1 # Social learning by mate-choice copying increases dispersal and reduces

2 # local adaptation

3

4 Manuel Sapage,[1,5] Susana A. M. Varela[1,2,3,6] & Hanna Kokko[4,7]

5 [1] *cE3c—Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências,*

6 *Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal.*

7 [2] *Instituto Gulbenkian de Ciência, 2780-156 Oeiras, Portugal.*

8 [3] ISPA – Instituto Universitário, 1149-041 Lisboa, Portugal.

9 [4] *Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich,*

10 *Switzerland.*

11 [5] *Email: masapage@fc.ul.pt*

12 [6] *Email: smvarela@igc.gulbenkian.pt*

13 [7] *Email: hanna.kokko@ieu.uzh.ch*

14

15 **Corresponding Author**

16 **Name:** Manuel António Pinto Sapage

17 **Mailing Address:** cE3c—Centre for Ecology, Evolution and Environmental Changes, Faculdade de

18 Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal.

19 **E-mail:** masapage@fc.ul.pt

20

23

24

Statement of authorship

All authors helped to conceive the problem and contributed to the design of the study. MS wrote the code to the mathematical model, ran the simulations, analysed the data, and wrote the first draft of the manuscript. All authors contributed substantially to the writing.

Data accessibility statement

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dncjsxkz1, (Sapage *et. al.*, 2020)

Abstract

1. In heterogeneous environments, dispersal may be hampered not only by direct costs, but also because immigrants may be locally maladapted. While maladaptation affects both sexes, this cost may be modulated in females if they express mate preferences that are either adaptive or maladaptive in the new local population.

2. Dispersal costs under local adaptation may be mitigated if it is possible to switch to expressing traits of locally adapted residents. In a sexual selection context, immigrant females may learn to mate with locally favoured males. Mate-choice copying is a type of social learning, where

individuals, usually females, update their mating preferences after observing others mate. If it allows immigrant females to switch from maladapted to locally adapted preferences, their dispersal costs are mitigated as mate choice helps them create locally adapted offspring.

3. To study if copying can promote the evolution of dispersal, we created an individual-based model to simulate the coevolution of four traits: copying, dispersal, a trait relevant for local adaptation, and female preference. We contrast two scenarios with copying — either unconditional, or conditional such that only dispersers copy — with a control scenario that lacks any copying.

4. We show copying to lead to higher dispersal, especially if copying is conditionally expressed. This leads to an increase in gene flow between patches and, consequently, a decrease in local adaptation and trait-preference correlations.

5. While our study is phrased with female preference as the learned trait, one may generally expect social learning to mitigate dispersal costs, with consequent feedback effects on the spatial dynamics of adaptation.

Introduction

Mate-choice decisions may be based on innate preferences, individual experience, or on the observed choices of others. The last of these, mate-choice copying, is a type of social learning that involves updating mate preferences after observing others' choices (Wade & Pruett-Jones 1990; Dugatkin 1992, 1996; Pruett-Jones 1992). Females may prefer either the successful males themselves (Bowers *et al.* 2012), or generalize their preferences to males with similar phenotypes ("trait copying" or "mate-choice copying generalization", (Brooks 1998; White & Galef Jr 2000; Witte & Noltemeier 2002; Godin *et al.* 2005; Swaddle *et al.* 2005; Drullion & Dubois 2008; Mery *et al.* 2009; Bowers *et al.* 2012).

Mate-choice copying (synonymous with 'mate copying', Danchin *et al.* 2020) is documented in many taxa (Jones & DuVal 2019; Davies *et al.* 2020), e.g. birds (Swaddle *et al.* 2005; Kniel *et al.* 2017), fish (Dugatkin & Godin 1992; Schlupp & Ryan 1997; Witte & Ryan 1998; Heubel *et al.* 2008), mammals (Galef *et al.* 2008; Kavaliers *et al.* 2017), insects (Mery *et al.* 2009; Dagaeff *et al.* 2016; Germain *et al.* 2016; Monier *et al.* 2018) and spiders (Fowler-Finn *et al.* 2015). Empirical studies typically test whether copying occurs in a species or aim to evaluate conditions that make copying favoured over innate preferences. Theoretical studies have complemented the picture by exploring when copying is expected to invade and spread (Losey *et al.* 1986; Pruett-Jones 1992; Servedio & Kirkpatrick 1996; Stöhr 1998; Dubois *et al.* 2012; Santos *et al.* 2017) and how copying affects the direction and strength of sexual selection (Kirkpatrick 1982; Agrawal 2001; Santos *et al.* 2014).

Mate-choice copying is argued to be adaptive because it allows the female to mate with higher quality mates (Gibson & Höglund 1992; Nordell & Valone 1998; Valone & Templeton 2002; Danchin *et al.* 2004; Dugatkin 2005; Uehara *et al.* 2005; Wagner & Danchin 2010; reviews Vakirtzis & Roberts 2012, Varela *et al.* 2018). But this yields another question: why is copying needed to achieve a good outcome, i.e. why should any female not already possess preferences for best traits? If temporal changes are fast, i.e. the best mate for a given female varies through time (Ingleby *et al.* 2010), females

91   might need updated information regarding better adapted (Getty 2014; Wade 2014) and/or more

92   popular males (Kokko *et al.* 2007). Theoretical work that focuses on the 'informedness' of individuals

93   has, indeed, considered age effects. Young females are conceivably inexperienced, and although they

94   may possess innate preferences, observing and copying experienced females' behaviour can be of

95   benefit; still, it is not always clear why informedness should increase with age, i.e. why innate

96   preferences are insufficient. Older and experienced females may also opt for mate-choice copying if,

97   for example, their previous breeding attempt failed (Amlacher & Dugatkin 2005; Hill & Ryan 2006;

98   Danchin *et al.* 2008). In both cases, the probability of copying is argued to increase with the difficulty

99   of the discrimination task (Nordell & Valone 1998).

100   Irrespective of age and experience, some individuals may be poorly informed in settings where

101   spatial variation in environmental demands combines with local adaptation and gene flow (Holman &

102   Kokko 2014). Here, immigrant females may be uninformed of locally best traits. We show that this

103   creates population-level feedback where mate-choice copying may facilitate the evolution of dispersal

104   itself.

105   The reasoning is the following. Migrants experience an additional cost of dispersal when there

106   is spatial variation in the environment (Blanquart & Gandon 2014; Berdahl *et al.* 2015), because their

107   traits are shaped by past selection in their natal environment, with unknown (and likely worse)

108   performance in the environment they disperse to. For females, an additional complication is that their

109   mate preferences — if genetically determined — may be similarly shaped by past selection. If

110   preferences (and not just traits) are locally adapted, immigrant females may mate suboptimally. This

111   problem can be minimized through copying, assuming that dispersal is not so strong that immigrants

112   swamp locally adapted females, which would lead to uninformed immigrants copying each other's

113   choices. Copying thus allows immigrant-origin lineages gain locally adapted alleles and reduces the

114   costs of dispersal. As we show below, it also ultimately reduces the degree of local adaptation via

115   improved gene flow (reduction of genetic differentiation between different habitats).

116

Material and methods

We model populations of obligately sexual, haploid populations (which allows us to model one allele per locus, as our focus is not on effects of genetic dominance, see Kokko 2007), initialized in a locally adapted state with only short-distance dispersal (a negative exponential dispersal kernel with a low mean). We thereafter allow the dispersal kernel to evolve in populations with or without a mate-choice copying locus. This locus, if present, has two alleles c (for innate preference) and C (for copying), only expressed in females. We contrast three scenarios. In the *unconditional* scenario, females with the C allele copy the mate choice of others at every copying opportunity; in the *conditional* scenario, they only do so if they have emigrated from their natal patch. In the *control* scenario, females only express innate preferences (no mate choice copying evolves), while dispersal still evolves.

The population inhabits a toroid world (a doughnut-shaped continuous surface, each side having length 1). The benefit of using a toroid world is to avoid the need to specify what happens if individuals encounter the edge of the modelled world; under toroid assumptions, they can always continue moving in any direction even if the world is finite. The world is divided into 25^2 patches with environmental heterogeneity that translates into a spatially varying and positively autocorrelated optimum for individuals' trait values (note that we include spatial but not temporal variation of the environment). Positive spatial autocorrelation ensures that neighbouring patches do not differ very strongly from each other (details described in Step 1 below); in other words, it allows the scale of environmental variation to be broader than a single patch. This is of benefit since broadly similar conditions across several patches, combined with finite dispersal distances, allows local adaptation to proceed and overcome the effects of drift — even if local patches (demes) themselves are kept small for the sake of realistic mate choice (females do not evaluate very many males before mating, Roff & Fairbairn 2014; see below).

