/3 chance of pairing assortatively, plus 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 assortatively, but no female would forego pairing, 66.7% of pairings should be assortative (8 assortative and 4 disassortative pairs per aviary).

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

Methods

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

Ethics

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

Background of study populations and assortative mating

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

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

Experimental setup

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

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

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

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

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

Breeding procedures

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

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

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

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

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

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

Data analysis

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

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

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

Exploratory analyses

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

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

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

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

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

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Authors’ contributions

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

Competing interests

We have no competing interests.

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Data accessibility

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

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

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

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

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

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

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

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

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

Supporting Information

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

S2 Table. Number of genetically verified eggs laid per female as a function of treatment and female 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

S3 Table. Latency (in days, log10-transformed) to lay the first genetically verified egg as a function of 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

S4 Table. Probability of remaining socially unpaired (not recorded participating in one of 106 nest-attending 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

S5 Table. Number of social pair bonds observed per female (range 0-2) as a function of treatment and 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

S6 Table. Number of assortative social pair bonds observed per female (range 0-2) as a function of treatment 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

S7 Table. Number of disassortative social pair bonds observed per female (range 0-2) as a function of 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

S8 Table. Latency (in days, log10-transformed) to the first recorded egg in a clutch attended as one of the 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

S9 Table. Number of clutches attended as a single mother (range 0-2) as a function of treatment and female 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

S10 Table. Number of eggs which the female took care of (recorded as a social mother in any pairing 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

S11 Table. Number of genetically verified eggs by a female that were cared for by another female as a 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

S12 Table. Number of genetically verified eggs per female that she did not take care of as a function of 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

S13 Table. Relative counts of eggs that the female dumped (in a strict sense) versus her remaining eggs as a 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

S14 Table. Relative counts of eggs that the female dumped (in a wide sense) versus took care of as a 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

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

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:
823             Estimate Std. Error t value Pr(>|t|)
824 (Intercept)      0.95523    0.09704   9.844 < 2e-16 ***
825 trt2              0.06716    0.11884   0.565  0.57308
826 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:
831             Estimate Std. Error t value Pr(>|t|)
832 trt1              0.95523    0.09704   9.844 < 2e-16 ***
833 trt2              1.02239    0.06861  14.901 < 2e-16 ***
834 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:
842             Estimate Std. Error t value Pr(>|t|)
843 (Intercept)      0.91436    0.10175   8.987 5.94e-15 ***
844 trt2              0.12846    0.12779   1.005  0.31691
845 scale(Fped, scale = F) -3.53541    1.25551  -2.816  0.00573 **
846 scale(Npeers, scale = F) -0.01711    0.01174  -1.457  0.14777
847 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:
855   Groups   Name      Variance Std.Dev.
856 NatalAV   (Intercept) 0.1557  0.3945
857 ExpAV     (Intercept) 0.2179  0.4668
858 Residual                12.4647  3.5305
859 Number of obs: 120, groups: NatalAV, 15; ExpAV, 10
860
861 Fixed effects:
862             Estimate Std. Error      df t value Pr(>|t|)
863 (Intercept)      8.5633    0.5931  34.7822  14.439 2.94e-16 ***
864 trt2              0.6400    0.7032  20.1072   0.910  0.37351
865 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:
872   Groups   Name      Variance Std.Dev.
873 NatalAV   (Intercept) 0.006107  0.07815
874 ExpAV     (Intercept) 0.000000  0.00000
875 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

```

Model 10

```
m10<-lmer(Eggselfcaredfor~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m10)
```

Random effects:

Groups	Name	Variance	Std.Dev.
NatalAV	(Intercept)	0.00	0.000
ExpAV	(Intercept)	1.13	1.063
Residual		10.14	3.185

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

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	7.4139	0.6055	28.6811	12.245	6.51e-13 ***
trt2	-0.7834	0.6167	108.0893	-1.270	0.206713
scale(Fped, scale = F)	-23.6450	6.3432	111.6922	-3.728	0.000305 ***

Model 11

```
m11<-lmer(Eggsdumpedstrict~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m11)
```

Random effects:

Groups	Name	Variance	Std.Dev.
NatalAV	(Intercept)	0.000	0.000
ExpAV	(Intercept)	0.000	0.000
Residual		4.145	2.036

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

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	0.7984	0.3219	117.0000	2.480	0.0146 *
trt2	0.8274	0.3943	117.0000	2.098	0.0380 *
scale(Fped, scale = F)	2.6959	3.7360	117.0000	0.722	0.4720

Model 12

```
m12<-lmer(Eggsdumpedwide~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV),data=dd); summary(m12)
```

Random effects:

Groups	Name	Variance	Std.Dev.
NatalAV	(Intercept)	0.2326	0.4823
ExpAV	(Intercept)	0.0000	0.0000
Residual		6.9173	2.6301

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

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	1.1143	0.4466	38.9532	2.495	0.01694 *
trt2	1.4819	0.5455	44.0411	2.717	0.00939 **
scale(Fped, scale = F)	3.5141	5.0345	86.4795	0.698	0.48704

Model 13

```
dd$Propdumpedstrict<-cbind(dd$Eggsdumpedstrict,dd$Eggsnotstrictlydumped)
m13<-glmer(Propdumpedstrict~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV)+(1|Ind_ID),data=dd,
family=binomial); summary(m13)
```

Random effects:

Groups	Name	Variance	Std.Dev.
Ind_ID	(Intercept)	1.969e+00	1.403e+00
NatalAV	(Intercept)	2.590e-10	1.609e-05
ExpAV	(Intercept)	1.431e-09	3.783e-05

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

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.9587	0.3536	-8.367	<2e-16 ***
trt2	0.8687	0.3931	2.210	0.0271 *
scale(Fped, scale = F)	6.7587	3.7493	1.803	0.0714 .

Model 14

```
dd$Propdumpedwide<-cbind(dd$Eggsdumpedwide,dd$Eggsnotwidelydumped)
m14<-glmer(Propdumpedwide~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV)+(1|Ind_ID),data=dd,
family=binomial); summary(m14)
```

Random effects:

Groups	Name	Variance	Std.Dev.
Ind_ID	(Intercept)	2.38	1.543
NatalAV	(Intercept)	0.00	0.000
ExpAV	(Intercept)	0.00	0.000

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

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.6595	0.3582	-7.425	1.13e-13 ***
trt2	1.3551	0.4065	3.334	0.000857 ***
scale(Fped, scale = F)	12.4515	4.0355	3.085	0.002032 **

Model 15

```
dd$Propeggsuccess<-cbind(dd$juvd35,dd$Eggsfailed)
m15<-glmer(Propeggsuccess~trt+scale(Fped,scale=F)+(1|ExpAV)+(1|NatalAV)+(1|Ind_ID),data=dd,
family=binomial); summary(m15)
```

Random effects:

Groups	Name	Variance	Std.Dev.
Ind_ID	(Intercept)	7.807e-01	8.836e-01
NatalAV	(Intercept)	1.758e-10	1.326e-05
ExpAV	(Intercept)	7.669e-02	2.769e-01

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

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.06413	0.20909	0.307	0.7591
trt2	-0.03649	0.23081	-0.158	0.8744
scale(Fped, scale = F)	-6.50954	2.84856	-2.285	0.0223 *