141   We model genotypes with five different loci (S, T, P, C, D), some of which have sex-limited

142   expression. The S locus determines sex, with alleles 0 (for females) and 1 (for males). The T locus (T

143   stands for *trait*) has a pleiotropic effect. In both males and females, its value (real number between 0

144   and 1) relative to an environmental (spatially varying) optimum determines viability; in males, it

145   additionally codes for a phenotype directly observable to females. The P locus likewise takes allelic

146   values between 0 and 1 but is only expressed in females; it specifies a preference for specific

147   phenotypes of males. Females prefer males whose trait locus matches the female's preference locus,

148   which allows females to show local adaptation for locally adapted male traits. The C locus, with 2

149   alleles c and C, is likewise only expressed in females and controls female copying behaviour. Finally,

150   the D locus, expressed in all individuals, determines the mean of the individual's dispersal kernel, with

151   values between 0 and 1 (where 1 would imply a mean distance equal to the length of the entire world).

152   Each run of the simulation proceeds as follows: (1) creation of the patch-specific environmental

153   values, (2) population initialization, (3) survival, (4) dispersal, (5) mate choice by females, and (6)

154   reproduction. The simulation starts following steps 1 through 6, thereafter repeating steps 3 through 6

155   for each generation. Note that the order of the events dictates that viability selection is applied at the

156   natal patch. Generations are non-overlapping.

157   In step 1, to simulate environmental heterogeneity, an environmental value is attributed to each

158   patch using the algorithm described in Holman & Kokko (2014) that creates a matrix of environmental

159   values with an adjustable spatial autocorrelation. The algorithm first generates a random value between

160   0 and 1 for each patch, then, for $25^2 \times 100$ iterations (a large enough number so that each patch, on

161   average, experiences 100 impacts), it updates a randomly chosen patch p by setting its environmental

162   value E_p to $\mu_p + r(1 - \beta)$, where μ_p is the mean environmental value of the eight patches surrounding

163   patch p. These successive iterations bring the autocorrelation between neighbouring patches to a level

164   that is controlled by the parameter β ($0 \leq \beta < 1$). $\beta = 0$ implies there is no spatial autocorrelation, and

165   when $\beta \approx 1$, neighbouring patches are very similar to each other. After all iterations, the resulting

166   matrices were rescaled to have mean environmental value 0.5 and standard deviation 0.2 (see figure

167   S1 in Supporting Information for examples).

168   In step 2, we give 20000 young individuals random coordinates $0 \leq x,y < 1$. The sex of each

169   individual is randomly chosen (S locus is randomized to be 0 or 1), and we assume initial local

170   adaptation with the following procedure. Values for T and P alleles are drawn randomly from a

171   Gaussian distribution with mean E_p (where p is the patch that the individual's coordinates imply it

172   resides in) and standard deviation 0.05. Values that fall below 0 or exceed 1 are given a value of 0 or

173   1, respectively. Mate-choice copying is initially absent, i.e. all individuals are initialized with the c

174   allele at the copying locus; C alleles are introduced later via mutation (see below). For the dispersal-

175   determining D locus, individuals are initialized with random values drawn from a uniform distribution

176   ranging between 0 and 0.005.

177   Viability selection (step 3) is applied in a density-dependent manner. At most 16 individuals

178   survive in each patch. The value is chosen to allow each female to observe a low number of males and

179   females (we expect patches to contain close to 8 females and 8 males; in nature, examples of more

180   than 10 males sampled before mating appear rare, Roff & Fairbairn 2014), and also to produce a global

181   population of maximally 10000 adults. No viability selection occurs in patches containing up to 16

182   individuals. In patches with more than 16 individuals, we first compute an adaptedness value for each

183   individual i in patch p:

$$v_{Ai} = e^{-S_N(a_{Ti} - E_p)^2}, \tag{1}$$

185   where $S_N > 0$ scales the strength of natural selection and a_{Ti} is the allele value of individual i at the T

186   locus. This expression is close to 1 when the difference between a_{Ti} and E_p is small, indicating little

187   mismatch between the phenotype and the environment, and declines at a rate controlled by S_N as the

188   mismatch increases. Actual survival probability depends on v_{Ai} relative to competitors, and to generate

189   stochasticity that allows mild differences in individual v_{Ai} to translate to different rank orders when

190   competing for the 16 survival 'slots', we compute the relative success $v_{Ai}{}^*$ for individual i by drawing

191   from an exponential distribution with mean v_{Ai}. At each generation, the 16 individuals with the highest

192   v_A* of each patch are retained, while the others die.

193   In step 4, dispersal distances are drawn for each individual from a negative exponential

194   distribution with a mean equal to the allelic value at the D locus. The direction of dispersal is random.

195   The toroid arrangement of the patches ensures that the dispersal kernel can be applied even if dispersal

196   distances exceed 1, the width of the world. More importantly (given that very long-distance dispersal

197   is unlikely), short dispersal distances may mean not leaving the natal patch; coordinates are still

198   updated, but the environmental value that the individual experiences does not change. We apply

199   dispersal mortality of 0.05 to each individual whose new coordinates bring it outside its natal patch.

200   In step 5 (mate choice), females only perceive males who reside in the same patch as potential

201   mates. Females only mate once; males may mate multiply. While we impose no restrictions on male

202   mating capacity, their realized success is limited by the fact that males can only be chosen by females

203   residing in the same patch. Within each patch, non-copier females mate first, after which copier

204   females choose mates based on observations of all non-copier females' matings. There are three

205   categories of non-copiers: (i) all females with the c allele, (ii) females with a C allele who have not left

206   their natal patch in the conditional scenario, and (iii) females who attempt to copy but their patch offers

207   no non-copier female whose behaviour they could observe. Non-copier females (of any category)

208   observe all the males in their patch and preferentially mate with a male whose value at the T locus is

209   close to the female's value at her P locus. Specifically, each non-copier female f assigns a preference

210   value v_{Pfm} for each male m according to the equation

$$v_{Pfm} = e^{-S_S\left(a_{Pf} - a_{Tm}\right)^2},$$
(2)

212   where $S_S \geq 0$ scales the strength of sexual selection that female choice can impose on males, a_{Pf} is the

213   female's allelic value at the P locus, and a_{Tm} is the male's allelic value at the T locus. The expression

214   reaches its highest possible value, 1, when the male trait perfectly matches the female's preference,

215   and declines towards zero for increasing levels of mismatch. The probability that female f chooses

216   male m^* in the presence of other competitors is

217    $$Prob(f, m^*) = \frac{v_{\mathrm{P}fm^*}}{\sum_{m=1}^{M_p}(v_{\mathrm{P}fm})},$$ (3)

218   where M_p is the number of males in patch p.

219   A higher value of S_S means that females are choosier, i.e. realized matings more closely match

220   their innate preferences. Values at the P locus do not modulate the strength of preferences, but instead

221   indicate which phenotypes of males are preferred by each female. If $S_\mathrm{S} = 0$, mating is random, i.e.

222   values at the P locus do not impact realized mate choice.

223   While non-copier females choose, copier females observe. We assume trait-based mate-choice

224   copying (Danchin *et al.* 2018), i.e., copying females update their preferences for certain phenotypes

225   rather than specific males (thus a male with zero success so far can become favoured should he be

226   phenotypically similar to a male observed to mate). If choices made by non-copier females yield a

227   single winner among the males, copier females replace, phenotypically, their innate preferences with

228   a value that equals the T of this winner: $a_{\mathrm{P}f}^* = a_{\mathrm{T}m^{**}}$, where m** is the identity of the winner. In case

229   of a tie, one of the males is randomly chosen to be the winner, independently so for each of the copier

230   females.

231   A copier female f then assigns the value $v_{\mathrm{P}fm}$ to each male m analogously to the non-copier

232   case above,

233    $$v_{\mathrm{P}fm} = e^{-S_\mathrm{S}\left(a_{\mathrm{P}f}^* - a_{\mathrm{T}m}\right)^2},$$ (4)

234   and the actual choice of a mate follows eqn. 3 above.

235   In step 6, reproduction occurs in all patches with at least one male and one female. These

236   patches produce 32 offspring each. Each offspring has a mother and a father. The mother is chosen

237   randomly (as we assume no fecundity differences among females), and the sire is the mother's chosen

238   mate as determined above. Breeding is density dependent with these assumptions: a female breeding

239   in patch with a total of F_p females present will produce, on average, $32/F_p$ offspring. The expected

240   number of offspring produced by a focal male is $32/F_p$ times the number of females who chose this

241   male. Density dependence is relevant as it causes selection for dispersal to avoid competing with kin

242   (Hamilton & May 1977; Li & Kokko 2019). Offspring are initially placed at in the same coordinates

243   as their mothers.

244   For each locus, offspring inherit one allele, randomly chosen from either parent, without any

245   linkage between loci. The T, P, and D loci have a mutation probability of 0.01. Mutation is

246   implemented by adding, to the original allelic value, a random value drawn from a Gaussian

247   distribution with mean 0 and standard deviation 0.05, 0.05 or 0.005 for T, P and D loci, respectively.

248   Post-mutation allelic values below 0 or above 1 are assigned the value of 0 or 1, respectively. For the

249   biallelic mate-choice copying allele, a mutation changes the value of the allele from c to C and *vice*

250   *versa*, and the mutation probability was time-dependent: it was first set to zero for a burn-in period of

251   7500 generations (such that C individuals remain absent), and to 0.001 thereafter, except for the control

252   scenario (which never permits mate choice copying). The 'burning in' phase of 7500 generations

253   allows for all other loci to evolve to equilibrium values, and for dispersal specifically to show a balance

254   between avoidance of kin competition on the one hand and avoidance of dispersal costs (direct and

255   indirect) on the other.

256   After breeding, all adults die, and the offspring experience viability selection as described

257   above. Each simulation was run for 15000 generations, 20 times for each parameter value of S_S (taking

258   the values of 0, 25, 50, 75, and 100) and for each scenario (control, unconditional and conditional).

259   From generation 7500 onwards, we recorded the genotype and coordinates of all individuals every

260   2500 generations. This census was performed after the dispersal step and its associated mortality.

261   To understand the impact of mate-choice copying on local adaptation, we created a local

262   adaptation score (L) for each population. This measure quantifies the degree to which trait values, a_{Tp},

263   align with the environmental value in the (E_p) in the breeding patch:

$$264 \qquad L = -\frac{\sum_p \left(a_{\mathrm{T}p} - E_p\right)^2}{N}, \tag{5}$$

265   where N is the global number of surviving adults after dispersal. The negative sign in eqn. (5) implies

266   that high L corresponds to better local adaptation.

267   We compared mean allelic D values, C allele proportions, the local adaptation score L, and

268   trait-preference correlation coefficients across scenarios using one-way ANOVA tests (among all three

269   scenarios) or Welch two samples t-tests (between the conditional and unconditional scenarios).

270   Pairwise t-tests were used for comparisons of two different time points within populations. Significant

271   differences were followed by a post-hoc Tuckey's honest significance test. To account for multiple

272   testing, we applied Bonferroni corrections so that the corrected p-value = min $\{n \times p, 1\}$, where p is the

273   original p-value and n the number of hypothesis being tested. This may lead to a higher number of

274   false negatives than other methods (McDonald 2014), thus our conservative approach should provide

275   a strong argument for all significant cases that we find and discuss.

276   The Shapiro-Wilk test of normality revealed that some of our data deviate significantly from

277   normality. Although the tests we employed are robust against deviations from normality, as a

278   precaution, we repeated all the analyses for the significantly non-normal data using nonparametric

279   statistical tests. Since the results were similar, we only report parametric results.

280   The code for the mathematical model (programmed in C, using the GNU Scientific Library,

281   version 2.3, Galassi *et al.* 2009) have been deposited in the Dryad Digital Repository (Sapage *et al.*

282   2020). The statistical analyses were done with R, version 3.6.1 (R Core Team 2019).

283

284   **Results**

285   **1) Presence of mate-choice copying increases dispersal**

286   Scenarios did not differ with respect to dispersal at generation 7500 (all corrected p-

287   values > 0.05 for differences in mean D allele values, table S1), an expected outcome since copying

288   was not yet present in any of the scenarios. The control scenario that continued to lack mate-choice

289   copying in subsequent generations did not show any significant difference in dispersal tendency

290   between generations 7500 and 15000 (all corrected p-values > 0.05, table S2). In scenarios where the

291   C allele was introduced by allowing mutations to occur from generation 7500 onwards, dispersal

292   experienced a new evolutionary boost followed by reaching a new equilibrium (figure 1), as evidenced

293   by no significant difference when contrasting mean D allele values between generations 12500 and

294   15000 (all corrected p-values > 0.05, table S2).

295   We only expect differences in dispersal across scenarios if $S_S > 0$: non-random mating is

296   required for copying to mitigate the costs of dispersal that we envisage. Indeed, $S_S = 0$ yielded no

297   differences across scenarios (corrected p-value > 0.05, table S1) for allelic values of D at generation

298   15000, while differences emerged when $S_S > 0$: most populations with copying evolved significantly

299   higher mean values of D than control populations (figure 1). The exception, which we attribute to a

300   type II error, was the comparison between the conditional and the control scenarios at $S_S = 25$, where

301   the p-value remained marginally above significance (Tuckey HSD p = 0.05006).

302

303   **2) If sexual selection is strong, conditional copying increases dispersal more strongly than**

304   **unconditional copying**

305   Significant differences in the mean D allelic value at generation 15000 arose between the

306   conditional and the unconditional copying scenarios, when $S_S \geq 75$ (figure 1). Here, conditional

307   scenarios consistently produced more dispersal.

308

309   **3) Associations of the C allele and high dispersal within a population remain weak**

310   Are the above results driven by (i) C individuals (potential copiers) themselves dispersing at

311   higher rate than individuals with the allele c, or (ii) the presence of C in a population elevating dispersal

312   for everyone? At generation 15000, there was a tendency for C individuals to disperse more than c

313   individuals (in both scenarios where C alleles existed), but the difference was usually too small to be

314 significant (figure 2). Thus, any evidence for a statistical association between C and the allelic value

315 for D remains too weak to favour the first interpretation.

316

317 **4) Unconditional copying only evolves if sexual selection is suitably weak; conditional copying**

318 **does so across a range of strengths of sexual selection**

319   The frequency of the C allele remained constant (did not change significantly) between

320 generations 12500 and 15000 (all corrected p-values > 0.05, table S3), thus the proportion of copiers

321 had reached an equilibrium by generation 12500. In conditional as well as unconditional scenarios,

322 random mating ($S_S = 0$) should make the C allele neutral, and with sufficient time its frequency should

323 reach 0.5. This prediction was supported: the frequency of the C allele not differ significantly from 0.5

324 at generation 15000 (figure 3). Under non-random mating ($S_S > 0$), both scenarios deviated

325 significantly from the neutral expectation, but the effect depended on the strength of sexual selection.

326 At a low value of S_S ($S_S = 25$), the frequency of the copier allele C was elevated more in the

327 unconditional than the conditional scenario and exceeded 0.5 in both cases. This conclusion reversed

328 for $S_S \geq 50$, where unconditional copying led to a significantly lower frequency of the C allele than the

329 conditional scenario, with the former frequencies falling significantly below the neutral expectation

330 0.5 (figure 3).

331

332 **5) Mate choice copying weakens local adaptation and trait-preference correlations**

333   The local adaptation score L showed no significant differences between scenarios in generation

334 7500 (all corrected p-values > 0.05, table S4). As expected, control scenarios without copying also

335 yielded no significant differences in L between generations 7500 and 15000 (all corrected p-

336 values > 0.05, table S5), and L also did not differ between scenarios in generation 15000 under random

337 mating ($S_S = 0$, p-value > 0.05). Differences emerged when mating was non-random, and they became

338 significant once sexual selection was strong: when $S_S \geq 75$, scenarios with copying showed

339   significantly less local adaptation than the control scenario (figure 4a). Whether mate-choice copying

340   operated conditionally or unconditionally did not significantly impact the local adaptation score.

341   To understand the impact of mate-choice copying on the correlation between male traits and

342   female preferences, we calculated Pearson's correlation coefficients for the corresponding alleles.

343   They were not significantly different between scenarios in generation 7500 (all corrected p-

344   values > 0.05, table S6), control scenarios did not show any significant difference in the correlation

345   coefficient between generations 7500 and 15000 (all corrected p-values > 0.05, table S7), and the

346   correlation coefficient did not differ between scenarios in generation 15000 when mating was random

347   ($S_S = 0$, corrected p-value > 0.05). Introducing sexual selection ($S_S > 0$) increased these correlations,

348   but the magnitude of this response was scenario-dependent: at generation 15000, control populations

349   showed a significantly higher correlation coefficient than either scenario with mate-choice copying.

350   This was true across all positive values of S_S (figure 4b). The conditional scenario showed a

351   significantly higher correlation coefficient than the unconditional one when sexual selection was weak

352   ($S_S = 25$), but this result was reversed as S_S increased, and the reversed finding became significant for

353      $S_S = 75$ or higher (figure 4b).

354

355   **6) Sexual selection increases the effect of mate-choice copying on dispersal**

356   To investigate whether stronger sexual selection (high S_S) can amplify the effect of mate-choice

357   copying on dispersal, we created a linear model where the response variable was the mean D value at

358   generation 15000 and the predictors were S_S, the scenario, and their interaction. The control scenario

359   was used as the baseline. We also tested a linear model with the explanatory variable S_S transformed

360   to $\log(S_S + 1)$, because of the nonlinearity in eqn. (4); the model with the transformation fitted the data

361   better (AIC calculated by the 'extractAIC' function from the R statistical software (Venables & Ripley

362   2002), without transformation: –4312; with transformation: –4393). Diagnostic plots did not show any

363   major deviation from model assumptions. According to this model, when $\log(S_S + 1) = 0$ (i.e., $S_S = 0$),

364 mean dispersal did not differ between control populations and unconditionally copying populations

365 (allelic values for D; difference estimate: -2.40×10^{-4}; t $= -1.12$; p $= 0.233$), but both were

366 significantly higher than dispersal in conditionally copying populations (difference estimate: $-$

367 4.24×10^{-4}; t $= -2.11$; p $= 0.035$). Given that all populations should evolve identically under random

368 mating, and the previous results showed no significant difference between populations in this case

369 (figure 1), we regarded this particular result as an artefact of a model fit that is predominantly impacted

370 by the evolutionary responses to higher values of S_S.

371   The linear model shows S_S to increase dispersal in all scenarios. An increase of one $\log(S_S + 1)$

372 unit creates a significant increase of 1.96×10^{-4} in the mean allelic value of D in control populations

373 lacking copying (t $= 5.02$; p < 0.001), with an additional significant increase of 3.14×10^{-4} in the

374 unconditional copying scenario (t $= 5.677$; p < 0.001) and an additional significant increase of

375 5.38×10^{-4} in the conditional copying scenario (t $= 9.756$; p < 0.001). Overall, the dispersal-enhancing

376 effect of sexual selection is significantly strengthened by mate-choice copying, and it reaches its

377 maximum effect if copying is conditional on dispersal.

378

379 **Discussion**

380   Results show that mate-choice copying increases dispersal, especially when females are

381 choosier (sexual selection is stronger). Dispersal, in turn, has knock-on effects on gene flow and local

382 adaptation. Gene flow becomes stronger, and local adaptation becomes weaker, when immigrant

383 females can compensate for lack of local knowledge by copying the choices of others. Mate-choice

384 copying also decreased the correlation between the male trait and the female preference alleles. These

385 phenomena, taken together, counteract the depletion of male trait genetic variation by persistent innate

386 female preferences.

387   The evolution of mate-choice copying can be hampered when innate female preferences

388 coevolve with the male trait (Servedio & Kirkpatrick 1996; Santos *et al.* 2017), raising the question of

389   how sufficient variation in preferences can be maintained for a female to have any reason to switch

390   from her innate to an observed preference (in the absence of variation, a switch should never be

391   worthwhile). In their population-genetic models, Servedio & Kirkpatrick (1996) maintained the

392   polymorphism in preferences by mutation, while Santos *et al.* (2017) did so by randomly distributing

393   the preference locus each generation. In our case, environmental heterogeneity was the responsible

394   factor. Our finding that mate-choice copying can spread, but that it can also make local populations

395   less well adapted, is a novel twist on the idea that local adaptation of both traits and preferences,

396   combined with dispersal, can maintain a persistent supply of locally acting selection gradients (thus

397   helping to make the so-called lek paradox disappear, (Holman & Kokko 2014).

398   Sexual selection can be switched off in our model by assuming random mating. Dispersal

399   evolves to be low in such a setting. Complete philopatry still does not evolve as it would make

400   individuals compete for breeding resources (females) or matings (males) with close kin (Li & Kokko

401   2019), but dispersal mortality, as well as the risk of being maladapted to faraway parts of the landscape,

402   keeps dispersal rates low. Sexual selection can make this latter cost smaller, but this only works if

403   dispersing females subsequently mate with locally adapted males (and not, e.g., with males who are

404   themselves maladapted immigrants). Dispersal readily responds to this cost reduction, and evolves to

405   be higher, when the option of mate-choice copying is available. Copying allows choosy females to

406   express a different phenotype than her P locus would dictate. An immigrant female's offspring will

407   therefore, all else being equal, be better locally adapted than in the absence of mate-choice copying.

408   However, we also show that all else is not equal: when the evolutionary process with mate-choice

409   copying involves higher dispersal, this also improves gene flow and reduces local adaptation in the

410   global population as a whole.

411   Dispersal was particularly enhanced if mate-choice copying was conditionally expressed by

412   females who had dispersed, confirming the intuitive prediction that copying is best performed in

413   unfamiliar surroundings. For philopatric females, copying may lead to counterproductive updating of

414   preferences to those of immigrants, whose preferences have been shaped by selection elsewhere;

415   expressing one's own innate preferences may then be favoured. Conditional copying, then, appears the

416   superior way to alleviate the local adaptation cost of dispersal; it accordingly produces a more robust

417   feedback between copying and dispersal across different strengths of sexual selection, compared with

418   unconditional copying. This result is in line with earlier findings that indiscriminate copying can be

419   maladaptive (Dubois *et al.* 2012; see also Kendal *et al.* 2018). We are unaware of empirical studies

420   documenting differences in copying behaviour between immigrants and philopatric females; such

421   plasticity appears worth looking for.

422   Our results do not rely on assortative mating or other processes (e.g. physical linkage) creating

423   a statistical association between the C allele (copying) and the D allele (dispersal). While, in principle,

424   only high-D individuals 'need' the C allele (assuming philopatric individuals should not copy), such

425   associations remain weak at the genetic level. This does not strictly exclude any possibility for linkage

426   disequilibria: an immigrant non-copier would presumably mate non-ideally and thus high-D combined

427   with c would be selected against at the stage when her offspring viabilities are tested. But as her choices

428   are blind with respect to the dispersal status or (unexpressed) C locus of the sire, any effects here

429   remain weak. Instead, it appears that a high frequency of C in a population facilitates high D mainly

430   via (i) an overall expectation that preference updating is frequently an option for individuals in a

431   lineage (all female offspring who have inherited C from the mother or from the father can do so), and

432   (ii) a reduction of the overall importance of local adaptation. The latter is a general finding in the

433   literature on local adaptation and dispersal: once dispersal is relatively frequent, the costs of settling

434   in a new location are reduced, because recurrent gene flow prevents strong local adaptation in the first

435   place (Blanquart & Gandon 2011; Berdahl *et al.* 2015). Our contribution is to show that mate-choice

436   copying can amplify this effect quite substantially.

437   Note that the C allele in our model only experienced indirect selection, via its effects on the

438   identity of a female's chosen mate. Earlier population genetic work has investigated both direct and

439   indirect selection on copying (Servedio & Kirkpatrick 1996; Santos *et al.* 2017). Direct selection,

440   which we ignore, could either favour or disfavour copying: copying might help reduce the time and

441   energy costs of assessing male quality, or there may be mild costs inherent to the copying process itself

442   (e.g. costs of learning) or pleiotropic effects (Servedio & Kirkpatrick 1996). While our chosen focus

443   on the coevolution of copying and dispersal (via local adaptation) made us leave direct costs outside

444   our study, it is intuitively clear that copying may reach higher frequencies than reported by us if it also

445   helps to avoid direct costs.

446   Our contrasts between different scenarios were run in parallel, without the conditional strategy

447   directly competing with the unconditional one. Even so, it is still useful to reflect whether the

448   differences in the evolved frequencies of the C allele are a measure of 'success' of a certain kind of

449   copying strategy. Usually, high frequencies of C associate with conditional expression, but an

450   exception is found at weak sexual selection ($S_S = 25$), potentially explicable as a result of the quite

451   variable realized matings at low value of S_S (Box 1). Matings are in this case impacted by stochasticity,

452   whether the choices follow innate preferences or updated (copied) ones; the net effect is that non-

453   copier females may lose to copier females (in terms of mate quality) particularly when S_S is low (Box

454   1). Given that females with a C allele are much more likely to be copiers in the unconditional scenario

455   than in the conditional one, the situation described by Box 1 arises more often in the unconditional

456   scenario. This provides new insight into the debate (Nordell & Valone 1998; Giraldeau *et al.* 2002;

457   Vakirtzis 2011; Witte *et al.* 2015; Kendal *et al.* 2018; Varela *et al.* 2018) regarding the conditions

458   under which mate-choice copying can be adaptive.

459   Note that although the model has many parameters, it simultaneously presents a simplified

460   view of dispersal and mate-choice copying in a heterogeneous environment. For example, we modelled

461   dispersal as a simple exponential kernel, ignoring e.g. sex-biased dispersal (Li & Kokko 2019),

462   dispersal kernels with flexibilities offered by more than one variable (Chapman *et al.* 2007; Bonte *et

463   al.* 2010; Poethke *et al.* 2011; Nathan *et al.* 2012; Tung *et al.* 2018), or any decision-making during

dispersal (which can have a strong impact on the kernel in settings with two sexes, Shaw & Kokko 2014). Also, to avoid having to specify effects of genetic dominance on several traits, we also chose to investigate haploidy. Dominance relationships between two alleles at a diploid locus can take very many forms when fitness effects also depend on spatial location; we ignored these real-life complications to focus on a minimal genetic setup that permits all the intended feedbacks between mate-choice copying, dispersal, and local adaptation to occur. This obviously leaves avenues for further study.

More generally, mate-choice copying is just one example of social learning, which happens to be expressed in a sexual selection context (Verzijden *et al.* 2012; Kendal *et al.* 2018). If there is a need to locally adapt to new conditions after dispersal, and social learning offers a way to acquire a new set of behaviours (Varela *et al.* 2020), then our model's conclusions should generalize to situations where behaviours other than mate choice are learned. The prediction that social learning enhances dispersal appears quite generally applicable — as does its flipside, i.e. local adaptation may become less strong in the long term due to homogenization of traits over the spatial range of a species when learning and dispersal together promote strong gene flow (Varela *et al.* 2018). This finding, should it generalize, could be of importance in cultural evolution as a whole.

References

Agrawal, A.F. (2001). The evolutionary consequences of mate copying on male traits. *Behav. Ecol. Sociobiol.*, 51, 33–40. https://doi.org/10.1007/s002650100401

Amlacher, J. & Dugatkin, L.A. (2005). Preference for older over younger models during mate-choice copying in young guppies. *Ethol. Ecol. Evol.*, 17, 161–169. https://doi.org/10.1080/08927014.2005.9522605

489 Berdahl, A., Torney, C.J., Schertzer, E. & Levin, S.A. (2015). On the evolutionary interplay between

490   dispersal and local adaptation in heterogeneous environments. *Evolution*, 69, 1390–1405.

491   https://doi.org/10.1111/evo.12664

492 Blanquart, F. & Gandon, S. (2011). Evolution of Migration in a Periodically Changing Environment.

493   *Am. Nat.*, 177, 188–201. https://doi.org/10.1086/657953

494 Blanquart, F. & Gandon, S. (2014). On the evolution of migration in heterogeneous environments.

495   *Evolution.*, 68, 1617–1628. https://doi.org/10.1111/evo.12389

496 Bonte, D., Hovestadt, T. & Poethke, H. (2010). Evolution of dispersal polymorphism and local

497   adaptation of dispersal distance in spatially structured landscapes. *Oikos*, 119, 560–566.

498   https://doi.org/10.1111/j.1600-0706.2009.17943.x

499 Bowers, R.I., Place, S.S., Todd, P.M., Penke, L., Asendorpf, J.B. (2012). Generalization in mate-

500   choice   copying   in   humans.   *Behavioral   Ecology*,   23,   112–124.

501   https://doi.org/10.1093/beheco/arr164

502 Brooks, R. (1998). The importance of mate copying and cultural inheritance of mating preferences.

503   *Trends Ecol. Evol.*, 13, 45–46. https://doi.org/10.1016/S0169-5347(97)01253-6

504 Chapman, D.S., Dytham, C. & Oxford, G.S. (2007). Modelling population redistribution in a leaf

505   beetle: An evaluation of alternative dispersal functions. *J. Anim. Ecol.*, 76, 36–44.

506   https://doi.org/10.1111/j.1365-2656.2006.01172.x

507 Dagaeff, A.C., Pocheville, A., Nöbel, S., Loyau, A., Isabel, G., Danchin, E., *et al.* (2016). Drosophila

508   mate copying correlates with atmospheric pressure in a speed learning situation. *Anim. Behav.*,

509   121, 163–174. https://doi.org/10.1016/j.anbehav.2016.08.022

510 Danchin, E., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004). Public Information : From Nosy

511   Neighbors   to   Cultural   Evolution.   *Science.*,   305,   487–491.

512   https://doi.org/10.1126/science.1098254

513 Danchin, E., Giraldeau, L.-A. & Wagner, R.H. (2008). An Information-Driven Approach to Behaviour.

514   In: *Behavioural Ecology* (eds. Danchin, E., Giraldeau, L.-A. & Cézilly, F.). Oxford University

515   Press, Oxford, UK, pp. 97–130.

516 Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A.-C., Demay, L., Alphand, M., *et al.* (2018). Cultural

517   flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science*,

518   362, 1025–1030. https://doi.org/10.1126/science.aat1590

519 Danchin, E., Nöbel, S., Pocheville, A. & Guillaume, I. (2020). First evidence for a significant effect

520   of the regression to the mean fallacy in mate copying: a comment on Davies et al. *Behav. Ecol.*,

521   araa076, https://doi.org/10.1093/beheco/araa076

522 Davies, A.D., Lewis, Z. & Douherty, L.R. (2020). A meta-analysis of factors influencing the strength

523   of   mate-choice   copying   in   animals.   *Behav.   Ecol.,*   araa064,

524   https://doi.org/10.1093/beheco/araa064

525 Drullion, D. & Dubois, F. (2008). Mate-choice copying by female zebra finches, Taeniopygia guttata:

526   What happens when model females provide inconsistent information? *Behav. Ecol. Sociobiol.*,

527   63, 269–276. https://doi.org/10.1007/s00265-008-0658-5

528 Dubois, F., Drullion, D. & Witte, K. (2012). Social information use may lead to maladaptive decisions:

529   A game theoretic model. *Behav. Ecol.*, 23, 225–231. https://doi.org/10.1093/beheco/arr179

530 Dugatkin, L.A. (1992). Sexual Selection and Imitation: Females Copy the Mate Choice of Others. *Am.*

531   *Nat.*, 139, 1384–1389. https://doi.org/10.1086/285392

532 Dugatkin, L.A. (1996). Copying and mate choice. In: *Social learning in animals: The roots of culture*

533   (eds. Heyes, C.M. & Galef. B. G.). Academic Press, London, pp. 85–105.

534 Dugatkin, L.A. (2005). Mistakes and the evolution of copying. *Ethol. Ecol. Evol.*, 17, 327–333.

535   https://doi.org/10.1080/08927014.2005.9522586

536 Dugatkin, L.A. & Godin, J.G. (1992). Reversal of female mate choice by copying in the guppy

537   (Poecilia reticulata). *Proc. Biol. Sci.*, 249, 179–184. https://doi.org/10.1098/rspb.1992.0101

538 Fowler-Finn, K.D., Sullivan-Beckers, L., Runck, A.M. & Hebets, E.A. (2015). The complexities of

539   female mate choice and male polymorphisms: Elucidating the role of genetics, age, and mate-

540   choice copying. *Curr. Zool.*, 61, 1015–1035. https://doi.org/10.1093/czoolo/61.6.1015

541   Galassi, M., Davies, J., Theiler, J., Gough, B., Gerard, J., Allen, P., *et al.* (2009). *GNU Scientific*

542   *Library Reference Manual*. 3rd Revise. Network Theory Ltd.

543   Galef, B.G., Lim, T.C.W. & Gilbert, G.S. (2008). Evidence of mate choice copying in Norway rats,

544   *Rattus norvegicus*. *Anim. Behav.*, 75, 1117–1123. https://doi.org/10.1016/j.anbehav.2007.08.026

545   Germain, M., Blanchet, S., Loyau, A. & Danchin, E. (2016). Mate-choice copying in Drosophila

546   melanogaster: Impact of demonstration conditions and male-male competition. *Behav. Processes*,

547   125, 76–84. https://doi.org/10.1016/j.beproc.2016.02.002

548   Getty, T. (2014). GEIs when Information Transfer is Uncertain or Incomplete. In: *Genotype-by-*

549   *Environment Interactions and Sexual Selection* (eds. Hunt, J. & Hosken, D.J.). John Wiley &

550   Sons, West Sussex, pp. 19–40.

551   Gibson, R.M. & Höglund, J. (1992). Copying and sexual selection. *Trends Ecol. Evol.*, 7, 229–232.

552   https://doi.org/10.1016/0169-5347(92)90050-l

553   Giraldeau, L.A., Valone, T.J. & Templeton, J.J. (2002). Potential disadvantages of using socially

554   acquired information. *Philos. Trans. R. Soc. B Biol. Sci.*, 357, 1559–1566.

555   https://doi.org/10.1098/rstb.2002.1065

556   Godin, J.-G.J., Herdman, E.J.E. & Dugatkin, L.A. (2005). Social influences on female mate choice in

557   the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim. Behav.*,

558   69, 999–1005. https://doi.org/10.1016/j.anbehav.2004.07.016

559   Hamilton, W.D. & May, R.M. (1977). Dispersal in stable habitats. *Nature* 269:578-581.

560   https://doi.org/10.1038/269578a0

561   Heubel, K.U., Hornhardt, K., Ollmann, T., Parzefall, J., Ryan, M.J. & Schlupp, I. (2008). Geographic

562   variation in female mate-copying in the species complex of a unisexual fish, Poecilia formosa.

563   *Behaviour*, 145, 1041–1064. http://dx.doi.org/10.1163/156853908784474533

564   Hill, S.E. & Ryan, M.J. (2006). The role of model female quality in the mate choice copying behaviour

565   of sailfin mollies. *Biol. Lett.*, 2, 203–205. https://doi.org/10.1098/rsbl.2005.0423

566   Holman, L. & Kokko, H. (2014). Local Adaptation and the Evolution of Female Choice. In: *Genotype-*

567   *by-Environment Interactions and Sexual Selection* (eds. Hunt, J. & David J. Hosken). John Wiley

568   & Sons, West Sussex, pp. 41–62.

569   Ingleby, F.C., Hunt, J. & Hosken, D.J. (2010). The role of genotype-by-environment interactions in

570   sexual selection. *J. Evol. Biol.*, 23, 2031–2045. https://doi.org/10.1111/j.1420-

571   9101.2010.02080.x

572   Jones, B.C. & DuVal, E.H. (2019). Mechanisms of Social Influence: A Meta-Analysis of the Effects

573   of Social Information on Female Mate Choice Decisions. *Front. Ecol. Evol.*, 7, 1–14.

574   https://doi.org/10.3389/fevo.2019.00390

575   Kavaliers, M., Matta, R. & Choleris, E. (2017). Mate-choice copying, social information processing,

576   and the roles of oxytocin. *Neurosci. Biobehav. Rev.*, 72, 232–242.

577   https://doi.org/10.1016/j.neubiorev.2016.12.003

578   Kendal, R.L., Boogert, N.J., Rendell, L., Laland, K.N., Webster, M. & Jones, P.L. (2018). Social

579   Learning Strategies: Bridge-Building between Fields. *Trends Cogn. Sci.*, 22, 651–665.

580   https://doi.org/10.1016/j.tics.2018.04.003

581   Kirkpatrick, M. (1982). Sexual Selection and the Evolution of Female Choice. *Evolution*, 36, 1–12.

582   https://doi.org/10.2307/2407961

583   Kniel, N., Müller, K. & Witte, K. (2017). The role of the model in mate-choice copying in female

584   zebra finches. *Ethology*, 123, 412–418. https://doi.org/10.1111/eth.12611

585   Kokko, H. (2007). *Modelling for field biologists and other interesting people*. Cambridge University

586   Press, Cambridge.

587   Kokko, H., Jennions, M.D. & Houde, A. (2007). Evolution of frequency-dependent mate choice:

588   keeping up with fashion trends. *Proc. R. Soc. B*, 274, 1317–1324.

589   https://doi.org/10.1098/rspb.2007.0043

590   Li, X.Y. & Kokko, H. (2019). Sex-biased dispersal: a review of the theory. *Biol. Rev.*, 94, 721–736.

591   https://doi.org/10.1111/brv.12475

592   Losey, G.S., Stanton, F.G., Telecky, T.M. & Tyler, W.A. (1986). Copying Others, an Evolutionarily

593   Stable Strategy for Mate Choice: A Model. *Am. Nat.*, 128, 653–664.

594   https://doi.org/10.1086/284595

595   McDonald, J.H. (2014). *Handbook of Biological Statistics*. 3rd ed. Sparky House Publishing,

596   Baltimore, Maryland.

597   Mery, F., Varela, S.A.M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I., *et al.* (2009). Public versus

598   personal information for mate copying in an invertebrate. *Curr. Biol.*, 19, 730–734.

599   https://doi.org/10.1016/j.cub.2009.02.064

600   Monier, M., Nöbel, S., Isabel, G. & Danchin, E. (2018). Effects of a sex ratio gradient on female mate-

601   copying and choosiness in *Drosophila melanogaster*. *Curr. Zool.*, 64, 251–258.

602   https://doi.org/10.1093/cz/zoy014

603   Nathan, R., Klein, E., Robledo-Arnuncio, J.J. & Revilla, E. (2012). Dispersal kernels: review. In:

604   *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M.).

605   Oxford University Press, Oxford, UK, pp. 187–210.

606   Nordell, S.E. & Valone, T.J. (1998). Mate choice copying as public information. *Ecol. Lett.*, 1, 74–76.

607   https://doi.org/10.1046/j.1461-0248.1998.00025.x

608   Poethke, H.J., Gros, A. & Hovestadt, T. (2011). The ability of individuals to assess population density

609   influences the evolution of emigration propensity and dispersal distance. *J. Theor. Biol.*, 282, 93–

610   99. https://doi.org/10.1016/j.jtbi.2011.05.012

611   Pruett-Jones, S. (1992). Independent Versus Nonindependent Mate Choice: Do Females Copy Each

612   Other? *Am. Nat.*, 140, 1000–1009. https://doi.org/10.1086/285452

613   R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for

614   Statistical Computing, Vienna, Austria.

615 Roff, D.A. & Fairbairn, D.J. (2014). The evolution of phenotypes and genetic parameters under

616   preferential mating. *Ecol. Evol.* 4:2759–2776. https://doi.org/10.1002/ece3.1130

617 Santos, M., Matos, M. & Varela, S.A.M. (2014). Negative Public Information in Mate Choice Copying

618   Helps the Spread of a Novel Trait. *Am. Nat.*, 184, 658–672. https://doi.org/10.1086/678082

619 Santos, M., Sapage, M., Matos, M. & Varela, S.A.M. (2017). Mate-choice copying: A fitness-

620   enhancing behavior that evolves by indirect selection. *Evolution.*, 71, 1456–1464.

621   https://doi.org/10.1111/evo.13235

622 Sapage, M., Varela, S.A.M., Kokko, H. (2020) Data from: Social learning by mate-choice copying

623   increases dispersal and reduces local adaptation. Dryad Digital Repository

624   https://doi.org/10.5061/dryad.dncjsxkz1

625 Schlupp, I. & Ryan, M.J. (1997). Male Sailfin mollies (Poecilia latipinna) copy the mate choice of

626   other males. *Behav. Ecol.*, 8, 104–107. https://doi.org/10.1093/beheco/8.1.104

627 Servedio, M.R. & Kirkpatrick, M. (1996). The Evolution of Mate Choice Copying by Indirect

628   Selection. *Am. Nat.*, 148, 848–867. https://doi.org/10.1086/285959

629 Shaw, A.K. & Kokko, H. (2014). Mate finding, Allee effects and selection for sex-biased dispersal. *J.*

630   *Anim. Ecol.*, 83, 1256–1267. https://doi.org/10.1111/1365-2656.12232

631 Stöhr, S. (1998). Evolution of mate-choice copying: a dynamic model. *Anim. Behav.*, 55, 893–903.

632   https://doi.org/10.1006/anbe.1997.0674

633 Swaddle, J.P., Cathey, M.G., Correll, M. & Hodkinson, B.P. (2005). Socially transmitted mate

634   preferences in a monogamous bird: a non-genetic mechanism of sexual selection. *Proc. Biol. Sci.*,

635   272, 1053–1058. https://doi.org/10.1098/rspb.2005.3054

636 Tung, S., Mishra, A., Shreenidhi, P.M., Sadiq, M.A., Joshi, S., Sruti, V.R.S., *et al.* (2017).

637   Simultaneous evolution of multiple dispersal components and kernel. *Oikos*, 127, 34–44.

638   https://doi.org/10.1111/oik.04618

639 Uehara, T., Yokomizo, H. & Iwasa, Y. (2005). Mate-Choice Copying as Bayesian Decision Making.

640   *Am. Nat.*, 165, 403–410. https://doi.org/10.1086/428301

641 Vakirtzis, A. (2011). Mate choice copying and nonindependent mate choice : a critical review. *Ann.*

642   *Zool. Fennici*, 48, 91–107. https://doi.org/10.5735/086.048.0202

643 Vakirtzis, A. & Roberts, S.C. (2012). Human nonindependent mate choice: is model female

644   attractiveness   everything?   *Evol.*   *Psychol.*,   10,   225–237.

645   https://doi.org/10.1177/147470491201000205

646 Valone, T.J. & Templeton, J.J. (2002). Public information for the assessment of quality: A widespread

647   social   phenomenon.   *Philos.   Trans.   R.   Soc.   B   Biol.   Sci.*,   357,   1549–1557.

648   https://doi.org/10.1098/rstb.2002.1064

649 Varela, S.A.M., Matos, M. & Schlupp, I. (2018). The role of mate-choice copying in speciation and

650   hybridization. *Biol. Rev.*, 93, 1304–1322. https://doi.org/10.1111/brv.12397

651 Varela, S.A.M., Teles, M.C. & Oliveira, R.F. (2020). The correlated evolution of social competence

652   and social cognition. *Funct. Ecol.*, 34, 332–343. https://doi.org/10.1111/1365-2435.13416

653 Venables, W.N. & Ripley, B.D. (2002). *Modern Applied Statistics with S*. 4th edn. Springer, New

654   York.

655 Verzijden, M.N., ten Cate, C., Servedio, M.R., Kozak, G.M., Boughman, J.W. & Svensson, E.I.

656   (2012). The impact of learning on sexual selection and speciation. *Trends Ecol. Evol.*, 27, 511–

657   519. https://doi.org/10.1016/j.tree.2012.05.007

658 Wade, M.J. (2014). Genotype-by-Environment Interactions and Sexual Selection: Female Choice in a

659   Complex World. In: *Genotype-by-Environment Interactions and Sexual Selection* (eds. Hunt, J.

660   & Hosken, D.J.). John Wiley & Sons, West Sussex, pp. 1–18.

661 Wade, M.J. & Pruett-Jones, S.G. (1990). Female copying increases the variance in male mating

662   success. *Proc. Natl. Acad. Sci.*, 87, 5749–5753. https://doi.org/10.1073/pnas.87.15.5749

663 Wagner, R.H. & Danchin, E. (2010). A taxonomy of biological information. *Oikos*, 119, 203–209.

664 https://doi.org/10.1111/j.1600-0706.2009.17315.x

665 White, D.J. & Galef Jr, B.C. (2000). "Culture" in quail: social influences on mate choices of female

666 Coturnix japonica. *Anim. Behav.*, 59, 975–979. https://doi.org/10.1006/anbe.1999.1402

667 Witte, K., Kniel, N. & Kureck, I.M. (2015). Mate-choice copying: Status quo and where to go. *Curr.*

668 *Zool.*, 61, 1073–1081. https://doi.org/10.1093/czoolo/61.6.1073

669 Witte, K. & Noltemeier, B. (2002). The role of information in mate-choice copying in female sailfin

670 mollies (*Poecilia latipinna*). *Behav. Ecol. Sociobiol.*, 52, 194–202.

671 https://doi.org/10.1007/s00265-002-0503-1

672 Witte, K. & Ryan, M.J. (1998). Male body length influences mate-choice copying in the sailfin molly

673 *Poecilia latipinna*. *Behav. Ecol.*, 9, 534–539. https://doi.org/10.1093/beheco/9.5.534

674

Supporting information

676 Additional supporting information may be found in the online version of this article.

677 • Figure S1 Examples of simulated environmental values landscapes for $\beta = 0.99$

678 • Table S1 ANOVA comparison of the mean allelic value of D between control, unconditional,

679 and conditional mate-choice copying scenarios at generations 7500 and 15000

680 • Table S2 Pairwise t-test comparing the mean allelic value of D between generations 7500 and

681 15000 (control) or 12500 and 15000 (unconditional and conditional)

682 • Table S3 Pairwise t-test comparing the proportion of individuals with the C allele between

683 generations 12 500 and 15000

684 • Table S4. ANOVA comparison of the local adaptation score (*L*) between control,

685 unconditional, and conditional scenarios at generations 7500 and 15000

686 • Table S5. Pairwise t-test comparing the local adaptation score (*L*) in the control scenario

687 between generations 7500 and 15000

693

Figures

Figure 1. Mate-choice copying selects for higher dispersal. Line plots: evolution of D for each

sexual selection strength (S_S) as indicated in the plot and mate-choice copying scenario ("control",

"unconditional", and "conditional" as indicated by colour). Lines depict the means (across 20

simulation runs) of (population-wide) D and the standard deviations of the means (shading); the

vertical line denotes the generation at which mutation towards copying is introduced, and the

coevolution with dispersal begins. Box plot: distribution of D at generation 15000. Thick lines depict

the medians of the distribution of each population's mean D; box, the 25% and 75% interquantile

range; vertical dashed lines, the most extreme values within 1.5 of the interquantile range; opened

circles, extreme values outside of this range. Stars indicate pairwise differences between populations

within each case (Tuckey HSD test for cases where the ANOVA test with the Bonferroni correction

was significant, see Methods). *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Other parameters: $\beta = 0.99$, $S_N =$

50.

710   **Figure 2. Overall, individuals with c and C alleles show no significant differences in dispersal**

711   **across a wide range of values for the strength of sexual selection.** The distribution of the mean

712   allelic value of D at generation 15000 over 20 simulations for each set of parameters, graphed as in

713   figure 1, but separately for individuals with the c or C allele. Significance was calculated using a

714   pairwise t-test: *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Parameters as in figure 1.

715

716   **Figure 3. Unconditional copying evolves when sexual selection is weak, conditional copying**

717   **evolves across a wide range of values for the strength of sexual selection.** Box plot design follows

718   the conventions of figure 1 and 2, with data now giving the proportion of individuals with the C allele

719   at generation 15000 over 20 simulations for each set of parameters. Stars below each box represent

720   significant differences from 0.5 (one sample t-test), stars above give significance for differences

721   between populations with "unconditional" and "conditional" mate-choice copying for identical values

722   of S_S (Welch two sample t-test); for both tests, $*p < 0.05$, $** p < 0.01$, $*** p < 0.001$. Parameters as in

723   figure 1.

724

725 **Figure 4. Mate-choice copying (a) reduces local adaptation when sexual selection is high, and (b)**

726 **weakens trait-preference correlations.** The box plots (design as in figures 1–3) are complemented

727 with stars that indicate statistical significance (*p < 0.05, ** p < 0.01, *** p < 0.001) of pairwise

728 differences between scenarios at generation 15000 over 20 simulations for each set of parameters

729 (Tuckey HSD test, calculated for cases where the ANOVA test with the Bonferroni correction was

730 significant, see details in methods). Parameters as in figure 1.

731

Box 1. Example of the effect of S_S on Mate-choice copying

Consider a case where the environmental value $E_p = 0.5$, and there are three males M_A, M_B, M_C with trait values 0.4, 0.5, and 0.6, respectively.

First, assume strong sexual selection, $S_S = 100$, and assume that there is a locally adapted female with a with a value of 0.5 at the P locus. Following equations (2) and (3), she will choose a male with probability $Prob(F_A,M_A) = Prob(F_A,M_C) \approx 0.212$ and $Prob(F_A,M_B) \approx 0.576$. A copier female F_B ignores her innate preferences and updates her preferences to 0.4 if F_A chose M_A, to 0.5 if F_A chose M_B, and to 0.6 if F_A. The actual probabilities of mating, conditional on F_A having chosen M_A, are $Prob(F_B,M_A \mid F_A,M_A) \approx 0.721$, $Prob(F_B,M_B \mid F_A,M_A) \approx 0.265$, $Prob(F_B,M_C \mid F_A,M_A) \approx 0.013$. The probabilities are similarly calculated for all other choices of female F_A. In the end, the probability of female F_B choosing a less adapted male than F_A did is approximately 0.244, the probability for her to choose an equally adapted male is ≈ 0.643, and the probability of her choosing a better adapted male is ≈ 0.112.

These probabilities become more 'egalitarian' with respect to the two females if there is more randomness in the outcome. Assuming $S_S = 25$, $Prob(F_A,M_A) = Prob(F_A,M_C) \approx 0.305$ and $Prob(F_A,M_B) \approx 0.391$. In this case the probability for female F_B to choose a less adapted male than F_A is still considerable, approximately 0.238, but the probability to choose an equally adapted male is clearly lower than before, 0.541, and the clear increase is in the probability of choosing a better adapted male, ≈ 0.221.
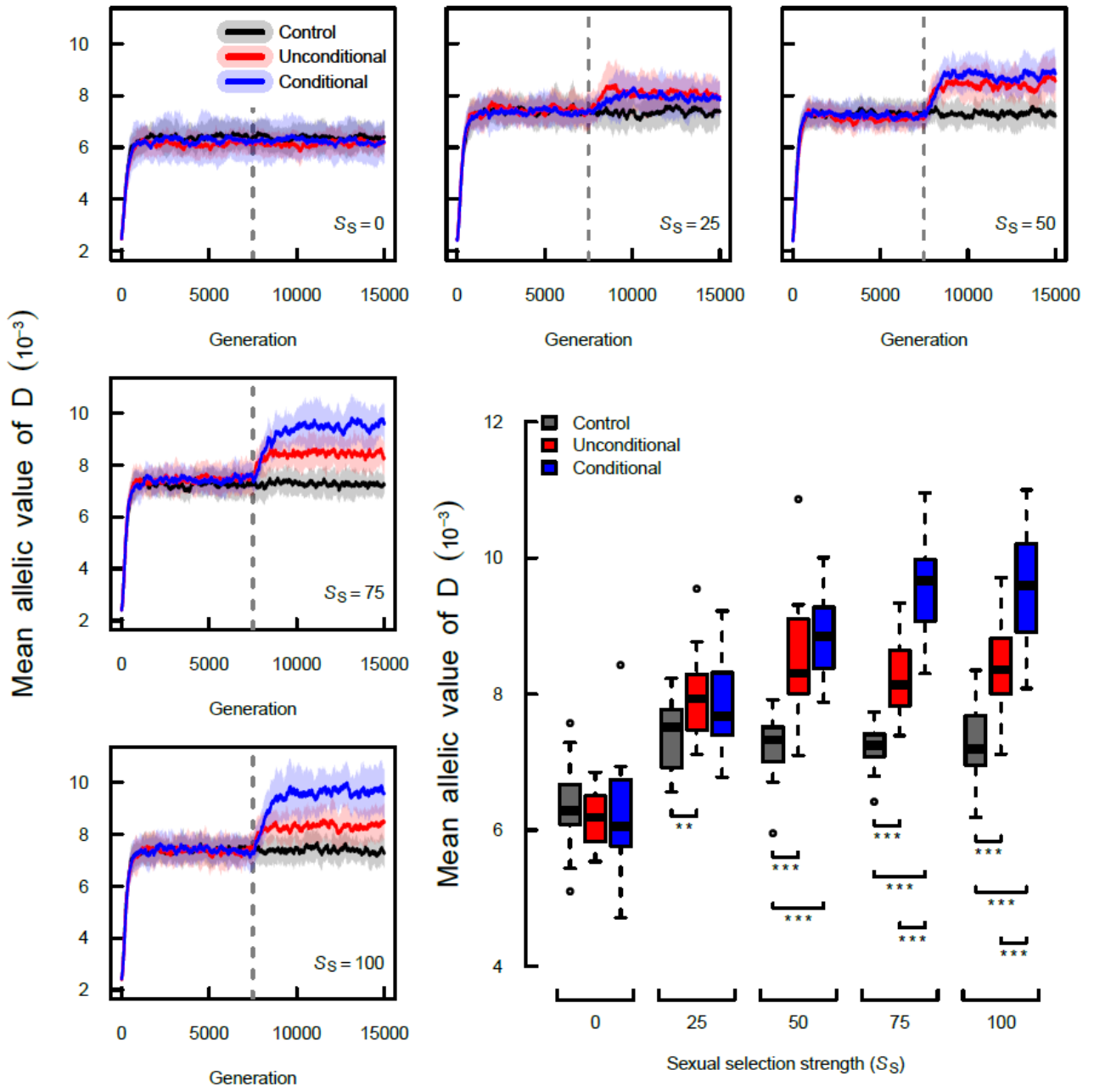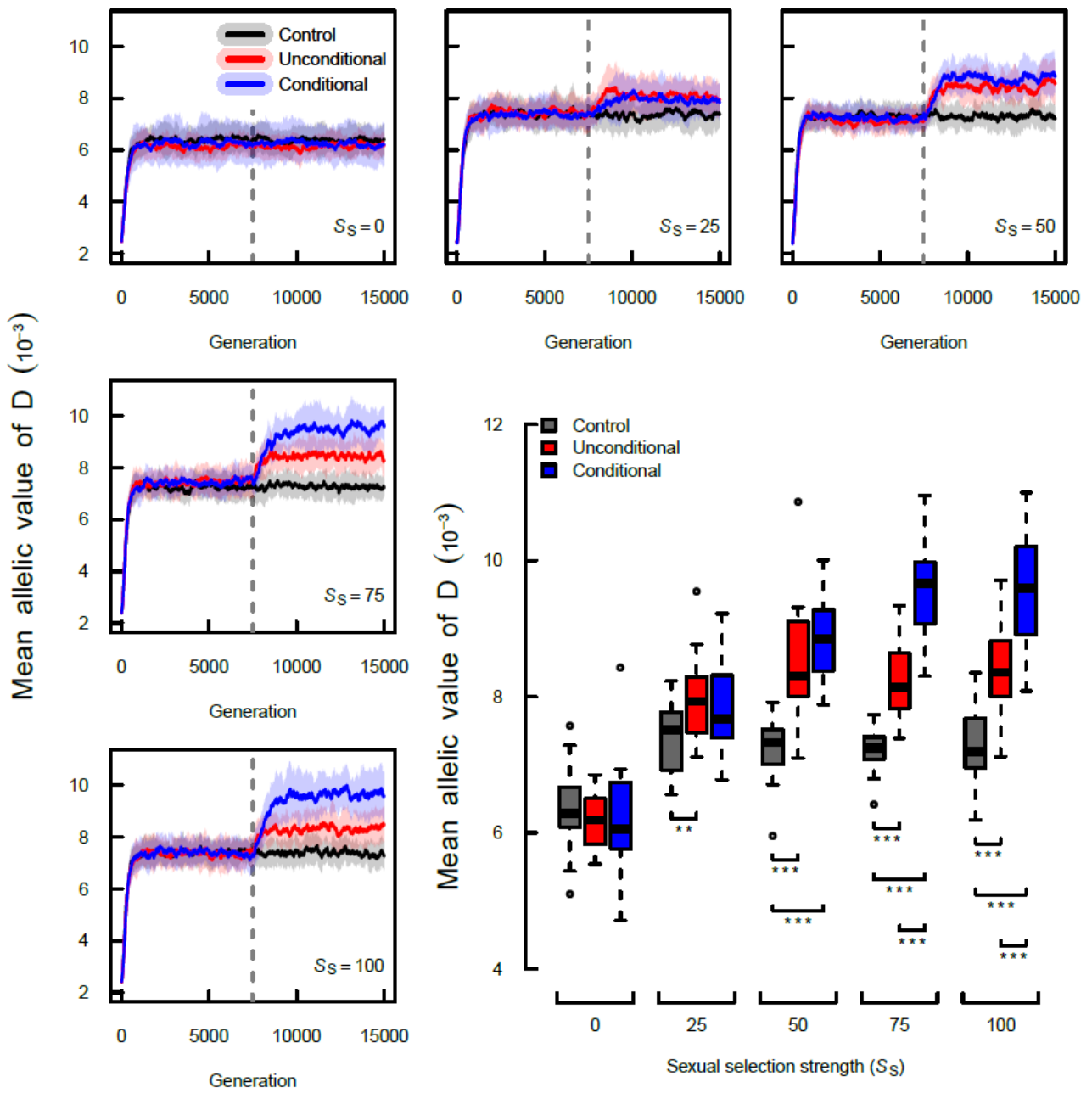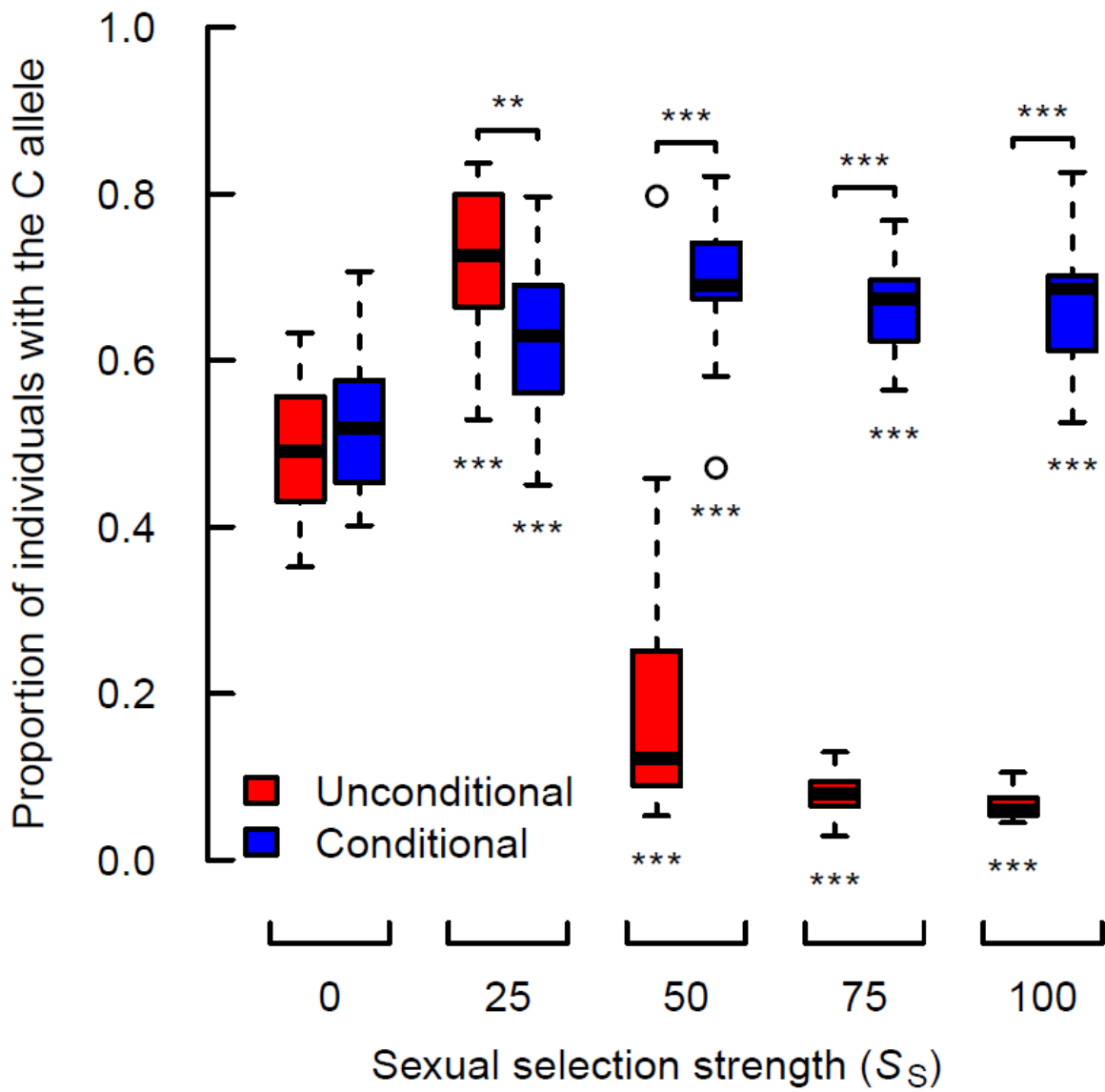
752

753

Figure 1

754
755   Figure 2
756

Figure 3

(a)

(b)

760

761

Figure 4